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SCIENTIFIC PERSPECTIVES

Theoretical Expected Genetic Gains for Among-and-Within-Family Selection Methods in Perennial Forage Crops

Michael D. Casler* and E. Charles Brummer

ABSTRACT

Genetic gains in forage yield lag far behind the gains made in grain yield of cereal crops, partly because of the use of inefficient selection methods that make little use of additive genetic variance within half-sib or full-sib families. The objectives of this study were (i) to compute expected genetic gains for among-and-within-family (AWF) selection methods, (ii) to compare these selection methods to standard family and progeny-test selection methods, and (iii) to define the conditions under which AWF selection methods may be superior to progeny-test selection. Among-and-within-family selection is equal to or better than family selection under all circumstances provided the within-family selection criterion (X or Y) is heritable and has a positive genetic correlation with the desired trait (Y). Among-and-within-family selection is favored over progeny-test selection by (i) high heritability on an individual-plant basis (relative to heritability on a family-mean basis), (ii) within-family selection intensity ≥ among-family selection intensity, and (iii) possibly a shorter cycle time (for some species and some breeding programs). These conditions are more frequently achieved for half-sib mating systems due to the greater partitioning of additive genetic variance within families, but AWF selection can also be heavily favored in a full-sib mating system under conditions that are a bit more restrictive.

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Abbreviations: AWF, among-and-within-family; AWFX, among-and-within-family selection for different traits; AWFX-FS, among-and-within-family selection with different selection criteria among vs. within families using full-sib families; AWFX-HS, among-and-within-family selection with different selection criteria among vs. within families using half-sib families; FSF, full-sib family; FSPT, full-sib family progeny-test; G×E, genotype × environment; HSF, half-sib family; HSPT, half-sib family progeny-test.

It is well documented that gains in forage yield from breeding forage crops are low to nonexistent, despite over 100 years of breeding efforts in some forage species (Casler et al., 1996; Casler, 1998; Humphreys, 1999, 2005). Most estimates of gains in forage yield are less than 10% of the gains made for grain yield of cereal crops. Humphreys (1999) and Casler (1998) discussed several reasons for this yield lag in forage crops relative to grain crops: (i) a longer breeding cycle for forage crops, most of which are perennials, (ii) lack of a "harvest index" trait to aid dry-matter partitioning into the economic product, (iii) inability to exploit heterosis in commercial cultivars, and (iv) our focus on a wide array of economically important traits of forage crops, many of which are not specifically correlated or may be negatively correlated with forage yield (Casler, 2001).

The most notable exception to the lack of yield progress in forages is the Pensacola bahiagrass (*Paspalum notatum* Flüggé var. *saurae*

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Parodi) breeding program led by the late Glenn Burton at Tifton, GA. This program documented gains in forage yield of 21% cycle^{-1}, sustained over 18 cycles of selection and realized in both spaced plantings and sward-plot trials (Gates et al., 1999; Burton and Mullinix, 1998). In addition, recent results of several selection experiments suggest that forage yield can be increased by breeding, at rates of gain far surpassing the rates of 1.0 to 4.0% decade^{-1} typically cited (Humphreys, 1999, 2005). In orchardgrass (*Dactylis glomerata* L.), one cycle of intensive half-sib family selection resulted in significant gains in all three source populations, with an average increase in forage yield of 6.5% or 1.3% yr^{-1} (Casler et al., 2002). In perennial ryegrass (*Lolium perenne* L.), four cycles of among-and-within-family (AWF) selection resulted in a gain in forage yield of 12.8% or 1.1% yr^{-1} (Wilkins and Humphreys, 2003). Other reports of progress from selection for forage yield have been published (summarized in Casler et al., 1996; Brummer and Casler, 2008).

The lack of yield improvement can be ascribed in many cases to simply not selecting for yield per se (Brummer, 2005). Many other traits—including nutritive value, disease resistance, and winter hardiness—also need to be improved, and because yield is not easily measured, it is often not the focus of the program. Additionally, the ultimate trait that forage producers need, forage yield in a solid seeded sward, is rarely measured. Visual vigor ratings are often used as a proxy for yield, although the genetic correlation between forage yield and vigor rating may not be strong. Further, when measured directly, yield is often evaluated on spaced plants rather than swards, even though the genetic correlation of yield under these two conditions is known to be low in most cases (Wilkins and Humphreys, 2003). Although forage producers have not exerted strong pressure on breeders to create cultivars with higher forage yield, the recent worldwide focus on breeding dedicated bioenergy crops has increased attention on improving biomass yield as one of the most important breeding goals (Perlack et al., 2005).

We conclude from these studies that rates of gain for forage yield and other traits of forage crops can be improved by use of more efficient and focused breeding methods. Vogel and Pedersen (1993) estimated that AWF selection should be more efficient than half-sib progeny-test selection under the fairly restrictive conditions of equal among-family and within-family phenotypic variances. Apart from their computations, no theoretical framework exists to compare family, progeny-test, and AWF selection methods. The objectives of this review are (i) to compute expected genetic gains for AWF selection methods in which within-family selection is based on the same or different trait(s) as among-family selection, using both half-sib and full-sib mating schemes, (ii) to compare these selection methods to standard among-family and progeny-test selection methods, and (iii) to define the conditions under which AWF selection methods may be superior to progeny-test selection. We expand on the computations and framework of Vogel and Pedersen (1993) by defining the efficiency of two different forms of AWF selection using either half-sib or full-sib families, compared with both family selection and progeny-test selection. More specifically, we define the conditions under which AWF selection is superior to other selection methods for a range of AWF heritabilities and selection intensities. Furthermore, our purpose is to provide direct and explicit comparisons among recombination and selection methods within both half-sib and full-sib family mating schemes, not specifically to compare among different mating schemes or family structures. Other researchers have provided explicit comparisons among selection methods with different family structures (Hill and Haag, 1974). The latter authors demonstrated the theoretical difference between family and progeny-test selection methods on changes in allele frequencies, while Haag and Hill (1974) provided an empirical comparison of family vs. progeny-test selection. Neither study investigated AWF selection methods.

MATERIALS AND METHODS

Expected gains were computed assuming disomic inheritance, linkage equilibrium, no epistasis, and random mating equilibrium within the population (Falconer and Mackay, 1996; Hallauer and Miranda, 1988). Most perennial forage crops are polyploid, exhibiting both disomic and polysomic inheritance (Harlan and deWet, 1975). Because polyploids transmit multiple alleles within a locus to their progeny, covariances of relatives for autopolyploids are more complex than for diploids. Among-family variances (σ^2_F) are

$$\sigma^2_F = (1/4)\sigma^2_A \text{ (half-sib, diploid)},$$

$$\sigma^2_F = (1/4)\sigma^2_A + (1/36)\sigma^2_D \text{ (half-sib, autotetraploid)},$$

$$\sigma^2_F = (1/2)\sigma^2_A \text{ (full-sib, diploid), and}$$

$$\sigma^2_F = (1/2)\sigma^2_A + (2/9)\sigma^2_D + (1/12)\sigma^2_T + (1/36)\sigma^2_Q \text{ (full-sib, autotetraploid)}$$

where σ^2_A is additive genetic variance, σ^2_D is dominance genetic variance (diploid) or digenic genetic variance (autotetraploid), σ^2_T is trigenic genetic variance, and σ^2_Q is quadrigenic genetic variance (Gallais, 2003). Empirical estimates of nonadditive genetic variances were considerably lower than estimates of additive genetic variances in autotetraploid alfalfa, *Medicago sativa* L. (Dudley et al., 1969), indicating that these small fractions of nonadditive genetic variances can reasonably be ignored for the purpose of comparing selection methods (Wricke and Weber, 1986; Gallais, 2003).

Four selection methods were modeled in this study: family selection with recombination of random plants within selected families, AWF selection with recombination of selected plants within selected families, AWF selection with recombination of naturally selected (surviving) plants from sward plots of selected families, and progeny-test selection with recombination of saved parental clones (Fig. 1). Each of the four selection methods was modeled for two mating systems: half-sib or polycross families and full-sib families.

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The first two events shown in Fig. 1 involve establishment of the initial parents in polycross or full-sib crossing blocks and development of the first group of families for field evaluation. This process may be completed in one year (using greenhouse facilities with limited quantities of seed), two years in the field (with no selection of parental plants), or multiple years in the field (with phenotypic selection of parental plants). Our purpose is to develop expected gains for multiple cycles of recurrent selection in a dedicated, long-term breeding program for agronomic traits, such as forage yield and/or other agricultural fitness traits. Therefore, we considered these first two events to be preparatory to the initiation of all family selection methods; that is, each cycle of family selection, including the first cycle, begins with the establishment of N families in field trials and ends with the generation of a new set of N families. In this regard, we differ from the goals and breeding methodology presented by Vogel and Pedersen (1993). We also differ from Vogel and Pedersen (1993) in that we believe that progeny-test selection is not necessarily a single-cycle "dead-end" selection method even though the parents for the next cycle must be drawn as seeds from the previous recombination event and this method requires two recombination events per cycle (Fig. 1).

For simplicity, we have purposely ignored genotype × environment (G×E) interactions in all of our expected gain derivations. Because G×E interactions are a component of phenotypic variance, there is much greater potential to use multilocation testing, multiple years, and family replication to reduce the among-family phenotypic variance relative to the within-family phenotypic variance. The latter can be reduced only by use of clonal replication. Although numerous authors have used clonal replication for the purpose of estimating genetic variance components and population genetic structure (e.g., Dudley et al., 1969; Aastveit and Aastveit, 1990), clonal replication is unlikely to be used on a routine basis due to excessive time and expense. Evidence that individual plants are subject to extreme G×E interac-

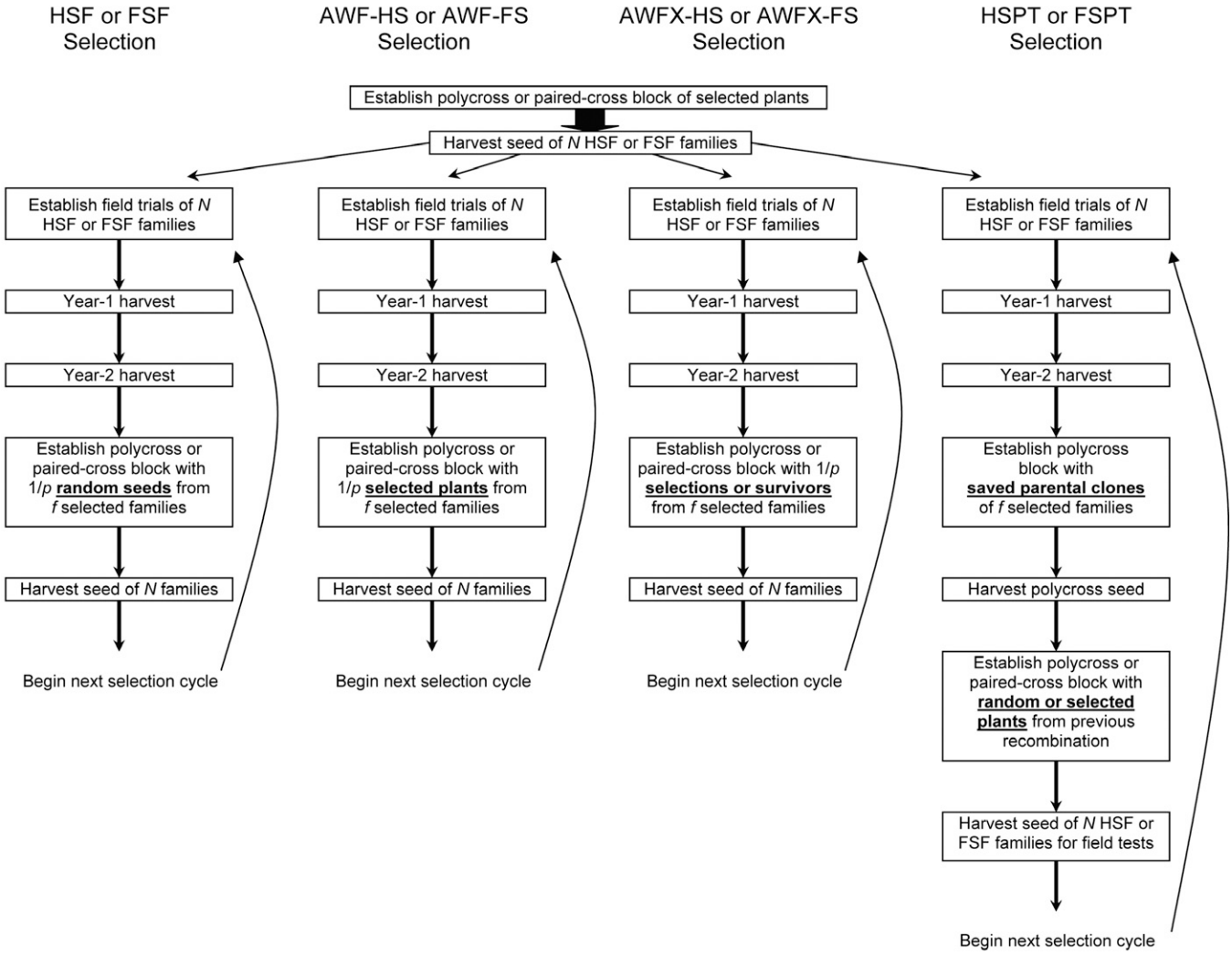

Figure 1. Schematic flow diagram of four family-selection methods differing in recombination unit, assuming 2 yr of data collection before selecting the best families. Each selection method begins with the development of N half-sib families (HSF) or full-sib families (FSF), which are planted in field trials for phenotypic measurement of trait Y. Half-sib family (HSF) and full-sib family (FSF) selection utilize $n = 1/p$ random plants from $f = Np$ selected families as the recombination unit, where p = proportion of families selected. Among-and-within family selection utilizes plants selected from the best families for trait Y (AWF-HS and AWF-FS) or plants selected for an alternative trait (X) within families (AWFX-HS and AWFX-FS). Half-sib progeny test (HSPT) and full-sib progeny test (FSPT) selection methods use saved parental clones as the recombination unit, requiring establishment of an additional recombination nursery to increase the number of families back up to N for continuation of the next selection cycle.

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tions, such as genotype × harvest interactions, would be a good reason to use clonal replication.

Among-Family Selection Methods

Half-sib family (HSF) selection, the simplest selection method presented here, involves the evaluation of N half-sib or polycross families, followed by recombination using n random plants from remnant seed of f selected families to create $N = fn$ new families for the next cycle (Fig. 1; column 1). The expected gain for HSF is shown in Eq. [1] of Table 1, where $c = 1/2$ because selection is on female gametes only (Falconer and Mackay, 1996; Hallauer and Miranda, 1988). Half-sib progeny-test (HSPT) selection involves the evaluation of half-sib or polycross families, followed by recombination using saved parental plants, after which a new set of half-sib families must be generated to begin the next cycle of selection (Fig. 1; column 4). The expected genetic gain for HSPT selection is shown in Eq. [2] in Table 1, where $c = 1$, providing an expected gain twice that of HSF in Eq. [1].

Similarly, full-sib family (FSF) selection involves the evaluation of a number of full-sib families, followed by recombination using random plants from remnant seed of selected families to create new families for the next cycle (Fig. 1). The expected genetic gain for FSF selection is shown in Eq. [5] of Table 1, where $c = 1/2$ if selection is conducted on only one of the two sexes (Hallauer and Miranda, 1988). Full-sib progeny-test (FSPT) selection involves the evaluation of full-sib families, followed by recombination using saved parental plants, after which a new set of full-sib families must be generated to begin the next cycle of selection (Fig. 1). The expected genetic gain for FSPT selection is shown in Eq. [6] in Table 1, where $c = 1$ if selection is for both male and female parents, providing an expected gain twice that of FSF selection in Eq. [5]. Hallauer and Miranda (1988) indicate that selection is usually practiced on both sexes in maize (*Zea mays* L.), and we agree that this is also the most common practice for FSPT selection in perennial forage crops.

Among-and-Within-Family Selection for the Same Trait

Among-and-within-family selection as generally practiced in forage crops involves the use of replicated and randomized designs in which families are replicated and each family plot is made up of a fixed number of unreplicated plants from that family (Fig. 1; column 2). The most common application of AWF selection involves establishment of large spaced-planted nurseries in an arbitrary spacing with or without a companion crop (Vogel and Pedersen, 1993). Families are typically planted in rows (Vogel and Pedersen, 1993) or may be planted in other rectangular arrangements (Casler, 2005; Casler et al., 2005). van Dijk and Winkelhorst (1978) and van Dijk (1983) developed the innovative system of evaluating "spaced plants in swards," in which spaced plants of the target species are planted into a sward of a contrasting species as a uniform competitor. Individual plant data is collected in AWF selection, allowing plot/family means to be used to select the best families and individual-plant data to be used to select the best plants within the best families. The number of plants selected per family (n) must be sufficiently large to offset the reduction in number of families from N to f, so that $n = 1/p$, where p = the proportion of families selected.

The expected gain for AWF selection using half-sib families (AWF-HS) is shown in Eq. [3] in Table 1, where $c = 1/2$ (Falconer and Mackay, 1996; Hallauer and Miranda, 1988). The expected gain for AWF selection using full-sib families (AWF-FS) is shown in Eq. [7] in Table 1, where $c = 1/2$ if families are selected on the basis of only one sex or $c = 1$ if families are selected on the basis of both sexes (Hallauer and Miranda, 1988).

Among-and-Within-Family Selection for Different Traits

There are two likely scenarios for conducting AWF selection for different traits (AWFX). The first, reported by Casler (2008), involves establishment of families in seeded sward plots. Forage yield is determined for one or two years by harvesting forage from all plots in a randomized and replicated design (Fig. 1; column 3). Individual-plant mortality rates are high within sward plots (Charles, 1961), severely reducing the number of genotypes that may be present two or three years after establishment. A random sample of surviving plants can be dug from plots of selected families to be used as recombination units, selecting for survivorship within families (Casler, 2008). Among-family selection is based on trait Y, forage yield or some other agronomic trait(s), and within-family

Table 1. Expected gains per cycle of selection for trait Y from eight family selection methods used in breeding perennial forage crops.

Selection method†	Family mating system	Recombination unit (and within-family selection criterion)	Expected gain per cycle of selection‡	Equation no.
HSF	Half-sibs	Random plants	$\Delta G_{HSF} = k_F c(1/4)\sigma^2_A/\sigma_{PF}$	[1]
HSPT	Half-sibs	Parental clones	$\Delta G_{HSPT} = k_F c(1/4)\sigma^2_A/\sigma_{PF}$	[2]
AWF-HS	Half-sibs	Selected plants (trait Y)	$\Delta G_{AWF\text{-}HS} = k_F c(1/4)\sigma^2_A/\sigma_{PF} + k_W c(3/4)\sigma^2_A/\sigma_{PW}$	[3]
AWFX-HS	Half-sibs	Selected plants (trait X)	$\Delta G_{AWFX\text{-}HS} = k_F c(1/4)\sigma^2_A/\sigma_{PF} + k_W c(3/4) r_g h_X \sigma_A$	[4]
FSF	Full-sibs	Random plants	$\Delta G_{FSF} = k_F c(1/2)\sigma^2_A/\sigma_{PF}$	[5]
FSPT	Full-sibs	Parental clones	$\Delta G_{FSPT} = k_F c(1/2)\sigma^2_A/\sigma_{PF}$	[6]
AWF-FS	Full-sibs	Selected plants (trait Y)	$\Delta G_{AWF\text{-}FS} = k_F c(1/2)\sigma^2_A/\sigma_{PF} + k_W c(1/2)\sigma^2_A/\sigma_{PW}$	[7]
AWFX-FS	Full-sibs	Selected plants (trait X)	$\Delta G_{AWFX\text{-}FS} = k_F c(1/2)\sigma^2_A/\sigma_{PF} + k_W c(1/2) r_g h_X \sigma_A$	[8]

†HSF, half-sib family selection; HSPT, half-sib progeny-test selection; AWF-HS, among-and-within-family selection on half-sib families; AWFX-HS, among-and-within-family selection on half-sib families where trait X is the within-family selection criterion; FSF, full-sib family selection; FSPT, full-sib progeny-test selection; AWF-FS, among-and-within-family selection on full-sib families; AWFX-FS, among-and-within-family selection on full-sib families where trait X is the within-family selection criterion.

‡k_F, the standardized selection differential among families; c, parental control factor; σ^2_A, additive genetic variance; σ_{PF}, the phenotypic standard deviation among families; k_W, the standardized selection differential within families; σ_{PW}, the phenotypic standard deviation within families; r_g, the genetic correlation between X and Y; h_X, the square root of heritability for trait X; h_Y, the square root of heritability for trait Y (Falconer and Mackay, 1996; Hallauer and Miranda, 1988).

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selection is based on trait X, survivorship. As with AWF selection, the number of plants selected per family is $n = 1/p$.

The second scenario involves the use of spaced plantings as described for AWF selection. Families are planted in plots made up of a fixed number of spaced plants. Forage yield data can be collected on a plot basis, using a mechanized harvesting system and allowing plot yields to be used as the among-family selection criterion. Differential plant spacings among vs. within plots (Casler, 2005; Casler et al., 2005) may be advantageous in this scenario, creating separation between adjacent plots for ease of harvest, but maintaining a relatively narrow plant spacing within plots to simulate realistic sward-type competition (Hayward and Vivero, 1984). Within-family selection can be accomplished by collecting individual-plant data for other trait(s), such as visual scores of plant vigor, disease resistance, morphological traits, forage quality traits, or any other trait(s) of interest.

The expected gain in yield for AWF selection based on two different traits (e.g., Y = yield of families, X = survivorship of plants within families) using half-sib families (AWFX-HS) is obtained by substituting expected correlated responses for trait Y due to selection for trait X, obtained from Falconer and Mackay (1996), into the within-family portion of Eq. [3] in Table 1, as follows

$$G_{\text{AWFX-HS}} = k_F c(1/4)\sigma^2{}_A/\sigma_{PF} + k_W c(3/4) r_g h_X h_Y \sigma_{PW}$$

where r_g is the genetic correlation between X and Y, h_X is the square root of within-family heritability for trait X, and h_Y is the square root of within-family heritability for trait Y (Falconer and Mackay, 1996; Hallauer and Miranda, 1988). Within-family heritabilities are generally based on individual unreplicated plants and are defined as $\sigma^2{}_A/\sigma^2{}_{PW}$, hereafter termed *individual-plant heritability* and equivalent in concept to the family-deviations heritability of Walsh and Lynch (2007; Chapter 8). This equation can be simplified to obtain Eq. [4] in Table 1, by substituting σ_A for $h_Y\sigma_{PW}$, so that additive genetic variance for trait Y becomes a direct component of both the among-family and within-family components and the within-family phenotypic variance for trait Y drops out. The expected gain for AWF selection based on two different traits using full-sib families (AWFX-FS) is shown in Eq. [8] in Table 1, where $c = 1/2$ if families are selected on the basis of only one sex or 1 if families are selected on the basis of both sexes (Hallauer and Miranda, 1988).

Expected Gain Computations

Heritability of trait Y, on a family-mean basis, was set to a constant value of 0.2, by setting $\sigma^2{}_A = 0.2$ and $\sigma^2{}_{PF} = 1.0$. Selection intensity among families was also set to a constant value of $p_1 = 0.05$. Setting these values to constants forces the results of Table 1, Eq. [1], [2], [5], and [6] to be constants as well. Equations [3] and [7] for AWF were evaluated for differential values of the within-family selection intensity ($p_2 = 0.05$ to 0.50) and the within-family phenotypic variance ($\sigma^2{}_{PW} = 1$ to 100). Values of $\sigma^2{}_{PW}$ corresponded to heritability on an individual-plant basis ranging from $h^2{}_Y = 0.20$ (for $\sigma^2{}_{PW} = 1$) to $h^2{}_Y = 0.002$ (for $\sigma^2{}_{PW} = 100$). This was based on our assumption that heritability on an individual-plant basis may be equal to heritability on a family-mean basis, but is more likely to be significantly smaller than heritability on a family-mean basis. Equations [4] and [8] in Table 1 for AWFX selection were evaluated for differential values of the within-family selection intensity ($p_2 = 0.001$–0.50) and the product $r_g h_X = 0.00$ to 0.30. Results of Eq. [2], [3], and [4] were expressed as a percentage of the results for Eq. [1] for half-sib family matings. Results of Eq. [6], [7], and [8] were expressed as a percentage of the results for Eq. [5] for full-sib family matings. For all full-sib breeding methods, we assumed a constant parental control factor (c); that is, that selection was based either on one sex ($c = 1/2$) or on both sexes ($c = 1$) for all full-sib breeding methods, regardless of recombination unit. Because all expected gains were reported as values relative to HSF or FSF selection (within mating schemes), the choice of one vs. both sexes in full-sib selection schemes is irrelevant here.

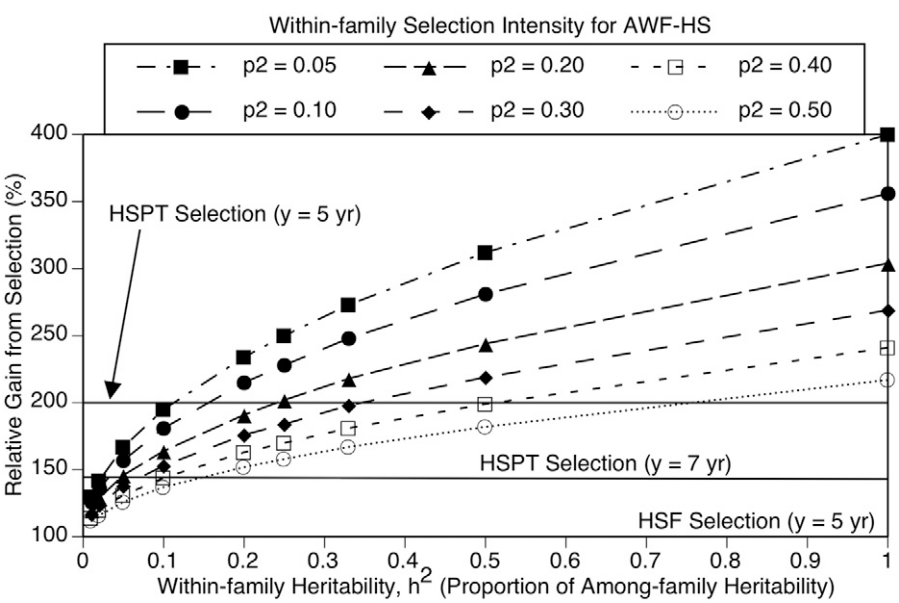

Figure 2. Expected gains from half-sib progeny-test (HSPT) selection (two solid lines, one for a 5-yr cycle time and one for a 7-yr cycle time) and among-and-within-family (AWF-HS) selection for six different within-family selection intensities (p_2) (dashed lines, all for a 5-yr cycle time), expressed as a function of the within-family (individual-plant) heritability. All expected gains for HSPT and AWF-HS selection are expressed as a percentage of gains for half-sib family (HSF) selection. Within-family heritability (x axis) is expressed as a proportion of the among-family heritability, 0.20).

RESULTS

For any positive value of individual-plant (within-family) heritability, AWF-HS selection is more efficient than HSF selection (Fig. 2). For low values of individual-plant heritability, AWF-HS selection is always less efficient than HSPT selection, but this is highly dependent on cycle time. If the second recombination event in HSPT selection can be accomplished within the same cycle time, using the greenhouse and/or off-season nurseries, HSPT selection remains more efficient than AWF-HS selection as within-family selection intensity increases. However, if the second recombination event requires

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an additional two years to accomplish, as is typically the case with grasses that require vernalization, AWF-HS selection rapidly exceeds HSPT selection in efficiency for any within-family selection intensity and individual-plant heritability exceeding 15% of the among-family heritability. If individual-plant heritability is at least 50% of the among-family heritability, then AWF-HS selection is more efficient than HSPT selection for all within-family selection intensities less than $p_2 = 0.40$. For individual-plant heritability exceeding 75% of the among-family heritability, AWF-HS selection was always more efficient than HSPT selection.

Because FSF matings have twice the additive genetic variance apportioned among families, compared with half-sib matings, AWF-FS selection is generally far less efficient than FSPT selection for an equal-length cycle time (Fig. 3). The two selection methods have equal efficiency only when among-family heritability and individual-plant heritability are equal and when among-family and within-family selection intensities are also equal ($p_1 = p_2 = 0.05$ in our example). The AWF-FS selection method is expected to be more efficient than FSPT selection only under some fairly restrictive conditions: longer cycle time for FSPT selection, moderate to high individual-plant heritability (relative to among-family heritability), and fairly high selection pressure within families ($p_2 < 0.20$–0.30).

For the AWFX-HS selection method, selection within families is based on trait X; so either $r_g = 0$ or $h_X = 0$ is sufficient to eliminate any advantage of this selection method over HSF selection (Fig. 4). Increases in efficiency of AWFX-HS are a linear function of the product $r_g h_X$, as can be seen from Eq. [4] in Table 1, and the efficiency of AWFX-HS exceeds that of HSPT at relatively small values of $r_g h_X$. However, this relationship is highly dependent on within-family selection intensity. For relatively mild within-family selection pressures, values of $r_g h_X$ must exceed 0.2 to 0.3 for AWFX-HS selection to be more efficient than HSPT selection. Conversely, for relatively intense within-family selection, AWFX-HS selection is nearly always more efficient than HSPT selection for any value of $r_g h_X > 0.1$. As an example, this would correspond to potential values of $r_g = 0.25$ and $h_X^2 = 0.16$. Thus, it is clear that only moderate values of r_g and h_X^2 are required to make AWFX-HS selection more efficient than HSPT selection. Of course, this effect is magnified if HSPT selection requires additional years to complete the second recombination event.

The AWFX-FS selection method requires a value of $r_g h_X > 0.30$ and extremely intensive within-family selection or a value of $r_g h_X > 0.45$ and within-family selection intensity equal or greater than among-family selection intensity to be more efficient than FSPT selection with an equal-length cycle time (Fig. 5). For traits with a high genetic correlation with Y and a moderate to high individual-plant heritability, AWFX-FS selection is likely to be more efficient than FSPT selection for any selection intensity equal to or greater than that used for among-family selection. For example, a trait X with $h_X^2 = 0.81$ and $r_g = 0.5$ would result in the minimum value of $r_g h_X = 0.45$ to meet this qualification. In contrast, for mild within-family selection intensities, required for the scenario in which spaced plants are used for the entire selection nursery, AWFX-FS selection will rarely exceed FSPT selection in efficiency, only under the circumstances when both r_g and h_X^2 are high.

DISCUSSION

Using expected gain formulas based on a model of disomic inheritance, we have defined a number of conditions under which AWF selection is expected to be more efficient at improving a primary trait Y, such as forage yield, compared with family or progeny-test selection. A number of assumptions were required in preparation to using these formulas for this purpose. We minimized the potential consequences of making invalid assumptions by expressing all expected gains, on a relative basis, to family

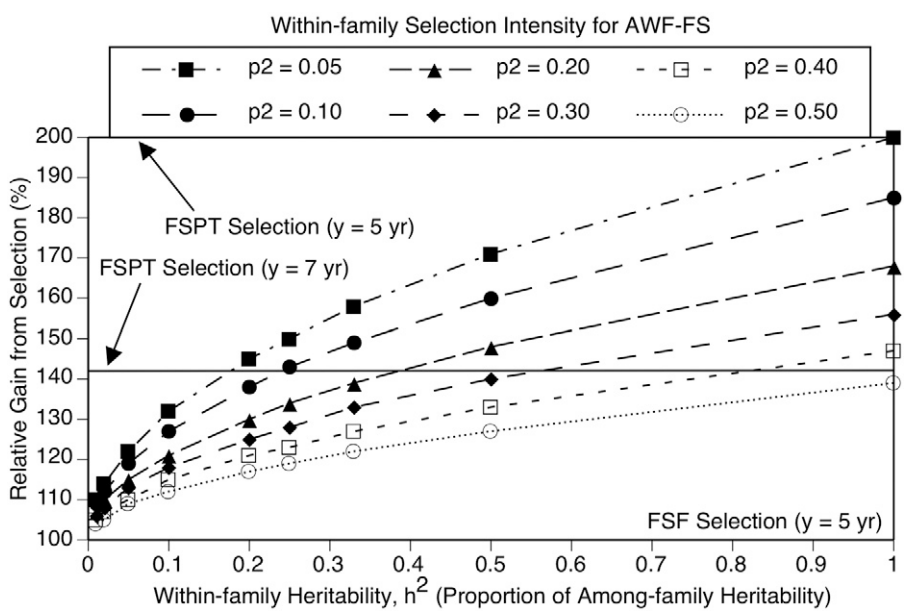

Figure 3. Expected gains from full-sib progeny-test (FSPT) selection (two solid lines, one for a 5-yr cycle time and one for a 7-yr cycle time) and among-and-within-family (AWF-FS) selection for six different within-family selection intensities (p_2) (dashed lines, all for a 5-yr cycle time), expressed as a function of the within-family (individual-plant) heritability. All expected gains for FSPT and AWF-FS selection are expressed as a percentage of gains for full-sib family (FSF) selection. Within-family heritability (*x* axis) is expressed as a proportion of the among-family heritability, 0.20).

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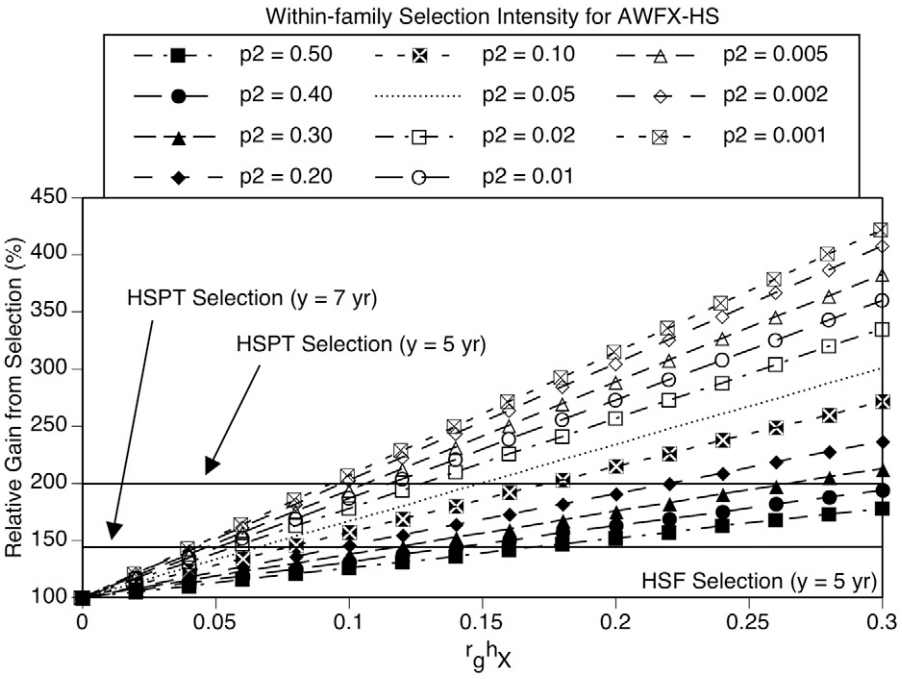

Figure 4. Expected gains from half-sib progeny-test (HSPT) selection (two solid lines, one for a 5-yr cycle time and one for a 7-yr cycle time) and among-and-within-family (AWFX-HS) selection for two traits (Y among families, X within families) for 11 different within-family selection intensities (p_2) (dashed lines, all for a 5-yr cycle time), expressed as a function of $r_g h_X$, the product of the genetic correlation between X and Y (r_g) and the square root of individual-plant heritability for X (h_X). All expected gains for HSPT and AWFX-HS selection are expressed as a percentage of gains for half-sib family (HSF) selection.

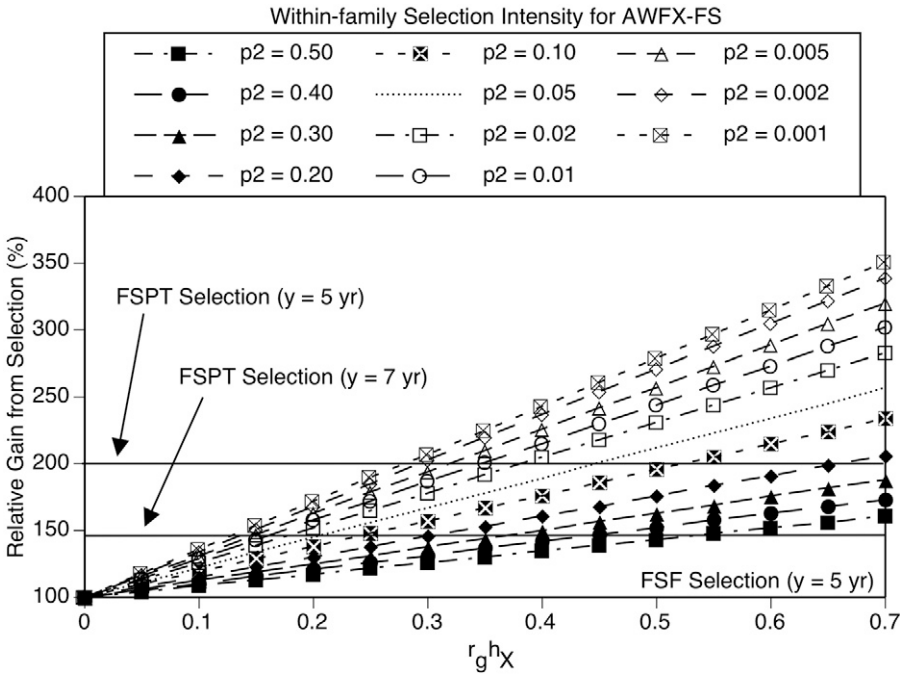

Figure 5. Expected gains from half-sib progeny-test (FSPT) selection (two solid lines, one for a 5-yr cycle time and one for a 7-yr cycle time) and among-and-within-family (AWFX-FS) selection for two traits (Y among families, X within families) for 11 different within-family selection intensities (p_2) (dashed lines, all for a 5-yr cycle time), expressed as a function of $r_g h_X$, the product of the genetic correlation between X and Y (r_g) and the square root of individual-plant heritability for X (h_X). All expected gains for FSPT and AWFX-FS selection are expressed as a percentage of gains for half-sib family (FSF) selection.

selection within each mating scheme. We recognize that linkage, epistasis, and nonadditive gene action could all disrupt expected gains for AWF selection by altering the relative amounts of genetic variability that is apportioned among vs. within families in both half-sib and full-sib mating schemes. Therefore, the results of these formulas should be taken as guidelines, not to infer that any particular ratio of $\sigma^2_{PW}/\sigma^2_{PF}$ or value of $r_g h_X$ is the magic value to make AWF selection the most efficient selection scheme under any conditions.

In general, three sets of conditions create an advantage for AWF selection over progeny-test selection. Among-and-within-family selection is favored by greater selection intensity within families, relatively low within-family phenotypic variance (i.e., high individual-plant heritability), and in the case where within-family selection is based on a different trait, positive genetic correlation between X and Y combined with moderate to high individual-plant heritability for trait X. A fourth condition is highly dependent on the biology and mating system of the target species. Because progeny-test selection requires an additional recombination event within each cycle, plants that have a long juvenility phase and/or a vernalization requirement for flowering will require at least one or perhaps two additional years per cycle, particularly if sward plots are used for family evaluation.

Among-Family vs. Within-Family Selection Intensities

The ability to increase within-family selection intensity to a level sufficient to create an advantage for AWF selection is highly dependent on the breeder's resources. Assuming N = 100 half-sib families are evaluated as spaced plants and f = 5 families are selected (p_1 = 0.05), n = 20 plants per family must be selected to generate 100 new half-sib families for the next cycle of selection. Maintaining p_2 = p_1 = 0.05 would require 400 plants per family or a spaced-plant nursery of 40,000 plants. A nursery of this size, devoted to a single population of one species, is prohibitive for most breeding programs that

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deal with several species and several populations within each species. Even the large European breeding programs that focus heavily on perennial ryegrass deal with multiple populations with a range of heading dates, diverse origins, and differential environmental adaptation.

A spaced-plant nursery of 4000 to 10,000 plants is more realistic for most breeding programs that handle multiple populations and, especially, multiple species. For $N = 100$ and $p_1 = 0.05$, a nursery of 4000 plants would allow a within-family selection intensity of only $p_2 = 0.50$, while a nursery of 10,000 plants would allow a within-family selection intensity of $p_2 = 0.20$. Wilkins and Humphreys (2003) improved forage yield of perennial ryegrass using 9600-plant selection nurseries (100 plants within each of 96 families) and $p_1 \approx p_2 \approx 0.08$ to 0.12 in an AWFX-HS selection scheme. A smaller nursery size of 4000 plants would not allow sufficient selection pressure to create an advantage for AWF selection, compared with progeny-test selection, regardless of the mating design (with the exception of very high individual-plant heritability in a half-sib mating system; Fig. 2). Use of spaced plantings to conduct AWF selection will require relatively large nurseries (≥10,000 total plants) and moderate within-family selection intensity ($p_2 \leq 0.20$) to have any reliable advantage over progeny-test selection. Furthermore, this is true only for half-sib matings. For full-sib matings, forcing $p_2 \leq p_1$ is the only way that AWF can have an advantage over progeny-test selection when the two methods have the same cycle time, creating a prohibitively large population size. Finally, if the breeding program could sustain a larger nursery size for AWF selection to achieve a desirable selection intensity, then the program could also evaluate a larger number of families in a HSPT selection program, further improving gain by HSPT relative to AWF selection. Thus, comparisons between methods need to be made carefully, between systems with similar resource expenditures. Such comparisons may be difficult, largely because the costs of evaluating families is different in AWF and HSPT selection methods, due to the added cost of evaluating individual plants in the AWF selection method. Furthermore, the cost ratio will vary among breeding programs, species, and traits, linking it closely to the specific breeding objectives.

One way to solve the problem of large nurseries for AWF selection is to relax selection intensity among families, allowing an increase in within-family selection intensity. Sandha and Twamley (1973) used mean selection intensities of $p_1 = 0.28$ and $p_2 = 0.10$ in AWF-HS selection for increased seed yield in birdsfoot trefoil (*Lotus corniculatus* L.), resulting in genetic gains over two AWF selection cycles 81% greater than genetic gains for HSPT selection. Over four cycles of AWF selection for seed yield, gains averaged 11% cycle^{-1} (Tomes et al., 1983). Twamley (1974) conducted three cycles of AWF-HS selection for increased seedling vigor in birdsfoot trefoil with mean $p_1 \approx p_2 \approx 0.16$. The AWF-HS selection had average genetic gains of 13% cycle^{-1}, with 63% greater gains for AWF-HS selection than for HSPT selection (Twamley, 1972, 1974).

Alternatively, the use of sward plots for family evaluation has two distinct advantages. First, sward plots provide a more realistic assessment of forage yield than spaced plants. In perennial grasses, the genetic correlation between spaced-plant and sward-plot forage yield is highly inconsistent, ranging from zero to relatively high, positive values (Casler et al., 1996; Casler, 2008). Selection for spaced-plant forage yield can be highly deceiving when it has a high heritability per se, but zero or low genetic correlation with forage yield on a narrow, or more realistic, plant spacing (Hayward and Vivero, 1984). Of course, the high genetic correlation between spaced-plant and sward-plot forage yield of Pensacola bahiagrass contributed to the most prominent example of successful spaced-plant selection for increased forage yield (Burton and Mullinix, 1998). Unfortunately, these relationships appear to be somewhat species specific, perhaps even population specific. Although traits such as rhizomatous or stoloniferous growth habit may explain differences among certain species in the relationship of spaced-plant and sward-plot yields, they are not universally explanatory. To our knowledge, no biological factor can be used to predict the genetic correlation between spaced-plant and sward-plot forage yield for a given species.

Second, sward plots allow the use of considerably higher within-family selection intensities than spaced-plant nurseries. For many perennial forage crops, seeding rates range from approximately 500 to 2000 pure live seeds m^{-2}, depending on species, purpose, and environment. In this case, within-family selection intensity is limited not by the labor and land area required to transplant and maintain huge spaced-plant nurseries but by land area, harvesting equipment, and seed production systems to routinely conduct family selection. Using the same example as above with $N = 100$ and $p_1 = 0.05$, assume that sufficient seed has been produced to allow two replicates of each family in plots that are 5 m^2 in size at a planting rate of 1000 pure live seed m^{-2}, a very realistic assumption for field-grown crossing blocks that have a full season to become established (Fig. 1; Casler, 2008). As with the spaced-plant nursery, we require $n = 20$ plants per family, achieved by digging 10 survivors from each of the two replicates, resulting in $p_2 = 10/[5(1000)] = 0.005$. Recall from Fig. 4 that only small positive values of $r_g h_X$ are required to make AWFX selection more efficient than progeny-test selection at this within-family selection intensity in a half-sib mating scheme.

It is virtually impossible to walk into a sward plot and visually select the best plants for any phenotypic trait, largely because individual plants cannot be distinguished reliably by eyesight, plants will have different levels of competition

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with neighboring plants, and (at least for some species) only a single tiller, stolon, or rhizome can be selected to provide assurance that each parent for the next generation is a unique genotype. Of course, DNA markers could be used to distinguish individual plants within plots, but this would be prohibitive in terms of both time and cost. Thus, selection of survivors relies heavily on selection pressures that have been present within family-evaluation plots between the planting date and the selection date.

Mortality rates are high within perennial-forage sward-plots, with estimates of up to 90% mortality within the establishment year for several grasses (Charles, 1961) and more than 85% for alfalfa (Brummer et al., 2002), leading to meaningful selection pressures observed within three production years in some species (Falkner and Casler, 2000; Casler, 2008). Is this mortality, and the mortality that may occur in subsequent years, meaningful to the plant breeder? Plants are selected largely for survivorship, a nebulous term that may account for a wide range of physiological and morphological traits. Do these survivors have better, equal, or worse agricultural fitness than random plants from these families? That is, is the genetic correlation between survivorship and forage yield positive, zero, or negative? Some evidence from alfalfa experiments suggests that survivors have higher forage yield than random plants. Yield of plots seeded with as low as 50% (Viands et al., 1988) or 80% (Velde et al., 2002) hybrid seed produced the same yield as 100% hybrid plots, which had better production than the nonhybrid control.

In grasses, results are mixed between no difference vs. a forage-yield advantage for survivors (see reviews of Casler et al., 1996; Falkner and Casler, 2000). Survivors from long-term pastures tend to have a more prostrate growth habit, later heading date, more tillers, and smaller tillers compared with their unselected siblings (Casler et al., 1996; Falkner and Casler, 2000). Casler (2008) indirectly estimated the genetic correlation between survivorship and forage yield by conducting one cycle of half-sib family selection and one cycle of AWFX selection in eight populations of orchardgrass, smooth bromegrass (*Bromus inermis* Leyss.), and hybrid wheatgrass [*Elytrigia* × *muctonata* (Opiz ex. Bercht.) Prokud.]. In orchardgrass, a nonrhizomatous bunchgrass, AWFX selection and family selection did not differ in genetic gains, indicating that three-year-old survivors were equal in forage yield potential to their random siblings; that is, the genetic correlation between survivorship and forage yield was zero. Conversely, in the two rhizomatous species, AWFX-HS selection was 5.8-fold more effective at increasing forage yield than HSF selection, averaged across four populations (Casler, 2008). Because within-family selection intensities ($p_2 = 0.027$) were only slightly greater than among-family selection intensities (mean $p_1 = 0.042$) in that study, the results imply a fairly high value of $r_g h_X \approx 0.60$ to 0.70, that is, moderate to high values of both the survivorship heritability and the genetic correlation between survivorship and forage yield. Casler (2008) attributed these results to the use of a constant and infrequent harvest system for both the half-sib family evaluation and the evaluation of selection progress, so that natural selection within plots acted to favor traits related to forage yield and survival under infrequent harvesting. In addition, plants were not under livestock grazing pressure, which creates a different selection environment than does mechanical harvesting and which may be expected to be antagonistic to yield.

Among-Family vs. Within-Family Phenotypic Variance

Family selection is generally based on plot values over a large number of plants and multiple plots per family, both factors acting as replication to improve the precision of estimates of family performance. Family selection is highly amenable to multilocation testing, providing a mechanism to reduce the G×E interaction component of phenotypic variance. In contrast, within-family selection is based on individual plant performance for which replication in space would require vegetative propagation, a practice that is rarely used in family selection schemes because of added cost and time. The intensive effort required to clonally propagate plants can have its rewards. In one case, heritability on a clonally replicated individual-plant basis was 1.4 to 2.5 times greater than heritability on a family-mean basis (Aastveit and Aastveit, 1990). An alternative form of individual-plant replication would be repeated measures in which multiple ratings are taken on each plant over time, although this form of replication is not as effective at improving precision as spatial or clonal replication (Casler et al., 2008).

In its simplest form, ignoring G×E interaction and using the half-sib mating system, the phenotypic variance among families has the expectation

$$\sigma^2_{PF} = \sigma^2_w/rs + \sigma^2_e/r + (1/4)\sigma^2_A$$

where σ^2_w is the within-plot error variance, σ^2_e is the error variance, r is the number of replicates for each family, and s is the number of plants per family in the family field test. Similarly, the phenotypic variance within families has the expectation

$$\sigma^2_{PW} = \sigma^2_w + \sigma^2_e + (3/4)\sigma^2_A$$

for individual plants that are unreplicated, as will generally be the case. For high-heritability traits, both σ^2_w and σ^2_e approach zero relative to σ^2_A, so that σ^2_{PW} approaches $3\sigma^2_{PF}$ as h^2 approaches 1.0.

As heritability approaches zero, these two equations are more difficult to evaluate. Setting $\sigma^2_A = 0$, taking the ratio of the two phenotypic variances, and simplifying, gives

$$\sigma^2_{PW}/\sigma^2_{PF} = r(\sigma^2_w + \sigma^2_e)/(\sigma^2_w/s + \sigma^2_e)$$

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the value of which depends largely on the ratio σ^2_w/σ^2_e and the number of plants per family. For a large number of families (>200), s is likely to be small; as s approaches 1, $\sigma^2_{PW}/\sigma^2_{PF}$ approaches r. Fewer families allow more plants to be evaluated per family and as s becomes large, the ratio $\sigma^2_{PW}/\sigma^2_{PF}$ approaches $r(1 + \sigma^2_w/\sigma^2_e)$, greatly decreasing individual-plant heritability relative to among-family heritability, particularly if $\sigma^2_w >> \sigma^2_e$. Thus, larger values of s result in decreased individual-plant heritability relative to among-family heritability, an effect that is exacerbated by greater environmental variability within plots. The net result is that larger family sizes tend to decrease the merit of AWF versus HSPT selection, largely by improving the reliability of family mean values, increasing the efficiency of among-family selection compared with within-family selection.

Lack of hard knowledge about the relative magnitudes of σ^2_w and σ^2_e (and among-family vs. individual-plant heritability) for any given trait is, in our opinion, the greatest weakness in assessing the practical implications of our expected gain computations for all AWF selection methods. For biomass yield of switchgrass (*Panicum virgatum* L.), Rose et al. (2007) observed individual-plant heritabilities ranging from 0.17 to 0.70 (mean of 0.48) relative to among-family heritabilities, trending toward the center of Fig. 2. Clonal replication of individual plants would increase these values, conferring greater advantage to AWF over HSPT selection by reducing σ^2_{PW}. But the time, expense, and additional record keeping involved argue against its use, and we are not aware that the method is widely practiced in breeding programs.

Genetic Correlation Between Traits X and Y

Perhaps the most surprising result of our computations was the observation that only relatively small values of $r_g h_X$ are necessary for AWF selection to be favored over HSPT selection. These results indicate that indirect selection for a trait that is positively correlated with trait Y can be highly effective, provided it is combined with selection for trait Y on a family-mean basis. Use of a yield-component or yield-related trait as the within-family selection criterion is one mechanism to help ensure a positive correlation between X and Y. In the study of Casler (2008), survivorship in sward plots can be considered a component of forage yield because forage yield is a function of ground cover, and the ability to survive in a competitive sward is likely related to the ability to fill in gaps or openings in the sward of a rhizomatous grass, which, to complete the circle, is necessary to maintain stand productivity. The genetic correlation between biomass yield and ground cover of switchgrass is also a relatively high and positive value, suggesting that survival may also be a component of biomass yield in a bunchgrass that relies on tillering to compensate for gaps between plants (Casler et al., 2004, 2007). The success of AWF selection for a common selection criterion among and within families, particularly when applied to forage yield, is actually dependent on two genetic correlations. First, family selection is based on plot yields, the sum of harvested biomass on all s plants within a plot and r replicates of a family. Biomass or forage yields are rarely taken on individual plants because of the time and expense of individual-plant harvest. Second, within-family selection is based on individual-plant vigor scores. Both spaced-plant forage yield, on a plot basis, and plant vigor scores should have a positive genetic correlation with forage yield on a sward-plot basis. Results from selection experiments on perennial grasses are mixed, with implied genetic correlations ranging from zero to highly positive, depending on species (Casler et al., 1996; Casler, 2008). Heavy reliance on spaced plantings by forage breeders may be an additional important factor in limiting long-term genetic gains of forage crops. The use of overseeding a competitor in a spaced-plant nursery or transplanting spaced plants into an existing stand of an alternative species (van Dijk and Winkelhorst, 1978; van Dijk, 1983) is becoming more frequent as forage breeders recognize the potential pitfalls of selection for forage yield in spaced plantings and are taking more steps to resolve this problem. Wilkins and Humphreys (2003) used AWFX-HS selection on spaced-plant nurseries of perennial ryegrass, using forage yield on a plot basis to select families and visual ratings to select plants within selected families. Their gains of 1% yr^{-1} suggest that within-family selection very likely contributed to the success of this selection protocol, implying a positive genetic correlation between visual vigor ratings and forage yield in this particular case.

Flowering, Seed Production, and Cycle Time

The efficiency of any selection method is highly dependent on the decisions made by the breeder regarding the specific protocols to utilize in testing plants and families and in recombining selections. Depending on biological characteristics of the species, facilities available, and resource availability at critical times of the year, AWF selection could be logically conducted in a one- to five-year selection cycle. If winter survival is not an issue, meaningful data on trait Y can be collected during the establishment year. If plants do not require vernalization to induce flowering, families and plants can be selected at the end of the establishment year, moved into a greenhouse or crossing chamber, intercrossed during winter, and their progeny can be planted in a selection nursery during the following growing season (Sandha and Twamley, 1973; Twamley, 1974). Plants that require vernalization to induce flowering may qualify for a one-year cycle time if the breeder has access to cold chambers and proper lighting to artificially induce flowering (Ikegawa et al., 1985).

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As more restrictions are added to the selection protocol, such as the need for a winter survival assay (Vogel and Pedersen, 1993), slow establishment that prevents meaningful data collection during the establishment year (Vogel and Pedersen, 1993), genotype × year interactions that demand a minimum of two years for data collection (Casler, 2005), or seed production requirements that can only be met by intercrossing in the field (Casler, 2008), cycle time may lengthen to up to five years in the most extreme case (each box in Fig. 1 represents one growing season). In this worst-case scenario, progeny-test selection requires an additional two years per cycle compared with AWF selection (seven vs. five years, as shown in Fig. 2–5). However, any mechanisms that can be used to reduce cycle time for AWF selection can also be used to reduce the two-year extension for the second recombination event in progeny-test selection. Therefore, our choice of a seven- vs. a five-year-cycle represents the worst-case scenarios for both selection methods. If cycle time is held constant, progeny-test selection has a 200% relative efficiency (twice as efficient as family selection), but this efficiency is reduced to 200(5/7) = 143% if cycle time is lengthened from five to seven years (the two horizontal lines in Fig. 2–5). Wilkins and Humphreys (2003) used a three-year cycle for AWF-HS selection, using greenhouse facilities for crossing. Using their methodology, HSPT selection would only require an additional fourth year under the most recalcitrant conditions, resulting in a selection efficiency of 200(3/4) = 150% for HSPT selection. Under the best circumstances, where facilities and timely labor are available, the second recombination of HSPT or FSPT selection may only require an additional few months of off-season time, resulting in a relative selection efficiency of 200% for comparison to all AWF curves in Fig. 2–5. Of course, all of these decisions are highly dependent on external factors that draw the breeder's time, attention, and resources away from any particular population or population-improvement program.

The use of off-season greenhouse or crossing chamber facilities may not be practical in the AWFX-HS or AWFX-FS selection methods if sward plots are used in field tests of families. Even two replicates of relatively small plots may require up to 3000 or more viable seeds per family, which may not be possible or reliable in an off-season greenhouse or crossing chamber where seed production is likely to be reduced compared to field-grown crossing blocks. Seeded row plots (Casler and Walgenbach, 1990), extremely low seeding rates (Casler and Undersander, 2006), or the spaced-plants-in-swards method (van Dijk and Winkelhorst, 1978) may be used to reduce seed requirements and allow use of off-season seed production, but the necessary trade-off will be having to tolerate a reduction in within-family selection intensity simply because of a reduced number of plants within families.

A final, practical consideration for which AWF selection has a distinct advantage over progeny-test selection is that parental clones do not need to be saved. Saving parental plants is a nuisance for most breeders, often drawing precious time and resources away from other activities.

CONCLUSIONS

Among-and-within-family selection is favored by high heritability on an individual-plant basis (relative to heritability on a family-mean basis), within-family selection intensity equal to or greater than among-family selection intensity, and possibly a shorter cycle time (for some species and some breeding programs). These conditions are more frequently achieved for half-sib than full-sib mating systems due to the greater partitioning of additive genetic variance within families in half-sib systems, but among-and-within-family selection can also be heavily favored in a full-sib mating system, under conditions that are a bit more restrictive. Two options exist to increase within-family selection intensity relative to among-family selection intensity, both of which are supported by our theoretical computations and published empirical results: (i) relax selection intensity among families to allow an increase in within-family selection intensity without the need for a prohibitive population size or (ii) use sward plots to evaluate families, making plots (i.e., number of pure live seeds planted) as large as possible within the restrictions of available land area, equipment size limitations, and available seed stocks of the families to be tested. If the seed production system borders on supplying sufficient seed for testing all families, a larger number of families could be produced in each cycle of selection, adding seed production as an additional selection criterion for families without increasing cycle time. Finally, AWF selection is equal to or better than family selection, in which random plants from remnant seed stocks are used as the recombination unit, under all circumstances except one: when the within-family selection criterion (X) has positive heritability, but a negative genetic correlation exists between X and the among-family selection criterion (Y). This could be the case if X is a forage-quality trait and Y is forage yield (Casler, 2001). Apart from this isolated condition, AWF selection offers almost-universal advantages over family selection and frequent advantages over progeny-test selection. We conclude that breeders should carefully design their breeding program to make the most efficient use of selection methodologies that will maximize expected gains within the biological and physical constraints of the species, facilities, and goals of the program. There are many cases in which forage-crop breeders should use AWF selection more frequently than is implied by the relatively low frequency of published articles on this topic.

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