Theor Appl Genet (1990) 79:618–624

THEORETICAL AND APPLIED GENETICS

Theory and application of open-pollination and polycross in forage grass breeding

A. H. Aastveit [1] and K. Aastveit [2]

[1] Department of Mathematical Sciences, Agricultural University of Norway, N-1432 Aas-NLH, Norway
[2] Department of Genetics and Plant Breeding, Agricultural University of Norway, N-1432 Aas-NLH, Norway

Received November 20, 1989; Accepted January 22, 1990
Communicated by P. M. A. Tigerstedt

Summary. Progeny testing and selection of forage grasses by means of growing half-sib (HS) families from open-pollination and polycross have been considered from theoretical and practical points of view. Special attention has been paid to the genetic variation within half-sib families, which is expected to be large as compared to the genetic variation between families. Based on observations of individual plants within plots, the environmental component of the variation is expected to be large and nonestimatable. The results of an experiment in meadow fescue (*Festuca pratensis* Huds.) are presented. In this experiment, randomly selected individual plants within HS-families were cloned and laid out in randomized blocks. For the characters observed (earliness and raw matter yield) no significant variance component for dominance was found. The highly significant additive component estimated for earliness, as well as for yield, after each of three cuts and in total were about three times as large within as between families, as expected from the theoretical considerations. The estimated response to selection was much higher for a combination of between- and within-family selection as compared to free clone or family mean selection alone. It is suggested that a program for progeny testing and selection in a base population of perennial forage grasses should start with an experiment in which a large number of randomly selected parental clones and a fixed number of clones from each of the half-sib families derived from the mother genotypes are grown simultaneously. The selected clones within superior families could later on be further cloned, placed in a polycross field, and the new HS-families could be sown in ordinary field trials at various locations for further selection.

Key words: Open-pollination – Polycross – Genetic variation – Genetic correlation – Bootstrapping

Introduction

The general aim in the breeding of cross-pollinated, perennial forage grasses has so far been to develop improved synthetic populations. The characters of greatest interest for improvement are in most cases forage yield and quality, persistency, seed yield, and stability over years and locations. These characters are all quantitative, showing continuous variation in genetically heterogeneous populations and being highly influenced by environmental factors of various kinds. In order to plan an effective program, information on the extent and nature of the genetic variation and covariation of the various characters within the base population is necessary. From a breeding point of view, the common forage perennial grasses provide the advantage of being relatively easy to clone. Experimental growing of clones is therefore, in most cases, the initial step in the process of investigating the genetic variation in base populations. Experiments with clones from a randomly pollinated base population do not, however, allow a separation of the additive and nonadditive genetic variation. Progeny testing is therefore needed. The most common systems of mating and progeny testing of perennial forage grasses are open-pollination of individual plants or clones, polycross, pair matings, and top-crosses. Among these methods, open-pollination and the polycross method originally introduced by Frandsen (1940), Frandsen and Frandsen (1948), and by Tysdal et al. (1942) have probably found the widest application, mainly because of the simplicity in respect to the equipment needed and the labor required.

In most cases, the progeny testing after open-pollination or polycross is limited to experimental growing of half-sib families on whole plots laid out with replications at one or more locations, and the biometrical analysis of the experimental data is often limited to estimation of the

genetic and environmental variation of the HS-family means. This analysis will always provide an estimate for general combining ability as defined by Wricke and Weber (1986), irrespective of ploidy level and genotypic composition of the parental population.

If the parents are randomly selected from a diploid population in linkage equilibrium, the genetic component of the variation between the progeny means is an estimate of the additive component of the variation in the sense of Mather and Jinks (1982).

The variation among family means does, however, uses only one-fourth of the total additive variation in the base population. This means that the difference of three-quarters of the additive and the total of the nonadditive variation is hidden within the families. In their theoretical considerations, Hill (1981) and Nguyen and Sleper (1983) were aware of the great within-family variation and pointed to the possibility of within-family selection based on observations of individual plants within plots. This technique does not, however, allow for a separation between the genotypic and environmental variation within HS-families. Experience has shown that the environmental influence on typical quantitative characters of individual plants of forage grasses is high. There is, therefore, good reason to assume that selection based on mesurements of individual plants within plots would be rather inefficient.

In this paper we present results from an experiment in diploid meadow fescue (*Festuca pratensis* Huds.), in which a fixed number of plants from each HS-family after a polycross were cloned and then laid out in a randomized block experiment. Our intention from the beginning was to estimate and compare the genetic components of the variation between and within HS-families. Analysis of this experiment has, however, lead us to consider from a theoretical and practical point of view how progeny testing in forage grasses by means of open-pollination and polycross should be conducted in order to give maximal genetical information and maximal response to selection.

Theoretical considerations

We consider a breeding population of a diploid, perennial, and sexual species with complete random mating and in linkage equilibrium. Further, we assume that each quantitative character is governed by many loci, each with only two alleles, normal meiosis, no mutations, and no cytoplasmic effects. The additive gene contribution of the genotypes in each locus is designated d and $-d$ for the increasing and decreasing effects of the two homozygous genotypes, respectively, while the dominance effect is designated by h (Mather and Jinks 1982). If interallelic and genotype-environment interactions are absent, the total expected phenotypic variation of a character in the population is then

$$V_{pop} = V_{\bar{p}} = 1/2\,D_R + 1/4\,H_R + E,$$

where

$$D_R = 4 \sum_{i=1}^{k} u_i v_i (d_i + (v_i - u_i) h_i)^2,$$

and

$$H_R = 16 \sum_{i=1}^{k} u_i^2 v_i^2 h_i^2.$$

E stands for the environmental component of the variation, u and v designate the frequencies of increasing and decreasing alleles, respectively.

If c plants are chosen at random from the population, each selected plant cloned, and the clones laid out in a randomized experiment, the sum of the additive and dominance components $(1/2\,D_R + 1/4\,H_R)$ and E can be estimated from an analysis of variance according to Table 1.

In this table σ_e^2 represents E, while σ_c^2 represents $1/2\,D_R + 1/4\,H_R$. Based on clone means averaged over replications, heritability in the broad sense can be estimated as

$$h_{b.s.} = \frac{\sigma_c^2}{\sigma_c^2 + \frac{\sigma_e^2}{r}}.$$

Random mating in a cross-fertilizing population does not change genefrequencies over generations provided that selection, mutation, or random drift do not occur. The mean and total genetic variation of the progeny population should, therefore, be the same as for the parental population. If the progeny population consists of half-sib families produced from open-pollination of randomly selected plants or clones, it is possible to split up the total variation into components for between- and within-HS-families. If clones within families are used, it is then also possible to estimate D_R and H_R. Clones within families do not, however, permit testing for goodness of fit to a genetic two-parameter model (additive and dominance effects). Inclusion of parental clones together with clones of HS-families in the same experiment would give two useful additional statistics, namely the variation between

Table 1. Analysis of variance of an experiment with randomly selected clones

Source	*df*	Expected mean square
Replications	$r-1$	
Clones	$c-1$	$\sigma_e^2 + r\sigma_c^2$
Clones × repl.	$(c-1)(r-1)$	σ_e^2

parental clones ($V_{\bar{P}}$) and the covariance between parental clones and HS-family means ($W_{\overline{HS}/\bar{P}}$). Then the following equations would be available:

Variance between parental clones

$$V_{\bar{P}} = 1/2\,D_R + 1/4\,H_R + E_1 = \sigma^2_{c(p)}. \quad (1)$$

Variance between HS-family means

$$V_{\overline{HS}} = 1/8\,D_R + E_2 = \sigma^2_{\overline{HS}}. \quad (2)$$

Mean variance of HS-families

$$\overline{V}_{HS} = 3/8\,D_R + 1/4\,H_R + E_2 = \sigma^2_{\bar{W}}. \quad (3)$$

Covariance between parental means and HS-means

$$W_{\overline{HS}/\bar{P}} = 1/4\,D_R = \sigma_{\bar{P},\overline{HS}}. \quad (4)$$

Environmental variance of P-clones

$$E_1 = \sigma^2_{(1)}, \quad (5)$$

and HS-clones

$$E_2 = \sigma^2_{(2)}. \quad (6)$$

The different variance components $\sigma^2_{c(p)}$, $\sigma^2_{\overline{HS}}$, $\sigma_{\bar{P},\overline{HS}}$, $\sigma^2_{(1)}$, and $\sigma^2_{(2)}$ can all be estimated from an analysis of variance and covariance. There are six equations and four parameters to be estimated, leaving two degrees of freedom for testing goodness of fit by means of a Chi-square. If interallelic interaction is present or if one or more of the other assumptions do not hold, the Chi-square test for goodness of fit should be significant.

The total variation in the progeny population based on means over replications is

$$\mathrm{Var(pop)} = V_{\overline{HS}} + \overline{V}_{HS} = 1/8\,D_R + E_2/r + 3/8\,D_R + 1/4\,H_R + E_2/r = 1/2\,D_R + 1/4\,H_R + E_2/r,$$

and heritability in the narrow sense

$$h^2_{\mathrm{n.s.}} = \frac{\frac{1}{2}D_R}{\frac{1}{2}D_R + \frac{1}{4}H_R + E_2/r}.$$

Genetic response to selection (R) of clones within HS-families and intermating of the selected clones in an isolated polycross is then expected to be

$$R = k\,h^2_{\mathrm{n.s.}}\,\sigma_{\mathrm{pop}} = \frac{k\,\frac{1}{2}D_R}{(\frac{1}{2}D_R + \frac{1}{4}H_R + E_2/r)^{1/2}},$$

where k is the standardized selection differential (selection intensity).

As pointed out by Nguyen and Sleper (1983), it is possible to predict the response to a combined selection of HS-families (R_1) and selection of genotypes within HS-families (R_2). The expected gain will be

$$R = R_1 + R_2 = \frac{k_1\,\frac{1}{8}D_R}{(\frac{1}{8}D_R + E_2/r)^{1/2}} + \frac{k_2\,\frac{3}{8}D_R}{(\frac{3}{8}D_R + \frac{1}{4}H_R + E_2/r)^{1/2}},$$

where k_1 and k_2 designate the standard selection differentials among and within families, respectively.

If heritability on an individual genotype basis is low because of large environmental effects, family selection would be preferred to individual selection (Falconer 1981). Cloning of individual genotypes within HS-families does, however, lead to more precise estimates of genotypic values within families.

The disadvantage of using clones is, of course, the great labor involved in cloning and planting, which often results in small plots and thereby an environment that is somewhat different from mass-seeding.

The genetic expectations are the same in a polycross as they are for open-pollinations, provided that the clones in the polycross are not selected. It is, however, common to apply selection of the clones that are put into the polycross. Since the additive as well as the non-additive genetic components of the variation are frequency-dependent, they will all be biased by selection. In such cases one should be very careful in drawing genetic conclusions. One has to rely on general combining ability based on the mean performance of HS-families. The great advantage of a polycross as compared to half-sib families from individual plants after open-pollination is that great quantities of seed can be produced at low cost allowing large plots with natural stands in replicated trials at several locations. Family-environment interactions can thereby be taken into account in the process of selection.

Materials and methods

The material used in the present experiment came from Svanhovd, which is situated in the northeastern part of Norway at a latitude of 69°25′N and 45 m above sea level. The original population, designated 021012, was a 7-year-old ley characterized as natural meadow but originally sown with the variety Løken. Seeds were harvested from an area of about 0.3 ha from 100 randomly selected plants in 1973. The seeds were brought to the State Research Station Holt, where 100 randomly selected plants from a seed mixture of the collected population were cloned, the clones were grown in a randomized-block experiment and observed visually over two seasons (I. Schjelderup, personal communication). In 1984, 22 of the clones with the best general performance were transferred to the Agricultural University outside Oslo (59°40′N), where they were further cloned and planted in a polycross field laid out according to the design suggested by Olesen and Olesen (1973). From the seed harvested from this polycross in 1985, 20 randomly selected plants of each of the 22 HS-families were cloned and planted in a randomized-block experiment in 1987. Planting was done from 29 May to 4 June. Each plot had five ramets, set 30 cm apart in a row, and the row distance was 60 cm.

Table 2. Results of analyses of variances; mean squares and significance levels. The raw matter yields are devided by 100

Source	*df*	Panicle emergence	Cut 1	Cut 2	Cut 3	Total
Replication	1	12.53	110.15	3.40	61.24	271.53
HS-families	21	71.86***	262.97**	14.48**	32.69	436.53***
HS-fam. × repl.	21	2.28	6.07	0.60	2.80	15.19
Clones within HS-families	418	17.68***	36.50***	2.70***	7.44***	73.65***
Clones within HS-fam. × repl.	418	2.60	6.28	0.51	2.66	12.01
Total	879					

** $0.001 < P < 0.01$
*** $P < 0.001$

Table 3. Distribution of clones within HS-families for total RM yield. Class intervals = 200 g. Class 1 < 1,000 g

HS-family	Class												*n*	$\bar{x}$	Var./100
	1	2	3	4	5	6	7	8	9	10	11	12			
1			1		3	3	3	1	5	1	2	1	20	2,246	2,266
2	2	1			1	5	3	2	1	1	2	2	20	2,089	5,791
3	1			2		3	1	4	2	5	2		20	2,241	3,648
4				3	2	4	3	1	3	2	2		20	2,165	2,190
5					1	2	2	5	1	5	1	3	20	2,502	1,697
6				1	3		2	2	4	3	2	3	20	2,458	2,927
7	3			2	2	1	5	2		1	2	2	20	2,000	5,806
8	2		2	1	1	2	2	3	3	2		2	20	2,058	7,006
9				1	2	2	3	4	2	3	1	2	20	2,329	2,200
10			1		1	5	3	3	3	4			20	2,203	1,490
11	2	1	1	3	1	4		3	1	2	2		20	1,904	5,506
12		2	1			3	2	2	3	1	3	3	20	2,352	4,928
13	6	1	2	1	1	6	1		1		1		20	1,527	3,994
14	3			2	4	4	5			2			20	1,734	3,944
15						2	2	3	2	6	1	4	20	2,574	1,616
16	1		1	1	1	2	1	7	2	4			20	2,143	4,096
17	1		4	1	2	2	4	3	3				20	1,915	2,440
18		1		1	1	6	1	1	3	3	2	1	20	2,212	2,884
19	1		1		1	4		7	3	2		1	20	2,176	3,540
20	1			3			1	1	5	2	5	2	20	2,415	4,679
21	5	4	2	1	2	1	1	4					20	1,401	4,422
22	5	2	5	1	2	1	1	1	1		1		20	1,428	4,020
Sum	33	12	21	24	31	62	46	59	48	49	29	26	440	2,094	3,686

In the planting year the grass was cut without weighing at the end of August. The next year three cuts were taken. The first cut was at panicle emergence, the second 43 days there-after, and the third cut 41 days after the second cut. The grass yield after all cuts was determined by weighing the raw matter immediately after cutting each plot by hand. According to previous results, the raw matter yield determined in this way is closely correlated genotypically with the dry matter yield and should be a good measure of productivity (Aastveit and Aastveit 1989). Panicle emergence was determined in the ordinary way, i.e. in terms of days from an arbitrary date and until three plants of each plot had started panicle emergence.

Results

Table 2 shows that there were highly significant mean squares for earliness as well as for raw matter yield after all cuts and in total. Table 3 shows the distribution of HS-family means and within-family clone means averaged over blocks, as well as the within-HS-family variances for total raw matter yield. This table shows that the variation within families was large as compared to the variation among family means, and there was also a great variation among HS-families in the within variances. The within-family variances were not correlated with total yield.

Table 4. Estimates of variance components for HS-family means (σ^2_{HS}) and clones within HS-families (σ^2_W) with standard errors (SE). The yields are divided by 100

Character	Between HS-family means		Clones within HS-families	
	$\hat{\sigma}^2_{HS}$	SE ($\hat{\sigma}^2_{HS}$)	$\hat{\sigma}^2_W$	SE ($\hat{\sigma}^2_W$)
Panicle emergence	1.35	0.55	7.55	0.62
RM yield:				
Cut 1	5.66	2.03	15.11	1.28
Cut 2	0.29	0.11	1.09	0.10
Cut 3	0.61	0.24	2.38	0.27
Total	9.07	3.37	30.74	2.56

Table 5. Least-square estimates of D_R and H_R. The standard deviations are given in parentheses. The numbers for yields are based on the yields divided by 100

Characters	D_R		H_R	
Panicle emergence	10.8***	(4.4)	13.9	(7.0)
RM yield:				
Cut 1	45.29***	(16.24)	−7.49	(24.74)
Cut 2	2.36***	(0.89)	0.83	(1.38)
Cut 3	4.85***	(1.96)	2.25	(3.08)
Total	72.58***	(26.96)	14.11	(41.37)

*** $P<0.001$

Table 4 shows the estimates of the variance components for HS-family means (σ^2_{HS}) and clone variation within HS-families (σ^2_W), with their respective standard errors. All components have a high degree of significance. For panicle emergence, the within-family component is more than five times as large as the family component, while for RM yield the σ^2_W is, roughly speaking, about three times as large as σ^2_{HS}.

Based on Eqs. (2), (3), and (6), D_R and H_R have been estimated by the method of least squares. The estimates with their standard errors are presented in Table 5. The table shows that D_R is significant for all characters, while H_R is not significant in any case. It should be noticed that the standard errors of the H_R estimates are high as compared to the standard errors of D_R. Since we had only three equations available for estimation of three parameters, there were no degrees of freedom left for testing goodness of fit.

The genotypic correlations have been estimated on the basis of family means as well as within families. Tables 6 and 7 show relatively good correspondence between the two sets of estimates. In the tables, we have included the standard errors of the estimates. These standard errors are estimated by the Bootstrap method described by Aastveit (1989, 1990). In the Bootstrap method we have sampled both between and within families. The tables show that there were negligible genotypic correlations between earliness and the yield characters. High correla-

Table 6. Genotypic correlations estimated from HS-family means ± the standard deviations of the estimates (estimated by the Bootstrap method)

Character	Panicle emergence	RM yield			
		Cut 1	Cut 2	Cut 3	Total
Panicle emergence	1.0	−0.04±0.26	0.28±0.25	−0.03±0.29	0.01±0.28
RM yield					
Cut 1		1.0	0.25±0.30	0.31±0.31	0.92±0.05
Cut 2			1.0	0.85±0.13	0.60±0.20
Cut 3				1.0	0.65±0.20
Total					1.0

Table 7. Genotypic correlation coefficients within HS-families ± the standard deviations of the estimates (estimated by the Bootstrap method)

Character	Panicle emergence	RM yield			
		Cut 1	Cut 2	Cut 3	Total
Panicle emergence	1.0	0.01±0.16	0.30±0.11	0.12±0.14	0.10±0.16
RM yield					
Cut 1		1.0	0.40±0.09	0.56±0.09	0.93±0.02
Cut 2			1.0	0.66±0.11	0.66±0.06
Cut 3				1.0	0.80±0.05
Total					1.0

Table 8. Narrow-sense heritability estimates ($h^2_{n.s.}$)

Character	Based on all clones in the population	Based on HS-family means	Based on clones within HS-families
Panicle emergence	0.68	0.54	0.74
RM yield:			
Cut 1	0.79	0.65	0.84
Cut 2	0.68	0.49	0.90
Cut 3	0.47	0.23	0.58
Total	0.73	0.54	0.82

Table 9. Expected response (R) to three types of selection for RM yield (g/plot). b_1 = selected families (in %) and b_2 = selected clones within families (in %)

% selected	Selection of HS-families	Free selection of clones	Combined family and clone selection	
b_1	(R_1)	(R_2)	b_2	(R_3)
44	199	460	10	1,028
			5	1,173
20	311	719	10	1,140
			5	1,285
10	390	902	10	1,219
			5	1,364

tions were found between each of the three cuts and total yield, and between the yield at the second and third cut. The other correlations seem to be rather low compared to these estimated standard deviations. It can also be seen that the standard deviations of the estimates are lower for the within-family estimates as compared to the between-family estimates.

Narrow-sense heritabilities based on means of HS-families and clones within families averaged over replications are given in Table 8.

The table shows that the heritability estimates are highest when based on clones within HS-families. This may be due to some dominance variation, although none of the H_R estimates were significant.

Expected response to selection

Among the characters studied, selection for total yield is most important. Three methods of selection are possible.

(1) Selection based on clone means averaged over replication without attention to family. It is assumed that the selected clones are removed from the field and placed in a new polycross. The mixed progeny will then be the new population or syn-1 that should be compared to the original population.

(2) Selection of HS-families. It is assumed that seeds from the selected HS-families produced by the respective parental clones in the polycross are mixed in equal proportions and multiplied.

(3) Selection of the best clones within the best families. Also in this case it is assumed that the selected clones are removed from the field and placed in a new polycross.

Table 9 presents the expected responses after the three selection methods for various selection intensities. In the case of method 3, b_1 indicates the percentage of selected families, while b_2 indicates the percentage of selected clones within the selected families. Free selection among all clones is more efficient than selection among families. Selection of the best clones within the best families seems, however, to be most efficient in this case. Selection in a crop such as meadow fescue, with a strong, two-loci incompatibility system (Lundquist 1955, 1961), must take into account the risk of sterility and other undesired effects of inbreeding. Consequently, the number of selected families or clones selected within families should not be too low. A reasonable number of families in this case would, in our opinions be ten, or 44%. Furthermore if 10% or the two highest yield clones within these ten families were selected, we would expect a very high response of combined-family and clone within-family selection as compared to the two other methods.

Discussion and conclusions

Planning and conducting breeding programs in the perennial cross-pollinating forage grass crops requires information as to the size and nature of the genetic variation for the various characters of economic interest and the genetic relationship between the characters. Such information is expressed in terms of statistical parameters for broad-sense and narrow-sense heritabilities, genetic and environmental correlations, genotype × environment interactions, and predicted and observed response to selection. The information needed can be obtained from experiments with clones and progenies from various types of mating systems. Among the systems reported in the literature, progeny from open-pollination of individuals or clones in polycross fields seem to be among the most extensively used in the forage grasses. From a theoretical genetic point of view, progeny from open-pollination and poycross fields are the same, provided that the clones in a polycross are not selected. The difference between the two systems is that a relatively low number of clones in a polycross are arranged in such a way that the chance for random pollination is optimized. In a polycross field, large amounts of seed can be produced; thus, half-sib progeny families can be laid out in seed-sown trials at many locations. The amount of seed available from open-pollination of individual plants is so low that

the half-sib families have to be grown on small plots, often as spaced plants. In contrast to polycross, it is easy to have great numbers of families after open-pollination.

From a theoretical point of view, the additive component of variation among family means is expected to be low (1/8 D_R). Response to selection based on family means is therefore expected to be low. Several authors, e.g., Hill (1981) and Nguyen and Sleper (1983), are aware of the great genetic variation within HS-families (3/8 $D_R + 1/4\ H_R$). They do, however, assume that this variation is measured and used in selection by observing individual plants within plots. In that case, the environmental component of the variation will be very large and cannot be estimated.

This paper presents the results from an experiment in which 20 randomly selected plants from each of 22 HS-families from a polycross were observed for earliness and raw matter yield after three cuts. The dominance component of the variation was not siginificant for any of the characters. The additive component was, however, highly significant for all characters and, for yield was about three times as large within as between families. Thus, there was good agreement between theoretical expectation and observations. The expected response to selection for total yield was much higher for a combined between- and within-family selection as compared to family selection alone or free clone selection.

From a theoretical point of view, we think that an ideal program for progeny testing and selection within a base population should start with an experiment in which a large number of randomly selected parental clones and a fixed number of clones from each half-sib family produced by the same genotypes as the parental clones are grown simultaneously. The parental clones would add additional statistics so that the genetic model could be tested for goodness of fit. After analysis of the data from such an experiment, combined between- and within-family selection could be applied. The selected clones within families could then be removed from the field, cloned further, planted in a polycross, and the HS-families from this polycross could be laid out in a series of trials at several locations for further selection.

Acknowledgements. The authors wish to thank Mr. E. Berg for excellent technical assistance.

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