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Prediction of progeny variation in oat from parental genetic relationships

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Summary. The ability to predict agronomic performance of progeny from a cross would be a great benefit to plant breeders in selecting parents. The predictive value of parental genetic relationships estimating F_1 progeny means and F_4 family variances of nine argronomic traits was tested in 76 oat crosses, using genetic distance measures based on coefficients-of-parentage, quantitatively inherited morphological characters, and discretely inherited biochemical and morphological characters. Coefficients-of-parentage were better predictors of F_1 performance than similarity measures derived from plant morphology or discretely inherited characters. Combined distance measures were better estimators of F_1 specific combining ability (SCA) effects than any single measure. Among cultivars of similar adaptation and quantitative morphology, crosses between parents with high coefficients-of-parentage gave higher SCA effect values than crosses of distantly related parents for grain yield and total biomass. The opposite was found for crosses among cultivars of different adaptation or quantitative morphology. The best predictor of trait variances among F_4 families was coefficients-of-parentage. Crosses between more distantly related parents produced larger variances among families than crosses between closely related parents for plant biomass. For grain yield, test weight, heading date, grain filling period, and maturity date, crosses between more closely related parents produced larger among-family variances than crosses of distantly related parents. Crosses between more distantly related parents involved at least one parent unadapted to central New York, and resulted in most of the progeny being generally unadapted. This, in part, may account for the low genetic variances for heading date, test weight, and grain yield in crosses of distantly related parents.

Key words: *Avena* – Genetic distance – Coefficient-of-parentage – Heterosis – Specific combining ability

Introduction

Being able to accurately predict the progeny value from a cross would be of great benefit to crop breeding programs. It would allow breeders to focus on parental combinations with the greatest breeding potential. Studies of progeny value prediction have generally focused on estimation of F_1 hybrid performance (Moll et al. 1965; Shamsuddin 1985; Frei et al. 1986; Damerval et al. 1987; Lamkey et al. 1987). These studies attempted to predict hybrid performance based on measures of genetic distance, the average divergence of parental genomes. Moll et al. (1965) found increasing hybrid heterosis in maize (*Zea mays* L.), with increasing divergence between parental populations as measured by known crop histories. Genetic distance based on allozyme dissimilarity was of limited use for prediction of single cross hybrid maize performance (Frei et al. 1986; Lamkey et al. 1987), but was most predictive among closely related inbreds (Frei et al. 1986). Damerval et al. (1987) studied differences among two-dimensional gel electrophoresis patterns of total leaf proteins and concluded that single cross hybrid maize performance could be predicted by genetic divergence of genomic protein 'regulatory' sequences, but not protein coding sequences. This suggests that divergence of some genes may contribute more than others to heterosis.

Jenkins (1969) found greater F_1 heterosis in oat (*Avena sativa* L. and *A. byzantina* C. Koch) crosses between parents of different hexaploid species than between parents within a species. Shamsuddin (1985), in a

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study of wheat (*Triticum aestivum* L. em. Thell.), reported positive correlation of genetic distance, as measured by dissimilarity of quantitatively inherited characters, with hybrid heterosis. Cox and Murphy (1990), in a study of a wide range of winter wheat crosses, observed correlation of genetic distance, based on morphology and disease reaction, with F_2 heterosis. Kinship measures were poorer predictors of F_2 heterosis than measured genetic distance. Combining the two relationship measures, however, accounted for the greatest proportion of variation in F_2 heterosis between crosses (Cox and Murphy 1990). Cowen and Frey (1987a, b) used parentage relationships and quantitatively inherited morphological traits to measure genetic distance among parental oat genotypes from the midwestern U.S. Cowen and Frey (1987a) found a positive correlation between F_1 heterosis and distance based on plant morphology, but limited usefulness of parentage information for prediction of trait heterosis (Cowen and Frey 1987b).

Genetic variances in segregating populations are expected to be correlated to genetic distance between parents because the greater the parental divergence, the greater the proportion of segregating loci in inbred generations (Martinez et al. 1983). This assumes that all loci contribute equally to plant phenotype, that segregation of a limited number of 'major' genes cannot produce similar genetic variances to segregation of larger numbers of 'minor' genes. This is likely not a valid assumption unless there is uniform distribution of 'major' factors among parents. Cowen and Frey (1987a, b) found correlation of parental genetic distance based on either parentage of morphology multivariate genetic variances with yield traits among F_4 and F_5 oat families, but poor correlation with individual components of yield.

Souza and Sorrells (1989, 1991a, b) determined genetic relationships among North American oat cultivars using three methods: coefficients-of-parentage, quantitative morphological characters, and discrete morphological and biochemical characters. Evaluation of coefficients-of-parentage (COP) data from 205 North American oat germ plasms and cultivars revealed that approximately half of all genotypes and nearly all of the recently developed genotypes fell into a single large cluster, named, for convenience, the Central cluster (Souza and Sorrells 1989). Older genotypes tended to be placed in smaller regional germ plasm pools with a high degree of relatedness to specific ancestral lines. These regional germ plasm clusters were generally named after the ancestral parent with the greatest relationship to the cultivars of that pool (e.g., Red Rustproof cluster). Seventy North American oat genotypes were evaluated for similarity of 13 quantitative morphological characters (QMCs), such as grain yield, heading date, and height (Souza and Sorrells 1991a). Cluster analysis using these metric traits produced four large clusters of cultivars. Using QMCs to measure relatedness, cultivars of similar latitude of adaptation and maturity were generally clustered together. Relationships based on quantitative morphological traits were strongly influenced by heading date (Souza and Sorrells 1991a), which is controlled by a limited number of factors, such as photoperiodic and vernalization loci. In a related study, relationships of 70 genotypes were measured using discrete morphological and biochemical characters (DMBCs) (e.g., seedling pigmentation and avenin seed proteins), which represented a minimum of 26 loci. Clustering by DMBCs produced six large clusters, with division of genotypes that also generally corresponded to latitude of adaptation and ancestral origin (Souza and Sorrells 1991b). For convenience, in the QMC study clusters were named by maturity characteristics and in the DMBC study clusters were named for area of adaptation or the ancestral parent common to most of the cultivars in a cluster (Souza and Sorrells 1991a, b). These three methods produced different relative measures of genetic relationships among the individual cultivars and groups of cultivars. However, coefficients-of-parentage and discrete character distances were more similar to each other than to quantitative trait distance measures (Souza and Sorrells 1991b).

The purpose of this study was to identify methods of measuring genetic relationships which, singularly or in combination, most accurately predict progeny genetic variation of performance in oat crosses representing a broad range of genetic divergence. This study assumed that, with the range of crosses studied, greater genetic distance between parents would result in greater genetic variances among derived inbred progeny. The primary test of desirability of a distance measure for parental selection in this study was its ability to significantly predict F_1 specific combining ability. This is based on: (1) the assumption that the number of heterozygous loci should increase with increasing genetic distance (differences in relative proportions of loci that are heterozygous should be reflected in changes in specific combining ability); and (2) the fact that the mean effects of specific combining ability are easier to measure than trait variances among inbred progeny. Prediction of genetic variances among inbred progeny by genetic distance measures is the best test of the validity of the use of genetic distances as a parental selection tool in oat. Therefore, variation among F_4 progeny was also examined with the understanding that the larger experimental error of variance estimates may produce ambiguous results.

Materials and methods

Analysis of F_1 oat hybrids

Seventy-six F_1 hybrids were evaluated for 2 years in two locations near Ithaca, NY. Four adapted cultivars (used as females) – Astro, Marathon, Ogle, and Porter – were crossed with 19

Table 1. Parents in the Design II, F_1 experiment with state or province of origin and genetic relationship among parents

Cultivar	Origin	COP[a] cluster	QMC[a] cluster	DMBC[a] cluster	Genetic distance between parents[b]							
					Astro		Marathon		Ogle		Porter	
					J_r	J_{joint}	J_r	J_{joint}	J_r	J_{joint}	J_r	J_{joint}
Females (adapted)												
Astro	NY	Victoria	Fall	Kherson	–	–	0.472	0.548	0.289	0.708	0.591	0.762
Marathon	WI	Central	Late spring	Kherson	0.472	0.548	–	–	0.465	0.608	0.477	0.528
Ogle	IL	Central	Early spring	Bond-Hajira	0.289	0.708	0.465	0.608	–	–	0.347	0.718
Porter	IN	Central	Late spring	Core spring	0.591	0.762	0.477	0.528	0.347	0.718	–	–
Male (regional)												
Orbit	NY	Victoria	Early spring	Core spring	0.180	0.406	0.472	0.444	0.467	0.477	0.591	0.761
Calibre	Alberta	Central	Late spring	Core spring	0.675	0.833	0.583	0.607	0.573	0.811	0.504	0.605
Cascada	Alberta	Central	Late spring	Kherson	0.678	0.905	0.689	0.915	0.675	1.181	0.643	0.963
Fidler	Manitoba	Central	Late spring	Core spring	0.678	0.703	0.689	0.522	0.675	0.797	0.643	0.616
Lancer	SD	Central	Fall	Core spring	0.641	0.716	0.401	0.271	0.385	0.608	0.413	0.552
SD 790400	SD	Central	Late spring	Bond-Hajira	0.347	0.679	0.406	0.314	0.396	0.482	0.492	0.549
Spear	SD	Central	Early spring	Core spring	0.614	0.753	0.305	0.360	0.284	0.412	0.319	0.545
Bates	MO	Central	Fall	Core fall	0.469	0.812	0.555	0.816	0.522	0.907	0.588	0.900
Clintford	IN	Central	Early spring	Core spring	0.633	0.771	0.455	0.600	0.433	0.637	0.309	0.640
Nodaway 70	Mi	Central	Early spring	Bond-Hajira	0.524	0.851	0.641	0.687	0.609	0.540	0.654	0.775
Chilocco	OK	Rustproof	Fall	Core fall	0.575	0.743	0.694	0.621	0.617	0.819	0.643	0.811
TAM 301	TX	Central	Fall	Byzantina	0.519	0.797	0.646	0.900	0.593	0.968	0.653	1.072
TAM 312	TX	Central	Fall	Core fall	0.519	0.800	0.646	0.969	0.447	0.966	0.635	1.102
Brooks	NC	Rustproof	Fall	Core fall	0.570	0.732	0.638	0.790	0.601	0.890	0.612	1.032
Salem	NC	Canadian	Fall	Trispernia	0.401	0.514	0.377	0.628	0.593	0.926	0.465	0.725
Windsor	VA	Central	Fall	Core fall	0.462	0.682	0.604	0.680	0.633	0.959	0.675	0.830

[a] COP cluster: coefficient-of-parentage cluster; QMC cluster: quantitative morphological characters cluster; DMBC cluster: discrete biochemical and morphological characters clusters

[b] J_r: Jaquard's transformation of parental COP values; J_{joint}: genetic distance of parents of all three methods of measuring genetic distance combined (See Table 2)

pollen sources including 16 'regional' cultivars and three of the four adapted cultivars (Design II, with fixed effects; Comstock and Robinson 1948). Adapted and regional cultivars used as males are listed in Table 1. The F_1 hybrids and parental cultivars were grown in split plots, with crosses (hybrid and parents) assigned to whole plots. One replication was grown per location, with three plants per split plot, 20 cm between plants within a row and between rows. Seedlings were germinated in the greenhouse, acclimated in outdoor shelters, and transplanted to the field in late April at the three-leaf stage. In 1986 and 1987 trials were grown at two locations (McGowan Farm, Niagara silt loam; and Ketola Farm, Erie Channery silt loam) on the Cornell University Agricultural Experimental Station, Ithaca, NY. Approximately 225 kg ha^{-1} of 10/20/20 fertilizer (10% elemental nitrogen, 20% P_2O_5, and 20% K_2O, by weight) was applied preplant, and during plant tillering the plots were top-dressed with 100 kg ha^{-1} 14/14/14 fertilizer and 20 kg ha^{-1} $Ca(NO_3)_2$ (17% elemental nitrogen). Bromoxynil (trade name 'Brominal') was applied at a rate of 210 g ha^{-1} active ingredient to control broad-leaf weeds. In 1987, 'Pyrmore' (Primicarb: 2, dimethylamino-5,6-dimethylpyrimidin-4yl-dimethylcarbamate) insecticide was applied for aphid control in three applications at a rate of 400 g ha^{-1} at 2-week intervals starting 22 May.

Agronomic traits were measured using standard methods (Souza and Sorrells 1991a). Plots were evaluated for heading date, height, tiller number, maturity date, grain fill period, grain yield, grain yield per tiller, and total biomass. Test weight was not measured because of the small grain quantities. Nonuniform damage due to barley yellow dwarf (BYDV) infection occurred in 1986 and, at harvest, plants with obvious disease symptoms were discarded to avoid bias. Traits were analyzed as a randomized complete block design with genotype-by-location interactions within years as an error term. Only F_1 plots were included in the analysis. Plot means for biological yield, grain yield, and tiller number were standardized by expressing them on a per-plant basis, and plot means for all characters were weighted in the analysis of variance by the number of plants harvested from the plot, to reduce variation due to unequal sampling within plots (SAS Institute 1985). Cross means averaged across locations and years were used to estimate parental specific combining ability (SCA) and general combining ability (GCA), following Comstock and Robinson's (1948) mating Design II model.

Estimation of variances among inbred progeny using F_4 families

Genetic variances of characters within crosses were estimated from variances among 30 random F_4 families per cross. The 20 crosses used in the F_4 experiment were derived from crosses of the four adapted cultivars (Astro, Marathon, Ogle, and Porter) to five other cultivars (Bates, Calibre, Lancer, Orbit, and Salem). Thirty random seeds from a single F_1 plant were planted in each cross and advanced by single-seed descent to F_3 seed. F_3 plants were grown in the greenhouse and harvested separately to produce F_4 families. The 30 F_4 families from each cross were grown at three locations near Ithaca, NY in 1987 on the Ketola (Erie Channery silt loam), McGowan (Niagara silt loam), and Caldwell (Williamson silt-loam soil) farms of the Cornell Uni-

Table 2. Genetic distance measures used for prediction of progeny performances in the F_1 and F_4 experiments

Name	Abbreviation	Equation[a]	Reference
Coefficient-of parentage Jaquard's transformation	J_r	$J_r = [e^{(1-r)}] - 1$	Cowen and Frey 1987b
Covariance of alleles Jaquard's transformation	J_{cov}	$J_{\mathrm{cov}} = [e^{(1-\mathrm{cov})}] - 1$	Smith 1984
Euclidean distance	E_m	$E_m = [\sum(\mathrm{P1}_i - \mathrm{P2}_i)^2]^{0.5}$	Martinez et al. 1983
Joint genetic distance	J_{joint}	$J_{\mathrm{joint}} = [J_r + J_{\mathrm{cov}} + \ln(E_m)]/3$	Souza 1983

[a] Abbreviations used in the equations: r = COP between parents, cov = covariance of alleles between parents estimated from observed similarities of discrete characters, P1 and P2 = parent one and parent two evaluated for i morphological traits

versity Agricultural Experimental Station, Ithaca, NY. Ten families of each cross were grown at a single location, with families crosses completely randomized within a location. Sixty seeds of each family were planted in a single plot consisting of a single 1-m row, with 20 cm between rows. Two families of each cross were replicated once within a location to estimate random error. To adjust for families with less than 60 seeds per plot, seed number per plot was used as a covariate in the analysis of variance. Average seed number was 58.4 per plot, with no family having fewer than 30 seeds. Two replications of the parental genotypes also were grown at each location. Planting dates were 13 April at the Ketola farm, 18 April on the Caldwell farm, and 24 April on the McGowan farm. Fertilizer, herbicide, insecticide rates, and timing of application were identical to the F_1 experiment. Plots were evaluated for heating date, height, physiological maturity, grain filling period, plot biomass, grain weight, and grain test weight, as in Souza and Sorrells (1991a).

Trait variances were estimated from the analysis of variance using the mean-square term for families within a cross (MS_{Fam}) after estimating the mean effects of locations. Assuming a random model, MS_{Fam} can be partitioned into variance components: $s^2 e + n(s^2 g)$, where $s^2 e$ is the random error term estimated from family replications within locations (MS_{Error}), n is the number of family replications (average 1.2), and $s^2 g$ is the genetic variance for the trait (Snedecor and Cochran 1980). The genetic variance among F_4 families derived from single-seed descent, assuming no epistasis, represents 1.5 of the additive variation (A) and 3/16 of the dominance variation (D) within a cross (Horner and Weber 1956). The population mean for randomly derived inbred lines is expected to be identical to the midparent mean of the cross (Jinks and Pooni 1981). The genetic mean of the F_4 families tested should deviate from the midparent mean only by residual dominance effects and sampling error. Trait variances of a population of inbred lines derived from a hybrid should have a normal distribution in the absence of epistasis and linkage disequilibrium (Jinks and Pooni 1981). Trait genetic variances for a cross were estimated from the MS_{Fam} term and the MS_{Error} term determined for each cross, estimated from family replications within a cross. Negative estimates of variance components were assumed to equal zero.

Prediction of progeny performance

Three measures of parental genetic relationships were used to predict progeny performance: (i) coefficients-of-parentage (COP), (ii) similarly of quantitative morphological characters (QMC), and (iii) covariance of alleles estimated from discrete morphological and biochemical characters (DMBC). Using each method of determining genetic distance, crosses were divided into two groups: (i) crosses between parents within a cluster of related cultivars, and (ii) crosses between parents from different clusters. Clustering methodology and descriptions of clusters are given in Souza and Sorrells (1989, 1991a, b).

Prediction of SCA in the F_1 experiment was tested by comparing the average SCA of crosses among genetically similar parents (within clusters) to the average SCA for crosses among genetically dissimilar parents (between clusters), using only one of the three methods of clustering (single classification). The usefulness of combining two clustering methods (double classification) was tested using three 2 × 2 factorial analyses of variance to measure the significance of the interactions between pairs of classification methods.

Cross SCA effects were also examined for linear and quadratic relationships to the genetic distance between parents. Four measures of genetic distance were used in the regression: (i) Jacquard's transformation of coefficient-of-parentage (J_r) (Cowen and Frey 1987a); (ii) Jaquard's transformation of the covariance of alleles between parents, as estimated from discrete morphological and biochemical traits (J_{cov}) (Souza and Sorrells 1991b); (iii) morphological euclidean distance (E_m) (Martinez et al. 1983), estimated from the quantitative morphological characters (Souza and Sorrells 1991a); and (iv) the 'Joint Measure' of genetic distance (J_{joint}) derived from: J_r, J_{cov}, and the natural logarithm of the euclidean distance measure to transform E_m to approximately the same scale as the other distance measures (Table 2). Jacquard's transformation was used for parentage and discrete trait distances to convert the similarity measures into distance measures with larger distribution ranges. For each genetic distance measure, 24 regressions were calculated: each of the eight traits were evaluated from estimated genetic distance, using (i) all crosses, (ii) only crosses involving parents from within the same QMC cluster, and (iii) only crosses involving parents from different QMC clusters. Genetic distances between parents are given in Souza (1988); COP, QMC, and DMBC clusters of parents and the J_r and J_{joint} between parents are listed in Table 1. The Astro/Orbit cross was excluded from regressions using the J_r genetic distance in the F_1 and F_4 study. The sib relationship of the two parents was well beyond the range of relationships for the other crosses and always produced a highly significant, but artifactual, polynomial regression.

Genetic variances within crosses in the F_4 experiment were tested for linear and second-order polynomial relationships to each of the four genetic distance measures described in the F_1 experiment. The genetic variances were transformed using the natural logarithm to meet the assumption of uniform distribution of variances throughout the range of the regression. Traits with genetic variances of zero are undefined using this transformation and were not included in the regression model.

Results

General description of the F_1 experiment

Significant male and female effects and specific combining ability effects were observed for each of the traits measured, except for plant height, biomass, and number of tillers per plant which had only significant

Table 3. Single classification comparisons. Specific combining ability (SCA) effects for crosses between parents placed in the same and differrent quantitative morphological clusters (QMC), coefficient-of parentage clusters (COP), and discrete morphological and biochemical clusters (DMBC)

Character	Units	COP clusters		QMC clusters		DMBC clusters	
		Similar	Dissimilar	Similar	Dissimilar	Similar	Dissimilar
		Average SCA effects		Average SCA effects		Average SCA effects	
Heading date	days	0.00	0.00	0.96	−0.39**	0.02	−0.02
Maturity date	days	0.74	−0.96*	1.90	−0.78**	0.08	−0.61
Grain-fill period	days	0.74	−0.96*	0.95	−0.39	0.01	−0.58
Height	cm	1.11	−1.45**	1.61	−0.66*	1.19	−1.82*
Biomass	g plant^{-1}	−0.13	0.21	0.45	−0.16	0.29	−0.44
Grain yield	g plant^{-1}	−0.07	0.09	0.94	−0.38	−0.01	0.02
Tillers plant^{-1}		−0.31	0.41*	0.03	−0.01	−0.33	0.50*
Grain tiller^{-1}	g tiller^{-1}	0.01	−0.02	0.09	−0.04	0.03	−0.05*
Average distance[a]		0.51	0.54	3.2	4.0	0.00	0.45
No. of crosses		43	33	17	59	22	54

*, ** Paired groups of crosses within a classification system significantly different at 95 and 99% confidence interval, respectively.

[a] Distance measures are J_r, E_m, and J_{cov} for the first, second, and third pairs of columns, respectively

Table 4. Double classification comparisons. Specific combining ability (SCA) effects crosses based on parental relationships as determined by two clustering methodologies: quantitative morphological character clusters (QMC) in combination with either coefficients-of-parentage clusters (COP) or discrete morphological and biochemical character clusters (DMBC)

Trait of SCA effects	Units	Similar COP cluster		Dissimilar COP cluster		Similar DMBC cluster		Dissimilar DMBC cluster	
		Similar QMC	Dissimilar QMC	Similar QMC	Dissimilar QMC	Similar QMC	Dissimilar QMC	Similar QMC	Dissimilar QMC
		Average SCA effects		Average SCA effects		Average SCA effects		Average SCA effects	
Heading date	days	1.30	−0.57	0.46	−0,17	1.08	−0.61	0.53	−0.14
Maturity date	days	3.41	−0.42	−0.28	−1.21**	1.33	−0.91	−0.56	−0.62*
Grain-fill period	days	2.11	0.14	−0.74	−1.05*	0.54	−0.30	−1.09	−0.48
Height	cm	4.13	−0.20	−2.02	−1.23**	3.21	0.01	−3.81	−1.43*
Biomass	g plant^{-1}	2.68	−1.34	−2.77	1.33**	0.36	0.25	0.48	−0.63
Grain yield	g plant^{-1}	1.70	−0.84	−0.16	0.19*	1.56	−0.93	−1.17	0.25*
Tillers plant^{-1}		−0.65	−0.17	1.01	0.18**	−0.41	−0.28	1.51	0.30
Grain tiller^{-1}	g tiller^{-1}	0.25	−0.10	−0.14	0.03**	0.20	−0.08	−0.31	0.00*
Mean E_m distance		3.1	4.0	3.3	3.9	3.4	3.5	3.1	4.1
Mean 2nd distance[a]		0.53	0.49	0.51	0.55	−0.08	0.04	0.41	0.46
No. of crosses		13	30	9	24	7	10	15	44

*, ** Interaction of two methods of classifications significant at the 95 and 99% confidence interval, respectively

[a] Second distance measures are J_{cov} and J_r for the first four and second four columns, respectively

male and female effects. Generally, the F_1 plants were taller and had later heading dates and fewer tillers than their parents. Tillering reduction was particularly prominent in the crosses with Astro, a high-tillering cultivar. Because of the low planting density, the high-tillering parents often had higher grain yield per plant than the F_1 hybrid but lower grain yield per tiller. In 1986, Barley yellow dwarf virus (BYDV) infections were observed in some plants. The crosses to Ogle and Porter, BYDV-resistant cultivars, had less disease symptoms than crosses to the susceptible females Astro and Marathon. In 1987, expression of BYDV symptoms occurred later in the season (following anthesis) and was less obvious than the previous year. Culling plants with severe symptoms was not necessary, except in the crosses of Astro or Marathon to each other or to the breeding line SD790400.

SCA effects for different clustering methods

Significant differences in SCA effects for physiological maturity date, grain filling period, height, and tillers-per-plant were observed for crosses within versus between the more distantly related parents from different COP clusters. Heading date for crosses between parents within a QMC cluster had an average SCA effect of 1.35 days later than crosses between parents in different QMC clus-

Table 5. Prediction of specific combining ability effects of crosses using three genetic distances measures in regressions with all 76 crosses and subsets of crosses; only significant prediction models presented

Distance measure	Relationship of parents	R^2	Trait estimated	
J_r	Between QMC	$Y=7.5-154.6\,J_r+630.7\,(J_r)^2$	0.11 *	Biomass plant^{-1}
E_m	Between QMC	$Y=12.2+8.0\,E_m-1.1\,(E_m)^2$	0.13 *	Height
J_{joint}	All crosses	$Y=42.5-70.4\,J_{\text{joint}}+28.1\,(J_{\text{joint}})^2$	0.08 *	Biomass plant^{-1}
J_{joint}	Within QMC	$Y=3.2-7.0\,J_{\text{joint}}+3.1(J_{\text{joint}})^2$	0.28 *	Tillers plant^{-1}
J_{joint}	Between QMC	$Y=-0.4-2.0\,J_{\text{joint}}+5.9\,(J_{\text{joint}})^2$	0.14 **	Maturity date
J_{joint}	Between QMC	$Y=-53.9+154.9\,J_{\text{joint}}-103.6\,(J_{\text{joint}})^2$	0.34 **	Height
J_{joint}	Between QMC	$\mathrm{Y}=63.6-102.2\,J_{\text{joint}}+39.7\,(J_{\text{joint}})^2$	0.17 **	Biomass plant^{-1}
Models tested		*Percent of models significant*		
All distance measures[a]		7.3%		
J_r distance measure		8.3%		
J_{cov} distance measure		0.0%		
E_m distance measure		4.2%		
J_{joint} distance measure		20.8%		
J_{joint} distance measure for crosses between QMC clusters		37.5%		

*, ** Linear regression model significant at the 95 and 99% significance levels, respectively

[a] Three models were fit for each combination of genetic distance measure and trait: quadratic polynomial regression for (1) all crosses, (2) crosses within QMC clusters, and (3) crosses between QMC clusters. Significant models had p-value less than 0.05 for regression slope F-test

ters (Table 3). Significant differences were also observed in SCA effects for physiological maturity date and height for crosses within versus between QMC clusters. Significant differences in SCA effects were observed for plant height, tiller number, and grain yield per tiller between crosses within DMBC clusters and crosses between DMBC clusters.

The SCA effects of crosses divided into four groupings using double classification produced significant interaction models for predictions using QMC clusters in combination with either of the other two classification methods. Significant interaction models were found for SCA effects of physiological maturity date, grain-fill period, height, tillers per plant, and grain per tiller using the double classification of QMC clusters and COP clusters (Table 4). The single classification using parentage clusters had no significant SCA effect differences between the cross grouping for plant biomass. However, in crosses within a QMC cluster, parental combinations within a COP cluster had an average of 4.0 g plant^{-1} greater biomass SCA effect than crosses between COP clusters. By comparison, in crosses between QMC clusters, crosses between COP clusters had an average biomass SCA effect of 4.1 g plant^{-1} less than crosses within COP clusters (Table 4). Double classification using QMC clusters and DMBC clusters had more similar effects to double classification with QMC clusters and COP clusters than COP-DMBC double classification (Table 4). Interactions for prediction of SCA effects were not significant using double classification with DMBC clusters and COP clusters after partitioning single classification effects.

Prediction of SCA effects using continuous genetic distances

The parental distance J_{joint} produced the greatest number of significant prediction models. Of the models tested for prediction of SCA effects, 5 of the 24 J_{joint} models were significant. For crosses within QMC clusters, three of the eight models of J_{joint} models for crosses within QMC clusters were significant (Table 5). The percentage of significant SCA effects prediction models using the other genetic distance measures were at the level expected by random chance alone. The SCA effects for biomass declined with increasing genetic distance between parents using the J_{joint} measure. Negative associations between parental genetic distance (J_{joint}) and SCA effects for height, heading, and maturity also were observed. The SCA values for tillers per plant were positively associated with the J_{joint} between parents.

Prediction of F_4 variances by genetic distance measures

Trait variances were positive for most of the observed characters. Harvest index was exceptional as only one cross, Astro/Salem, was found to have a nonzero genetic variance among families. Therefore, harvest index was not included in subsequent analyses. The greatest genetic variance for grain yield was observed in the cross Marathon/Lancer (7398). Crosses to the winter cultivar, Salem, segregated for vernalization requirement, and approximately 5% of the families did not head until after 1 August. Therefore, the Salem crosses tended to have high genetic variances for most traits due to the delayed heading of the winter segregates. Means and variances for test

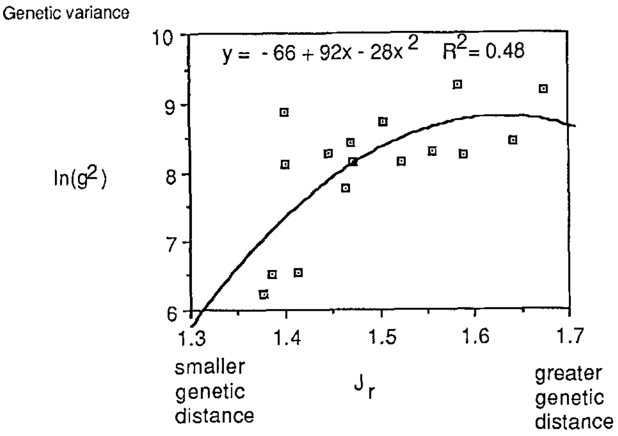

Fig. 1. Prediction of genetic variances among F_4 families within crosses for above-ground biomass by the genetic distance J_r between parents of a cross. The J_r value is a distance measure derived from the coefficient-of-parentage between parents. Genetic variances transformed by the natural logarithm

Table 6. Best prediction equations for genetic variances among F_4 families within crosses from each genetic distance measure. Only significant prediction models presented

Dependent variable	Model[a]	R^2
Test weight	$\ln(y) = 146.1 - 187.2\,J_r + 60.5\,J_r^2$	0.38**
Biomass	$\ln(y) = 65.0 + 91.8\,J_r - 28.2\,J_r^2$	0.48**
Grain yield	$\ln(y) = 15.0 - 5.6\,J_r$	0.24*
Heading date	$\ln(y) = 44.6 - 48.3\,J_r + 13.6\,J_r^2$	0.43**
Grain filling	$\ln(y) = 167.9 - 213.4\,J_r + 67.9\,J_r^2$	0.38**
Maturity date	$\ln(y) = 10.7 - 5.6\,J_r$	0.25*

Models tested	*No. of models*	*Percent of models significant*
All distance measures[b]	56	17.9%
J_r distance measure	14	64.2%
J_{cov} distance measure	14	0.0%
E_m distance measure	14	0.0%
J_{joint} distance measure	14	0.0%

*, ** Significant at the 95 and 99% confidence interval, respectively

[a] Genetic variances were transformed by the natural logarithm

[b] A linear and quadratic model was fit for prediction of the variance of each of the seven traits, 14 models for each genetic distance measure

weight, biomass, and grain yield were compared to expected values. Means for the three traits for all 20 populations were not significantly different from the midparent means. Population variances were not greatly skewed (Coefficients of Skewness, **b**, were less in absolute value than the standard deviation of the population) for the three traits. The exception was test weight variances in crosses involving Salem, which had negative **b** values in the range of 1.2 to 1.8 times the standard deviation. For the three traits, none of the populations had significant **b** values, defined as **b** greater than 4 times the population's standard deviation (Snedecor and Cochran 1980).

Genetic distance measures were poor predictors of F_4 variances. The best predictor of genetic variances among F_4 families within a cross was J_r, which had significant R^2 values for either linear of second-order polynominal regressions, or both, for all characters evaluated except height (Table 6). The best model, as measured by R^2 values, was the prediction of biomass genetic variance by J_r genetic distance with a second-order polynominal regression model ($R^2 = 0.48$). Genetic variance for biomass increased with increasing genetic distance, but the rate of increase declined with increasing genetic distance (Table 6, Fig. 1). In contrast, test weight, heading date, physiological maturity date, and grain-filling period had decreasing genetic variances with increasing genetic distance.

Discussion

Comparisons of genetic distance measures

The hypothesis tested by these experiments was that progeny performance can be predicted by measurement of genetic distances between the parents. Implicit in this hypothesis is the assumption that the genetic distance measurements are accurate. The F_1 and F_4 experiments have dichotomous results. In the F_1 experiment, the combined genetic distance measures (J_{joint} and double classification) best predict SCA effects; in the F_4 experiment, fewer prediction models were significant and only J_r reliably predicts the variances among families. The difference in the progeny parameters estimated in the two experiments partially explains this dichotomy. Prediction of progeny performance in the F_4 is more difficult than in the F_1: the parameter predicted in the F_1 study is a mean effect (SCA), while the parameter predicted in the F_4 study is a variance, which has greater error than prediction of a mean.

The F_1 experiment provides useful information for selecting parents for inbred development. The parental relationships based on quantitative morphological characters (QMC clusters and E_m) are probably measures of differences in parental adaptation (Souza and Sorrells 1991 a). Quantitative morphological characters, however, are strongly affected by a few simply inherited traits (photoperiod, vernalization, and stature) with large epistatic effects. The prediction models in the F_1 experiment support the supposition that vernalization and photoperiod factors affect the QMC clusters and E_m. Height, heading date, and maturity date are the only SCA effects predicted by the QMC clusters alone, and these traits would be expected to be strongly affected by photoperiod, vernalization, and stature genes. The QMC clusters complement the information provided by the COP and

DMBC clusters. The double classification models are similar for both COP and DMBC clusters used in conjunction with the QMC clusters. COP clusters in double classification with DMBC clusters produced no significant interaction models, suggesting that relationships derived from parentage and relationships derived from allele identity were similar, but that relationships derived from gross morphology were dissimilar to the other two distance measures. Cox and Murphy (1990) found in winter wheat that morphology was a better predictor of F_2 heterosis than parentage but, as in this study, the two measures of parental relationship were complementary and combined distance measures explained the greatest proportion of variation.

The F_4 experiment results suggest that J_r is the best predictor of progeny variances. Although J_{cov} is similar to J_r, it is an inferior predictor to J_r, probably because J_{cov} is an inferior measure of genetic distance. The parents used in this study all had extensive pedigree information; thus, the relative relationships of the parents were well defined. The J_{cov} distance, by contrast, is based on the similarity among parents at a minimum of 26 loci, a small sample of the possible divergent loci. Perhaps the J_{cov} would improve as a predictor of progeny variances if more loci were evaluated. E_m and J_{joint} were not predictive of F_4 progeny variances. This does not mean that factors determining gross morphology are not important sources of variation, but that, unlike F_1 SCA effects, progeny variances are not predictable from observed parental classes for these traits.

Relationships between progeny performance and genetic distance

In the F_1 experiment, the largest positive SCA effects for all traits except tillers per plant were observed in crosses among the parents with the closest genetic relationships. Jenkins (1969) and Cowen and Frey (1987a) found that the greatest F_1 heterosis occurred in the crosses between the most distantly related parents. Different testing environments and methodology may account for part of the variance in observations between this study and those of Cowen and Frey (1987a) and Jenkins (1969). For example, the lower planting density used in this study may also have resulted in tillering differences not present in other studies, which affected yield trait variation. There are also differences in the range of parental diversity between this study and those of Jenkins (1969) and Cowen and Frey (1987a) that may explain these differences in observations. Jenkins (1969) studied crosses between *A. sativa* and *A. byzantina,* while Cowen and Frey (1987a) studied crosses of elite *A. sativa* cultivars and breeding lines from the Midwest.

This study found complex relationships between both types of crosses and the correlations of genetic distance with trait SCA effects. Examining biomass and grain yield only, Jenkins (1969) compared oat cultivars with divergent pedigrees from both *A. sativa* and *A. byzantina. A. byzantina* cultivars are normally better adapted to Mediterranean climate and would likely be unadapted to the English testing environment. A comparison between crosses of divergent *A. sativa* cultivars and crosses of *A. sativa* and *A. byzantina* would be similar to comparisons in this study between crosses of parents of dissimilar COP clusters/similar QMC clusters and crosses of parents from dissimilar COP clusters/dissimilar QMC clusters (Table 4). Comparing only those crosses, this study also found that crosses between parents of greater diversity had greater positive SCA effects for grain yield and plant biomass than crosses of closely related parents. This finding agrees with Jenkins (1969). Cowen and Frey (1987a, b), in contrast, used parents that would probably be placed within a similar COP cluster and similar QMC cluster relative to the range of genotypes used in this study. Within closely related genotypes, increasing distance of parents may result in increasing levels of heterosis; this type of parental-progeny relationship was not examined specifically in this study.

The inverse relationship of SCA effects with genetic distance is an indication of the behavior of heterosis in oat. Dobzhansky (1952) hypothesized that many effects of heterosis in allogamous species were due to the masking of deleterious recessive alleles in the hybrid. In an autogamous species, such as oat, deleterious recessive alleles would be selected against by nature and breeding programs, except when masked by dominant homoeoalelles. The main hybrid effect observed for the range of oat genetic diversity studied here was a lowering of F_1 vigor with increasing genetic distance between parents. Crosses of divergent parents had a higher frequency of heterozygous loci and exhibited a lower agronomic vigor than crosses of closely related parents. This suggests that an important form of interallelic interaction in oat is reduced agronomic fitness of the heterozygote. Moll et al. (1965) found that hybrid vigor in maize crosses increased initially but declined in crosses among the most divergent parents. In these experiments, SCA effects for traits such as plant biomass and height declined with increasing parental genetic distance before starting to increase among the most divergent crosses. Although the response curves are different between these experiments, Moll et al. (1965) provides a precedent for nonlinear and nonpositive relationships between parental genetic distance and hybrid response, as occurred in this study.

In the F_4 experiment, the biomass genetic variances of crosses increased with increasing genetic distance between parents. This result was anticipated based on theory and previous experimentation (Cowen and Frey 1987a, b). However, declining genetic variances with increasing parental distances (J_r) were found for traits such as test weight and grain yield. One explanation for these results was the adaptation of the parents. Although the female parents were adapted to New York conditions, only one male parent, Orbit, was adapted to the northeast region. As genetic distance among crosses increased, the male parent was less well adapted (e.g., Calibre and Salem). Although genetic variances for characters such as test weight may have been high for divergent crosses, the variance may not have been expressed due to the poor progeny adaptation. For example, the cross Marathon/Calibre had a very high J_r value but a low genetic variance for test weight [2.4 (kg $hl^{-1})^2$] because many of the progeny headed too late (average 29 June) in the season to produce well-filled seed. Ogle and Porter, well-adapted cultivars, headed on 19 and 24 June, respectively. The Marathon/Calibre families had the lowest average test weights of any of the crosses (33.1 kg hl^{-1}). That variance for plant biomass was positively correlated with genetic distance may indicate that plant biomass has a lower environmental sensitivity than grain mass, test weight, or heading date. The variances of the latter traits may be more strongly affected by oligogenic traits (such as dwarfing, vernalization, and photoperiod loci) than by total biomass, and may therefore be less predictable by parental distance.

For cultivar development programs, breeders should concentrate on crosses between divergent, adapted parents because heritabilities will be greatest for agronomic traits in progeny of such crosses. This does not preclude the use of unadapted, genetically divergent germ plasm, but these experiments indicate that the full range of genetic variation will not be expressed in the adapted-by-unadapted cross due to poor progeny adaptation. Therefore, identification of superior adapted lines will require large populations for selection. Genetic distance measures also provide additional objective criteria for efficient selection of parental combination. This is of particular importance for new breeders unfamiliar with the available germ plasm, or for experienced breeders who need criterial for culling through potential parents that have been found to be locally adapted, but which have not been used previously in a crossing program.

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