RESEARCH

Forage Rye Improvement in the Southern United States: A Review

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ABSTRACT
Rye (Secale cereale L.) is an important crop worldwide for grain and forage production. Stocker cattle (Bos spp.) production in the southern United States relies on rye for forage from autumn to spring when warm-season perennials remain dormant. Because rye has high-stress tolerance with respect to both soil and environment, it fills a particular niche that spans the winter months for the region. Rye forage yield has not improved over time, due in part to limited breeding effort. Many of the cultivars currently grown in the region were released as early as the 1950s. Similar to other forage crops, gains in forage yield have been small or nonexistent; therefore, an evaluation of the crop in relation to past and current breeding strategies could contribute to the future improvement of the crop. The objectives of this manuscript are to review the rye crop in relation to its cropping system, the genetic considerations for rye in relation to breeding, and past and current breeding efforts and selection processes and then to propose breeding methodologies for the improvement of rye with major focus on forage yield. Methods of selection that rely on family performance in multienvironment trials are recommended. With advancements in breeding methods, rye poses a unique opportunity among the forage crops to enable rapid cycling for development of improved cultivars.

RYE OVERVIEW
Cereal rye, hereafter referred to as rye, is an important grain crop worldwide with most of the area harvested in Poland, Russia, Germany, Belarus, and the Ukraine (FAOSTAT, 2010). Worldwide, rye accounts for only 0.7% of cereal production (Feuillet et al., 2007). In 2010, the total area of rye harvested for grain in the United States was approximately 107,000 ha. Assuming all 107,000 ha was grown for forage the following year, this would support over 13 million ha of rye planted as a forage crop. Although the area harvested in the United States is low compared to other small grain crops, including wheat (Triticum aestivum L.), barley (Hordeum vulgare L.), and oat (Avena sativa L.), it is an important forage crop. Across the United States the majority of the rye is not used for grain but rather for animal feed in a graze-out production system (Morey and Barnett, 1980). In a graze-out system, the crop is used as forage until late spring as warm-season perennial forages, such as bermudagrass [Cynodon dactylon (L.) Pers.], begin actively growing (Bowman et al.,...
2008). Rye could also be used in a graze-grain system, in which the crop is grazed until the jointing phenological stage, thus allowing for grain production and harvest; however, this system is usually followed mainly in wheat (Rao et al., 2000). Much of the rye forage production in the United States occurs in the south; however, it is used as forage throughout the United States. In the southern region, defined as the area between Texas and Oklahoma eastward toward Florida and Georgia, rye is planted in late summer or early autumn and grown as winter forage from October through May (Ball et al., 2007). Rye is more suitable for grazing systems than other small grains due to its greater forage production (Poya, 1985), especially during the winter months (Bruckner and Raymer, 1990), and because it may have less potential for causing grass tetany due to greater Ca and Mg concentrations (Mayland et al., 1976). Rye has excellent forage quality (approximately 120 g crude protein kg⁻¹ and 700 g in vitro dry matter digestibility kg⁻¹) sufficient for growing cattle (NRC, 1996; Islam et al., 2011; Butler et al., 2012). Rye–annual ryegrass (Lolium multiflorum Lam.) pastures, which were predominantly rye, produced on average 1.05 kg d⁻¹ average daily gain (ADG), 448 steer grazing days ha⁻¹ (duration on pasture), 491 kg ha⁻¹ total live weight gain, and US$279 ha⁻¹ yr⁻¹ expected net return (Islam et al., 2011). However, ADG (0.81–1.20 kg d⁻¹), grazing days (161–734 d ha⁻¹), and total gain (130–844 kg ha⁻¹) varied over the 5-yr period and was highly dependent on rainfall. Breeding rye for forage has been limited with the exception of two institutions (the University of Florida and the Samuel Roberts Noble Foundation) in the south; however, this system is usually followed mainly in wheat and 75 to 100 kg ha⁻¹ for the graze-grain system (Bishnoi, 1980; Rao and Horn, 1995; Ball et al., 2007). This system has been typical of the High Plains, Southeast, and wheat belt of Oklahoma and Kansas (Beck et al., 2008). Rye is also well known for its overwintering ability and has the highest tolerance to cold temperatures, drought, salt, and Al stress among all of the small grain cereals (Geiger and Miedaner, 2009). Rye is also the best adapted of the winter annuals in high-stress, low-yield environments (Bruckner and Raymer, 1990). In addition to these attributes, rye is also highly valued for its superior disease resistance. The value of rye for disease resistance was demonstrated by the IRS chromosome from rye, which provided race-specific disease resistance to major rust diseases when introduced into wheat via a 1BL/IRS chromosomal translocation (Zarco-Hernandez et al., 2005). There is also a considerable interest in rye for its contribution to the development of triticale (×Triticeae Wittm. ex A. Camus) as a forage crop (Feuillet et al., 2007).

GENETIC CONSIDERATIONS FOR BREEDING

Unlike most small grain crops, rye is unique in that it is a true diploid (Lundqvist, 1956) and allogamous. Rye has 14 chromosomes (2n = 2x = 14) with a relatively large genome size, estimated to be on the order of 8 Gbp (Doležel et al., 1998). In relation to some of the other small grains, the rye genome is estimated to be larger than barley (4.9 Gbp) but smaller than oat (11.3 Gbp) and wheat (16.5 Gbp). Because rye is primarily grown as forage in the United States, grows tall with a tendency to lodge, is an obligate outcrossing species, and is a poor seed producer, breeding rye has been difficult (Barnett et al., 2002). Outcrossing is enhanced by a strong self-incompatibility system (Lundqvist, 1956). Therefore, the majority of cultivars released across the south are open-pollinated varieties (OPVs), also referred to as synthetics, that are both heterogeneous and heterozygous. Released cultivars have probably changed genetically over time due to unintended natural selection processes during seed increase and maintenance (Chebotar et al., 2003) or failure of seed production in isolation. Outside of the United States, namely in Germany, hybrid rye cultivars for grain production have been successfully developed (Tomerius et al., 2008). Similar to other hybrid breeding programs, hybrid production in rye depends on a cytoplasmic male sterility (CMS) system for seed production (Havey, 2004). In Germany, the best hybrids produce from 10 to 20% greater grain yield than the best OPVs (Geiger and Miedaner, 2009). Whether these production levels transfer to forage production or if the cost of hybrid seed production would be economical for forage in the United States remain in question.
CURRENT BREEDING EFFORTS

The major breeding programs that have contributed to improvement of rye for forage in the past have been the Samuel Roberts Noble Foundation, Texas AgriLife Research, the University of Georgia, and the University of Florida. Currently, only the Noble Foundation and the University of Florida maintain active rye breeding programs. All released cultivars currently grown as forage are OPVs and are derived from open-pollinated single plant visual selections from earlier cultivars, single crosses, or poly-crosses (Table 1). Interestingly, the pedigrees of most of the current cultivars are derived from ‘Abruzzi’, originally collected from Italy, or ‘Maton’, derived from a polycross of 43 collections of ‘Balbo’ made from various states and 10 cultivars including Abruzzi. Although most of the recent cultivars are derived from these few released OPVs, the released OPVs are not static populations but most likely differ with respect to their spatial and temporal origin. For the region surrounding the Samuel Roberts Noble Foundation, much of the forage rye produced consists of ‘Elbon’ and Maton, cultivars released in 1956 and 1975, respectively. In the Southeast, most of the acreage of rye is planted in ‘Wrens Abruzzi’, released in 1970. A major difficulty in the development of new cultivars is the difficulty to develop cultivars with greater forage yield than these early releases (R. Barnett, personal communication, 2012). The current and past breeding methods for the crop need to be adjusted to improve the response to selection to develop populations that outperform current cultivars.

In contrast to the phenotypic recurrent selection breeding methods implemented in the United States, other regions have produced hybrid rye specifically for grain production (Geiger and Schnell, 1970). Hybrid superiority to OPVs is well documented across a wide range of species including maize (Zea mays L.; Duvick, 1999) and rice (Oryza sativa L.; Budar and Pelletier, 2001). The appeal of hybrid production is due to the generally superior performance of hybrids over OPVs with respect to overall performance, including stress tolerance and yield. An excellent model for this system in rye has been applied in Germany since around 1970 and has been highly successful (Geiger and Miedaner, 2009). The yield increases in hybrids are attributed to heterosis, the superiority in performance of hybrids in comparison to their parents (Fehr, 1987). The system that is widely used in Germany (Geiger and Miedaner, 2009) for hybrid rye production is dependent on (i) self-fertility to develop inbred lines, (ii) CMS for production of hybrid seed, and (iii) heterotic pools that maximize heterosis. The highly effective self-incompatibility system in rye can be overcome by self-fertility genes that have been detected in various European germplasm sources. Given self-fertility, inbred lines are produced by continued self-fertilization of single plants. Both line and testcross performance are used as selection criteria during inbreeding; testcross seed is produced based on CMS. There are various sources of CMS available in rye, although most hybrids are produced using the Pampa cytoplasm (Lapiński and Stojałowski, 2001). Recent findings of restorer genes for the Pampa cytoplasm that are stable across environments have greatly improved seed production (Miedaner et al., 2000, 2005). Lastly, early research determined that two heterotic pools exist that exhibit the greatest hybrid performance, referred to as the Petkus and Carsten gene pools (Hepting, 1978).

Table 1. Most commonly grown winter forage rye cultivars for the southern region. Information for each cultivar includes the type of cultivar, year of release, pedigree, primary method of selection, the source of primary release, and the reference associated with the release if available.

<table>
<thead>
<tr>
<th>Cultivar name</th>
<th>Type of cultivar</th>
<th>Year released</th>
<th>Pedigree</th>
<th>Selection method</th>
<th>Source†</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abruzzi</td>
<td>OPV</td>
<td>Early 1900s</td>
<td>Collected in Italy</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Elbon</td>
<td>OPV</td>
<td>1956</td>
<td>Abruzzi from Oregon</td>
<td>–</td>
<td>NF</td>
<td>–</td>
</tr>
<tr>
<td>Wrens Abruzzi</td>
<td>OPV</td>
<td>1970</td>
<td>Abruzzi</td>
<td>Natural selection</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Maton</td>
<td>OPV</td>
<td>1975</td>
<td>OP Tenn 1/4062 population (43 collections of Balbo plus 10 cultivars [Caribou, Emory, Elbon, Elk, Explorer, Gator, Pierre, Rosen, Weser, and Abruzzi])</td>
<td>F2 single plant selection</td>
<td>NF</td>
<td>Bates (1979)</td>
</tr>
<tr>
<td>Wrens 96</td>
<td>OPV</td>
<td>1996</td>
<td>Wrens Abruzzi</td>
<td>Seven cycles of recurrent phenotypic selection</td>
<td>FL and GA</td>
<td>Bruckner et al. (1999)</td>
</tr>
<tr>
<td>AGS 104</td>
<td>OPV</td>
<td>2003</td>
<td>Mixture of five strains that included Bates, Maton, BR1, Florida 401 (Pflaum et al., 1986), WALC7, and NF 73</td>
<td>Bulk selection</td>
<td>FL and GA</td>
<td>–</td>
</tr>
</tbody>
</table>

†Source refers to The Samuel Roberts Noble Foundation (NF), Texas AgriLife Research (TX), the University of Florida (FL), and the University of Georgia (GA).

†OPV, open-pollinated variety.

†OP Tenn, open-pollinated Tennessee.
Regardless of the success of hybrid rye programs, the question remains as to whether a hybrid system would be economical for rye forage producers in the United States. This question is largely dependent on whether the gain in forage yield as a result of heterosis can overcome costs for seed production. Unfortunately, there is a far lower mean heterotic increase for forage yield compared to grain yield—12 and 32%, respectively (Roux et al., 2010)—and this result was later verified (Miedaner et al., 2010, 2012), indicating that hybrid rye production for forage may not be economically feasible for the southern United States.

**BREEDING OBJECTIVES**

Increase in autumn and total forage yield are the major breeding objectives for rye in the southern United States. Typically, forage yield is measured by mechanical harvest- and selections can be based on autumn, winter, and/or total forage yield in a given field season. For rye, visual evaluation of individual genotypes for vigor or height, which are (assumed to be) traits correlated to forage yield, are used as the primary selection criteria. A restricted recurrent phenotypic selection program (adapted from Burton [1982]) basing selection on visual forage potential of spaced plants in a gridded nursery was successful at improving yield on a per plant basis (Bruckner et al., 1991). However, the gains found in spaced plants were not realized when populations were evaluated under more competitive conditions similar to producer densities. Visual forage potential ratings were primarily based on plant size but also involved assessment of plant leafiness and growth habit (Bruckner et al., 1991). Although recurrent phenotypic selection on spaced plants has been successful in some species (Gates et al., 1999; Burton and Mullinix, 1998), the lack of yield improvement in forages, and possibly in the case of rye, can be attributed to simply not selecting for yield per se (Brummer, 2005). Selection based on correlated traits, such as visual forage potential, may not have a strong correlation or maybe even negatively correlated to forage yield in swards (Casler and Brummer, 2008). At the Samuel Roberts Noble Foundation, recent emphasis has been placed largely on early autumn to winter forage production. The most recent released cultivar, Maton II (Baker et al., 2008), has 55 and 6% greater early autumn to winter and total forage production than Maton, respectively. However, selection for early autumn to winter forage production may result in early maturing plants, thus decreasing the duration of the field season. For grain crops this is a large advantage, but in the case of forage crops, later maturity results in plants that are vegetative longer in the season and may extend the forage availability of the crop. Besides selection for forage yield in rye, very little emphasis is placed on plant pests or diseases, as this does not generally pose a large problem for the region. With the major breeding objective and hurdle being forage yield, little effort has been placed on forage quality traits including crude protein, dry matter percentage, acid or neutral detergent fiber, or in vitro dry matter digestibility.

**FUTURE GENETIC IMPROVEMENT**

**Improved Germplasm Use**

Given the apparently narrow germplasm base of southern U.S. cultivars, perhaps a valuable resource that has not been extensively explored for rye improvement are germplasm resources. Unlike production of rye for grain production, rye produced for forage does not need to meet seed quality requirements. For many crops, including rye, germplasm resources are often underused for many reasons (Geiger and Miedaner, 2009), including the lack of adaptation to the target environment and large differences in phenotypic performance between genebank accessions and commercial cultivars. The National Plant Germplasm System (NPGS) in the United States maintains a collection of rye and its relatives. The NPGS Germplasm Resources Information Network (GRIN) currently describes 2049 world accessions of the various species and subspecies of Secale, 1962 of which are cultivated rye. Evaluation of the germplasm in the southern United States target environment may identify useful resources that are not currently being exploited. The NPGS does evaluate many traits that enable initial selection of lines for evaluation; a starting point for rye in the south would be for winter types. After evaluation of winter types, the origin of the selected lines could be a useful criterion to further explore the accessions in the NPGS. An alternative approach for testing, due to the fact that much of the germplasm lacks adaptation to the target environment, is to produce testcross seed with adapted cultivars followed by evaluation. This could enable identification of valuable germplasm accessions that would otherwise be discarded due to the lack of adaptation to the target environment. Even germplasm that has been evaluated previously may have changed genetically over time due to procedures for population maintenance (Chebotar et al., 2003), which may warrant a reevaluation. In any case, molecular markers in many crops have shown that valuable alleles are present in wild or untapped germplasm resources ( Tanksley and McCouch, 1997), and the situation in rye is unlikely to be different.

**Improved Selection Methodologies**

A lack of yield improvement among forage crops compared to grain crops has been well documented ( Humphreys, 1999; Casler, 1998). The lack of progress for yield improvement could be due to selection for a wide variety of economically important traits, particularly if one or more of them is negatively correlated to on-farm forage yield (Casler, 2001). Yield in forages, including rye, could be improved by more efficient and focused breeding
methods including half-sib and full-sib selection methods (Casler and Brummer, 2008). A first step in future genetic improvement of rye requires a more focused selection approach and determination of a selection criterion positively correlated with on-farm forage yield. The half-sib family (HSF) approach outlined by Casler and Brummer (2008) would be suitable for rye (Fig. 1), resulting in calculation of breeding values based on the general combining ability of a specific genotype rather than the visual phenotype of spaced plants. In short, HSFs are generated from open-pollination of random seed from a population and evaluated in replicated, multienvironment trials (METs) in seeded rows or swards (depending on seed quantities available). Seed for the next cycle is generated from a poly-cross of random remnant HSF seed of the selected parents (Fig. 1). However, because a HSF would be derived from a single plant involved in a poly-cross, selection based on HSFs would need to be accomplished with only a small amount of seed. Hill plots are used to evaluate yield in oat and are highly correlated to grain yield under production conditions (Frey, 1965). Hill plots could be easily adapted to selection for forage yield among HSFs in rye. For oat, hill plots generally consist of 30 seeds planted in a single hole on 30-cm centers (i.e., each hill plot is 30 cm apart). Thirty seeds were used for oat based on the seeding rate of 125 kg ha$^{-1}$ planting density, which is in accordance with common planting densities for oat as grain. Typically for rye, 112 kg pure live seed per ha$^{-1}$ are planted; therefore, about 40 seeds per hill with 30-cm centers would meet normal plant densities for forage. Depending on the number of seed available, the same plant density could be achieved with 15-cm centers using 10 seeds per hill plot. An option such as this could enable the breeder to evaluate large numbers of HSFs directly for forage yield by cuttings of individual hills in METs. Most importantly, selection among HSFs would be grown in plant densities typical of producers. The hill-plot method assumes that forage yield in hills is positively correlated to on-farm forage yield. Various studies have found hill plot grain yield to be highly correlated with on-farm yield in other small grain crops (Frey 1965; Jellum et al., 1963). In fact, Frey (1965) determined that genetic correlations between rod rows and hill plots were 0.98, 0.96, and 0.96 for grain yield, plant height, and heading date, respectively. A possible mechanism for such a correlation between hill plots and on-farm yield is due to the high inter- and intraplot competition that occurs among hill plots. In contrast, visual selection of spaced plants, which may not be indicative of yield in high competition stands typically found on-farm, may not result in yield gains. The empirical results of rye breeding programs suggest this is the case.

A potential downside of HSF selection is the fact that both the female parent and tester are heterozygous. Theoretically, the additive genetic variance among HSFs is only one-fourth of the overall additive variance (Lynch and Walsh, 1998). An alternative and complementary method to overcome this issue would be selection among full-sib families (FSFs) in a HSF–FSF design. The additive variance among FSFs (one-half) is double that of HSFs and selection among FSFs could be used in tandem with HSF selection. The proposed HSF–FSF design would follow the same principle outlined in Fig. 1 except the addition of developing FSFs from random seeds between selected HSFs. Due to the greater time requirement for production of FSFs, a much smaller number of FSFs would be produced compared to HSFs. This HSF–FSF design would enable greater selection and provide a preselection of seed before large amounts of time are devoted to developing FSFs. Regardless of whether HSF selection has this issue, it is substantially more effective than current methods of selection that are practiced in rye. However, the HSF–FSF design lends a possible solution that attempts to overcome this issue concerning HSF selection.

Genetic Markers to Increase Selection Gain

The improvement of quantitative traits using molecular markers can enhance the response to selection (Heffner et al., 2009). For rye in the southern United States, selection has not been conducted using molecular marker information. The efficiency of marker-assisted selection (MAS) as compared to phenotypic selection is greater for traits with low heritability and smaller family size (Lande and Thompson, 1990). In traditional MAS, quantitative trait loci (QTL) are identified in a biparental population and selection for the desired allele is conducted. The selection...
criteria can be based purely on markers or a combination of marker and phenotypic selection. For rye, the production of biparental populations for QTL detection would not adequately sample the allelic diversity in the crop; therefore, other methods are more appropriate. More recently, genome-wide association studies (GWAS) have been used to identify QTL in large populations of existing breeding lines and can be used even if the population of lines contains individuals with different levels of relatedness or is structured into subpopulations (Yu et al., 2006). Quantitative trait loci that are identified by GWAS can then be used as the basis of selection using traditional MAS. Given the allogamy of rye, GWAS would be a preferred method for sampling the high levels of allelic diversity present, both within and between current cultivars. Potential target traits for QTL in rye using MAS would be those that are controlled by a few large-effect QTL such as self-incompatibility, plant height, and heading date. Identification of such traits could also enable identification of potential accesses from GRIN, for example, with proper heading date for the target environment. Genomic selection (GS) (Heffner et al., 2009), on the other hand, can be used to predict the genetic value of individuals, also referred to as the genomic estimated breeding value, based on marker alleles (Meuwissen et al., 2001). By using many genome-wide markers, selection is based on a larger proportion of the genetic variation, including markers that do not statistically associate with QTL in a GWAS context, resulting in more accurate estimates of breeding values (Goddard and Hayes, 2007; Solberg et al., 2008). The properties of GS lend itself to selection of traits with a large number of small-effect QTL controlling the trait of interest. For rye, GS would be appropriate for forage quality traits and forage yield. All mapping relies on linkage disequilibrium (LD), the nonrandom association of alleles at two loci (Falconer and Mackay, 1996), in the working population. With advances in molecular marker development, single nucleotide polymorphisms (SNPs) can be identified even for relatively large genomes with large amounts of highly repetitive DNA (Elshire et al., 2011), as is the case for rye (Bartoš et al., 2008). The extent of LD in rye has been explored for genes involved in frost response (Li et al., 2011a), as is the case for rye (Bartoš et al., 2008). In short, across five populations in 11 candidate genes, significant LD declined within 520 bp. The LD likely decays more rapidly in rye than the other small grains, including oat (Newell et al., 2011), wheat (Chao et al., 2007), and barley (Hamblin et al., 2010), attributed to the large number of effective recombinations in rye due to its allogamy. From the preliminary data on the decay of LD in rye, efficient application of genome-wide methods will require large numbers of SNPs to capture adequate levels of genetic variation across the genome. Assuming the extent of significant LD of Li et al. (2011b) of 0.16 (measured as $r^2$), 76,000 SNPs would be required, on average, to explain just 16% of QTL variance. Whether this level of LD is typical of breeding populations in the southern United States and whether gains from selection based on markers is worth the cost are still unknown.

Implementing Genome-Wide Association Studies and Genomic Selection in Rye

Various GWAS have been implemented on a wide range of species including mice (Mus spp.) (Farber et al., 2011), humans (Homo sapiens sapiens) (Sturm et al., 2008), and crop plants (Neumann et al., 2011) including the small grains (Newell et al., 2012). In general for plants, an association panel that covers the range of diversity in the species is both genotyped and phenotyped (Long and Langley, 1999). However, for rye this approach is not applicable given that it is both heterogenous and heterozygous. As a result, each plant is genetically different and cannot be replicated for measurement of phenotype. Therefore, for solving this issue in addition to capitalizing on the out-breeding nature of rye, genotyping on single plants and phenotyping their HSF progeny in METs is an alternative, hereafter referred to as the HSF design. Such approaches have been successful in Drosophila melanogaster (Kennington et al., 2007) and theoretical approximations of power have demonstrated that the HSF design is more powerful than the traditional approach for traits with low heritability (Chenoweth and Visscher, 2009). A major advantage of the HSF design is that it is easily incorporated into the recommended recurrent HSF approach for rye improvement in previous sections (Fig. 1). Therefore, its only additional cost is that for genotyping given the fact that phenotyping the HSFs is already completed to make selections within an applied breeding program. The panel for implementation of GWAS in rye could essentially comprise a series of HSFs derived from a poly-cross of individual plants. Another avenue for population development would be to derive a randomly mating population from a cross between two cultivars followed by multiple generations of random mating (Li et al., 2011a).

A major limitation of the HSF breeding scheme (Fig. 1) are the number of selection cycles conducted on a per-year basis. Selection can only take place once every 2 yr given crossing and selections are made in alternating field seasons. This is consequently a major limitation for the time required to release a new cultivar. Three methods can be implemented to alleviate this limitation: (i) use a smaller number of lines in the initial poly-cross and have multiple poly-crosses in a given field season, (ii) implement two programs simultaneously in alternating field seasons, and/or (iii) implement GS for off-season selection within HSFs. If a small panel is used initially for the poly-cross, and/or (iii) implement GS for off-season selection within HSFs, it could be completed in the greenhouse; however, this assumes a suitable amount of seed would be produced for field evaluation in METs. Of the three approaches to
alleviate this major limitation of the HSF breeding design, the first two fail to use off-season greenhouses or nurseries for selection whereas the latter does enable selection in the off-season (Fig. 2). Although rye is largely different from other small grain species because of its allogamy and self-incompatibility system, GS for other small grains and simulations has been proven successful for accelerating the breeding cycle (Jannink, 2010; Asoro et al., 2011). In addition to the advantage of GS on a per-year basis (Heffner et al., 2010), a major advantage of such an approach would be the ability to select not only among HSFs but also within HSFs. The expected gains of among- and within-HSF selection relative to HSF selection are greatly improved and positively correlated with the within-family heritability (Casler and Brummer, 2008). For example, given a within-family heritability of 0.3, the relative gain varies from about 160 to 275% for among- and within-HSF selection relative to HSF selection for varying within-family selection intensities. Therefore, implementation of GS would enable within-HSF selection to be practiced in the off-season greenhouse or nursery and the selected plants as a result of GS would be used for poly-cross establishment in the field. The major modifications to HSF selection (Fig. 1) to implement among- and within-HSF selection using GS (Fig. 2) are genotyping plants involved in the initial poly-cross, training the GS model followed by validation, two cycles of selection within selected HSFs between field seasons, and poly-cross establishment with $1/p$ selected seeds from the selected $f$ families. Selection in the off-season greenhouse or nursery would only occur every other year; therefore, further modifications could be made to incorporate GS and make selections in every off-season cycle.

**CONCLUSIONS**

Rye improvement has been limited in recent years even though the stocker cattle industry in the southern United States...
States relies on rye for forage from autumn to spring. Rye improvement has been predominantly based on recurrent phenotypic selection of spaced plants, and little gain for forage yield has been made. As a result, much of the acreage grown across the south consists of old cultivars, all OPVs, developed before 1980. This is a similar situation for many of the forage crops and has been attributed to (i) selection for traits with little or no correlation with on-farm yield and (ii) a lack of efficient and focused breeding methods. Given the difficulty in developing OPVs with superior performance, we suggest several improved methods that could make yield gains for forage rye in the future. The hill plot method could be a viable and testable approach to indirectly select for on-farm forage yield. The hill plot method of evaluation has high correlations with on-farm grain yield for other small grains and allows evaluation of large numbers of families in METs when seed is a limited resource. Casler and Brummer (2008) discuss methods of selection for forage crops to initiate more efficient and focused breeding methods; it is concluded here that selection among HSFs or a HSF–FSF design could vastly improve selection for on-farm forage yield in rye. The combination of these two methods, HSF or HSF–FSF selection and hill plot evaluation, would enable selection among families for a trait most likely to have reasonable correlation with on-farm forage yield in METs covering the target environment. Such a selection approach that combines these two processes, to our knowledge, has yet to be tested or implemented for improvement of forage yield in the small grains. An added benefit of a more efficient and focused breeding method is the adaptation of GWAS and GS methods. Application of GS in such a scheme would enable selection in off-season nurseries within HSFs, thus increasing the number of selections per year from one to as many as three and doubling or even tripling the genetic gain per year. Additionally, selections within HSFs in off-season nurseries or greenhouses theoretically improve the response substantially relative to selection among HSFs. Therefore, among the forage crops, rye poses a unique opportunity for testing improved methods of selection with rapid cycling to deliver improved cultivars with greater forage yield.

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