Journal of Agricultural Science, Cambridge (2001), **137**, 173–178. © 2001 *Cambridge University Press*
DOI: 10.1017/S0021859601001265 *Printed in the United Kingdom*

Comparative efficiency of three selection methods in *Dactylis glomerata* L. and *Agropyron cristatum* L.

E. M. ABRAHAM[1]* AND A. C. FASOULAS[2]

[1] *Department of Range Science, Aristotle University of Thessaloniki, Greece*
[2] *Department of Genetics and Plant Breeding, Aristotle University of Thessaloniki, Greece*

(*Revised MS received 10 April 2001*)

SUMMARY

Two populations, one non-improved of *Dactylis glomerata* and one improved of *Agropyron cristatum* were selected in an isolated spaced plant environment (80 cm) by three selection procedures: (1) Mass honeycomb selection (MHS), (2) pedigree honeycomb selection (PHS) and (3) pedigree honeycomb selection-combined criterion (PHS-CC). The third procedure is a between-families selection based on increased family mean and reduced family coefficient of variation (CV). Response to selection assessed in sward trials in the first and second harvest year was effective for the three procedures, which ranked PHS-CC > PHS > MHS. Evaluation was based on consistent efficiency as measured by both cloned and half-sib families. The precision of assessing progeny performance under sward conditions on the basis of single plant evaluation in the isolation environment, increased with a reduction in competition among plants, the use of moving-ring selection, and the application of high selection pressures (1·6%). The efficiency of selection between unimproved families increased when families were selected concurrently for high family mean and reduced family coefficient of variation.

INTRODUCTION

The amount of progress in breeding perennial forage grasses over a long period of time was assessed by Turner (1987) for *Lolium perenne* under UK conditions. The reported progress over 50 years was 0·3% per annum which is far behind the average 1% progress reported over the last 60 to 80 years in annual crops like barley, oats, wheat, sorghum and maize (Wych & Rasmusson 1983; Wych & Stuthman 1983; Duvick 1984; Miller & Kebete 1984; Schmidt 1984; Waddington *et al*. 1986; Cox *et al*. 1988; Feil 1992). The reasons for this reduced efficiency may be attributed to a perennial habit, an outcrossing system of reproduction, and the breeding methods used. According to Casler *et al*. (1997) the usual methods of breeding perennial forage grasses are: (1) single plant phenotypic selection (spaced-planting stage), and (2) polycross progeny test selection (sward-plot stage). They also stated that there are currently no means of determining the importance of one method relative to the other. Measures of forage yield per se in spaced-plant nurseries are generally considered to be of poor predictive value for sward-plot yield (Hayward & Vivero 1984; Casler & Hovin 1985; Carpenter & Casler 1990). Nevertheless, there are documented cases in which spaced-plant selection for forage yield has been responsible for increasing forage yield in sward plots of Italian ryegrass *Lolium multiflorum* Lam. (Fujimoto & Suzuki 1975), of rye *Secale cereale* L. (Bruckner *et al*. 1991); and of pensacola bahiagrass, *Paspalum notatum* (Burton 1992).

Better results may be expected by a combination of the two breeding methods, which in essence represents pedigree selection, i.e. joint selection between and within families. In fact, Aastveit & Aastveit (1990) estimated that response to selection was much higher when a combination of between and within family selection was used as compared to free clone or family mean selection alone. According to Fasoula & Fasoula (2000) the conditions that drastically reduce the efficiency of phenotypic selection are (1) competition, (2) heterozygosity and (3) genotype by environment (GE) interaction. Competitive ability which is negatively correlated with yielding ability limits response to selection (Kyriakou & Fasoulas 1985; Fasoula 1990). Heterozygosity is also undesirable as response to selection presupposes fixation of favourable additive alleles. More detrimental is the effect of GE interaction as the same genotypes will exhibit different phenotypes when exposed to environmental diversity. Honeycomb breeding overcomes the aforementioned difficulties firstly by selecting in the absence of

* To whom all correspondence should be addressed.
Email: eabraham@for.auth.gr

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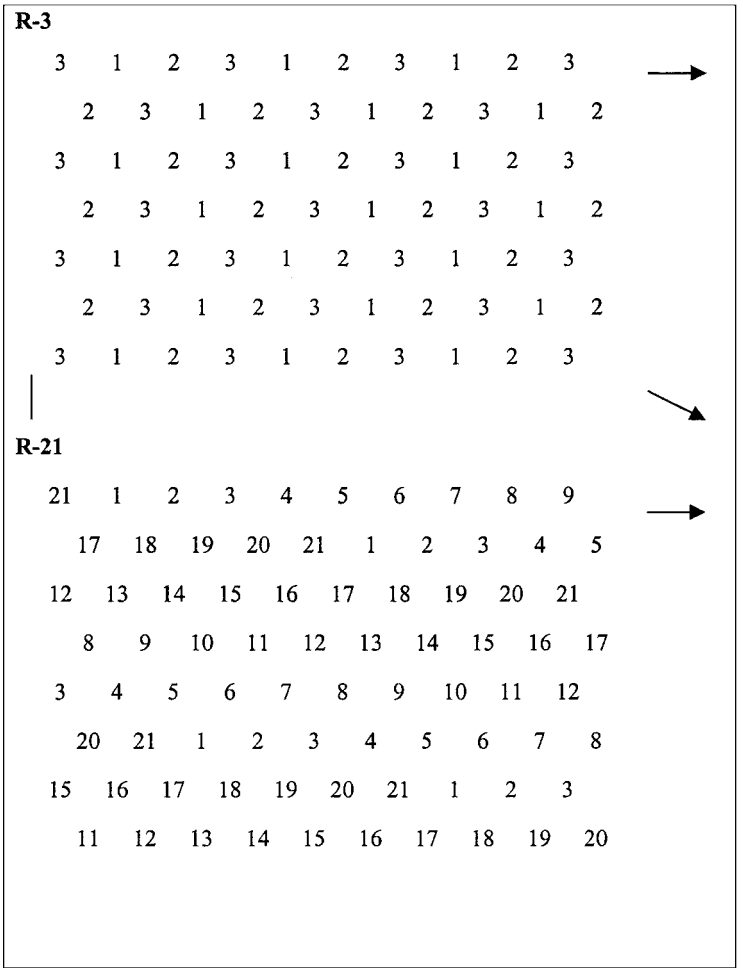


Fig. 1. The R-3 and R-21 honeycomb designs (Fasoulas & Fasoula, 1995).

competition, secondly by enhancing gene fixation by three means: (1) wide spacing that favours self-fertilization, (2) confinement of intermating among selected plants only and (3) application of high selection pressures. Genotype by environment interaction is overcome by selection for reduced GE interaction across the target area of adaptation, using honeycomb designs that sample effectively for environmental diversity and allow selection among and within families, as well as for general and specific adaptability. Since single plant selection for yield under sward conditions is generally ineffective, the objective of the present investigation was to assess efficiency when selection methods were compared in an isolated spaced-plant environment. The compared methods were: (1) mass honeycomb, (2) pedigree honeycomb and (3) pedigree honeycomb based on increased family mean and reduced family CV. The materials used were a non-improved population of *Dactylis glomerata* and an improved population of *Agropyron cristatum*.

MATERIALS AND METHODS

In 1992 a replicated-3 honeycomb trial (Fig. 1) was grown in the isolation environment, where code no. 1 was assigned to plants of a non-improved population of *Dactylis glomerata* (D.gl) (local ecotypes), code no. 2 to plants of an improved population of *Agropyron cristatum* (A.cr.) introduced from Canada, and code no. 3 to plants of a local non-improved population of *Festuca vallesiaca*. Plant spacing was 80 cm and the total number of plants was 330, i.e. 110 per species.

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All plants were harvested individually. Moving-ring selection was applied (Fasoulas & Fasoula 1995) and the best 21 plants were selected from each of the first two species to form 21 half-sib families. The third species was not included because of its low performance (Abraham *et al*. 1997).

In 1993 two replicated-21 honeycomb trials (Fig. 1) were grown, one for the 21 half-sib families of D.gl. and the other one for the 21 half-sib families of A.cr. Plant spacing was 80 cm and each family was represented by 30 plants. The total number of plants in each R-21 experiment was 630. All plants were harvested individually and their yield was recorded using software developed by Batzios & Roupakias (1997). A selection pressure of 1·6% was applied and 10 superior plants were selected using three different procedures, i.e.: (1) the 10 best plants using mass honeycomb selection (moving-ring selection), (2) the 10 best plants using pedigree honeycomb selection (i.e. the best two plants from the best five families), and (3) the 10 best plants by pedigree honeycomb selection using the combined criterion $CC = \bar{x}^2(1-CV)/CV$ that selects jointly for high family mean ($\bar{x}$) and reduced family CV. From each of the best five families on the basis of CC, the two highest-yielding plants were finally selected.

In 1994 two RCB (randomized complete block) trials with four replicates each were grown to test response to selection relative to the base population under sward-plot conditions. The eight populations tested comprised six from each species plus two base populations, four belonging to cloned families and four to half-sib families, as follows. Cloned families: (a) base population, (b) selected plants from MHS, (c) selected plants from PHS, (d) selected plants from PHS (CC); Half-sib families: (a) base population, (b) selected plants from MHS, (c) selected plants from PHS, (d) selected plants from PHS (CC).

The area occupied by each plot was 1·8 m² in which 30 plants spaced 30 × 30 cm were harvested individually and their yield was determined after drying at 60 °C for 48 h. Individual yields were combined to give a plot yield in g/m². Data were subjected to analysis of variance and significant mean differences were evaluated by the L.S.D. test (Steel & Torrie 1980) at a probability 0·05 level. The effect of competition on the CV values of single plants was estimated by using the mean, standard deviation and CV of the selected plants under nil-competition (80 cm) and cloned replicates under competition (30 cm) during the second year of RCB experiment (1995).

RESULTS AND DISCUSSION

According to Fasoula & Fasoula (1997*a*, *b*, 2000) the reliability of compared means is reflected by their coefficients of variation (CV) which may be impaired by two conditions: (1) competition and (2) the load of deleterious genes. The detrimental effects of competition on CV values of single plant yields were discussed by Hamblin *et al*. (1978) who found that in barley the CV values of single plant's yields were increased from 32 to 51% for plants spaced 40 and 4 cm respectively. Similar results were obtained by Kyriakou & Fasoulas (1985) in rye where the CV values were increased from 33 to 53% for plants spaced 90 and 15 cm respectively. This was despite the fact that at 15 cm the occupied area was 35 times smaller than at 90 cm, indicating that the masking effects of competition are larger than those of soil heterogeneity. Our results, presented in Table 1, corroborate these findings since the CV values obtained for 80 and 30 cm spacing were respectively 46 and 64% for D.gl. and 37 and 53% for A.cr. The larger CV values under competition indicate that competition reduces the reliability of means. Table 1 also indicates that (in accordance with Hamblin *et al*. 1978; Kyriakou & Fasoulas 1985) higher values for phenotypic standard deviations are obtained in the absence of competition. The fact that nil-competition produces higher values of phenotypic standard deviations, suggests that it will also produce higher responses to selection according to the general response equation $R = i.h^2.\sigma_p$ (Falconer 1989). Given that heritability improves in the absence of competition (Lin *et al*. 1971; Gibori *et al*. 1978), whereas at high selection pressures nil-competition ensures maximal positive response and competition maximal negative response (Kyriakou & Fasoulas 1985), it is self-evident that the three parameters of the general response equation are optimized in the absence of competition and minimized under competition.

Table 1. *The effects of competition on the mean, the phenotypic standard deviation, and the coefficient of variation of a non-improved population of* Dactylis glomerata *and of an improved population of* Agropyron cristatum

Species	Nil-competition (80 cm)	Competition (30 cm)
Dactylis glomerata		
x	79 g/plant	11 g/plant
σ_p	36	7
CV	46%	64%
Agropyron cristatum		
x	53 g/plant	11 g/plant
σ_p	19	3
CV	37%	53%

The effect of the load of deleterious genes on the CV values of single plant yields was extensively discussed by Fasoula & Fasoula (1997*a*, *b*). The

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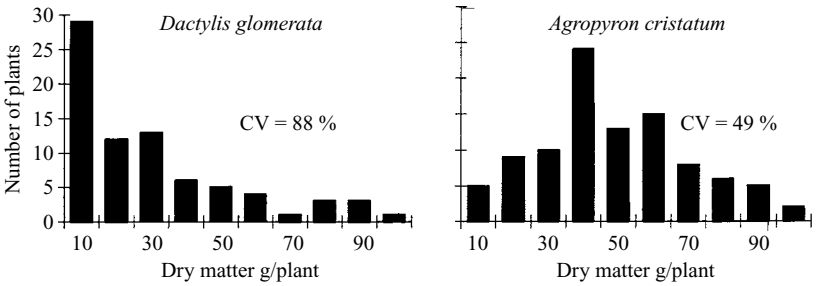


Fig. 2. When plants grow in the absence of competition (80 cm), the CV values quantify the load of deleterious genes which is higher in the non-improved population of *Dactylis glomerata* compared to the improved population of *Agropyron cristatum*. The load of deleterious genes affects also the normality of the yield frequency distribution the skewness of which increases according to the magnitude of the load.

Table 2. *Dry matter production of* Dactylis glomerata *under sward conditions, in the first and the second year after establishment as a percentage of the cloned base population*

	First harvest year		Second harvest year	
Selection method	Cloned families %	Half-sib families %	Cloned families %	Half-sib families %
Base population	100*	53	100†	97
Mass honeycomb	145	173	116	140
Pedigree honeycomb	167	108	144	113
Pedigree honeycomb (CC)*	203	138	131	132
LSD		36 %		20 %

* Cloned base population $100 = 42 \pm 11$ g/m^2 (D.F. = 24).
† Cloned base population $100 = 130 \pm 19$ g/m^2 (D.F. = 24).

authors pointed out that when plants grow in the absence of competition, the CV values increase as the load of deleterious genes increases, whereas the yield frequency distribution departs from normality accordingly. Therefore, the higher the CV value of a population in the absence of competition, the higher the load of deleterious genes and the greater the expectations for prolonged response to selection through effective replacement of deleterious by favourable alleles. Fig. 2 shows clearly that the non-improved population of D.gl. carries a much higher load of deleterious genes compared to the improved population of A.cr. It also shows that effective selection for reduced CV essentially improves the population through replacement of deleterious by favourable alleles.

According to Fasoula & Fasoula (2000), deleterious genes affect crop yield by reducing individual buffering which interferes with the equal sharing of resources. Correlation coefficient between yield per plot under sward conditions and the CV of single plant yields within the plot, was significant and negative ($r = -0{\cdot}47$) for D.gl. and non-significant ($r = -0{\cdot}03$) for A.cr. This is another indication that a reduction of the load of deleterious genes improves individual buffering and performance under sward conditions.

Two-cycle responses to selection in the two populations are presented in Tables 2 and 3 respectively. Table 2 indicates that in the second harvest year, mass honeycomb selection gave a significant genetic gain of 40 % when assessed by half-sib families. Pedigree honeycomb selection gave a significant genetic gain of 44 % when assessed by cloned families. The pedigree honeycomb-combined criterion produces significant genetic gains of 31 and 32 % when assessed by cloned and half-sib families respectively. It is clear that inclusion of CV as a selection criterion in the third method renders response to selection more predictable. Similar results were obtained in A.cr. (Table 3). Here the reduced load of deleterious genes gives an advantage to pedigree honeycomb selection which is a between and within family selection without inclusion of CV. Good response relative to the base population at 1·6 % selection pressure, demonstrates the im-

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Table 3. *Dry matter production of* Agropyron cristatum *under sward conditions, in the first and the second year after establishment as a percentage of the cloned base population*

Selection method	First harvest year		Second harvest year	
	Cloned families %	Half-sib families %	Cloned families %	Half-sib families %
Base population	100*	99	100†	89
Mass honeycomb	195	199	127	105
Pedigree honeycomb	224	190	122	144
Pedigree honeycomb (CC)*	240	145	120	121
LSD		42%		22%

* Cloned base population $100 = 19 \pm 6$ g/m^2 (D.F. = 24).
† Cloned base population $100 = 88 \pm 13$ g/m^2 (D.F. = 24).

portance of nil-competition in relating high response to high selection pressure according to the general response equation. The second factor affecting efficiency, i.e. heterozygosity has to do with the load of deleterious genes. The higher the load of deleterious genes, the higher is the degeneration brought about by gene fixation, and the more reduced the individual buffering and stability of performance. Thus, joint selection in the absence of competition for high family mean and low family CV, leads to efficient selection for high and stable yield. As to the third factor affecting efficiency, i.e. GE interaction, an efficient discrimination between methods requires multi-environmental screening in order to expose families to the diversity encountered over the target area of adaptation, this allows selection for reduced GE interaction either by the CV or by the standardized mean ($\bar{x}/s$). Recently, Fasoula & Fasoula (2000) partitioned crop yield potential into three components assessed in the absence of competition, i.e. (1) mean yield assessed by the progeny mean, (2) tolerance to stresses including tolerance to sward conditions assessed by the progeny standardized mean, and (3) responsiveness to inputs assessed by the progeny standardized selection differential. These approaches provide good prospects to overcome the barriers impairing selection efficiency and should improve performance under sward conditions when evaluation and selection are practiced in the absence of competition.

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