International Journal of Plant Breeding ©2010 Global Science Books

Genetics, Breeding, and Ecology of Reed Canarygrass

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ABSTRACT

Reed canarygrass is a cool-season perennial with a circumglobal distribution in the northern hemisphere, native to Europe, Asia, and North America. It is tolerant of a wide range of environmental stresses including cold, heat, drought, and flooding, and utilized for many purposes, including pasture, hay production, biomass for bioenergy, and soil conservation. It has become notorious in North America, recently classified as "invasive" because it has opportunistically invaded wetlands across much of temperate North America. Numerous cultivars of reed canarygrass have been developed in Europe and North America. Early 20th-century cultivars represented seed increases from meadows and hay fields that were considered to have desirable agronomic traits. Cultivars developed later in the 20th century were products of selection for productive and persistent plants from long-term meadows and pastures. With the discovery of indole alkaloids and the strong linear relationship of alkaloid profiles, including both type and concentration, to palatability and preference of ruminant livestock, modern cultivars have been bred to contain only the more benign alkaloid gramine, generally in relatively low concentration. Indeed, the popularity of these new cultivars has led to complete replacement of older "wild-type" cultivars in the commercial sector, so that seed of old cultivars can often be obtained only from gene banks.

Keywords: alkaloids, bioenergy, invasive plants, *Phalaris arundinacea*

CONTENTS

INTRODUCTION

Reed canarygrass (*Phalaris arundinacea* L.) is a cool-season perennial with a circumglobal distribution in the northern hemisphere (Anderson 1961). It is native to Europe, Asia, and North America. Its status as a North American native was verified by herbarium samples collected in remote regions of the Pacific Northwest USA in the early 19th century, before European immigrants settled that region (Merigliano and Lesica 1998). European and North American reed canarygrass herbarium samples are largely indistinguishable from each other on a phenotypic basis, indicating that European and North American strains represent different populations or races of the species.

Reed canarygrass is one of three *Phalaris* species that are cultivated and have been subjected to selection and breeding. Reed canarygrass breeding has occurred primarily in the USA and Canada and secondarily in northern Europe, mainly for forage production and quality traits and secondarily for bioenergy feedstock production. Phalaris (*P. aquatica* L.) is the closest relative of reed canarygrass (Anderson 1961; Baldini 1995), originates in the Mediterranean region, and is adapted as a winter-growing perennial in warmer climates than reed canarygrass. Breeding activity has occurred primarily in Australia, the southern USA, and Argentina (Oram *et al.* 2009). Canary seed (*P. canariensis* L.) is a distantly related annual that has been bred as a grain crop for bird-seed production.

Reed canarygrass is tolerant of a wide range of environmental stresses including cold, heat, drought, and flooding. Strains of reed canarygrass differ in their ability to survive extreme cold or heat, in direct proportion to their latitude-of-origin and mean winter temperature at their point of origin (Klebesadel and Dofing 1990; Carlson *et al.* 1996). Considerable genetic variation exists for tolerance to acid soils and aluminium within the sister species *P. aquatica* L. (Requis and Culvenor 2004; Oram *et al.* 2009). There is also indirect evidence for genetic variation for heat and drought tolerance in the sister species *P. aquatica*, with the development of cultivars that tend to perform better under these conditions (Oram *et al.* 2009). Reed canarygrass is tolerant of a wide range of management practices, including grazing or conservation harvesting on a frequent or infrequent basis. As such, its use in agricultural systems is highly varied, including pasture, hay or silage production, straw or bedding for livestock, and soil conservation. There is no direct evidence for genetic variation in drought or flooding tolerance within reed canarygrass, but there is indirect evidence for constitutive resistance to stem-borer insects, as discuss later in this paper. In addition, reed canarygrass possesses genetic variability for salt tolerance, capable of rapid and heritable shifts in salt tolerance, commensurate with the degree of exposure to salt stress (Maeda *et al.* 2006).

Reed canarygrass is a very long-lived species that may persist indefinitely in areas where it is well adapted. It is frequently found in wetlands, riparian zones, along shore-

Received: 10 May, 2010. Accepted: 9 June, 2010.

Invited Mini-Review

lines of lakes and rivers, and in canals or ditches. Seeds, rhizomes, or axillary buds of culm nodes can all be used to propagate reed canarygrass. In the 1930s, it was frequently propagated by axillary buds on stem nodes tilled into highly erodible lands in the central and northern USA. It is a prolific seed producer and all genotypes are highly susceptible to seed dispersal by premature dehiscence. Seeds float on surface waters and can be carried for many kilometers (Casler, unpublished data), allowing reed canarygrass to colonize large areas. Annual seed production may lead to build-up of large seed banks in the soil of colonized areas. Although reed canarygrass can be controlled by systemic herbicides and repeated burning, long-term flooding may be the only way to eradicate the species once it has established a viable seed bank. Reed canarygrass seedlings are relatively low in vigor, leading to severe establishment difficulties in fields with high populations of annual weedy plants. Diligent management of reed canarygrass during the establishment year, including frequent clipping to maintain a canopy open to sunlight, will greatly enhance the probably of successful establishment.

TAXONOMY AND GENETICS

Reed canarygrass has two chromosome races, tetraploid ($2n = 4x = 28$) and hexaploid ($2n = 6x = 42$) (Anderson 1961). The tetraploid race originated in the cool temperate zone of Europe and spread into Asia and North America prior to recorded history. The hexaploid race is largely restricted to the Iberian Peninsula and may be derived from an interspecific hybrid between *P. arundinacea* and *P. aquatica* (McWilliam and Neal-Smith 1962).

The genus *Phalaris* consists of 21 species including annuals and perennials native to either Eurasia or North America. Reed canarygrass is the only member of the genus that is native to both the Old World and New World (Anderson 1961; Baldini 1995). *P. aquatica* ($2n = 4x = 28$) is its closest relative, with which it can be readily hybridized to create F_1s, backcrosses, and stable introgression lines (Carlson *et al*. 1996; Oram *et al*. 2009).

Reed canarygrass is wind pollinated with a strong self-incompatibility system that promotes a high degree of cross-pollination (Carlson *et al*. 1996). As such, individual populations of reed canarygrass are highly variable, demonstrating large amounts of phenotypic variability (e.g. Marum *et al*. 1979). Likewise, only 18% of variation for amplified fragment length polymorphism (AFLP) DNA markers could be attributed to differences among 15 European and North American cultivars, with the remainder of the variability attributed to plants within cultivars (**Fig. 1**; Casler *et al*. 2009). However, a significant portion (5%; $P<0.0001$) of this variability was related to European vs. North American origin of the cultivars. These results suggest a significant level of genetic differentiation between European and North American cultivars. More importantly, significant polymorphisms exist between modern North American cultivars and older North American cultivars that appear to represent source-identified ecotypes or land races. North American land races can be clearly discriminated from European cultivars by several single-nucleotide polymorphisms in non-coding regions of the cpDNA genome (Casler *et al*. 2009). Conversely, most modern North American reed canarygrass germplasm traces back to selections made from old pastures and hay fields that clearly originate from introduced European germplasm. Several North American cultivars appear to derive from parental clones of highly diverse origins, including potential North American, Scandinavian, and Continental European clades (Casler *et al*. 2009).

Very little molecular genetic research has been conducted with the genus *Phalaris*. Considerable DNA marker variation has been demonstrated in reed canarygrass nuclear and chloroplast genomes (Casler *et al*. 2009), *P. aquatica* (Rouf Mian *et al*. 2005), and *P. minor* (Dhawan *et al*. 2008). Somaclonal variants of several reed canarygrass genotypes were confirmed by the use of DNA markers, with some

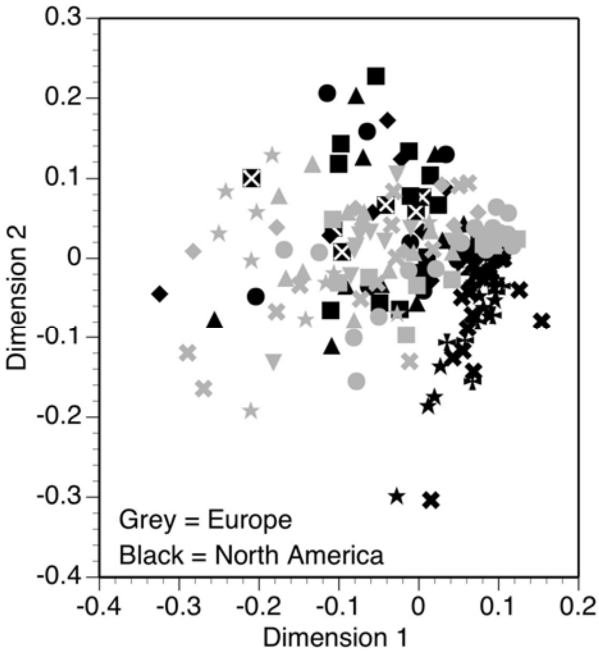

Fig. 1 Scatterplot of the first two dimensions of the matrix of 103 amplified fragment length polymorphism (AFLP) DNA markers scored on 205 reed canarygrass plants representing 15 North American and European cultivars, each cultivar represented by a different symbol. Adapted from Casler *et al*. 2009.

plants demonstrating potential agronomic value (Gyulai *et al*. 2003). *P. coerulescens* Desf. has served as a model species for map-based cloning of the S and Z self-incompatibility loci within the Avenae tribe (Bian *et al*. 2004). Reed canarygrass has not been a target for genetic modification by plant transformation, most likely due to its relatively low economic value as one of many forage-grass options and its classification as an "invasive" species by the ecological community. Genetically modified organisms are highly regulated in the USA, requiring millions of dollars in licensing, trialing, documentation, and legal expenses, especially when the candidate species is controversial or sensitive. Linkage and association mapping studies are currently underway, using breeding populations, cultivars, and collections from natural areas, in a collaborative effort between USDA-ARS in Madison, Wisconsin and Ithaca, NY and Cornell University.

BREEDING AND SELECTION

Reed canarygrass has received relatively little attention compared to many other forage crops, with breeding and selection originating in Iowa in the 1940s (Carlson *et al*. 1996). Early cultivars, such as 'Auburn', 'Ioreed', and 'Superior' were largely ecotypes or land races that had undergone natural selection and their favorable traits identified in early agronomic trials. The origin of these land races is not currently clear, whether they represent pre-Columbian native lineages or were introduced from Europe (Casler *et al.* 2009). It is clear that the earliest land races of reed canarygrass ('Auburn', 'AR Upland', 'Cana', 'Superior', and to a lesser extent, 'Ioreed') have unique DNA profiles compared to European germplasm and modern North American cultivars (Casler *et al.* 2009). These authors suggested that these land races may represent native North American lineages, but recent preliminary data suggests that they may alternatively represent the hexaploid Iberian race of reed canarygrass (Johnson, R.C., 2010, unpublished data). Research is currently underway to test this hypothesis.

Seedling vigor and establishment capacity, seed retention, and alkaloid profiles have served as the most important traits in reed canarygrass breeding programs during the past 30+ years. Palatability and livestock health problems

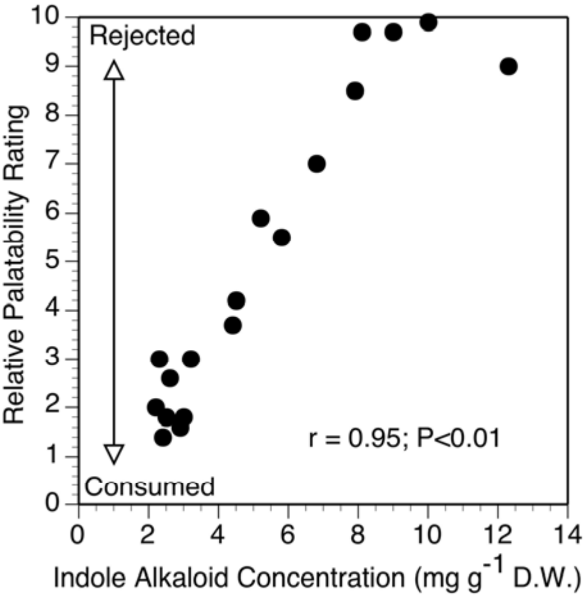

Fig. 2 Relationship of palatability, measured by grazing lambs, to indole alkaloid concentration of 18 reed canarygrass genotypes. Adapted from Simons and Marten 1971.

on reed canarygrass pastures led to the identification of specific indole alkaloids as antiquality compounds in reed canarygrass herbage. Palatability, intake, and liveweight gains of ruminant livestock are all suppressed by elevated levels of indole alkaloids in reed canarygrass herbage (Marten 1985, 1989). There is considerable genetic variability within reed canarygrass for alkaloid concentration and type. Early research identified a wide range in alkaloid concentration within reed canarygrass cultivars and breeding populations. Grazing trials demonstrated that lambs easily discriminated among reed canarygrass genotypes in terms of their preference and consumption of different reed canarygrass genotypes was highly dependent on alkaloid concentration (**Fig. 2**; Simons and Marten 1971). Reed canarygrass also contains non-indole alkaloids, such as hordenine, which are believed to be relatively benign to livestock (Goelz *et al*. 1980).

Alkaloid type has a significant effect on both liveweight gains and livestock health, with mixed-type cultivars (gramine, tryptamines, and β-carbolines) resulting in reduced liveweight gains and greater incidence of livestock health issues compared to cultivars with gramine as their only alkaloid (Marten 1985, 1989). The presence of tryptamines and β-carbolines in reed canarygrass herbage is governed by a simple two-locus inheritance model (Marum *et al*. 1979a), so it was relatively simple to identify true-breeding plants with gramine as the principal indole alkaloid. 'Vantage' was the first cultivar to be free of tryptamines and β-carbolines, leading to a slight increase in liveweight gains and a large increase in health of lambs grazing reed canarygrass (**Table 1**). 'Palaton' and 'Venture' represented the next generation of cultivars with reduced levels of gramine (Wittenberg *et al*. 1992). The improvement of reed canarygrass cultivars is clearly a two-step process with both removal of tryptamines and β-carbolines and subsequent reduction in gramine having independent effects on improving liveweight gains (**Table 2**). Low-alkaloid cultivars have become so dominant in the marketplace that old cultivars with

Table 2 Mean biomass yield of reed canarygrass under three harvest managements (two harvests in Spring or Autumn, one harvest in Autumn, or one harvest in late Winter) evaluated for three years at three locations in the North Central USA (adapted from Tahir *et al*. 2010).

Harvest management	Ames, Iowa	McNay, Iowa	Arlington, Wisconsin
	----------	Mg DM ha^{-1}	----------
Spring + Autumn	10.49	6.02	7.54
Autumn only	7.49	4.56	6.21
Winter only	3.23	1.45	2.46
LSD(0.01)	0.31	0.30	0.29

tryptamines and β-carbolines in their herbage have been discontinued and many can be found only in gene banks.

There were sporadic efforts to improve seed retention of reed canarygrass during the 20th century. The most significant of these was phenotypic selection for seed retention, as determined by tactile evaluation, in spaced-plant nurseries, resulting in the release of 'Palaton' and 'Venture' with improved seed production (Kalton *et al*. 1989a, 1989b). A single plant of *P. aquatica* was found to have an intact rachilla, resulting in improved seed retention, which has been incorporated into all recent cultivars of this species (Oram and Lodge 2003). This trait has been successfully incorporated into F_1s and backcrosses with *P. arundinacea*, but these materials have not yet been successfully transferred into reed canarygrass breeding programs. These interspecific hybrids and backcrosses have been used to transfer genes for aluminum and acid-soil tolerance from reed canarygrass into *P. aquatica* (Ridley *et al*. 2002).

Recent efforts have led to an increase in stand establishment capacity through the use of systematic natural selection methods (Casler and Undersander 2005). Natural selection for survival in competition with annual weeds led to progeny with increased seedling vigor, expressed as both increased root and shoot mass, leading to increased establishment capacity.

CHANGES IN STATUS AND PERCEPTION

Reed canarygrass was cultivated in Europe as early as the mid-18th century (Alway 1931). The first cultivation of reed canarygrass in North America likely occurred around the 1830s in the northeast USA and eastern Canada, about the same time that cultivation spread from Scandinavia into other parts of northern Europe (Schoth 1929; Alway 1931). At this time, cultivation consisted of harvesting seed from native stands and planting the species in disturbed areas, largely for reclamation of peatlands and marshes.

Natural European strains of reed canarygrass were imported into North America beginning sometime prior to 1924 and quickly dominated the marketplace (Schoth 1929). Agronomic research on reed canarygrass began sometime around 1920, with most efforts focused on comparing it to other perennial grasses, defining management systems, and improving seed production and harvesting methodology. In 1924, reed canarygrass was still considered to be of minor importance to agriculture, barely warranting mention in textbooks of forage crops (Piper 1924). The use of reed canarygrass in agriculture likely increased in the 1930s, as farmers and extension personnel were desperate for perennials that could withstand the severe drought that plagued the mid-western USA in the early 1930s. Reed canarygrass is one of the most drought tolerant cool-season grasses adapted to eastern North America (Wilkins and Hughes

Table 1 Alkaloid profiles, average daily gain, and diarrhea incidence for lambs grazing three reed canarygrass cultivars (adapted from Marten *et al*. 1981).

Cultivar	Alkaloid types	Alkaloid concentration (mg g^{-1} D.W.)	Average daily gain (g $lamb^{-1}$)	Diarrhea incidence (%)
Rise	Gramine, Tryptamine, β-carboline	3.0	68	20
Vantage	Gramine	2.7	80	2
MN-76	Gramine	0.9	116	1
LSD (0.05)		0.4	11	10

1932). The ability to propagate reed canarygrass by seed, sod, or stem cuttings was an additional advantage, partly responsible for the increased use of this grass in conservation programs. The results of these efforts can still be seen today in the abundance of reed canarygrass along roadsides, stream banks, and conservation strips within and between tilled fields. Despite these efforts and the increases in propagation of reed canarygrass, it was yet to be widely considered as an invasive species, even though early agronomists recognized its ability to create dense monocultures (Hoover *et al*. 1948).

Gradually, during the last half of the 20th century, reed canarygrass became recognized as an invasive species, because it was found in wetlands where it had never been observed and it typically became the dominant species within 5-6 years. Volker and Smith (1965) showed that reed canarygrass had invaded a native wetland in Iowa sometime between 1915 and 1961. During this period, 11 species disappeared, while reed canarygrass and several other invasive species became the dominant flora. Although it is not so well documented at other sites, this phenomenon seems to have occurred throughout temperate North America during the latter half of the 20th century. Because European germplasm was repeatedly introduced into North America beginning in the late 19th century, and it cannot be reliably distinguished from the native North American type on the basis of phenotype, there are unsubstantiated opinions and beliefs that European-derived cultivars represent a group of invasive genotypes that have overtaken native reed canarygrass populations (Lavergne and Molofsky 2004).

Many significant changes occurred to agriculture during the latter half of the 20th century, coincident with the increase in breeding and cultivation of reed canarygrass. Inexpensive fossil fuels and advances in agricultural mechanization led to more intensive and frequent tillage operations and huge increases in the use of non-organic fertilizers (McNeill and Winiwarter 2004). Tractors replaced horses, tractors and tillage equipment gradually became larger, pastures and prairies were replaced with grain crops, and inorganic fertilizers became commonplace. In addition, many wetlands were drained, converting them to croplands divided by roads, drainage ditches, and waterways (Prince 1997).

A steady increase in soil erosion has been one of the most significant changes in agriculture since World War II, directly related to increased use of tillage (Pimentel *et al*. 1995). Runoff induced by precipitation or irrigation carries sediments, pesticides, nutrients, minerals, and bacteria into rivers, streams, lakes, and estuaries. Indeed, the economic consequences of soil erosion to off-farm ecosystems are far greater than the effects on agronomic or livestock productivity (NRC 1986). Agriculture accounts for more than 50% of the suspended sediments discharged into surface waters of the USA (USDA 1987). Furthermore, 50-70% of the nutrients reaching surface waters originate from agricultural lands (USDA 1987).

Channelization of former wetlands into roads, drainage ditches, and waterways has provided a mechanism for reed canarygrass seeds to travel long distances in stormwater and runoff from agricultural lands. Sedimentation and nutrient loading of wetlands provides an ideal environment for germination of reed canarygrass seeds, establishment of seedlings, and colonization by adult plants (Werner and Zedler 2002). Sedimentation smothers native vegetation, reducing microtopography and species richness, and creating open ground available to colonization by introduced species. Elimination of native vegetation reduces cover canopy, increasing light interception, and enhancing germination of reed canarygrass seeds (Lindig-Cisneros and Zedler 2002a). Gaps in the canopy are also important for enhancing the success of seedling establishment (Lindig-Cisneros and Zedler 2002b). Growth of reed canarygrass is heavily favored by low vegetative cover, as found in these types of disturbed or low-density habitats (Morrison and Molofsky 1998). These authors also suggested that continual introductions of reed canarygrass seed increase the probability of successful colonization. High seed production and seed shattering of reed canarygrass, followed by precipitation, runoff, and frequent sedimentation events, likely results in repeated introduction of reed canarygrass seeds into this ideal establishment environment.

The nutrients that accompany sedimentation are also a key component of this equation. High-nutrient environments enhance the biomass production of reed canarygrass (Green and Galatowitsch 2001; Maurer and Zedler 2002), increasing its aggressiveness and suppressing effect on native plant species (Green and Galatowitsch 2002). Once established, high nutrient levels enhance the vegetative spread of reed canarygrass by rhizomes and tillers (Maurer and Zedler 2002). The opportunistic nature of reed canarygrass is illustrated by an alternative strategy under low-nutrient conditions – allocation of more resources to root growth and tillering closer to the parent clone (Maurer and Zedler 2002). These strategies lead to the inevitable succession of reed canarygrass as the dominant species, gradually replacing native wetland species and reducing wetland diversity (Spuher 1994; Barnes 1999; Galatowitsch *et al*. 1999; Lavoie *et al*. 2003). Perry *et al*. (2004) elegantly verified this effect, by demonstrating that the dominance of reed canarygrass over a native *Carex* species was reversed when a large portion of soil inorganic N was tied up by carbon enrichment, and this effect was reversed again when N fertilizer was applied to carbon-enriched plots. Clearly, the colonization of wetland habitats by introduced reed canarygrass is largely a function of landscape disturbances combined with agricultural systems that have promoted erosion, sedimentation, and nutrient loading of wetlands.

REED CANARYGRASS AS A BIOENERGY CROP

With increased interest in the development of bioenergy crops for diverse environmental conditions, interest in reed canarygrass has increased in recent years. Reed canarygrass has extremely high biomass yields compared to most other C3 grasses commonly used for hay or pasture production (Marten 1985; Jasinskas *et al*. 2008). Routine reed canarygrass biomass yields of 14 to 17 Mg DM ha^{-1} have been reported in temperate North America and Europe (Wrobel *et al*. 2009).

Biomass yield of reed canarygrass responds linearly to nitrogen fertilizer at least up to 200 kg N ha^{-1} with split applications in a multiple-harvest system (Malzer and Schoper 1984; Schmitt *et al*. 1999). Higher rates of nitrogen fertilizer are generally considered too high for profitable and sustainable biomass feedstock production; low to intermediate rates, approximately 100 kg N ha^{-1}, seem to be common for a one- or two-harvest management system (Landström *et al*. 1996; Cherney *et al*. 2003). Especially with a single-harvest management, nitrogen-use efficiency decreases rapidly above 100 kg N ha^{-1}, leading to inefficient use of fertilizer N and potential leaching into groundwater (Landström *et al*. 1996; Cherney *et al*. 2003; Lewandowski and Schmitt 2006). Furthermore, with a single-harvest management, reed canarygrass is capable of recycling N and other nutrients via translocation from shoot to roots, reducing the need for N fertilization in subsequent production seasons (Partala *et al*. 2001). Biomass yield of reed canarygrass responds well to application of municipal wastewater effluent and the species is capable of extracting large amounts of N, P, and other nutrients from the soil (Marten *et al*. 1979). Co-location of reed canarygrass production fields with a biomass-capable power plant and a source of wastewater from municipal effluent or agricultural processing facility would be a logical solution to develop a sustainable production system that minimizes or eliminates the need to transport expensive fertilizers and nutrients into the system.

Reed canarygrass is tolerant of a wide range of harvest managements and could produce large amounts of biomass under the relatively infrequent harvest systems used for biomass production. In a three-location study in the North Central USA, reed canarygrass biomass yield was highest under a two-harvest system in which first harvest was taken after anthesis but prior to seed ripening and second harvest was taken after killing frost (**Table 2**). Biomass yields were reduced by 18 to 29% when the first harvest was eliminated for a single harvest in autumn. Biomass yields were reduced by 67 to 76% when the first harvest was eliminated for a single harvest at the end of winter. The late winter harvest is utilized as a mechanism to allow plant biomass to naturally leach out moisture and minerals that are undesirable for a biomass feedstock used to generate energy in a combustion system. Numerous studies have shown that undesirable elements such as Cl and K are severely reduced in a reed canarygrass crop left standing over winter (Landström *et al*. 1996; Burvall 1997; Hadders and Olsson 1997; Tahir *et al*. 2010), greatly improving the biomass feedstock quality of reed canarygrass hay. Estimates of biomass yield loss during overwintering of a standing crop are generally about 25% with an associated decrease in moisture content of approximately 50% in Europe (Landström *et al*. 1996; Christian *et al*. 2006), but 57 to 68% in the North Central USA (**Table 2**). In the USA study, lodging was a severe problem, even though the rates of N fertilization were similar between the USA and European studies, eliminating the possibility of successful harvest approximately once every three years (Tahir *et al*. 2010). A distinct "ecosystem-service" advantage of a two-harvest system is that first harvest could be taken before any ripe seed is produced, completely eliminating the potential invasive threat of bioenergy-type reed canarygrass cultivars to neighboring ecosystems.

There are environments in which routine overwintering of reed canarygrass biomass appears to be a long-term sustainable enterprise for producing biomass feedstocks. In Ostrobothnia, Finland, a successful research and outreach effort led to rapid increases in land area devoted to reed canarygrass feedstock production to support several local coal-fired power plants, essentially saturating the marketplace within 4-5 years (Pahkala *et al*. 2008). This program has been strongly supported by management and production research, education and outreach, and a breeding program, all designed to deliver improved methods, information, and cultivars to reed canarygrass growers (Sahramaa 2003; Pahkala *et al*. 2008).

There is a large amount of genetic variation for biomass yield and quality traits that could be used to select cultivars with improved biomass yield and conversion efficiency (Marum *et al*. 1979b; Casler and Hovin 1985). Because management of reed canarygrass as a bioenergy feedstock is dramatically different than its use as a forage crop, breeding objectives and selection criteria must be dramatically altered to match the needs of both the feedstock producer, but also the end users who are concerned with energy production (combustion to produce heat, fermentation to produce liquid fuels, or thermochemical conversion to produce syngas). The issue is further confounded in that each conversion platform may demand highly significant modifications to the breeding objectives, e.g. reduced lignification or reduced cross-linking between lignin and cell-wall polysaccharides for fermentation (Casler *et al*. 2008), reduced Si, Cl, and K combined with lodging resistance for combustion (Lindvall 1997), or simply high biomass yield for thermochemical conversion (Boateng *et al*. 2008). Demonstrating the significant deviation of bioenergy feedstock breeding objectives from forage breeding objectives, Sahramaa *et al*. (2003) have shown that improvement of biomass yield for a one-harvest management system should focus on tall plants with many nodes and a high straw fraction, high panicle number, reduced leaf area index, and reduced axillary shoot development.

Due to the palatability and liveweight gain issues associated with alkaloids of reed canarygrass, germplasm used in pasture breeding programs has been severely restricted. Because alkaloids are not an issue in biomass conversion to energy, these restrictions need not apply to reed canarygrass breeding programs that focus on bioenergy. Because alkaloids may function to protect plants from insect predation and some environmental stresses, the use of genotypes with "wild-type" alkaloid profiles may be advantageous for developing dedicated bioenergy feedstocks. Reed canarygrass genotypes with high alkaloid concentrations are more resistant to infestation by stem borers such as frit fly, *Oscinella frit* (Byers and Sherwood 1979). Gramine is also a deterrent to aphid feeding in barley, *Hordeum vulgare* L. (Corcuera 1993), suggesting that alkaloids likely act as a mechanism of antibiosis to multiple families of insects.

Existing cultivars of reed canarygrass are clearly suboptimal for development and production of dedicated bioenergy feedstocks. Biomass yield and pest resistance are lacking in low-alkaloid germplasm, necessitating the need to discover, collect, evaluate, and refine new sources of germplasm suitable for bioenergy feedstock production. Sachs and Coulman (1983) found a wide range of Canadian accessions, collected from natural stands over a wide geographic area, that were considerably higher in biomass yield compared to existing cultivars. Because the focus of this collection and evaluation was for forage and pasture, this germplasm collection has yet to be exploited for improving biomass yields of reed canarygrass as a bioenergy feedstock in Canada. Casler *et al*. (2009) collected and evaluated 72 reed canarygrass accessions collected from natural and wild areas in the North Central and Northeastern USA, finding 39 of these accessions to rank higher in biomass yield than all eight cultivars evaluated. Four accessions had biomass yield 10% higher than the cultivar with the highest biomass yield (Casler *et al*. 2009). Collections made throughout Finland and Sweden are the foundation of new cultivar development initiatives in those two countries (Lindvall 1997; Sahramaa 2003).

CONCLUSIONS

In much of temperate North America, reed canarygrass is still considered to be one of the premier forage grasses, having utility as both a hay and pasture crop with adaptation to a wide range of soils and environmental conditions. Low seedling vigor and poor competitive ability against annual weeds, leading to poor and/or inconsistent establishment, is the major limitation to increased utilization of reed canarygrass in livestock agriculture. Research on naturally occurring alkaloids in reed canarygrass tissues and their role in palatability, intake, and health of grazing livestock resulted in drastic modifications to reed canarygrass cultivars, successfully transforming a highly toxic plant used largely for soil conservation into a healthy and nutritious pasture plant. Future use in bioenergy feedstock production systems will require comparable breeding efforts and genetic studies using specific harvest management schemes and focus on specific selection criteria and breeding objectives designed to improve biomass yield and standability, stress tolerances, and feedstock quality.

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