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A genetic approach to the multivariate differentiation of perennial ryegrass (*Lolium perenne* L.) populations

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Genetic differentiation among perennial ryegrass populations was studied using multivariate procedures incorporating a broad range of seasonal growth, quality and persistency traits. Principal components analysis, based on a genetic variance/covariance matrix, resulted in a correlation of 0.70 between the relative weighting (communalities) of traits in the first four principal components and the corresponding between population heritabilities. This was compared to correlations of 0.43 and −0.82 obtained for principal components, based on phenotypic and environmental variance/covariance matrices, respectively. Principal component communalities were more evenly related to heritabilities than those from canonical variates analysis which produced a correlation of 0.5 with heritabilities. Cluster analyses, based on principal component scores, produced four groups of populations separated by Mahalanobis distances ranging from 3.0 to 7.8. Considerable heterosis was obtained in crosses between populations from the more widely genetically separate groups.

Keywords: heritability, multivariate differentiation, perennial ryegrass, principal components.

Introduction

Assessment of genetic divergence between populations is vital to the success of plant breeding programmes designed to exploit gene recombination and the heterosis often produced by wide crossing. Strong positive relationships have been found between genetic distance and heterosis in a broad range of crop species (Balasch *et al.*, 1984; Shamsuddin, 1985; Spagnoletti Zeuli *et al.*, 1985; Lefort-Buson *et al.*, 1987; Peeters & Martinelli, 1989). Measures of genetic distance should have most value to breeding when based on a broad range of characteristics relevant to breeding objectives. Grass breeding programmes seek to improve many attributes including spring and summer growth, winter survival, disease resistance and quality factors such as digestibility and water-soluble carbohydrate content. Multivariate procedures have helped to evaluate germplasm collections used for breeding in a number of grass species (Charmet *et al.*, 1988; Falcinelli *et al.*, 1988; Veronesi & Falcinelli, 1988). However, little attention is often given to the validity of the methods used in terms of the genetic characteristics and relationships of measured traits and the genetic interpretation of results obtained from multivariate analysis.

Multivariate assessments are often made using phenotypic population means. If these are based on sufficiently large sample sizes and the traits measured show significant between-population differences, they can provide a reasonable representation of overall genetic performance. However, the standardization of most data in multivariate analyses gives equal weight to traits irrespective of differences in heritability and environmental interactions. Standardization is usually necessary because large differences in the scale of measurement are inevitable when dealing with a wide range of measured traits. Differences in scale can dominate the outcome of multivariate procedures if variances are not equalized, either by using correlation matrices or by correcting raw data prior to forming variance/covariance matrices.

In this paper information is extracted on genetic and environmental components of variability for a range of growth and quality traits among 81 perennial ryegrass populations of diverse origin. Genetic information is used to provide multivariate assessments of genetic distance between the ryegrass populations. The effect of separating genetic and environmental components on the relative weight of traits in these analyses is considered.

Materials and methods

Seedlings from 81 perennial ryegrass accessions were planted at the Department of Agriculture and Fisheries for Scotland, Agricultural Scientific Services, East Craigs site, Edinburgh on 19 July, 1982. The wide range of accessions included many grown in a previous trial at the Welsh Plant Breeding Station (Humphreys & Eagles, 1988) together with populations collected from old permanent meadows and pastures in Dyfed, Powys and Herefordshire (Humphreys *et al.*, 1980). Plants were spaced at 0.6-m intervals in the field in 10-plant row plots in each of two randomized blocks. During the period 1982 to 1984, 29 traits were measured as listed in Table 1. In 1983 and 1984 plants were topped in mid-March to remove winter growth and 377 kg ha^{-1} 20:10:10 NPK fertilizer applied. Plants were also topped after ear emergence in June 1983 and 277 kg ha^{-1} 20:10:10 fertilizer applied. The same quantity of fertilizer was used after each of the two cuts in 1983 and three cuts in 1984. Samples from each plot were taken at each cut, dried and used for analysis of water-soluble carbohydrates (WSC) (Thomas, 1977) and dry matter digestibility (DMD) (Jones & Hayward, 1975).

Genetic and environmental components of variance and covariance were calculated as in Humphreys (1989) with 80 degrees of freedom (d.f.) for between populations, 1 d.f. for between blocks and 80 d.f. for populations × blocks (used as the basic error term). Between-population heritabilities (h^2) were calculated for each trait as $h^2 = g/(g+e)$ where g is the between-population genetic component and e is the population environmental component (including interaction effects). Phenotypic variances and covariances were calculated as $p = g + e$ and $Cov_p = Cov_g + Cov_e$ respectively. Principal components analysis, canonical variate analysis and cluster analyses were performed on matrices derived from standardized raw data (giving a zero mean and standard deviation of 1 for each trait) using Genstat 5 packages (Payne *et al.*, 1987).

Results and discussion

Environmental and genetic components of variability from analyses of variance on non-standardized data for the 29 measured traits are given in Table 1. The range in values for these components reflects differences in scales of measurement used for the various traits and illustrates the need for standardization of variance prior to multivariate analyses. Of the 29 traits measured, five failed to show significant differences between populations and were omitted from further analyses.

Principal component analyses were carried out on phenotypic, genetic and environmental variance/covariance matrices derived from standardized data for 24 traits. Table 2 gives the cumulative percentage variance accounted for by the latent roots of the first four principal components in the analyses. It is clear that at least twice as much of the relevant matrix variance was represented by principal components derived from the genetic matrix compared to those derived from the environmental matrix. This reflects much stronger correlations between traits when based on genetic effects than on environmental effects and suggests a strong underlying genetic relationship between traits. Interactions with the environment were more independent between traits and tended to mask genetic relationships, as shown by the lower variance accounted for by principal components derived from the phenotypic matrix.

The relative contribution of each of the traits to the variance retained by the principal components is represented by the communalities presented in Table 3. Estimates of heritability for the traits are also given. Correlations between the heritability estimates and the communalities from the phenotypic, genetic and environmental matrices were 0.43, 0.70 and −0.82, respectively. Communalities indicate the relative weightings of traits in the total variance accounted for by the four principal components. The genetic matrix produced weights which were more strongly positively related to the heritability of traits than those produced by the phenotypic matrix. For example, HDAFT3 with a high heritability (0.78), had a higher communality (0.27), based on the four principal components from the genetic matrix than that based on the components from the phenotypic matrix (0.19). In contrast, PY831 with a low heritability (0.38) had a lower communality (0.19) in components from the genetic matrix than in the components derived from the phenotypic matrix (0.25). Weights produced by the environmental matrix had a strong negative relationship with heritability. Thus there were clear advantages to removing environmental effects from the phenotypic variance/covariance matrix. Godshalk & Timothy (1988) suggested that extraction of genetic matrices had little effect on rankings for principal component scores obtained from simple phenotypic matrices based on a limited range of traits. However, for the wide range of traits used in the current studies, and in the context of weighting traits for estimates of genetic distance, principal components derived from genetic matrices appear to have advantages. Virtually all the variation in the extracted genetic matrix was summarized in four principal components and the relative contribution of traits to these was directly related to their heritability.

Table 1 Chronological list of measured traits with associated environmental (e) and genetic (g) components of variability and significance level (P) of g

Trait	Measurement	Date	Code	e	g	P
Autumn growth	(1 poor–9 good)	28/9/82	(AUT82)	0.45	0.09	ns
Winter greeness	(1 little–9 lot)	21/1/83	(WTGRJN83)	0.08	0.07	***
Winter greeness	(1 little–9 lot)	9/3/83	(WTGRMR83)	0.10	0.23	***
Spring growth	(1 poor–9 good)	21/4/83	(SG83)	0.18	0.28	***
Ear emergence	(Days after 1/4/83)		(EE83)	7.40	325.70	***
Recovery growth	(1 poor–9 good)	4/7/83	(RECOV831)	0.71	1.00	***
Aftermath heads 1	(1 few–5 many)	4/7/83	(HDAFT1)	0.07	0.30	***
Yield Cut 1	(g per plant × 10)	3/8/83	(YLD831)	251.30	156.55	***
WSC Cut 1	(%)	3/8/83	(WSC831)	2.74	6.43	***
DMD Cut 1	(%)	3/8/83	(DMD831)	1.31	1.15	***
Aftermath heads 2	(1 few–5 many)	1/9/83	(HDAFT2)	0.09	0.24	***
Yield Cut 2	(g per plant × 10)	2/9/83	(YLD832)	369.40	11.00	ns
WSC Cut 2	(%)	2/9/83	(WSC832)	4.68	1.02	ns
DMD Cut 2	(%)	2/9/83	(DMD832)	1.83	0.85	**
Aftermath heads 3	(1 few–5 many)	19/10/83	(HDAFT3)	0.01	0.04	***
Autumn yield	(1 little–9 lot)	19/10/83	(AUTYLD83)	0.22	0.17	***
Spring growth	(1 little–9 lot)	18/4/84	(SG84)	0.16	0.24	***
Yield Cut 1	(g per plant × 10)	1/5/84	(YLD841)	232.10	353.15	***
Percentage DM Cut 1	(%)	1/5/84	(PDWT841)	3.58	0.24	ns
WSC Cut 1	(%)	1/5/84	(WSC841)	5.61	11.88	***
DMD Cut 1	(%)	1/5/84	(DMD841)	0.80	0.66	***
Yield Cut 2	(g per plant × 10)	19/6/84	(YLD842)	3252.00	8098.50	***
Percentage DM Cut 2	(%)	19/6/84	(PDWT842)	2.45	3.10	***
WSC Cut 2	(%)	19/6/84	(WSC842)	5.47	1.98	**
DMD Cut 2	(%)	19/6/84	(DMD842)	3.47	5.83	***
Yield Cut 3	(g per plant × 10)	24/8/84	(YLD843)	2303.00	3833.50	***
Percentage DM Cut 3	(%)	24/8/84	(PDWT843)	2.48	1.05	**
WSC Cut 3	(%)	24/8/84	(WSC843)	5.64	0.40	ns
DMD Cut 3	(%)	24/8/84	(DMD843)	8.95	1.66	*

Table 2 Cumulative percentage variance accounted for by successive principal components derived from phenotypic (p), genetic (g) and environmental (e) variance/covariance matrices for 24 traits

	Component number			
	1	2	3	4
p matrix	25	40	51	60
g matrix	40	76	86	96
e matrix	15	28	40	48

An alternative method of separating the between-population genetic effects from environmental effects is canonical variates analysis (Riggs, 1973; Tai, 1989). This analysis extracts components so that between-population variability (genetic) is maximized compared to the within-population (environmental) variability that remains. Essentially, it maximizes the overall heritability of canonical variates and places very large weight on traits with low levels of enviromental variability. The first four canonical variates derived from the standardized data for 24 traits accounted for 84 per cent of the between-population (genetic) variance. This compared with 96 per cent for the first four principal components on the extracted genetic matrix. Communalities based on the first four canonical variates are given in Table 4, together with values for genetic (g) and environmental (e) components of variance and their ratio (g/e) from analysis of standardized data. Unlike principal components analysis, communalities in canonical variate analysis are not constrained to lie in the range $(-1,1)$.

The correlation of the canonical variate communalities with the heritability estimates, listed in Table 3, was 0.50 which was slightly higher than the correlation (0.43) obtained with the principal component communalities from the phenotypic matrix but significantly lower than the correlation of 0.70 obtained with the communalities derived from the genetic matrix. However, a very high correlation (0.998) was obtained

Table 3 Communalities of 24 traits based on the first four principal components derived from phenotypic (p), genetic (g) and environmental (e) variance/covariance matrices and trait heritabilities

	Communalities			
Trait	p	g	e	Heritability
WTGRM83	0.25	0.25	0.02	0.70
SG83	0.23	0.23	0.06	0.61
EE83	0.19	0.23	0.00	0.98
HDAFT1	0.20	0.22	0.06	0.81
HDAFT2	0.22	0.25	0.09	0.73
HDAFT3	0.19	0.27	0.02	0.78
AUTYLD83	0.12	0.08	0.28	0.43
WTGRJN83	0.13	0.14	0.11	0.48
PY831	0.25	0.19	0.36	0.38
RECOV831	0.23	0.19	0.12	0.59
WSC831	0.12	0.12	0.03	0.70
DMD831	0.17	0.13	0.23	0.47
DMD832	0.16	0.12	0.61	0.32
SG84	0.18	0.20	0.14	0.60
PY841	0.25	0.26	0.11	0.60
PY842	0.17	0.20	0.07	0.71
PY843	0.12	0.13	0.10	0.62
PDWT842	0.18	0.15	0.22	0.56
PDWT843	0.08	0.07	0.32	0.30
WSC841	0.13	0.11	0.06	0.68
WSC842	0.14	0.11	0.43	0.27
DMD841	0.04	0.06	0.08	0.45
DMD842	0.17	0.19	0.14	0.63
DMD843	0.09	0.08	0.35	0.16

Table 4 Communalities based on the first four canonical variates for 24 traits and genetic (g) and environmental (e) components of variation with the (g/e) ratio derived from standardized data

Trait	Communality	g	e	g/e
WTGRM83	1.02	0.70	0.30	2.31
SG83	1.06	0.58	0.38	1.54
EE83	69.64	0.98	0.02	44.01
HDAFT1	3.94	0.78	0.19	4.21
HDAFT2	2.19	0.74	0.27	2.75
HDAFT3	3.79	0.78	0.22	3.47
AUTYLD83	0.13	0.42	0.56	0.74
WTGRJN83	0.57	0.44	0.48	0.91
PY831	0.41	0.38	0.62	0.62
RECOV831	1.51	0.59	0.41	1.42
WSC831	1.14	0.52	0.22	2.35
DMD831	0.34	0.45	0.51	0.88
DMD832	0.28	0.30	0.65	0.46
SG84	1.59	0.56	0.38	1.48
PY841	0.28	0.57	0.38	1.52
PY842	1.29	0.71	0.28	2.49
PY843	1.57	0.51	0.31	1.66
PDWT842	0.28	0.56	0.44	1.27
PDWT843	0.64	0.30	0.70	0.42
WSC841	0.71	0.57	0.27	2.12
WSC842	0.42	0.25	0.70	0.36
DMD841	0.15	0.35	0.42	0.83
DMD842	0.74	0.63	0.37	1.68
DMD843	0.11	0.14	0.76	0.19

between the canonical variate communalities and the g/e ratio shown in Table 4. By far the most dominant trait in the canonical variate analysis was the date of ear emergence (EE83). This had a very low environmental component which resulted in a very high g/e ratio and highlighted the disadvantage of using an analysis that depends on maximizing such a ratio. Extremely large weights were given to traits with low environmental interactions. This would be useful if minimizing genotype × enviroment interactions was of major concern in a breeding programme. However, weights more evenly related to individual heritabilities are probably more realistic in an overall plant improvement programme in which sufficient genetic variation is required for long-term genetic improvement irrespective of environmental effects. Thus, to determine genetic distances, principal component scores from a genetic variance/covariance matrix appear more useful than canonical variate scores.

Principal components can also be used in multivariate selection programmes as an alternative to more complex selection indices. Godshalk & Timothy (1988) found high rank correlations between scores from principal components analysis and scores derived from a Smith–Hazel index (Smith, 1936; Hazel, 1943). The relative contribution of traits to each principal component (component loading) can aid the interpretation of relationships between traits and identify combinations amenable to independent selection. Loadings for the first four principal components extracted from the genetic matrix are given in Table 5. In general terms the first component reflects many of the effects of heading date. Thus later heading was associated with low aftermath head production and more growth in late summer, autumn and winter. The second principal component reflects many aspects of quality also related to seasonal growth. Later heading plants tended to have lower soluble carbohydrates than earlier heading plants, especially in the first half of the growing season, and also lower digestibilities later in the season. Component 3 appears to be associated with winter and early spring growth, while component 4 generally reflects overall dry matter production. It should be noted that Varimax or Quartimax rotation did not assist in giving more detailed interpretation of

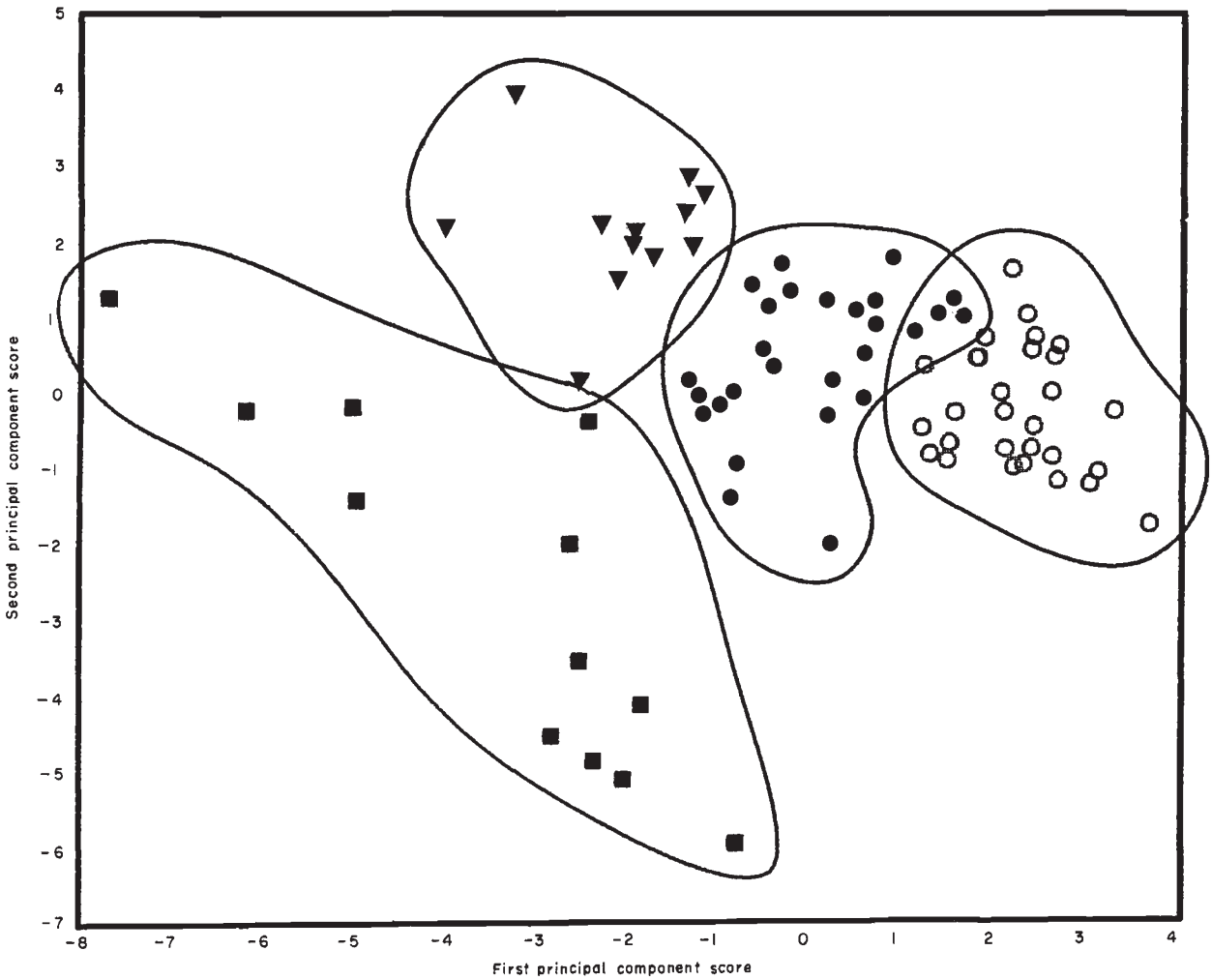

Fig. 1 Scatter plot of population scores for the first two principal components from a genetic variance/covariance matrix of 24 traits showing the four groups formed by non-hierarchical cluster analysis. (●) 4, (▼) 3, (■) 2, (○) 1.

these components. Loadings in the four *independent* components suggest that combinations of traits may be found which improve quality without decreasing yield, and that good overall productivity may be found in material over a range of heading dates. However, the fundamental effect of the wide range of heading dates found in perennial ryegrass, on the seasonality of many important growth and quality traits, is evident in these results. Previous work on winterhardiness in a separate trial (Humphreys, 1989) also illustrated the importance of heading date in relation to variation among perennial ryegrass populations.

To assess the overall genetic diversity among the 81 perennial ryegrass populations studied, the principal components loadings and population means for each trait were used to generate population scores. Essentially, these provided a summary of the genetic composition of each population in terms of traits relevant to breeding objectives. The population scores were subjected to average linkage hierarchical cluster analysis in order to identify groups based on genetic distances between populations. At the 95 per cent similarity level, the populations formed six groups while at the 90 per cent similarity level three groups were formed. On this basis non-hierarchical cluster analysis was applied assuming four groups using criteria which minimizes the determinant of the pooled within-class dispersion matrix and hence maximizes the total Euclidean distance between classes.

The four groups are shown in Fig. 1 on the scatter plot for the first two principal components. Mahalonobis distances representing the extent of genetic separation between groups are given in Table 6. This information may be used to determine which interpopulation crosses are likely to give most heterosis through genetic recombination. Considerable success has been achieved in making crosses between populations in Group 2, which comprise collections from N.

Table 5 Loadings for the first four principal components derived from the genetic variance/covariance matrix for 24 traits

	Component			
	1	2	3	4
WTGRM83	0.19	−0.06	0.45	−0.06
SG83	0.16	−0.18	0.39	0.13
EE83	0.35	0.28	−0.16	0.04
HDAFT1	−0.32	0.18	−0.07	0.29
HDAFT2	−0.14	0.36	0.15	0.28
HDAFT3	−0.28	0.06	−0.18	0.39
AUTYLD83	0.24	0.01	−0.03	0.16
WTGRJN83	0.18	−0.07	0.30	0.11
PY831	−0.02	−0.14	−0.10	0.39
RECOV831	−0.16	−0.33	−0.13	0.19
WSC831	−0.19	−0.25	−0.16	0.00
DMD831	0.15	−0.24	−0.08	−0.21
DMD832	0.10	−0.23	−0.22	0.03
SG84	0.11	−0.27	0.19	0.29
PY841	−0.06	−0.29	0.26	0.33
PY842	0.34	0.06	−0.08	0.27
PY843	0.27	0.02	−0.14	0.20
PDWT842	−0.28	−0.03	0.23	−0.14
PDWT843	0.00	0.16	0.22	0.04
WSC841	−0.27	−0.18	0.05	−0.06
WSC842	−0.04	−0.31	−0.10	−0.03
DMD841	0.03	0.12	−0.20	0.04
DMD842	0.26	−0.22	−0.27	0.03
DMD843	−0.02	−0.18	−0.05	−0.21

Table 6 Mahalanobis distances between the four groups iudentified by cluster analysis

Group				
1	0.00			
2	7.84	0.00		
3	5.42	6.03	0.00	
4	3.00	5.95	2.54	0.00

Italy and the Zurich Uplands, and those in Group 1 which contain generally late heading N. European cultivars (Humphreys, 1984; Wilkins, 1986). Heterosis has also been obtained in hybrids from crosses between populations in Group 2 and the early flowering Aberystwyth cultivar S.24. which falls into Group 4 (Kearsey *et al*; 1987). Work is in progress to investigate the performance of other hybrids between populations. Indications are that, as expected from the relatively low genetic distance between groups 3 and 4, heterosis is generally absent in hybrids between these groups and also in hybrids between populations within the same group.

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