Journal of Agricultural Science (2007), **145**, 599–610. © 2007 *Cambridge University Press*
doi:10.1017/S0021859607007332 *Printed in the United Kingdom*

Genetic variation and correlation among yield and quality traits in cocksfoot (*Dactylis glomerata* L.)

A. JAFARI[1]* AND H. NASERI[2]

[1] *Research Institute of Forests and Rangelands, Tehran, Iran*
[2] *Islamic Azad University, Brojerd, Iran*

(*Revised MS received 6 April 2007; First published online 1 August 2007*)

SUMMARY

The objective of the present research was to study the genetic variability for total dry matter (DM) yield, tiller number, heading date and three quality traits, namely content of digestible dry matter (DDM), water-soluble carbohydrate (WSC) and crude protein (CP), in cocksfoot (*Dactylis glomerata* L.). Twenty-five parents were randomly chosen from a genetically broad-based population, and their respective half-sib (HS) families were generated. Clonally-propagated parents and their HS family seeds were grown as individual plants using a randomized complete block design with two replications in Alborz Research Center, Karaj, Iran, during 2002–04. The results of combined analyses over 2 years showed significant variances between clonal parents for all traits except CP. In the HS generation, between-family variances were only significant for tiller number, heading date and WSC. Clone × year (S^2_{GY}) and family × year (S^2_{FY}) interactions were significant for all traits except for WSC in HS families. The estimates of broad-sense heritability (h^2_b) were moderate to high for all traits ($h^2_b = 0{\cdot}37$–$0{\cdot}69$), except CP. Narrow-sense heritability (h^2_n) estimates from analyses of progenies and from regression of HS progenies on parents (h^2_{op}) were moderate, relatively the same values as h^2_b for heading date, tiller number and WSC, which suggested that additive genetic variance was the main component controlling these traits. For DM yield and DDM, h^2_n and h^2_{op} estimates were low, whereas h^2_b estimates were moderate, which suggested that both additive and non-additive gene effects played an important role in the genetic regulation of these traits. Genetic correlations among CP with both WSC and DDM were generally negative, whereas WSC was positively correlated with DDM and tiller number. The genetic correlation among DM yield with DDM was weak and inconsistent and, in general, negative. DM yield had negative and positive correlation with heading date and tiller number, respectively. It was concluded that there was significant variation and moderate heritability for most traits in the cocksfoot populations evaluated to improve yield and quality traits. Selection for high WSC is a means to improve quality in general. The data also indicate that response to combined selection for both DDM and DM yield should be possible. Selection for DDM alone could result in reduction in yield.

INTRODUCTION

The botanical composition of rangelands is variable in Iran. Cocksfoot (*Dactylis glomerata* L.) is one of the main perennial grasses that naturally grow in temperate pasture and rangelands in northern and western Iran. It is used for grazing and hay production. Cocksfoot grows at altitudes of 500–2900 m (Rechinger 1970) having more than 300 mm annual participation (Niaky 1995). The improvement of total annual yield, persistency, disease resistance and extended grazing season are important objectives in most herbage breeding programmes. However, data from animal nutrition studies show the need to focus more attention on nutritive value in selection programmes. Wheeler & Corbett (1989) and Smith *et al.* (1997) ranked forage traits in terms of their nutritional value for live weight gain and dairy production, respectively. Improved digestibility and

* To whom all correspondence should be addressed. Email: aajafari@rifr-ac.ir

increased water-soluble carbohydrates (WSC) content were the two most important criteria on each of the two lists.

There are much published data which show that digestibility is a major factor affecting intake (Cooper 1973) and animal performance (Connolly *et al.* 1977). Carlier (1994) concluded that WSC are completely digestible and have an important role in ruminant animal nutrition, as they are a primary source of the readily available dietary energy necessary for efficient microbial fermentation in the rumen. Beever & Reynolds (1994) have shown that an adequate supply of soluble sugars is essential for good fermentation and protein utilization in the rumen, leading to improved feed efficiency and animal performance. When considered as a separate characteristic, crude protein (CP) content was ranked as moderate or low priority in terms of quality objectives (Wheeler & Corbett 1989; Smith *et al.* 1997). However, with regard to the important interaction between WSC and CP in the efficiency of protein metabolism as discussed above, it is clear that the combined evaluation of both characteristics is desirable in relation to selection for improved nutritional value in herbage.

From a plant breeding perspective, the possibility of improving forage quality by selection is a very attractive objective. The extent to which this is possible depends on the type of genetic control of the component characters and their interrelationship with other factors such as yield, disease resistance and persistence. To improve grass varieties for yield and quality traits, knowledge of genetic parameters is important for choosing an efficient selection strategy. Plant breeders have used the estimation of genetic variance and its additive components for selection proposes in perennial species because most breeding methods available to the forage breeder make little use of non-additive genetic variation (Nguyen & Sleper 1983).

The published data for cocksfoot suggest that genetic variation is present for digestibility (Cooper 1962; Christie & Mowat 1968; Frandsen 1986) and its improvement by selection should be possible. However, there is some evidence that the inheritance of digestibility in forage grasses is not purely additive but that dominance is present (Marum *et al.* 1979; Beerepoot *et al.* 1994). By comparison with other traits, there is little information on genetic control of WSC in cocksfoot. Cooper (1962) and Grusea & Oprea (1994) reported that genetic effects of WSC were additive. However, contrasting results were reported by Humphreys (1989*a*, *b*) in perennial ryegrass, who found that WSC behaved as a complex polygenic trait that was controlled by mainly non-additive gene effects. For CP in cocksfoot, Cooper (1962) and Shenk & Westerhaus (1982) found relatively high estimates of heritabilities ($h^2_n = 0{\cdot}55$) and ($h^2_n = 0{\cdot}39$–$0{\cdot}64$). For dry matter (DM) yield, both additive (Cooper 1962; Frandsen 1986; Annicchiarico & Romani 2005) and dominant variance (Casler 1998; Jafari 1998) have previously been reported.

Knowledge of correlation between traits of interest is useful in designing an effective breeding programme for a crop. Despite the increased emphasis on quality characteristics, total DM yield and seasonal yield distribution are of primary interest in herbage breeding. Consequently, the study of the potential for improvement in quality characteristics should be combined with the analysis of yield and its interrelationship with quality components. The extent to which various quality characters are correlated in forage grasses has been studied by a number of investigators (Frandsen 1986; Humphreys 1989*c*; Marum *et al.* 1994; Jafari *et al.* 2003*a*). In general, the correlation between CP and DM yield was negative and negative relationship between yield and digestible dry matter (DDM) was also frequently found. WSC was positively correlated with DDM, whereas the relationship between WSC and DM yield was inconsistent (Brown & Blaser 1970; Jafari *et al.* 2003*a*; Sanada *et al.* 2004). Cocksfoot has an important role in grassland productivity and any improvement in its herbage yield and quality would be very beneficial in terms of animal productivity. The present research project was conducted because relatively little breeding work has been done on this species and the information on its breeding behaviour, especially under the climatic conditions of Iran, is scanty. The objectives of the study were: (1) to estimate genetic variability and heritability for DM yield and quality traits, (2) to examine relationships among yield and quality traits and (3) to predict genetic gain from one cycle of selection.

MATERIALS AND METHODS

The cocksfoot genotypes used in the present study were derived from domestic accessions that were collected from temperate pasture and rangelands in northern and western Iran as follows: Uremia, Ardabil, Karaj, Sari and Gorgan. Five accessions were collected with a range of ear emergence of 7 days. Five seeds were taken randomly from each accession and sown in compost. The resulting 25 seedlings were vegetatively propagated to give six clones of each. The polycross consisted of 25 genotypes arranged randomly in six clonal replicate blocks and was established in the polycross nursery at the Research Institute of Forests and Rangelands, Karaj, Iran, in September 2001. The ear emergence date was recorded twice a week in May 2002. At harvest, seed from the clonal replicates of each genotype was bulked. Seed of HS families were sown for progeny test. From each HS family, eight seedlings were established in compost.

At the same time, eight clonal propagations were made from tillers of each parental genotype, planted under the same conditions as the HS seed progenies. The vegetative propagules of the parents, together with HS progeny seedlings, were transplanted to the field in October 2003. Two experiments were established using randomized complete-block designs with two replications for both parents and progenies. Spaced plants were established in rows 500 mm apart, with 400 mm spacing within rows. Fertilizer application rates were 50 or 100 kg nitrogen (N) and phosphorus (P)/h at sowing. Application of nitrogen was continued at 50 kg/h for the second and third years. The field was irrigated once a week during summer. Due to the dry conditions after transplanting, some seedlings died; therefore, only five out of eight plants per plot were evaluated. No measurements were taken in the establishment year. In 2004 and 2005, the plants were harvested three times. Before the first harvest, ear emergence date was measured as the number of days from 21 March to the stage at which three flowering shoots were visible. At harvest, fertile tillers were counted on spaced plants in the first and second cuts of both years. At the first cut of spaced plants, fertile tillers were assessed visually: the number of stems per plant was classified into five groups as 1 (1–10 stems), 2 (11–20 stems), 3 (21–30stems), 4 (31–40 stems) and 5 (more than 40 stems per spaced plant). The distribution of data for tiller number was non-normal, especially in the second cut. To normalize the data, they were transformed based on normal score with a mean of 2·5.

In each harvest, plants were cut, weighed, dried at 70 °C for 24 h, and reweighed to determine DM yield, then ground with a Retsch Impeller-type mill (1 mm screen). DM yields were measured for three cuts per year. Quality traits (DDM, WSC and CP) were estimated in the first and the second cuts for each year using near infrared spectroscopy (NIR). Details of the methodology and calibrations of NIR are given by Jafari *et al*. (2003*b*).

Statistical analysis

Data were collected for DM yield, morphological and quality traits. For each year, data were analysed for total annual DM yield (three harvests) and average annual quality value (two harvests). Data were also subjected to a combined analysis of variance across years using a split-plot-in-time design with years as sub-plots (Steel & Torrie 1980). Expected mean squares (EMS) were based on a random effects model for blocks, years, parents and HS families. Variance and covariance components were used to estimate heritabilities and genetic correlations. Broad-sense (h^2_b) and narrow-sense (h^2_n and h^2_{op}) heritabilities were estimated from analyses of parents, HS families, and regression of offspring on one parent, respectively (Nguyen & Sleper 1983; Falconer & Mackay 1996).

For individual years,

$$h^2_n = \frac{\sigma^2_G}{\sigma^2_G + \frac{\sigma^2_e}{r}}, \qquad h^2_n = \frac{\sigma^2_F}{\sigma^2_F + \frac{\sigma^2_w}{r}}, \qquad h^2_{OP} = 2b = \frac{V_A}{V_P}.$$

Combined across 2 years,

$$h^2_b = \frac{S^2_G}{S^2_G + \frac{S^2_{GR}}{y} + \frac{S^2_{GY}}{r} + \frac{S^2_e}{ry}},$$

$$h^2_n = \frac{S^2_F}{S^2_F + \frac{S^2_{FR}}{y} + \frac{S^2_{FY}}{r} + \frac{S^2_w}{ry}}, \qquad h^2_{OP} = 2b = \frac{V_A}{V_P},$$

where: b, r and y = regression coefficient, number of blocks and years, respectively. S^2_G, S^2_e, S^2_F and S^2_w = estimate of genetic, non-genetic, between- and within family variances, respectively. S^2_{GR}, S^2_{GY}, S^2_{FR} and S^2_{FY} = variance component due to parents × blocks, parents × years, family × block and family × year interaction effects, respectively.

Standard errors (S.E.) of h^2_b and h^2_n were computed as described by Dickerson (1969), whereas S.E. (h^2_{op}) = 2 × S.E. (b).

The reference unit to which all of these estimates apply was that of parents and family mean. Heritability estimates were obtained assuming a diploid inheritance model without epistasis and non-inbred parents chosen at random from the parent varieties. Negative variance components were considered to be zero in calculating heritabilities. Expected genetic gains per cycle of selection for parents and HS families were calculated for a selection intensity of 0·2 (standardized selection differential = 1·4), based on Nguyen & Sleper (1983), as follows:

$$R_P = ih^2_{op} \times \sqrt{S^2_{ph_P}}, \qquad R_F = iS^2_F \times \sqrt{S^2_{ph_F}},$$

where: R_P and R_F = expected gains for selection of clonal parents and HS families, respectively. h^2_{op} and S^2_F = narrow-sense heritability and genetic variance among HS families, respectively. $S^2_{ph_P}$ and $S^2_{ph_F}$ = phenotypic variance among parents and HS families, respectively.

The genetic correlations between traits measured for both parents and HS families were estimated from variance and covariance components of analysis. For parents, this is an estimate of the correlation of total genotypic effects (r_g). Because the variance and covariance of HS families are a measure of additive gene effects, the correlation based on these statistics is an estimate of the additive genetic correlation, i.e. correlation of the breeding values (r_a) (Falconer & Mackay 1996). Estimates of the non-genetic (error/environment) correlation coefficient (r_e) were also

https://doi.org/10.1017/S0021859607007332 Published online by Cambridge University Press

Table 1. *Summary of descriptive statistics for each trait derived from analyses of parents and HS families across 2 years for yield and quality traits*

	Parents				HS families			
Traits	Mean	S.E.M.	S.D.	Range	Mean	S.E.M.	S.D.	Range
DM yield (g/plant)	159	7·5	36·9	164	171	5·8	28·6	138
Heading date (day)	37·7	1·27	6·20	19·1	35·4	0·80	3·94	14·5
Tiller number (1–5)	2·6	0·12	0·58	2·0	2·7	0·09	0·46	1·6
Digestibility (mg/g)	589	36·2	178	64	578	21·3	102	41
Carbohydrates (mg/g)	141	38·1	188	72	118	32·1	156	56
CP (mg/g)	150	20·4	98	39	161	19·2	91	41

calculated for parents. Estimates of correlation were made for each year separately and the two years combined:

$$r_g = \frac{S_{G(xy)}}{\sqrt{S^2_{G_{(x)}} \cdot S^2_{G_{(y)}}}}, \qquad r_a = \frac{S_{F(xy)}}{\sqrt{S^2_{F_{(x)}} \cdot S^2_{F_{(y)}}}},$$

$$r_e = \frac{S_{E(xy)}}{\sqrt{S^2_{E_{(x)}} \cdot S^2_{E_{(y)}}}},$$

where: S^2_G, S^2_F, S^2_E, $S_{G(xy)}$, $S_{F(xy)}$, $S_{E(xy)}$ = estimate of genetic variances, between-family variances, error variance, genetic covariance, between-family covariance and error covariance components, respectively.

When the mean square of one or both traits was negative, no genetic correlation was calculated. Approximate standard errors of r_g and r_a were calculated as described by Becker (1984).

The phenotypic correlation (r_p) between two traits was then calculated as follows:

$$r_p = \frac{MP_{(X,Y)}}{\sqrt{MS_{(X)} MS_{(Y)}}},$$

where $MP_{(X,Y)}$ is the progeny or clone mean cross product for the characters X and Y and $MS_{(X)}$ and $MS_{(Y)}$ are the progeny or clone mean squares for the trait X and the trait Y, respectively.

RESULTS

Descriptive statistics for DM yield, morphological and quality traits derived from analysis of parents and HS families across years are summarized in Table 1. Estimates of components of genetic variance (S^2_G) and error variance (S^2_e), derived from analysis of parents, and between-HS families (S^2_{HS}) and within-HS families (S^2_w), derived from analysis of progenies and corresponding heritabilities values (h^2_b and h^2_n), are summarized in Table 2.

Both genetic and between family variances were significant for all traits ($P \leqslant 0{\cdot}01$) in both years, except for between-family variances for WSC in the second year (Table 2). The estimates of heritabilities for the various traits were different ($h^2_b = 0{\cdot}25 - 0{\cdot}96$ and $h^2_n = 0{\cdot}13 - 0{\cdot}85$; Table 2). The heritability estimates based on individual year were relatively high for more of the traits. This is expected, since heritability estimates based on one year are exaggerated if genetic × environment interaction variance is significant. The combined analyses across years and corresponding heritability values for parents and HS families are summarized in Table 3. Estimates of components of genetic variance (S^2_G) were significant in all cases except CP. The between-family variances (S^2_F) were significant only for heading date, tiller number and WSC. Parent × year and family × year interaction effects were significant in all cases except WSC for HS families (Table 3).

Three estimates of heritability were derived from the data (h^2_b, h^2_n and h^2_{op}) for individual years and combined across years; these are summarized in Table 4. The estimates of heritabilities based on combined analyses take account of genetic × environment interaction components and were, as expected, lower than those for individual years (Table 4). Based on combined analyses, h^2_n and h^2_{op} for DM yield were effectively zero (less than twice the corresponding S.E.; Table 4).

Expected genetic gains were calculated for all traits in parents and HS families. The expected genetic gains for phenotypic parental selection were higher than HS families except DM yield (Table 5).

The estimates of phenotypic (r_p), genotypic (r_g) and additive genetic (r_a) correlations from analysis of both parents and HS families are summarized in Table 6 for yield and morphological traits, Table 7 for yield and quality traits and Table 8 for three quality traits. The genetic and between-families variances for CP were negative or not significant in parents and HS families (see Table 3) and in such cases no r_g and r_a correlations were calculated. Genetic correlations had large sampling variances and the approximate S.E. values were large. Only

https://doi.org/10.1017/S0021859607007332 Published online by Cambridge University Press

Table 2. *Estimates of components of genetic variance* (S^2_G), *error variance* (S^2_e) *and broad-sense heritability* (h^2_b) *derived from analysis of parents and between-family variance* (S^2_F), *within family variances* (S^2_w) *and narrow-sense heritability* (h^2_n) *derived from analysis of HS families for yield and quality traits for individual years* (± S.E.)

		Parents			HS Families		
Traits	Year	S^2_G	S^2_e	h^2_b	S^2_F	S^2_w	h^2_n
DM yield (g/plant)	2004	1421 ± 505·6	3134	0·48 ± 0·111	1259 ± 481·7	3747	0·40 ± 0·096
	2005	959 ± 325·8	1709	0·53 ± 0·122	823 ± 314·8	2446	0·40 ± 0·096
Heading date (day)	2004	50·7 ± 15·19	32·8	0·76 ± 0·129	28·4 ± 9·76	54·1	0·51 ± 0·118
	2005	86·6 ± 24·27	7·87	0·96 ± 0·257	21·3 ± 6·18	7·73	0·85 ± 0·213
Tiller number (1–5)	2004	0·25 ± 0·078	0·28	0·63 ± 0·148	0·13 ± 0·052	0·45	0·37 ± 0·091
	2005	0·47 ± 0·153	0·65	0·59 ± 0·137	0·30 ± 0·110	0·78	0·43 ± 0·102
Digestibility (mg/g)	2004	205 ± 71·5	415	0·50 ± 0·115	198 ± 73·8	533	0·43 ± 0·101
	2005	538 ± 171·0	620	0·63 ± 0·148	428 ± 141·6	649	0·57 ± 0·131
Carbohydrates (mg/g)	2004	349 ± 117·7	597	0·54 ± 0·124	110 ± 40·2	276	0·44 ± 0·104
	2005	542 ± 175·4	718	0·60 ± 0·139	185 ± 142·5	2520	0·13 ± 0·053
CP (mg/g)	2004	265 ± 106·1	922	0·36 ± 0·089	162 ± 69·7	693	0·32 ± 0·081
	2005	39 ± 19·2	233	0·25 ± 0·071	38 ± 20·4	273	0·22 ± 0·066

Table 3. *Estimates of components of genetic variance* (S^2_G), *parents × blocks* (S^2_{GR}) *parents × years* (S^2_{GY}), *error variance* (S^2_e), *between-family variance* (S^2_F), *family × blocks* (S^2_{FR}), *family × years* (S^2_{FY}) *interaction effects and within family variances* (S^2_w) *derived from combined analysis of parents and HS families across 2 years for yield and quality traits* (± S.E.)

Parents	S^2_G	S^2_{GR}	S^2_{GY}	S^2_e	h^2_b
DM yield (g/plant)	952 ± 361·3	986 ± 196·5	238 ± 117·4	1435 ± 152·5	0·49 ± 0·188
Heading date (day)	42·0 ± 16·23	2·4 ± 1·54	26·6 ± 8·00	17·9 ± 1·91	0·69 ± 0·228
Tiller number (1–5)	0·15 ± 0·093	0·07 ± 0·035	0·25 ± 0·083	0·40 ± 0·042	0·37 ± 0·201
Digestibility (mg/g)	170 ± 92·5	68 ± 39·2	201 ± 71·7	449 ± 47·8	0·41 ± 0·196
Carbohydrates (mg/g)	304 ± 122·8	257 ± 53·1	141 ± 53·3	401 ± 42·6	0·50 ± 0·204
CP (mg/g)	0·0 ± 46·3	170 ± 45·2	218 ± 74·7	408 ± 43·4	0·00 ± 0·193
HS families	S^2_F	S^2_{FR}	S^2_{FY}	S^2_e	h^2_n
DM yield (g/plant)	351 ± 296·9	1090 ± 246·7	691 ± 262·5	2006 ± 213·3	0·20 ± 0·145
Heading date (day)	10·9 ± 6·00	2·6 ± 2·33	14·5 ± 5·03	28·3 ± 3·01	0·40 ± 0·186
Tiller number (1–5)	0·12 ± 0·063	0·12 ± 0·047	0·10 ± 0·045	0·50 ± 0·053	0·34 ± 0·165
Digestibility (mg/g)	0·0 ± 77·8	25 ± 44·5	322 ± 109·3	566 ± 60·2	0·00 ± 0·213
Carbohydrates (mg/g)	105 ± 66·7	31 ± 105·1	42 ± 61·7	1367 ± 145·3	0·23 ± 0·138
CP (mg/g)	0·0 ± 33·6	125 ± 38·3	39 ± 41·2	390 ± 33·9	0·00 ± 0·133

where the r_g or r_a value was greater than twice its S.E. was it considered to be significant. This approximate test was used previously for this statistic by Hill & Leath (1975). Estimates of the non-genetic (error/environment) correlation coefficient (r_e) for parents were calculated (Tables 6–8). With some exceptions, the r_e values were small and not significant (Tables 6–8). DM yield had strong negative and positive correlations (r_g and r_a) with heading date and tiller number, respectively. Heading date had strong negative r_g correlation with tiller number (Table 7). All the estimates of r_g and r_a among DM yield with both DDM and WSC were generally negative but not significant. However, the values for HS families were lower than those for parents (Table 7). The correlation between DM yield and CP was inconsistent across years. No r_g and r_a correlations were calculated in the combined analysis, because of negative values of genetic and family variance components (Table 7).

The correlations among heading date and quality traits were inconsistent, although any significant

https://doi.org/10.1017/S0021859607007332 Published online by Cambridge University Press

Table 4. *Summary of three estimates of heritability (±S.E.) broad-sense (h^2_b), narrow-sense (h^2_n) and parent-offspring (h^2_{OP}) heritability for yield and quality traits for parents and HS progenies analysis across 2 years*

h^2	Year	DM yield (g/plant)	Heading date (day)	Tiller number (1–5)	Digestibility (mg/g)	Carbohydrates (mg/g)	CP (mg/g)
h^2_b	2004	0·48±0·111	0·76±0·129	0·63±0·148	0·50±0·115	0·54±0·124	0·36±0·089
	2005	0·53±0·122	0·96±0·257	0·59±0·137	0·63±0·148	0·60±0·139	0·25±0·071
	Combined	0·49±0·188	0·69±0·228	0·37±0·201	0·41±0·196	0·50±0·204	0·00±0·193
h^2_n	2004	0·40±0·096	0·51±0·118	0·37±0·091	0·43±0·101	0·44±0·104	0·32±0·081
	2005	0·40±0·096	0·85±0·213	0·43±0·102	0·57±0·131	0·13±0·053	0·22±0·066
	Combined	0·20±0·145	0·40±0·186	0·34±0·165	0·00±0·213	0·23±0·138	0·00±0·133
h^2_{op}	2004	0·00±0·148	0·72±0·133	0·56±0·129	0·12±0·142	0·22±0·081	0·28±0·117
	2005	0·34±0·137	0·37±0·116	0·60±0·140	0·28±0·128	0·80±0·195	0·60±0·116
	Combined	0·10±0·136	0·34±0·128	0·79±0·129	0·18±0·119	0·62±0·125	0·46±0·111

Table 5. *Estimates of predicted selection response values per one cycle of selection for yield and quality traits for parents and HS progenies analysis across 2 years*

	Parents		HS families	
Traits	Values	Proportion of the mean	Values	Proportion of the mean
DM yield (g/plant)	5·75	0·04	9·26	0·05
Heading date (day)	3·44	0·09	2·25	0·06
Tiller number (1–5)	0·56	0·22	0·22	0·08
Digestibility (mg/g)	4·40	0·01	0·00	0·00
Carbohydrates (mg/g)	19·80	0·14	5·40	0·04
CP (mg/g)	7·70	0·05	0·00	0·00

values between heading date and DDM were positive (Table 7). Tiller number had positive relationship with DDM, but its relationship with CP was inconsistent. Estimates of additive correlation r_a between tiller number and WSC were also strongly positive and significant (Table 7). All the estimates of r_g and r_a between DDM and WSC were strongly positive and significant (Table 8). Genetic correlations among CP with both WSC and DDM were generally negative and some were significant. The r_e correlation for WSC *v*. CP was strong and negative for the first year and combined across years (Table 8).

DISCUSSION

The variations for DM yield, morphological and quality traits were always wider in parents than in HS families for all traits except CP. These differences between two generations are expected, since variation among parents is controlled by both additive and non-additive (dominant) genetic variance, whereas variation among HS families is only controlled by additive variance (Falconer & Mackay 1996). The mean of DM yield was relatively high for HS families. Jafari (1998) similarly detected higher DM yield in HS families of perennial ryegrass than those for parental clones and suggested that plants grown from clonal propagated tillers are less resistant to environmental hazards than those grown from seeds. In contrast, the average values of heading date, WSC and DDM were relatively high in parents compared with HS families. Since DM yield had negative relationships with both WSC and DDM (Table 8), this result might be expected.

Estimates of components of genetic variance (S^2_G) were significant in all cases except CP. The between-family variances (S^2_F) were significant only for heading date, tiller number and WSC, which suggests that additive genetic variance was the main component controlling these traits. Parent × year (S^2_{GY}) and family × year (S^2_{FY}) interaction effects were significant in all cases except WSC in HS families (Table 2). Marum *et al*. (1994) also found significant genotype × environment interactions for DDM in cocksfoot. In contrast, no significant genotype × environment interactions were found by Walters & Evans (1974) for DDM, Sanada *et al*. (2004) for WSC and Shenk & Westerhaus (1982) for CP. Buxton & Casler (1993), in a review, concluded that genotype × environment interactions should be smaller for forage quality than for DM yield and that quality traits might be relatively stable across environments. However, the results of the present study indicate the presence of genotype × environment interactions for DDM and

Table 6. *Phenotypic* (r_p), *genotypic* ($r_g \pm$ S.E., $r_a \pm$ S.E.) *and environmental* ($r_e \pm$ S.E.) *correlation coefficients among yield and morphological trait estimates from individual years and combined analysis across 2 years for parents and HS families*

Traits			DM yield (g/plant)			Heading date (day)		
			2004	2005	Combined	2004	2005	Combined
Heading date (day)	Parents	r_g	−0·33 ± 0·224	−0·45 ± 0·205	−0·40 ± 0·199			
		r_p	−0·38 ($P < 0·05$)	−0·43 ($P < 0·05$)	−0·34			
		r_e	−0·27 ± 0·132	−0·25 ± 0·131	−0·40 ± 0·135			
	HS	r_a	−0·21 ± 0·240	0·29 ± 0·213	0·02 ± 0·245			
		r_p	−0·27	0·25	−0·06			
Tiller number (1–5)	Parents	r_g	0·24 ± 0·224	0·84 ± 0·070	0·73 ± 0·165	−0·40 ± 0·203	−0·17 ± 0·206	−0·38 ± 0·164
		r_p	0·23	0·76 ($P < 0·01$)	0·66 ($P < 0·01$)	−0·36	−0·16	−0·33
		r_e	0·22 ± 0·132	0·35 ± 0·122	0·34 ± 0·123	−0·07 ± 0·138	−0·03 ± 0·139	−0·01 ± 0·138
	HS	r_a	0·29 ± 0·269	0·85 ± 0·100	0·69 ± 0·161	−0·05 ± 0·264	0·04 ± 0·227	0·15 ± 0·230
		r_p	0·27	0·77 ($P < 0·01$)	0·61 ($P < 0·01$)	−0·03	0·02	0·09

CP. When genetic × environment interactions are significant then evaluation prior to selection is more difficult. Ideally, more than one environment (e.g. years and locations) should be used to assess the breeding materials. The estimates of heritabilities based on combined analyses were lower than those for individual years (Table 4). Based on combined analyses, h^2_n and h^2_{op} for DM yield were effectively zero (Table 4). For DM yield, the results of h^2_n estimates were similar to those of Casler (1998) and Nguyen & Sleper (1983), but lower than those of Frandsen (1986) and Annicchiarico & Romani (2005), whose published data suggested that both additive and non-additive gene effects play an important role in the genetic regulation of DM yield. But in the present study, non-additive genetic variance is probably of greatest importance. For both heading date and tiller number, there was little difference between h^2_b and h^2_n, which suggests that genetic variations in these characteristics are controlled largely by additive gene action (Table 4).

Estimates of h^2_b for DDM were moderate, whereas h^2_n estimates were low and inconsistent, which suggest that genetic variation in this characteristic is controlled mainly by non-additive gene effects. This is in agreement with Beerepoot *et al*. (1994) and Marum *et al*. (1979) reported that both additive and dominance gene effects influence DDM. But Frandsen (1986) and Sleper *et al*. (1973) found that genetic variance for DDM was mainly additive. Estimates of h^2_b and h^2_{op} for WSC were moderate to high, whereas h^2_n estimates were low, suggesting that genetic variation in this trait is controlled by both additive and non-additive gene action. This is in agreement with Cooper (1962) and Grusea & Oprea (1994), who concluded that for WSC in cocksfoot, gene action was additive. However, in perennial ryegrass, Humphreys (1989*a*, *b*) found that WSC behaved as a complex polygenic trait, which was controlled mainly by non-additive gene effects. There was no significant variation for CP in either generation; the estimates of h^2_b and h^2_n values were low for individual years and they were effectively zero across years. The estimates of h^2_{op} based on regression analysis over 2 years, with two exceptions, were always higher than h^2_n estimated from variance components. This is in agreement with Vogel *et al*. (1980), who suggested that h^2_{op} would be overestimated if the parents and offspring shared the same plot. Therefore, they proposed that the regression of offspring in one replication and parents in another replication would remove such bias.

The expected genetic gains for phenotypic parental selection were higher than those for HS families, except DM yield. Based on the present findings, clonal evaluation appeared to be adequate to select parents for highly heritable characteristics, such as morphological and quality traits. Similar results for DM yield, were obtained by Pavetti *et al*. (1994), who

https://doi.org/10.1017/S0021859607007332 Published online by Cambridge University Press

Table 7. *Phenotypic* (r_p), *genotypic* ($r_g \pm$ S.E., $r_a \pm$ S.E.) *and environmental* ($r_e \pm$ S.E.) *correlation coefficients among yield, morphological and three quality traits: content of DDM, WSC and CP estimates from combined analysis of variance and covariance for parents and HS families across 2 years. P values* $>0{\cdot}05$ *are not included*

			DM yield (g/plant)			Heading date (day)			Tiller number (1–5)		
Traits			2004	2005	Combined	2004	2005	Combined	2004	2005	Combined
DDM (mg/g)	Parents	r_g	$-0{\cdot}30 \pm 0{\cdot}244$	$-0{\cdot}33 \pm 0{\cdot}232$	$-0{\cdot}30 \pm 0{\cdot}227$	$-0{\cdot}29 \pm 0{\cdot}212$	$0{\cdot}40 \pm 0{\cdot}177$	$0{\cdot}13 \pm 0{\cdot}211$	$0{\cdot}49 \pm 0{\cdot}204$	$0{\cdot}21 \pm 0{\cdot}216$	$0{\cdot}27 \pm 0{\cdot}211$
		r_p	$-0{\cdot}24$	$-0{\cdot}31$	$-0{\cdot}29$	$-0{\cdot}26$	$0{\cdot}38$ ($P<0{\cdot}05$)	$0{\cdot}06$	$0{\cdot}41$ ($P<0{\cdot}05$)	$0{\cdot}19$	$0{\cdot}25$
		r_e	$0{\cdot}02 \pm 0{\cdot}138$	$-0{\cdot}19 \pm 0{\cdot}137$	$-0{\cdot}18 \pm 0{\cdot}135$	$-0{\cdot}08 \pm 0{\cdot}138$	$0{\cdot}01 \pm 0{\cdot}139$	$-0{\cdot}04 \pm 0{\cdot}139$	$-0{\cdot}01 \pm 0{\cdot}139$	$0{\cdot}03 \pm 0{\cdot}139$	$0{\cdot}07 \pm 0{\cdot}138$
	HS	r_a	$-0{\cdot}04 \pm 0{\cdot}271$	$-0{\cdot}17 \pm 0{\cdot}248$	$-0{\cdot}34 \pm 0{\cdot}261$	$0{\cdot}28 \pm 0{\cdot}239$	$-0{\cdot}30 \pm 0{\cdot}201$	$0{\cdot}01 \pm 0{\cdot}222$	$0{\cdot}31 \pm 0{\cdot}227$	$0{\cdot}20 \pm 0{\cdot}237$	$0{\cdot}17 \pm 0{\cdot}243$
		r_p	$-0{\cdot}03$	$-0{\cdot}15$	$-0{\cdot}18$	$0{\cdot}23$	$-0{\cdot}22$	$-0{\cdot}18$	$0{\cdot}28$	$0{\cdot}17$	$0{\cdot}13$
WSC (mg/g)	Parents	r_g	$-0{\cdot}56 \pm 0{\cdot}184$	$-0{\cdot}37 \pm 0{\cdot}216$	$-0{\cdot}51 \pm 0{\cdot}183$	$-0{\cdot}32 \pm 0{\cdot}196$	$0{\cdot}32 \pm 0{\cdot}186$	$0{\cdot}03 \pm 0{\cdot}203$	$0{\cdot}54 \pm 0{\cdot}209$	$0{\cdot}12 \pm 0{\cdot}221$	$0{\cdot}24 \pm 0{\cdot}209$
		r_p	$-0{\cdot}49$ ($P<0{\cdot}01$)	$-0{\cdot}35$	$-0{\cdot}45$ ($P<0{\cdot}01$)	$-0{\cdot}29$	$0{\cdot}31$	$0{\cdot}09$	$0{\cdot}45$ ($P<0{\cdot}05$)	$0{\cdot}08$	$0{\cdot}21$
		r_e	$-0{\cdot}14 \pm 0{\cdot}135$	$-0{\cdot}21 \pm 0{\cdot}135$	$-0{\cdot}29 \pm 0{\cdot}132$	$0{\cdot}03 \pm 0{\cdot}139$	$0{\cdot}09 \pm 0{\cdot}138$	$0{\cdot}26 \pm 0{\cdot}135$	$-0{\cdot}12 \pm 0{\cdot}138$	$-0{\cdot}07 \pm 0{\cdot}139$	$-0{\cdot}12 \pm 0{\cdot}137$
	HS	r_a	$-0{\cdot}17 \pm 0{\cdot}260$	$0{\cdot}09 \pm 0{\cdot}265$	$-0{\cdot}11 \pm 0{\cdot}259$	$-0{\cdot}20 \pm 0{\cdot}243$	$0{\cdot}01 \pm 0{\cdot}229$	$0{\cdot}11 \pm 0{\cdot}230$	$0{\cdot}33 \pm 0{\cdot}207$	$0{\cdot}52 \pm 0{\cdot}215$	$0{\cdot}48 \pm 0{\cdot}211$
		r_p	$-0{\cdot}16$	$0{\cdot}07$	$-0{\cdot}09$	$-0{\cdot}16$	$0{\cdot}01$	$0{\cdot}02$	$0{\cdot}25$	$0{\cdot}39$ ($P<0{\cdot}01$)	$0{\cdot}38$ ($P<0{\cdot}05$)
CP (mg/g)	Parents	r_g	$0{\cdot}07 \pm 0{\cdot}244$	$0{\cdot}39 \pm 0{\cdot}197$	*	$0{\cdot}23 \pm 0{\cdot}213$	$-0{\cdot}16 \pm 0{\cdot}215$	*	$-0{\cdot}30 \pm 0{\cdot}214$	$0{\cdot}37 \pm 0{\cdot}207$	*
		r_p	$0{\cdot}05$	$0{\cdot}32$	$0{\cdot}27$	$0{\cdot}20$	$-0{\cdot}14$	$-0{\cdot}09$	$-0{\cdot}26$	$0{\cdot}35$	$-0{\cdot}05$
		r_e	$-0{\cdot}04 \pm 0{\cdot}138$	$0{\cdot}07 \pm 0{\cdot}137$	$0{\cdot}04 \pm 0{\cdot}139$	$-0{\cdot}07 \pm 0{\cdot}138$	$0{\cdot}00 \pm 0{\cdot}139$	$-0{\cdot}07 \pm 0{\cdot}139$	$-0{\cdot}02 \pm 0{\cdot}139$	$0{\cdot}21 \pm 0{\cdot}131$	$0{\cdot}07 \pm 0{\cdot}139$
	HS	r_a	$0{\cdot}02 \pm 0{\cdot}276$	$0{\cdot}45 \pm 0{\cdot}252$	*	$0{\cdot}13 \pm 0{\cdot}255$	$0{\cdot}08 \pm 0{\cdot}243$	*	$0{\cdot}17 \pm 0{\cdot}279$	$0{\cdot}46 \pm 0{\cdot}230$	*
		r_p	$0{\cdot}01$	$0{\cdot}33$	$0{\cdot}14$	$0{\cdot}11$	$0{\cdot}06$	$0{\cdot}05$	$0{\cdot}14$	$0{\cdot}35$	$0{\cdot}16$

* Mean square (MS) of one or both traits was not significant.

Table 8. *Phenotypic* (r_p), *genotypic* ($r_g \pm$ *S.E.*, $r_a \pm$ *S.E.*) *and environmental* ($r_e \pm$ *S.E.*) *correlation coefficients among content of DDM, WSC and CP estimates from individual years and combined analysis across 2 years for parents and HS families*

			DDM (mg/g)			WSC (mg/g)		
Traits			2004	2005	Combined	2004	2005	Combined
WSC (mg/g)	Parents	r_g	0·81 ± 0·111	0·76 ± 0·073	0·98 ± 0·051			
		r_p	0·70 ($P < 0·01$)	0·75 ($P < 0·01$)	0·79 ($P < 0·01$)			
		r_e	0·12 ± 0·137	0·59 ± 0·086	0·40 ± 0·117			
	HS	r_a	0·48 ± 0·215	0·70 ± 0·125	0·96 ± 0·108			
		r_p	0·43 ($P < 0·05$)	0·65 ($P < 0·01$)	0·74 ($P < 0·01$)			
CP (mg/g)	Parents	r_g	−0·66 ± 0·131	0·10 ± 0·231	*	−0·77 ± 0·100	−0·19 ± 0·223	*
		r_p	−0·56 ($P < 0·05$)	0·11	−0·52 ($P < 0·05$)	−0·74 ($P < 0·01$)	−0·16	−0·53 ($P < 0·05$)
		r_e	−0·03 ± 0·139	0·24 ± 0·131	0·46 ± 0·135	−0·54 ± 0·100	−0·04 ± 0·139	−0·30 ± 0·126
	HS	r_a	0·39 ± 0·248	0·20 ± 0·255	*	−0·36 ± 0·240	−0·12 ± 0·276	*
		r_p	0·29	0·15	0·12	−0·32	−0·15	−0·32

* Mean square (MS) of one or both traits was not significant.

suggested that progress with selection for improved herbage and DM yield is likely to be slow.

The results of the correlation analysis indicated general agreement in both sign and magnitude between genotypic and phenotypic correlations. This suggests that for all traits, genetic and phenotypic correlations have similar effects. In a comparison of the estimates of r_a and r_g, the results showed that where r_g or r_a values were considered to be significant, the relevant generation had the same sign; otherwise they were not significant. With few exceptions, r_e values were always small and not significant. This indicates that the phenotypic association for all other pair-wise combinations of traits measured on parental clones was due to genetic rather than environmental factors.

Genetic correlations between DM yield and heading date were strongly negative, similar to the findings of Martiniello (1998) and Kanapeckas *et al.* (2005). Both r_a and r_g correlations were positive and significant for DM yield with tiller number. This result was not unexpected because tiller number is a yield component. Heading date had a strong negative r_g correlation with tiller number. These results suggest that selection of early flowering accessions would lead to more tillers and increased DM yield in cocksfoot. All the estimates of r_g and r_a between DM yield *v.* DDM were generally negative but not significant. However, the values for HS families were lower than those for parents (Table 7). The negative correlation between DDM and DM yield has also been reported for cocksfoot (Brown & Blaser 1970; Marum *et al.* 1994). However, in contrast, some published data suggest that DDM is largely independent of DM yield (Frandsen 1986; Humphreys 1989*b*). The results from the current study do not agree with these conclusions and instead indicate a weak negative relationship between these traits. The r_g estimates for DM yield *v.* WSC were consistently negative, but the r_a values were inconsistent (Table 7). Brown & Blaser (1970) and Sanada *et al.* (2004) in cocksfoot, and Jafari *et al.* (2003*a*) and Marais *et al.* (2003) in ryegrass, found inconsistent relationships between these two traits, although significant values were generally positive. In the present study, the values of r_a are in agreement with those reported in the above publications, but the r_g obtained from analysis of parents indicate a weak negative relationship between these traits. The correlation between DM yield and CP was inconsistent for individual years, whereas, based on combined analysis because of negative values of genetic and family variance components, no r_g and r_a correlations were calculated (Table 7). Low and inconsistent relationships between these two traits have also been reported by Lamb *et al.* (1984) and Ray *et al.* (1996). In contrast, Jafari *et al.* (2003*a*) and Humphreys (1989*b*) in perennial ryegrass obtained negative correlations between these two traits under

https://doi.org/10.1017/S0021859607007332 Published online by Cambridge University Press

sward conditions. The latter author suggested that this negative relationship may be inconsistent where nitrogen availability is low.

The correlations between heading date and quality traits were inconsistent, although significant values between heading date and DDM were positive (Table 7). Hacker (1982), in a review, suggested that the correlations between heading date and quality traits are highly variable and depend on date of sampling and regrowth interval. Breese & Davies (1970) suggested that selection for high digestibility in cocksfoot was accompanied by faster growth rate and earlier heading date. The present results were in agreement with Quesenberry *et al.* (1978), who found significant positive correlation between digestibility and ear emergence date. However, when their comparisons were made at the same morphological stage of growth, early flowering types were usually more digestible. In this investigation, the relationships between heading date and WSC were inconsistent, although Sanada *et al.* (2004) found positive correlation between heading date and WSC in cocksfoot.

Tiller number had positive relationship with DDM, but its relationship with CP were inconsistent. Estimates of additive correlation r_a between tiller number and WSC were strong, positive and significant (Table 7). This positive correlation between DDM and tiller number was in agreement with results previously reported for spaced plants (Clements 1973; Humphreys 1989*c*). The positive estimates for spaced plants may be associated with the absence of competition under the present growth environment, where genotypes with large tillers (thicker stems) have high yield and such tillers also have high digestibility and low lignified vascular tissue (Ehlke & Casler 1985).

All the estimates of r_g and r_a for the relationship of DDM with WSC were strongly positive and significant (Table 8). Since WSC is completely digestible, a positive correlation between these two parameters is expected and is in agreement with Jafari *et al.* (2003*a*) and Humphreys (1989*b*) in perennial ryegrass. The r_g and r_p estimates between DDM and CP were negative and significant in the first year. But the r_a values were inconsistent and not significant (Table 8). Reports from the literature for a relationship between these two traits are inconsistent. The present results are in agreement with Jafari *et al.* (2003*a*) and Humphreys (1989*c*), who reported a strong negative relationship, whereas Frandsen (1986) and Marum *et al.* (1979) found positive correlations between the two traits. Radojevic *et al.* (1994) concluded that relationships between these two traits are strongly influenced by environmental effects such as drought, light intensity and nitrogen level during the growing season. The relationships between WSC and CP were generally negative and some r_g and r_p values were significant (Table 8). The r_e correlation was strongly negative in the first year and when combined across years, which suggested that the relationship between these traits is affected by environmental factors as well as by correlated genetic effects. Such environmentally induced effects have also been reported by Humphreys (1989*c*), who suggested that as growth increases with rapid uptake of nitrogen fertilizer, increase of CP and decrease of WSC content are environmentally induced effects.

It was concluded that genotype × year interactions were present for all traits except WSC in HS families, suggesting that more than one environment should be used to assess the breeding material. The results of analyses showed that the estimates of h^2_b were always larger than either h^2_n or h^2_{op}, indicating that some non-additive variance was present in almost all analyses. For DDM and WSC, the h^2_b estimates were relatively high, whereas the h^2_n and h^2_{op} estimates were low to moderate, indicating that both additive and non-additive effects were important in controlling the expression of this trait. With few exceptions, the value of h^2_{op} was more than that of h^2_n, indicating that narrow-sense heritability estimated from parents/offspring might be an overestimate. The h^2_b estimates for DM yield were moderate, whereas the h^2_n and h^2_{op} estimates were negligible, indicating that non-additive effects were important in controlling expression of this trait. Thus, to improve DM yield, recurrent selection based on progeny testing should be effective. The h^2_n and h^2_{op} estimates for heading date and tiller number were relatively high, about the same magnitude as h^2_b, which suggested that additive genetic variance was the main component controlling these traits and that response to selection would be likely.

The weak negative correlation between DDM and total DM yield indicates that combined selection for both DDM and DM yield should elicit a response. Selection for DDM alone could result in reduction in yield. Given the relationship between WSC, CP, DM yield and DDM, it is tempting to suggest that selection for high WSC is a means to improve quality in general. Beerepoot & Agnew (1997) have argued that this simple approach may not result in improved herbage quality because of possible negative effects on rumen pH. There is, however, indirect evidence that higher WSC in ryegrass may result in improved animal performance. On the basis of the present results, it is suggested that increased WSC, when CP is in excess, would improve herbage quality.

The study was part of a project for developing improved grass varieties (code: 1-016-11-7901). We thank Dr M. H. Assareh, Head of Research Institute of Forests and Rangelands that funded this research and Dr H. M. Arefi, Head of Iranian Natural Resource Gene Bank that provided seed samples.

REFERENCES

Annicchiarico, P. & Romani, M. (2005). Genetic variation, heritability and genetic correlation for forage quality and yield traits of Mediterranean tall fescue germplasm. *Plant Breeding* **124**, 99–101.

Becker, W. A. (1984). *Manual of Quantitative Genetics*, 4th edn. Pullman, WA: Academic Enterprises.

Beerepoot, L. J. & Agnew, R. E. (1997). Breeding for improved herbage quality in perennial ryegrass. In *Seeds of Progress* (Ed. J. R. Weddell), pp. 135–145. Occasional Symposium of the British Grassland Society, Vol. 31

Beerepoot, L. J., Bouter, W. & Dijkstra, J. A. (1994). Breeding for improved digestibility in perennial ryegrass. In *Breeding for Quality: Proceeding of the 19th EUCARPIA Fodder Crops Section Meeting, Brugge, Belgium, 5–8 October 1994* (Eds D. Reheul & A. Ghesquière), pp. 237–245. Wageningen, The Netherlands: EUCARPIA.

Beever, D. E. & Reynolds, C. K. (1994). Forage quality, feeding value and animal performance. In *Grassland and Society: Proceedings of the 15th EUCARPIA General Meeting of the European Grassland Federation, 6–9 June 1994* (Eds L.'t Mannetje & J. Frame), pp. 48–60. Wageningen, The Netherlands: Wageningen Pers.

Breese, E. L. & Davies, W. E. (1970). Selection for factors affecting nutritive value. In *Jubilee Report of the Welsh Plant Breeding Station 1919–1969*, pp. 33–35. Aberystwyth, Wales, UK: Welsh Plant Breeding Station.

Brown, R. H. & Blaser, R. E. (1970). Soil moisture and temperature effects on growth and soluble carbohydrates of orchardgrass (*Dactylis glomerata* L.). *Crop Science* **10**, 213–216.

Buxton, D. R. & Casler, M. D. (1993). Environmental and genetic effects on cell wall composition and digestibility. In *Forage Cell Wall Structure and Digestibility* (Eds H. G. Jung, D. R. Buxton, R. D. Hatfield & J. Ralph), pp. 685–714. Madison, WI: American Society of Agronomy.

Carlier, L. (1994). Breeding forage quality, feeding value and animal performance. In *Breeding for Quality: Proceeding of the 19th EUCARPIA Fodder Crops Section Meeting, Brugge, Belgium, 5–8 October 1994* (Eds D. Reheul & A. Ghesquière), pp. 25–27. Wageningen, The Netherlands: EUCARPIA.

Casler, M. D. (1998). Genetic variation within eight populations of perennial forage grasses. *Plant Breeding* **117**, 243–249.

Christie, R. B. & Mowat, D. N. (1968). Variability in *in vitro* digestibility among clones of brome grass and orchard grass. *Canadian Journal of Plant Science* **48**, 67–73.

Clements, R. J. (1973). Breeding for improved nutritive value of *Phalaris tuberosa* herbage: an evaluation of alternative sources of genetic variation. *Australian Journal of Agricultural Research* **24**, 21–34.

Connolly, V., do Valle Ribeiro, M. & Crowley, J. G. (1977). Potential of grass and legume cultivars under Irish conditions. In *Proceedings of the International Meeting on Animal Production from Temperate Grassland, Dublin, June 1977* (Ed. B. Gilsenan), pp. 23–28.

Cooper, J. P. (1962). Selection for nutritive value. In *Report of the Welsh Plant Breeding Station for 1961*, pp. 145–156.

Cooper, J. P. (1973). Genetic variation in herbage constituents. In *Chemistry and Biochemistry of Herbage*, Vol. 2 (Eds G. W. Butler & R. W. Bailey), pp. 379–417. London: Academic Press.

Dickerson, G. E. (1969). Techniques for research in quantitative animal genetics. In *Techniques and Procedures in Animal Production Research* (Ed. A. B. Chapman), pp. 36–79. New York: American Society of Animal Science.

Ehlke, N. J. & Casler, M. D. (1985). Anatomical characteristics of smooth bromegrass clones selected for *in vitro* dry matter digestibility. *Crop Science* **25**, 513–517.

Falconer, D. S. & Mackay, T. F. C. (1996). *Introduction to Quantitative Genetics*, 4th edn. London: Longman.

Frandsen, K. J. (1986). Variability and inheritance of digestibility in perennial ryegrass (*Lolium perenne*), meadow fescue (*Festuca pratensis*), and cocksfoot (*Dactylis glomerata* L.). II. F1 and F2 progeny. *Acta Agriculturae Scandinavica* **36**, 241–263.

Grusea, A. & Oprea, G. (1994). Variation and inheritance of quality of *Dactylis glomerata* varieties which were obtained by different breeding methods. In *Breeding for Quality: Proceeding of the 19th EUCARPIA Fodder Crops Section Meeting, Brugge, Belgium, 5–8 October 1994* (Eds D. Reheul & A. Ghesquière), pp. 145–149. Wageningen, The Netherlands: EUCARPIA.

Hacker, J. B. (1982). Selecting and breeding better quality grasses. In *Nutritional Limits to Animal Production from Pasture Proceedings of an International Symposium, Queensland, August 1981, Australia* (Ed. J. B. Hacker), pp. 305–326. Farnham, Surrey, UK: Commonwealth Agricultural Bureaux.

Hill, R. R. & Leath, K. T. (1975). Genotypic and phenotypic correlations for reaction of five foliar pathogens in alfalfa. *Theoretical and Applied Genetics* **45**, 254–258.

Humphreys, M. O. (1989*a*). Water soluble carbohydrates in perennial ryegrass breeding. II. Cultivar and hybrid progeny performance in cut plot. *Grass and Forage Science* **44**, 237–244.

Humphreys, M. O. (1989*b*). Water-soluble carbohydrates in perennial ryegrass breeding. III. Relationships with herbage production, digestibility and crude protein content. *Grass and Forage Science* **44**, 423–430.

Humphreys, M. O. (1989*c*). Assessment of perennial ryegrass (*Lolium perenne* L.) for breeding. II. Components of winter hardiness. *Heredity* **41**, 99–106.

Jafari, A. (1998). *Genetic analysis of yield and quality in perennial ryegrass* (Lolium perenne *L.*). Ph.D. thesis, Department of Crop Science, Horticulture and Forestry, University College Dublin, Ireland.

Jafari, A., Connolly, V. & Walsh, E. J. (2003*a*). Genetic analysis of yield and quality in full sib families of perennial ryegrass (*Lolium perenne* L.) under two cutting managements. *Irish Journal of Agricultural and Food Research* **42**, 275–292.

Jafari, A., Connolly, V., Frolich, A. & Walsh, E. J. (2003*b*). A note on estimation of quality parameters in perennial ryegrass by near infrared reflectance spectroscopy. *Irish Journal of Agricultural and Food Research* **42**, 293–299.

Kanapeckas, J., Tarakanovas, P. & Lemežienė, N. (2005). Variability, heritability and correlations of genetic resources in meadow fescue. *Biologija* **3**, 10–14.

Lamb, J. F. S., Vogel, K. P. & Reece, P. E. (1984). Genotype and genotype × environment interaction effects

on forage yield and quality of crested wheatgrass. *Crop Science* **24**, 559–564.

Marais, J. P., Goodenough, D. C. W., De Figueiredo, M. & Hopkins, C. (2003). The development of a *Lolium multiflorum* cultivar with low moisture content and an increased readily digestible energy to protein ratio. *Australian Journal of Agricultural Research* **54**, 101–106.

Martiniello, P. (1998). Influence of agronomic factors on the relationship between forage production and seed yield in perennial forage grasses and legumes in a Mediterranean environment. *Agronomie* **18**, 591–601.

Marum, P., Hovin, A. W., Marten, G. C. & Shenk, J. S. (1979). Genetic variability for cell wall constituents and associated quality traits in reed canarygrass. *Crop Science* **19**, 355–360.

Marum, P., Rognli, O. A., Aastveit, A. H. & Aastveit, K. (1994). Improved digestibility and protein content as breeding problems in Norwegian timothy (*Phleum pratense* L.) and cocksfoot (*Dactylis glomerata* L.). In *Breeding for Quality: Proceeding of the 19th EUCARPIA Fodder Crops Section Meeting, Brugge, Belgium, 5–8 October 1994* (Eds D. Reheul & A. Ghesquière), pp. 137–141. Wageningen, The Netherlands: EUCARPIA.

Nguyen, H. T. & Sleper, D. A. (1983). Genetic variability of seed yield and reproductive characters in tall fescue. *Crop Science* **23**, 621–626.

Niaky, S. (1995). *Land Grass Cover of Iran* (in Persian). Ahwaz, Iran: Chamran University Press.

Pavetti, D. I. T., Sleper, D. A., Roberts, C. A. & Krause, G. F. (1994). Genetic variation and relationship of quality traits between herbage and seed of tall fescue. *Crop Science* **34**, 427–431.

Quesenberry, K. H., Sleper, D. A. & Cornell, J. A. (1978). Heritability and correlation of IVDMD, maturity and plant height in Rhodes grass. *Crop Science* **18**, 847–849.

Radojevic, I., Simpson, R. J., St. John, J. A. & Humphreys, M. O. (1994). Chemical composition and *in vitro* digestibility of lines of *Lolium perenne* selected for high concentrations of water soluble carbohydrate. *Australian Journal of Agricultural Research* **45**, 901–912.

Ray, I. M., Karn, J. F. & Dara, S. T. (1996). Heritabilities of nutritive quality factors and interrelationships with yield in tetraploid crested wheatgrass. *Crop Science* **36**, 1488–1491.

Rechinger, K. H. (1970). *Flora Iranica*. No. 70. Graz, Austria: Akademische Druck und Verlagsanstalt.

Sanada, Y., Takai, T. & Yamada, T. (2004). Genetic variation in water-soluble carbohydrate concentration in diverse cultivars of *Dactylis glomerata* L. during vegetative growth. *Australian Journal of Agricultural Research* **55**, 1183–1187.

Shenk, J. S. & Westerhaus, M. O. (1982). Selection for yield and quality in orchardgrass. *Crop Science* **22**, 422–425.

Sleper, D. A., Drolsom, P. N. & Jorgensen, N. A. (1973). Breeding for improved dry matter digestibility in smooth bromegrass (*Bromus inermis* Leyss.). *Crop Science* **13**, 556–558.

Smith, K. F., Reed, K. F. M. & Foot, J. Z. (1997). An assessment of relative importance of specific traits for the genetic improvement of nutritive value in dairy pasture. *Grass and Forage Science* **52**, 167–175.

Steel, R. G. D. & Torrie, J. H. (1980). *Principles and Procedures of Statistics: A Biometrical Approach*, 2nd edn. London: McGraw-Hill Book Company.

Vogel, K. P., Haskins, F. A. & Gorz, H. J. (1980). Parent-progeny regression in indiangrass: inflation of heritability estimates by environmental covariances. *Crop Science* **20**, 580–582.

Wheeler, J. L. & Corbett, J. L. (1989). Criteria for breeding forages of improved feeding value: results of a Delphi survey. *Grass and Forage Science* **44**, 77–83.

Walters, R. J. K. & Evans, E. M. (1974). *Digestibility and Voluntary Intake of Be-6393 Cocksfoot*. Report of Welsh Plant Breeding Station for 1973, pp. 43–44. Aberystwyth, UK: Welsh Plant Breeding Station.