Theor Appl Genet (1991) 81:253–264

Genetic variation and covariation in a population of tetraploid *Dactylis* L. accessions

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Received January 10, 1990; Accepted July 25, 1990
Communicated by A. R. Hallauer

Summary. Efficient utilization of divergent germ plasm sources in breeding cultivated *Dactylis glomerata* L. ssp. *glomerata* Domin depends on knowledge of quantitative variation within and among accessions. This study was undertaken to quantify variation and covariation for forage yield, maturity, disease reaction, and ground cover within a population of tetraploid *Dactylis* accessions. Variation was observed among families within the population for each variable. Most genetic variation (73%–93% of the family sums of squares) was within country sources or within accessions. Thus, country boundaries, which are traditionally important factors used in defining limits of plant exploration expeditions, have limited expected use in targeting future exploration for specific sources of high yield, disease resistance, or ground cover. Maturity was the exception to this; late-maturing accessions were identified as originating exclusively from the USSR. Some relationships among traits, such as that for yield and disease reaction, differed for accessions and cultivars. Several accessions and families within accessions were identified to have performance superior to most or all cultivars included in this study. Existing germ plasm from several countries was identified to have potential in breeding orchardgrass, while that from other countries appeared to have little or no potential in supplying germ plasm for hay production in humid-temperate environments.

Key words: Germ-plasm evaluation – Germ-plasm preservation – Grass breeding

Introduction

Cultivated orchardgrass (*Dactylis glomerata* L. ssp. *glomerata* Domin) is a polysomic polyploid with $2n = 4x = 28$ (Müntzing 1937; Myers 1941). Evidence of tetrasomic inheritance suggests that this subspecies behaves generally as an autotetraploid (Lumaret 1988, Myers 1940, Tajimi 1974). Maximizing heterozygosity in autotetraploids is important in maximizing the performance of vigor-related traits (Bingham 1979). In natural collections of orchardgrass, high levels of polymorphism have been implicated in conditioning tolerance to aridity (Roy and Lumaret 1987) and widely fluctuating environmental conditions (Lumaret 1984), as well as conferring greater vigor and reproductive fitness to individuals (Lumaret 1984).

Germ plasm improvement in orchardgrass is based largely on recurrent selection or pedigree-type selection systems for phenotypic performance or general combining ability effects. Genotypes with superior performance per se or breeding value are polycrossed to create a synthetic cultivar. A major disadvantage of synthetic cultivars is that, for non-inbred parents, they tend to maximize heterozygosity in the Syn-1 generation (Busbice 1969), resulting in loss of vigor with generation advance (Busbice and Gurgis 1976). Inbreeding during generation advance becomes more severe with small numbers of parents (Busbice 1969). Thus, synthetic cultivars with relatively small numbers of parents do not favor preservation of individual polymorphism. While single- or double-cross hybrids would favor this genetic condition, economic limitations and lack of research efforts have prevented the development of viable hybrid cultivars.

Given the limitations of synthetic cultivars, the best parents are those with high mean performance and an ability to maintain vigor during inbreeding. Maximizing polymorphism of individual progenies in advanced synthetic generations can be done by ensuring maximum allelic diversity within the parental generation. Gilmore

(1969) suggested that synthetic cultivar performance is a function of allele frequencies, but not the level of inbreeding of the parents. Without selection during seed multiplication, parental alleles will be preserved and recombined into favorable tri- and tetra-allelic combinations. Based on current theories (Lumaret 1984, 1988), polymorphic parents can be identified presumably by superior phenotypic performance under widely fluctuating environmental conditions or by their superior performance in a wide range of environments. Tolerance to inbreeding can be identified by paired evaluations of parents and inbred progeny (Kalton et al. 1952), or by selection during inbreeding (Pfeiffer and Bingham 1983). Identification of genetically diverse parents could be done by one or more of four imperfect methods: (1) a sophisticated single-cross or topcross evaluation system meant to identify specific combining ability patterns, and requiring an extreme amount of hybridization and evaluation efforts, which may not be cost-beneficial if nonadditive genetic effects are small, as was observed in alfalfa, *Medicago sativa* L. (Hill et al. 1972); (2) isoenzyme analysis, which may fail due to unknown or nonexistant linkages between isoenzyme loci and quantitative trait loci; (3) restriction fragment length polymorphism analysis, which is based on structural DNA fragments in lieu of functional DNA segments and requires development of a detailed linkage map to accurately predict the number of polymorphisms for a trait; and (4) pedigree, typically a subjective judgement based on climate, geography, and phenotype.

Pedigree has historically been the only criterion used to judge parental diversity for orchardgrass synthetic cultivars. It is generally assumed that parents from diverse geographic or climatic locales are indeed genetically diverse. However, isoenzyme analysis suggests that 73%–79% of the genetic variation in wild, tetraploid *Dactylis* is contained within interbreeding populations (Lumaret 1985). This contrasts with wild diploids, for which only 38%–48% of genetic variation is within populations, while 50%–60% is between subspecies. Lumaret (1985) concluded that genetic variation which is scattered among the diploid subspecies has been concentrated within tetraploid subspecies. Polyploidy further serves to maintain high levels of genetic variation within localized populations. Lumaret (1985), advancing the speculations of Borrill (1978) and Stebbins and Zohary (1959), suggested that hybridization between diverse diploids led to autopolyploidization along diploid-diploid boundaries, followed by intercrossing of newly formed tetraploids to create populations with high internal genetic diversity. Finally, there is some evidence to suggest that tetraploid populations are beginning to differentiate (Borrill 1961; Guignard 1985; Lumaret 1988), as has been postulated to have occurred at the diploid level over 20 million years ago, during the Miocene epoch of the Tertiary period (Borrill 1978; Lumaret 1988; Stebbins and Zohary 1959). Ecotypic differentiation and evolution of new tetraploid forms (or even subspecies) should, due to genetic inertia, be a slower process in tetraploids than in diploids, requiring perhaps several hundred thousand more years to achieve a degree of interpopulation or intersubspecific diversity similar to that seen among diploid subspecies. Because tetraploids are more readily adaptable to disturbed areas (Lumaret et al. 1987), this process may have been hastened by human influences.

The objectives of this study were to (1) characterize the quantitative genetic variation in a collection of tetraploid *Dactylis,* and (2) to identify the extent to which geographic information might be useful in predicting breeding value of introduced *Dactylis* genotypes.

Materials and methods

Germ plasm

A total of 250 *Dactylis glomerata* L. accessions were selected at random from the US Department of Agriculture, National Plant Germplasm System collection. Twenty-two of these accessions belonged to the subspecies *hispanica*, while the remainder were the most common, tetraploid subspecies *glomerata*. Eighteen plants of each accession were grown in the greenhouse until they were 8 weeks old, then transplanted to the field in April 1981. The 18 plants of each accession were divided into three sets of 6 plants each. Thus, each complete set consisted of 6 plants from each of 252 accessions. The three sets were transplanted in isolation (at least 300 m) from each other and from other sources of *Dactylis*. The three sets were planted at Arlington, Wisconsin, USA (43°20′N, 89°23′W) into a Plano silt loam soil (fine-silty, mixed, mesic, Typic Argiudoll).

Plant spacings were 0.5 m in each direction. The space between each plant was bisected by seeding a single row of a topcross pollinator in perpendicular directions. Each of the three sets received a different topcross parent: 'Chinook', 'Potomac', or 'WO-1', the latter a Wisconsin experimental population. The three nurseries were clipped twice in 1981 and three times in 1982 to control annual weeds and to simulate a normal hay production management. Plots were fertilized with 56 kg N ha^{-1} in early spring and mid-summer of 1981 and 1982 and once in the early spring of 1983. All surviving transplants and rows of the topcross pollinators were allowed to produce seed in 1983. Random panicle counts indicated that, for each topcross nursery, average panicle composition was approximately 60% topcross tester/40% experimental spaced plants. Of the initial 4,536 transplants, approximately 66% were alive and produced at least one panicle in 1983. Seed from each plant was threshed, cleaned, and weighed.

Due to low panicle production, caused by winter injury, most surviving spaced plants did not produce enough seed for replicated progeny testing in seeded plots. Only 448 maternal plants (15% of those producing at least one panicle) yielded ≥ 8 g clean seed, which was the quantity required to establish four plots of each family. Of the 448 families, which represented 164 of the original 252 accessions, 227 came from the 'Chinook' nursery, 150 from the 'Potomac' nursey, and 71 from the 'WO-1' nursery.

Progeny test

The progeny test was seeded at Marshfield, Wisconsin (44°40′N, 90°10′W) on a Withee silt loam (fine-loamy, mixed, frigid, Aeric

Glossoboralf) and at Arlington in April 1986. Before planting, the 448 families were divided randomly into 24 sets with 14–20 families per set. There were 12 sets of 'Chinook' progenies, 8 sets of 'Potomac' progenies, and 4 sets of 'WO-1' progenies. The experimental design was a randomized complete block with two replicates per location, but with a randomization restriction within each complete block. Each set of families was restricted to an incomplete block of 20 plots; for those sets with fewer than 20 families, the remainder of the plots within the incomplete block were seeded with cultivars. Thirteen cultivars in total were used to fill in the remaining plots. Each cultivar as replicated two, four, or six times per location (i.e., one, two, or three times per complete block). Cultivars were selected at random from the population of North American cultivars. Plots measured 0.9×1.5 m, and consisted of five drilled rows; the rows were 15 cm apart. The seeding rate was 14.3 kg ha^{-1} for all entries.

Plots at both locations were clipped twice in 1986 to control annual weeds, and were fertilized with 56 kg N ha^{-1} after each cutting. Plots were fertilized with 112 kg N ha^{-1} in the spring of 1987 and 1988, after the first cutting in both years, and after the second cutting in 1987. Fertilization with P and K was according to soil test recommendations.

Forage from each plot was harvested with a flail-type harvester for three cuttings in 1987 and two cuttings in 1988 (there was no third cutting in 1988 due to drought). The fresh weight of each plot at each cutting was adjusted to a dry weight basis by using an average dry matter content from 15 forage samples per complete block. Maturity at first cutting was determined immediately prior to harvesting, using the 1 to 8 scale of Casler (1988). Leaf disease reaction was rated on the 1987 third cutting standing forage using a scale of 1 = no evidence of disease to 9 = leaves completely diseased. Leaf diseases were principally caused by *Drechslera dactylidis* and *Stagonospora arenaria* Sacc. and did not appear in 1988. Ground cover percentage was determined by visual rating immediately after the first cutting in 1988. Ground cover was considered to be important as a measure of an entry's ability to reduce water runoff, soil erosion potential, and weed encroachment. Severe winter kill, resulting from flooding in the fall of 1987 and subsequent ice sheet formation during the 1987/88 winter prevented forage yield, maturity, and ground cover from being determined at Arlington in 1988.

Statistical analysis

The frequencies of plants, from the original isolation nurseries, that were subsequently used for progeny testing were computed and analyzed by chi-square contingency tables (Steel and Torrie 1980). Single-degree-of-freedom chi-squares, based on the overall frequency, were computed for each country and each region of the world represented by half-sib families in the progeny test. Regions of the world were defined as: northern Europe (including accessions from Belgium, Denmark, Great Britain, The Netherlands, Poland, Sweden, and Switzerland), southern Europe (including accessions from Greece, Italy, Romania, Spain, and Yugoslavia), Middle East (including accessions from Iran and Turkey), USSR, Japan, Australia/New Zealand, and South America (including accessions from Argentina, Chile, and Uruguay). Chi-square and frequency computations were based on 4,068 of the 4,536 original plants, which included 429 of the 448 half-sib families tested. Countries for which all plants died before 1983 (these were Algeria with 1 accession, Austria with 1, Egypt with 1, France with 1, Morocco with 6, and Pakistan with 4), and 12 accessions whose origin was obscured by a mistake in the planting arrangement of one of the original nurseries were ignored in the frequency analysis presented in Table 1. The 12 unidentifiable accessions included 19 maternal plants which contributed half-sib families to the progeny test.

Analysis of variance using generalized least squares (Searle 1971) were computed separately for each of the 24 sets of half-sib families, after which sums of squares were pooled for sets within each tester population. Data collected on cultivars were also analyzed by analysis of variance using the same models as used for families. Forage yield and maturity were analyzed according to a split-plot-in-time-and-space model (Steel and Torrie 1980), but excluding the location × year component and its interaction with families, due to the fact that only three environments were available (Arlington and Marshfield in 1987 and Marshfield in 1988). Thus, the two degrees of freedom for environments were partitioned into effects of locations and years, and both family × location and family × year interactions were estimable. For disease reaction, a combined analysis of variance of 1987 data over locations allowed estimation of family main effects and family × location interaction. Family × environmental interactions were not estimable for ground cover. All effects in analyses of variance were assumed to be random.

Variance components for families, families × locations, and families × years were estimated by equating mean squares to their expectations (Gaylor et al. 1970). Cultivar variance components were computed in a similar manner. Confidence intervals for variance components are not known to exist for situations such as this case, where (1) mean squares are based on pooled sums of squares, and (2) there is imbalance in the factorial design (i.e., one environment missing). Jeyaratnam and Graybill (1980) defined approximate confidence intervals for complex varince components, those for which the estimators are linear functions of more than two mean squares. This estimator was used to estimate confidence intervals for the family and cultivar variance components for yield and maturity, with the realization that pooling sums of squares among sets and the factorial imbalance may cause violation of the assumptions implicit in the confidence interval computations. Confidence intervals for all other variance component estimates were computed according to the procedures of Milliken and Johnson (1984).

For each of the four variables, half-sib family means were estimated by averaging over all replicates and environments and subjected to a generalized least squares analysis of variance using the nested model

$$Y_{ijkl} = \mu + \alpha_i + \beta_{j(i)} + \gamma_{k(ij)} + \varepsilon_{l(ijk)}$$

where Y_{ijkl} = the ijklth half-sib family mean, μ = the overall mean, α_i = the effect of the ith region of the world, $\beta_{j(i)}$ = the effect of the jth country within the ith region, $\gamma_{k(ij)}$ = the effect of the kth accession deriving from the ijth country, and $\varepsilon_{l(ijk)}$ = the effect of the lth half-sib family deriving from the ijkth accession. Phenotypic correlation coefficients were computed among the four variables for half-sib families and for cultivars. Family versus cultivar correlation coefficients were compared for the same pair of variables using the Z transformation and test statistic (Steel and Torrie 1980).

For the 21 countries listed above, mean values and variances among all half-sib family means for accessions deriving from that country were computed. Thus, two 21×4 matrices were generated – one containing country means for each variable and the other containing within-country variances for each variable. Both matrices were subjected to principal components analysis (Morrison 1976) using the correlation matrices among the four variables.

Results and discussion

Selection of families for testing was based on winter survival and seed production of their maternal parents, the

Table 1. Frequency summary and chi-square analysis of plants producing sufficient seed for maternal half-sib family progeny testing, based on country and region of origin

Country or region	Initial no. of plants	No. of families tested	Frequency	X^2 (1 *df*)[a]	$P(>\chi^2)$
Country					
Belgium	18	2	0.111	0.006	<0.95
Denmark	270	29	0.107	0.011	<0.95
Great Britain	54	5	0.093	0.095	<0.90
The Netherlands	108	17	0.157	3.090	<0.10
Poland	126	9	0.071	1.547	<0.25
Sweden	72	5	0.069	0.990	<0.50
Switzerland	126	11	0.087	0.440	<0.75
Greece	90	5	0.056	2.376	<0.25
Italy	180	16	0.089	0.524	<0.50
Romania	72	3	0.042	3.106	<0.10
Spain	72	8	0.111	0.024	<0.975
Yugoslavia	216	16	0.074	2.255	<0.25
Iran	360	29	0.081	2.366	<0.25
Turkey	666	67	0.101	0.166	<0.75
USSR	1,368	189	0.138	15.507	<0.001
Japan	18	3	0.167	0.715	<0.50
Australia	162	2	0.012	14.888	<0.001
New Zealand	18	3	0.167	0.715	<0.50
Argentina	18	2	0.111	0.006	<0.95
Chile	36	6	0.167	1.430	<0.25
Uruguay	18	2	0.111	0.006	<0.95
Pooled	4,068	429	0.105		
Homogeneity (20 *df*)				50.263	<0.001
Region					
N. europe	774	78	0.101	0.180	<0.90
S. europe	630	48	0.076	5.720	<0.025
Middle East	1,026	96	0.094	1.538	<0.25
USSR	1,368	189	0.138	15.507	<0.001
Japan	18	3	0.167	0.715	<0.50
Aust. & N.Z.	180	5	0.028	11.514	<0.001
S. America	72	10	0.139	0.853	<0.50
Homogeneity (6 *df*)				36.026	<0.001

[a] Based on an expectation using the pooled frequency

latter of which was a function of winter injury symptoms following the winter of 1982/83. The overall selection frequency was 448/4,536 = 0.099, which was similar to the pooled frequency from the identifiable plants, deriving from 21 countries, represented in the progeny test (Table 1). Both countries and regions showed differences ($P<0.001$) in the frequency of plants represented in the progeny test. Country sources ranged in frequency from 0.012 for Australia, the accessions of which were mainly from subspecies *hispanica*, to 0.167 for 3 countries. Six countries contributed a lower frequency of germ plasm to the progeny test than the average, based on $P<0.25$. Three of these countries contributed *hispanica* germ plasm to the progeny test: Greece, Iran, and Australia, countries for which 40%, 5%, and 89%, respectively, of their original accessions were from subspecies *hispanica*. Most *hispanica* plants were dead by 1983, which was expected because this subspecies is winter-growing/summer-dormant and adapted to Mediterranean climates (Borrill 1978).

The Netherlands, USSR, and Chile contributed a higher-than-average ($P<0.25$) frequency of germ plasm to the progeny test (Table 1). Although there was some variation among countries within regions, variation among regions for the frequency of original plants included in the progeny test explained much of the variation among countries. Among regions, Soviet sources gave the only expectation of a higher-than-average frequency of useful germ plasm, based on the criteria used for inclusion in the progeny test. On average, southern European germ plasm was expected to be less useful, due to the low frequencies from several countries in this region. The low combined frequency of Australia and New Zealand reflected the low number of initial accessions

Table 2. Variance component estimates and their 90% confidence intervals for half-sib families and cultivars

Variable	Source of variation[a]	Half-sib families			Cultivars		
		Variance component estimate	Lower 90% limit	Upper 90% limit	Variance component estimate	Lower 90% limit	Upper 90% limit
Yield (Mg ha^{-1})	E	0.46*	0.35	0.57	−0.20	−1.36	1.26
	E × L	0.11	0.00	0.24	0.84	−0.05	3.46
	E × Y	−0.29	−0.36	−0.21	1.09*	0.08	4.02
	Error	2.21	2.07	2.36	3.07	2.57	3.76
Maturity	E	0.17**	0.13	0.22	0.66	−0.02	2.12
	E × L	−0.02	−0.03	0.01	0.13	−0.02	0.57
	E × Y	0.21**	0.17	0.26	0.74**	0.33	1.98
	Error	0.46	0.43	0.49	0.55	0.46	0.67
Disease reaction	E	0.31**	0.24	0.40	1.84**	0.60	4.88
	E × L	0.18**	0.11	0.25	0.62**	0.21	1.82
	Error	0.66	0.61	0.72	0.60	0.48	0.77
Ground cover (%)	E	16.0**	9.5	23.2	167.3**	76.2	413.0
	Error	63.0	56.5	70.8	40.0	30.0	58.0

*,** Mean square associated with variance component estimate was significant at $P<0.05$ or 0.01
[a] E, Entries (families or cultivars); L, locations; Y, years

from New Zealand and the apparent difference between *glomerata* (N.Z. and Aust.) and *hispanica* (Aust.) germ plasm collected in that region. Of these seven regions, only the European, Soviet, and Middle Eastern regions provided natural collections of *Dactylis* (Borrill 1978). Collections deriving from the other regions were introduced from natural collections made in Eurasia or from cultivated germ plasm.

Variation among families was detected ($P<0.05$) for forage yield, maturity, disease reaction, and ground cover (Table 2). Means, mean squares, and variance components for half-sib families did not differ ($P>0.10$) among the three topcross pollinators. Therefore, analyses of variance sums of squares were pooled across topcross pollinators. There was also some family × year interaction for maturity and family × location interaction for disease reaction. Cultivars varied only for disease reaction and ground cover, the lack of cultivar variation for yield and maturity being due to large cultivar × year interactions. Cultivar variation for disease reaction and ground cover was six and ten times greater, respectively, than for families. Confidence intervals for disease reaction and ground cover cultivar variance components did not overlap with those for family variance components. Greater cultivar variation for disease reaction and ground cover was possible due to (1) the concentration of favorable alleles for these two variables in some cultivars and (2) possible masking effects of the three topcross pollinators on family variances. The latter explanation appears unlikely because of the similarity in genetic parameter estimates for families of the three topcross pollinators despite the striking phenotypic dissimilarity among means of the three topcross pollinators per se (mean scores of 5.5, 5.6, and 3.1 for disease reaction and 89%, 80%, and 94% ground cover for 'Chinook', 'WO-1', and 'Potomac', respectively). Cultivars showed more genotype × environment (G × E) interaction effects for yield, maturity, and disease reaction than families, as illustrated by the minor overlap or lack of overlap in 90% confidence intervals for family × environment and cultivar × environment interaction variance components. This suggests that G × E interaction in *Dactylis* is, in part, a product of plant breeding efforts. While G × E interaction certainly exists among natural germ plasm sources, it can be made more important by breeding specific germ plasm sources for adaptation to specific types of environments. While broad adaptation is a goal of most forage breeders, cultivars are typically selected in a limited number of environments, creating potential cultivar differences in niche adaptation. This probably contributed to G × E interaction effects for the cultivars in this study.

Of the 448 half-sib families tested, 16 were derived from accessions classified as subspecies *hispanica* (Table 3). These represented the 396 original plants deriving from *hispanica* accessions, for a frequency of 0.04. On average, accessions of subspecies *hispanica* appeared to be less winter hardy than *glomerata* accessions. However, families deriving from accessions of *hispanica* versus *glomerata* subspecies did not differ in mean ground cover. Thus, based on the results of the progeny test, *hispanica*-derived individuals with adequate winter har-

Table 3. Mean performance of half-sib families derived from suspecies *glomerata* or subspecies *hispanica* maternal genotypes and of commercial North American cultivars

Group or subspecies	Number of families	Yield Mg ha^{-1}	Maturity	Disease reaction	Ground cover %
Glomerata (Gl)	432	12.10	6.4	4.1	86.4
Hispanica (Hp)	16	11.80	6.9	4.7	85.4
Cultivars	13	12.51	6.4	3.8	85.1
Comparison		*Probability of a greater Student's t-value*			
Gl vs. Hp		<0.0001	<0.0001	<0.0001	0.708
Cultivars vs. families		<0.0001	0.749	<0.0001	0.807

Table 4. Phenotypic correlation coefficients among four variables of 429 half-sib families (above diagonal) and 13 North American cultivars (below diagonal)

Variable	Yield	Maturity	Disease reaction	Ground cover
Yield		0.01	−0.23**	0.01
Maturity	0.16		0.04	0.14**
Disease reaction	−0.74**,[a]	−0.21		0.25**
Ground cover	0.48[a]	0.06	−0.17[a]	

** Correlation coefficient significantly different from zero at $P<0.01$. All others had $P>0.05$

[a] Z test for homogeneity of correlation for families vs. cultivars: $P=0.011$ for yield-disease, $P=0.067$ for yield-ground cover, and $P=0.121$ for disease-ground cover. All other Z tests had $P>0.35$

diness can be identified. Iran contributed the highest frequency of these families, with 7 of the original 18 Iranian *hispanica* plants included in the progeny test.

Families deriving from *hispanica* accessions were, on average, lower yielding, earlier maturing, and had greater average disease reaction than subspecies *glomerata* families (Table 3). Thus, *hispanica* accessions would be expected to have a lower probability than *glomerata* accessions of contributing superior germ plasm to breeding programs in similar temperate regions. The 45 families (10% of 448) with the highest mean forage yield included only 1 family derived from a *hispanica* accession. A similar truncation for late maturity, high disease resistance, or high ground cover means failed to identify a single *hispanica*-derived family. Thus, utilization of subspecies *hispanica* germ plasm under cultivation in environments similar to Wisconsin will require long-term objectives and mild selection pressures following hybridization with subspecies *glomerata* germ plasm, or a modification of the typical three-cuts-per-year hay management system.

North American cultivars were superior to the mean of all half-sib families for yield and disease reaction, but were similar in maturity and ground cover. Carlson and Moll (1962) reported a range of Turkish, Moroccan, and northern European accessions to be later in maturity than a group of unspecified commercial seed lots from Virginia, West Virginia, Kentucky, and Missouri. While breeding efforts have concentrated on yield and disease resistance, there appears to have been no average improvement in ground cover.

Forage yield and disease reaction were strongly correlated among the cultivars included in this study (Table 4). High-yielding cultivars had low disease reaction scores, suggesting that high disease levels tended to reduce yields, and/or breeding efforts for these two traits have been synchronous, leading to coincidental, rather than causal, changes. Review of the literature suggests that at least part of this relationship is due to the causal effect diseases generally have on reducing yield of forage grasses (Braverman 1986). This relationship was also observed for half-sib families ($P<0.01$), but to a considerably smaller degree ($r=-0.23$ versus -0.74; $P=0.011$) than for cultivars. Thus, the relationship between yield and disease reaction for cultivars is due partly to an inherent (likely causal) relationship that exists among natural collections and to synchronous breeding efforts for the two traits. Breeding of North American cultivars has also led to a positive relationship between forage yield and ground cover that was not present among progenies of the natural collections ($P=0.067$), and to an altered relationship between disease reaction and ground cover ($P=0.121$). Families with high ground cover tended to have more susceptible disease reactions, but this association was reduced among cultivars.

Because of the wide range in maturity among *Dactylis* accessions, germ plasm pools and cultivars are generally considered to be classified as early, medium, or late in maturity, with some introgression occurring between adjacent groups, but little between early and late populations. Thus, families and cultivars were separated, according to maturity score, into early (mean maturity score ≥ 7.0), medium (mean maturity score >5.0 and <7.0), and late (mean maturity score ≤ 5.0) classes, where scores of 5.0 and 7.0 indicate an average maturity stage of completely extended peduncle and anthesis, respectively, at the time of first cutting (Casler 1988).

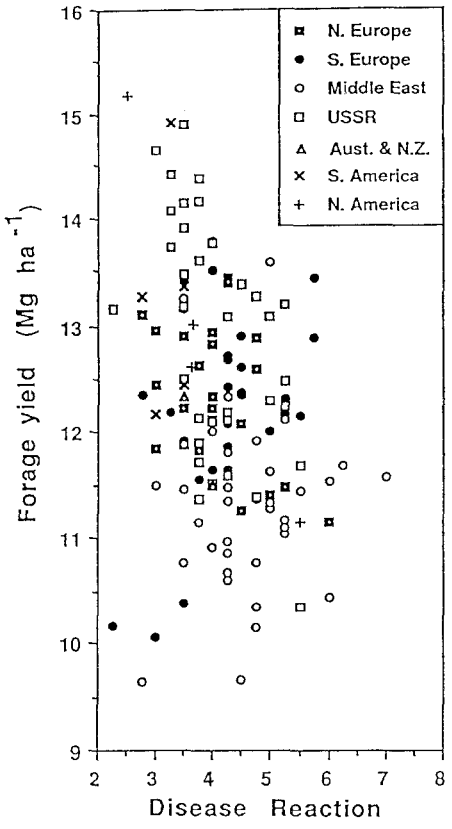

Fig. 1. Scatterplot of the relationship between disease reaction and forage yield of 139 early-maturing half-sib families and early-maturing cultivars, the latter of which were represented as North American germ plasm (+)

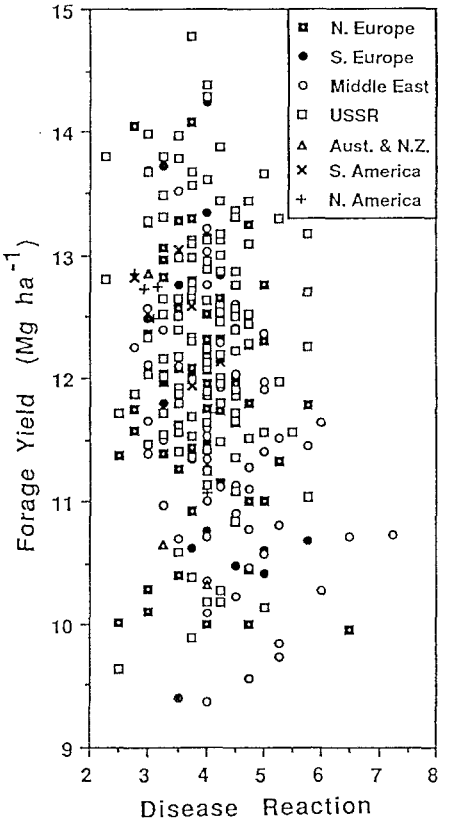

Fig. 2. Scatterplot of the relationship between disease reaction and forage yield of 275 medium-maturing half-sib families and 6 medium-maturing cultivars, the latter of which were represented as North American germ plasm (+)

Early-maturing cultivars had large ranges for mean yield and disease reaction: 75% and 63%, respectively, as great as for early-maturing families (Fig. 1). Yield (Y) was a linear function of disease reaction (D) for the cultivars classified as early in maturity ($Y = 17.65 - 1.23\ D$; $R^2 = 0.87$; $P = 0.067$). The relationship between yield and disease reaction for families was not symmetric. Selection among families for low disease reaction, with a 10% selection intensity, did not result in a difference in forage yield (mean of 12.20 Mg ha^{-1} for selected families versus 12.09 Mg ha^{-1} for all families; $P > 0.5$). However, selection of the 10% of families highest in yield resulted in a group of families with lower mean disease reaction (3.6 for selections versus 4.1 for all families; $P < 0.01$). Among the 14 highest-yielding, early-maturing families, 11 derived from Soviet sources, and 1 each derived from southern Europe, the Middle East, and South America. There was little regional clustering according to disease reaction; families with low disease levels were identified from germ plasm deriving from each region. In general, Soviet germ plasm was the most variable for yield in the early maturity group. Middle Eastern germ plasm clustered near the low end of the yield scale, while most European germ plasm clustered within the range from one phenotypic standard deviation (s_p) below the mean to two s_p units above the mean.

Medium-maturity cultivars had ranges in mean values for yield and disease reaction that were 32% and 67%, respectively, as large as those for half-sib families deriving from accessions (Fig. 2). Further, while the highest-yielding early-maturity entry was a cultivar (Fig. 1), the highest-yielding medium-maturity cultivar ranked 53rd out of 281 total medium-maturity entries. Therefore, the benefits of incorporating new germ plasm from various sources into cultivated germ plasm pools should be more immediate and more beneficial for medium-maturity pools than for early-maturity pools. This observation may be a result of more intensive cultivar breeding efforts in early-maturing germ plasm pools, due to prior, unpublished knowledge of the positive relationship between earliness and seed production, later documented by Godshalk (1985), Luedtke (1984), and Youngberg et al. (1986). The relationship between cultivar yield and disease reaction was similar to that for the early-maturity group ($Y = 15.98 - 1.12\ D$; $R^2 = 0.85$; $P = 0.009$).

Selection among medium-maturing families for yield or disease reaction gave similar results to those for the early-maturity group. The mean yield of the 10% of

families with the lowest disease reaction did not differ from the overall mean (12.21 versus 12.09 Mg ha^{-1}; $P>0.05$), while the mean disease reaction of the 10% higher yielding families was lower than the overall mean (3.7 versus 4.0; $P<0.001$) (Fig. 2). Among the 28 highest-yielding, medium-maturing families, 21 derived from Soviet sources, 3 from southern Europe, 2 from northern Europe, and 1 each from the Middle East and South America. Similar to observations for the early-maturity group, there was little regional clustering according to disease reaction. Soviet and European germ plasm were the most variable for yield, with family means scattered throughout the entire range of values. Middle Eastern germ plasm again clustered near the low end of the yield scale, but tended to provide a greater frequency of high-yielding families than for the early-maturity group.

Families deriving from Soviet sources comprised 42% of the half-sib families included in the progeny test. Thus, Soviet germ plasm contributed a greater-than-expected proportion of germ plasm when a 10% selection intensity was applied for yield (78%, $\chi_1^2=6.62$, $P<0.01$ for early-maturing families; 75%, $\chi_1^2=12.39$, $P<0.001$ for medium-maturing families). These results provide further evidence of the potential value of Soviet *Dactylis* germ plasm sources for improving forage yield or maintaining forage yield while improving other traits of cultivated germ plasm pools.

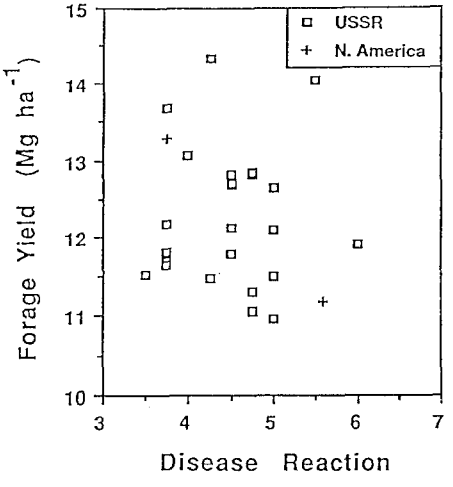

Fig. 3. Scatterplot of the relationship between disease reaction and forage yield of 23 late-maturing half-sib families and 2 late-maturing cultivars, the latter of which were represented as North American germ plasm (+)

Nutritional value of orchardgrass declines with advancing maturity (Van Soest 1982). Thus, when harvested on a specific date or according to the maturity stage of a companion (such as alfalfa, *Medicago sativa* L.), late-maturing cultivars are highest in nutritional value (Casler 1990). Late-maturing germ plasm in this study derived exclusively from the USSR (Fig. 3). The two late-maturing North American cultivars were both derived from Soviet accessions (Hanson 1972). Of the nine late-maturing orchardgrass cultivars listed by Hanson (1972), five trace exclusively or partly to Soviet sources, while three others are of Finnish or Swedish origin, and one is unknown. Therefore, the USSR and northern Scandinavia appear to be the only sources of late-maturing germ plasm in this collection and among North American cultivars. Therefore, identification of superior germ plasm sources from diverse climates and sites within these countries will be necessary to develop late-maturing cultivars while maintaining a broad genetic base within germ plasm pools and among cultivars. For most of the accessions that were evaluated in this study, local site data includes only the name of the nearest city and an occasional estimate of altitude or description of the habitat (e.g., USDA-ARS 1982). Thus, for these collections there is no substitute for an extensive field evaluation to identify superior sources of germ plasm from diverse sites.

The variances among accessions within countries and families within accessions made up the largest portions of the variance among half-sib families for each variable (Table 5). Region means and country means within regions made up a total of 7%–27% of the family sum of squares and had generally the smallest variance components. The remainder (73%–93%) of the variance among family means was within countries and accessions. Thus, geopolitical boundaries were not reliable predictors of mean performance for any trait, except maturity, due to the association of lateness with Soviet germ plasm sources. This was similar to results of Falcinelli et al. (1988) who found that variation among accessions within regions and plants within accessions were the most important sources of variation for heading date

Table 5. Estimated variance components of the total variance among half-sib family means for each variable. Values in parentheses are the percentage of the half-sib family sum of squares accounted for by each source of variation

Source of variation	*df*	Yield	Maturity	Disease reaction	Ground cover
Region	6	0.23 (15)	0.12 (21)	0.02 (8)	0.8 (3)
Country/Region	14	−0.03 (3)	0.03 (6)	0.06 (7)	0.1 (4)
Accession/Country	143	0.15 (36)	0.18 (45)	0.09 (37)	2.8 (36)
Family/Accession	265	0.82 (46)	0.24 (28)	0.51 (48)	43.2 (57)

and yield of Italian *Lolium perenne* L. accessions. Some of the variation among accessions could be ascribed to altitude and average annual rainfall of the collection site (Falcinelli et al. 1988). Two perennial ryegrass accessions, one collected from a pasture and one from near a path passing through the pasture, represented the entire range of phenotypic variation within the species (Tyler 1988). In *Dactylis*, aridity of the local climate was found to be the most important characteristic related to genetic variation among natural collections (Lumaret 1984; Roy and Lumaret 1987). Altitude of the original collection is also related to seedling leaf growth rate of *Dactylis* accessions (Broue and Kawanabe 1967). However, a range of panicle, spikelet, and leaf morphological traits of Italian *Dactylis* accessions were generally not related to rainfall, latitude, or longitude of the original collection site (Speranza and Cristofolini 1986). This suggests that environmental variation does not necessarily cause ecotypic differentiation for traits not closely related to sexual or asexual reproductive fitness.

The accessions described in this study derive from original collections that have been increased, en masse, once or twice without isolation of individual accessions. This was done mainly for convenience and cost reduction to avoid the labor and space requirements of isolated intercrossing or selfing within accessions (Burton 1979). Because approximately half of the observed genetic variation is contained within accessions, the population of accessions is already acting nearly as a single interbreeding population. Some assortative mating according to maturity has undoubtedly occurred. This was suggested by the relatively small amount of variance for maturity associated with families within accessions (Table 5). This is probably of little consequence because the relative patterns of variation and covariation were similar within early-, medium-, and late-maturing groups (Figs. 1–3).

Because the genetic variance structure of natural populations of tetraploid *Dactylis*, which have been maintained within their ecological niche, is similar to these accessions (Lumaret 1985), the method of seed multiplication appears to have had little effect on the genetic variance structure in the population. Thus, there is no evidence that the imposition of isolation mechanisms or any other change in seed multiplication would be beneficial and/or necessary when the initial accession seed increases were made without isolation of individual accessions. After two generations of nonisolated seed increase, only 25% of the original maternal alleles will exist within maternal sources, thereby reducing the usefulness of maternal pedigree maintenance and limiting the ability to identify and utilize collections from particular sources. Without accompanying climatic and altitudinal data, maintenance of individual accessions serves little purpose except for organizational purposes and maintenance of advanced-generation maternal pedigrees. Without initial isolated seed multiplication, routine maintenance of individual accessions or groups of accessions appears to have little biological value at more advanced stages in the processes of multiplication, maintenance, and preservation. Maximum utilization of genetic variation in this population will require that selection efforts be just as intensive within accessions as among accessions.

Long-term, temperature- and humidity-controlled storage is essential to preserve *Dactylis* germ plasm with minimum loss of viability (Rincker 1981), and thereby minimum loss of naturally-occurring alleles. Original seed of accessions may be kept viable for many years. Its usefulness will be limited by the amount of seed in the original collection and the degree to which it is subjected to nonisolated seed increase (Burton 1979). Occasional seed multiplication of the composite germ plasm pool, using spaced plants representing the entire pseudorandom-mating population, would avoid selection within solid-seeded rows of individual accessions and the efforts associated with maintaining individual accessions. For this purpose a location with mild winters and summers is essential to avoid selection based on winter or summer stresses. Collateral establishment of permanent field gene banks would allow (1) an annual opportunity to collect seed samples and (2) natural selection in a manner consistent with desired goals, depending on the management imposed. The use of multiple and diverse locations would minimize the overall loss of alleles from the collection (Roy and Lumaret 1987) and maximize the usefulness of the field collections for breeders and geneticists at various locations. If locations and management factors are carefully chosen, natural selection in field gene banks would do little more in this setting than in the natural setting, acting to modify allele frequencies of traits related to sexual and asexual reproductive fitness mediated by environmental constraints. If the goal is to minimize unpredictable genetic shifts, locations should be chosen to represent environments in which tetraploid *Dactylis* occurs naturally, e.g., temperate, mesic steppes and mountain meadows for subspecies *glomerata* and xeric steppes for *hispanica*. Alternatively, locations could be chosen to represent disturbed environments, as suggested by Gouyon et al. (1983). Disturbances could vary, depending on the objectives, but the specific nature of the disturbance can be expected to strongly influence the nature of genetic shifts in the gene bank (Snaydon 1987).

The three South American countries were among the four countries with the highest mean half-sib family yields (Table 6). This germ plasm, being non-native to South America (Borrill 1978), likely was introduced from Spain or Portugal. Support for this comes from Lumaret (1981), who found specific alleles of enyzme loci in South American germ plasm that were otherwise unique to Galician (northwestern Spain) and Portugese collections.

Table 6. Mean performance of half-sib families deriving from 21 countries

Country or region	n_i[a]	Yield Mg ha^{-1}	Maturity	Disease reaction	Ground cover %
Belgium	2	11.38	6.6	4.5	88.0
Denmark	29	12.20	6.6	3.8	85.9
Great Britain	5	12.27	7.0	3.6	86.0
The Netherlands	17	11.98	6.1	3.6	85.6
Poland	9	12.32	6.8	4.2	91.4
Sweden	5	11.93	6.6	3.6	86.2
Switzerland	11	11.54	6.1	4.8	89.9
Greece	5	11.44	6.9	3.8	83.6
Italy	16	11.97	6.6	3.9	90.4
Romania	3	12.56	5.9	3.7	88.3
Spain	8	12.74	7.2	4.4	87.5
Yugoslavia	16	11.98	7.0	4.3	90.0
Iran	29	11.35	6.8	4.7	84.8
Turkey	67	11.42	6.7	4.4	85.9
USSR	189	12.42	6.1	4.0	85.8
Japan	3	12.22	6.8	3.7	85.7
Australia	2	11.92	7.2	3.8	76.5
New Zealand	3	11.28	6.1	3.4	86.3
Argentina	2	12.70	6.8	3.5	86.5
Chile	6	12.70	6.9	3.4	87.5
Uruguay	2	13.55	7.0	3.1	90.0
Region means					
N. europe	78	12.04	6.5	3.9	87.2
S. europe	48	12.08	6.8	4.1	88.9
Middle East	96	11.40	6.8	4.5	85.6
Aust. & N.Z.	5	11.53	6.5	3.6	82.4
S. America	10	12.89	6.9	3.4	87.8
SE (family mean)[a]		0.607	0.28	0.41	5.61

[a] The standard error of difference between any pair of country or region means can be computed as SE9 $[(n_i+n_{i,})/n_in_{i,}]^{-1/2}$, where n_i is number of families

This is further supported by the observation that the mean yield of Spanish-derived families was also among the highest four country means. Both sources were among the earliest in average maturity. However, South American germ plasm had lower average disease reactions then Spanish germ plasm. This difference could arise from lack of adequate sampling or from natural disease selection pressures present in South America, but not in Spain.

Soviet, Romanian, Danish, British, and Polish accessions also produced high mean half-sib family yields. Although Soviet collections were the only source of late-maturing germ plasm, accessions from The Netherlands, Switzerland, Romania, and New Zealand contributed an average maturity similar to that of the average Soviet accession and, thus, would be potential sources of medium-maturity germ plasm. Countries and regions did not vary to a large degree in ground cover (Table 5), with the exception that Australian accessions contributed families with extremely low ground cover (Table 6). Both of the Australian families in the progeny test derived from *hispanica* accessions.

Principal components analysis of mean values in Table 6 resulted in the formation of two interesting components, which described 70% of the variation among country means (Table 7). The first component (PC1mean) had high values that were closely correlated with high yield, slightly correlated with earliness, closely correlated with low disease reactions, and uncorrelated with ground cover. The second component (PC2mean) had high values that mainly reflected lateness in maturity, slightly higher-than-average yield, and high ground cover. For within-country variances, the first and third principal components were the most interesting. High values of the first component for variances (PC1var) were associated with low variance for yield, average variance for maturity, and high variance for disease reaction and ground cover. High values of the third component (PC3var) for variances were correlated with high variance for yield and moderate variances for the other three variables.

British and Argentinian germ plasm were expected to provide the highest probability of success for short-term yield improvement of early-maturing germ plasm

Table 7. Eigenvectors and eigenvalues of principal components analyses of means over half-sib families and variances among half-sib families within 21 countries. Figures in parentheses are percentages of the total variance among countries accounted for by each of the four principal components

Statistic and variable	Eigenvector			
	1	2	3	4
Country means				
Yield	0.718	0.226	0.187	0.631
Maturity	0.264	−0.530	0.735	−0.329
Disease reaction	−0.642	0.085	0.535	0.542
Ground cover	0.040	0.813	0.371	−0.447
Eigenvalue	1.55 (39)	1.23 (31)	0.96 (24)	0.26 (6)
Within-country variances				
Yield	−0.477	0.128	0.864	0.097
Maturity	−0.082	0.920	−0.216	0.316
Disease reaction	0.645	−0.113	0.294	0.696
Ground cover	0.592	0.353	0.345	−0.637
Eigenvalue	1.58 (40)	1.06 (26)	0.83 (21)	0.53 (13)

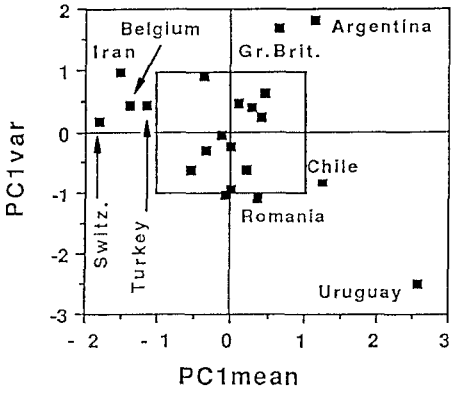

Fig. 4. Scatterplot of the first principal component for within-country variances (PC1var) versus the first principal component for country means (PC1mean)

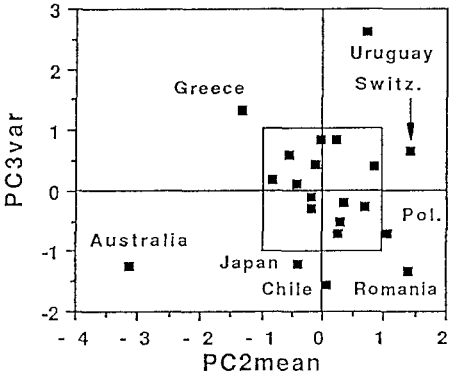

Fig. 5. Scatterplot of the third principal component for within-country variances (PC3var) versus the second principal component for country means (PC2mean)

(Fig. 4). Families derived from these two countries combined high scores of PC1var and PC1mean, thus providing a combination of high mean yield, low mean disease reaction, low variance for yield, and high variance for disease reaction and ground cover. Chilean germ plasm was similar in performance for PC1mean values, but had a near-average PC1var score. Uruguayan germ plasm appeared to be extremely valuable, in terms of mean performance, but was also extremely variable for yield and had low variation in disease reaction and ground cover. Iranian, Belgian, Swiss, and Turkish germ plasm sources were expected to provide the lowest probability of success for short-term yield gains in early-maturing orchardgrass germ plasm pools.

Uruguayan and Swiss germ plasm should be the most useful in a breeding program designed to improve yield of medium-maturity germ plasm, with a secondary goal of maintaining a high level of genetic variability (Fig. 5). Their high values of PC3var and PC2mean suggested high levels of yield variation that could be used to (1) sustain selection in a longer-term program, (2) infuse new variability into existing populations undergoing selection, or (3) maintain variability in short-term population improvement programs. Polish and Romanian germ plasm with similar PC2mean values did not possess adequate yield variation to meet this objective. Conversely, Greek germ plasm had a similar variance structure, but had low PC2mean scores, due to its low yield and earliness. Australian, Japanese, and Chilean germ plasm would be entirely inadequate for this objective.

Acknowledgement. I thank Dr. S. J. Knapp for his helpful advice regarding the computation of confidence intervals for variance component estimates.

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