Theor Appl Genet (2000) 100:889–894

M.T. Cheres · J.F. Miller · J.M. Crane · S.J. Knapp

Genetic distance as a predictor of heterosis and hybrid performance within and between heterotic groups in sunflower

Received: 1 September 1998 / Accepted: 14 September 1999

Abstract Heterosis is significant for seed yield and is one of the driving forces behind the hybrid seed industry in cultivated sunflower (*Helianthus annuus* L). Heterotic groups in sunflower, if any other than the female and male inbred-line groups exist, have not been well studied or described. The primary aims of this study were to assess the utility and validity of a series of proposed heterotic groups and estimate correlations between genetic distance, heterosis, and hybrid performance for seed yield in sunflower. Fortytwo female by male heterotic group (A × R) and 81 female by female heterotic group (A × B) single-cross hybrids were grown in Corvallis, Ore., and Casselton, N.D., in 1996 and 1997. Heterosis was significant for seed yield and plant height but not for seed oil concentration and days to flowering. Genetic distances were significantly correlated with hybrid seed yield when estimated from AFLP fingerprints (G_D) (r = 0.63 for A × R and 0.79 for A × B hybrids), but not from coancestries (G_C) (r = -0.02 for A × R and 0.54 for A × B hybrids). G_D (R^2 = 0.4) was a poor predictor of hybrid seed yield. The proposed heterotic groups in sunflower seem to have utility, but do not seem to be as strongly differentiated as those in corn (*Zea mays* L.). The highest-yielding hybrids were from the $B_C \times R_B$ heterotic pattern; however, several $B_C \times B_C$ hybrids (within-group hybrids) were among the top-yielding hybrids. The outstanding performance of certain $B_C \times B_C$ hybrids casts some doubt on the validity of the B_C group. Substantial genetic diversity seems to be present within and between heterotic groups in sunflower.

Communicated by G. Wenzel

M.T. Cheres · J.M. Crane · S.J. Knapp (✉)
Department of Crop and Soil Sci., Oregon State Univ.,
Corvallis, OR, 97331–3002 USA
e-mail: steven.j.knapp@orst.edu
Tel: +1541-737-5842, Fax: +1541-737-1334

J.F. Miller
USDA-ARS, Northern Crop Sci. Laboratory, Fargo,
ND 58105 USA

Key words Heterosis · Genetic distance · Sunflower · *Helianthus annuus*

Introduction

Genetic distances (G) between populations, individuals, or lines, whether estimated from coancestries or DNA fingerprints, have been widely used for descriptive analyses in crop plants, e.g., reconstructing breeding histories, describing patterns of genetic diversity, and assigning lines to heterotic or other biologically or economically important groups. Such analyses are appealing because G can be estimated without phenotyping the germplasm to be classified. Several such descriptive analyses have been reported in sunflower (*Helianthus annuus* L.) (Tersac et al. 1993; Berry et al. 1994; Gentzbittel et al. 1994; Zhang et al. 1995 b; Hongtrakul et al. 1997; Cheres and Knapp 1998). This research has shown that elite inbred-lines nearly always cluster into broad female and male inbred line groups and into market classes (oilseed versus confectionery).

Heterotic groups are important in corn (*Zea mays* L.) breeding and are well described from pedigree and DNA fingerprint analyses (Lee et al. 1989; Dudley et al. 1991; Smith et al. 1990, 1991, 1993; Smith and Smith 1992; Gerdes and Tracy 1994; Mumm and Dudley 1994; Mumm et al. 1994). Genetic distances tend to be narrow within and wide between heterotic groups in corn. And there is strong agreement between groupings produced by DNA fingerprint and coancestry analysis in corn (Smith OS et al. 1990; Smith JSC et al. 1991, 1993; Dudley et al. 1991; Smith and Smith 1992; Mumm and Dudley 1994; Mumm et al. 1994).

Heterotic groups and patterns have been much less studied in sunflower than corn and seem to have had a less important role in sunflower than corn breeding. Hongtrakul et al. (1997) and Cheres and Knapp (1998) proposed a series of heterotic groups for public inbred lines of sunflower developed in the US. Heterotic groups have not been formally proposed for other gene pools or from other studies in sunflower. Lines from the US gene pool comprise a subset of the germplasm used worldwide, but should also encompass key heterotic groups and patterns. The heterotic groups found in sunflower do not seem to be as rigid as those found in corn. Within-group genetic distances tend to be greater in sunflower than corn and between-group genetic distances tend to be greater in corn than sunflower (Dudley et al. 1991; Smith and Smith 1992; Mumm and Dudley 1994; Mumm et al. 1994; Cheres and Knapp 1998). Despite this difference, heterotic groups may have utility in sunflower breeding. They can, at the very least, be used to catalog diversity and direct the process of introgressing new alleles and creating new heterotic groups.

The utility of genetic distances for predicting hybrid performance has been widely studied. The correlation between genetic distance and general combining ability (GCA) for seed yield was weak (0.24) in the only predictive study reported thus far in sunflower (Tersac et al. 1994). Tersac et al. (1994) did not report correlations between genetic distance and seed yield, and heterosis for seed yield. Smith et al. (1990) reported a strong correlation between seed yield, heterosis for seed yield, and genetic distance among 37 inbred lines of corn selected to cover a broad range of diversity. Lee et al. (1989), Godshalk et al. (1990), Melchinger et al. (1990), and Smith and Smith (1992), in contrast, reported weak correlations between hybrid performance and genetic distance in corn. Similarly, weak correlations have been reported between *G* and hybrid seed yield in rapeseed (*Brassica napus* L.) (Diers et al. 1996), wheat (*Triticum aestivum* L.) (Martin et al. 1995), and rice (*Oryza sativa* L.) (Zhang et al. 1995 a). Although positive trends between genetic distance and seed yield were reported in each of these studies, hybrid seed yields were not accurately predicted by genetic distance in any of them. The basis for this inaccuracy is clear. Charcosset et al. (1991) and Bernardo (1992) showed that genetic distance does not accurately predict hybrid performance unless the DNA markers used in the analysis are associated with (linked to) genes affecting the trait.

The aims of the present study were to: (1) assess the validity of a series of proposed heterotic groups, (2) estimate heterosis effects among public inbred lines for economically important traits, and (3) estimate correlations between genetic distance, heterosis, and hybrid performance for seed yield in sunflower.

Materials and methods

Plant materials and field experiments

This study was performed using inbred lines from ‘female’ and ‘male’ heterotic groups. The female heterotic group was composed of unbranched, isogenic, cytoplasmic-genic male-sterile (A) and sterility maintainer (B) inbred-line pairs. The B-lines were HA89, HA370, HA372, HA382, HA383, HA384, HA385, HA390, HA821, HA822, HA850, HA851, HA852 and HA853. The male heterotic group was composed of branched, fertility restorer (R) lines. The R-lines were RHA274, RHA373, RHA377 and RHA801.

A-, B-, and R-lines were grown in a crossing nursery at East Farm, Corvallis, Ore., in 1995. Seed was produced for 42 of 56 possible A × R crosses. A × R hybrids were unbranched and male-fertile. Seed was produced for 81 of 91 possible A × B crosses (without reciprocals). A × B hybrids were unbranched and male-sterile.

The experiment was grown at Corvallis, Ore., and Casselton, N.D., in the summer of 1996 and 1997 using a simple square (12 × 12) lattice experiment design with four complete blocks (replications). The 144 entries were 14 B-lines, four R-lines, 42 A × R hybrids, 81 A × B hybrids, and three check hybrids from Pioneer Hi-Bred (Pioneer 6230, 6339 and 6451). One complete block was re-planted at Corvallis in 1996 because of bird damage to seedlings. We dropped seven A × R crosses (HA850 × RHA801, HA390 × RHA274, HA851 × RHA801, HA821 × RHA274, HA821 × RHA377, HA850 × RHA274 and HA852 × RHA373) and five A × B crosses (HA383 × HA850, HA370 × HA383, HA370 × HA382, HA385 × HA390 and HA372 × HA852) from the 1997 experiment because of insufficient seed. Plots of these hybrids were planted with one of the check hybrids (data were not recorded for these plots).

Forty seeds of each entry were sown in 6-m rows spaced 0.76 m apart at Corvallis. The Corvallis experiments were sown on 14 May 1996 and 15 May 1997 at East Farm. One and a half- to two-meter alleys were used between complete blocks. There were 12 incomplete blocks and 144 entries per complete block. The soil at East Farm is a Chehalis series dark-brown-silt loam. Seeds were planted with a cone seeder at a depth of 13 mm. Nitrogen (53.8 kg ha^{-1}) and phosphorus (67.2 kg ha^{-1}) were incorporated prior to planting. The experiment was hand-weeded and sprinkler-irrigated. We applied 0.84 cm of water after planting and 2.54–3.38 cm of water every 13–22 days until the end of August in 1996. We applied 2.54 cm of water on 22 July and 4 August in1997. The experiments were hand-harvested and threshed using a combine. Plots were harvested on 5 and 12 September in 1996 and 3 and 4 September in 1997. The threshed seed was stored in cotton bags, oven dried at 38 °C for 3 weeks, cleaned using an air-screen cleaner, and weighed.

Forty seeds of each entry were sown in 6-m rows spaced 0.91 m apart at Casselton, N.D. The Casselton experiments were sown on 23 May 1996 and 27 May 1997. The soil at Casselton is a Beardon silty clay loam (fine silty frigid Aeric Calciaquoll). Seeds were planted with a cone seeder at a depth of 5 cm. Nitrogen was applied at a rate of 58.0 kg ha^{-1} in 1996 and 66.9 kg ha^{-1} in 1997 and incorporated prior to planting. Triflualin (a, a, a-trifluoro-2, 6-dinitro-N,N-dipropyl-p-toluidine) was applied at a rate of 0.56 kg ha^{-1} AI. Plots were combine-harvested on 10 October 1996 and 14 October 1997. The threshed seed was dried at 43 °C for 3 days, cleaned using an air-screen cleaner, and weighed.

We measured days to flowering, plant height, seed yield, and seed oil concentration. The flowering date for an experimental unit (plot) was recorded when half of the plants reached the R5.1 growth stage (Schneiter and Miller 1981). Plant heights were recorded at physiological maturity. Oil concentrations were measured on 15-g seed samples (10% moisture) using nuclear magnetic resonance (Oxford Instruments, Concord, Mass.) (Robertson and Morrison 1979).

Statistical analyses

Analyses across locations and years were performed with the effects of entries (inbred lines and hybrids) fixed and the effects of years, locations, years × locations, entries × years, entries × locations, entries × locations × years, replications nested in years and locations, and incomplete blocks nested in replications random. Least square means (LSMs) for entries (entry means adjusted for incomplete block differences) were estimated using the PROC MIXED routine of the Statistical Analysis System (SAS) (Cary, N.C.). Tests for significant differences between entry means

Table 1 Heterotic group assignments and names for 14 sterility maintainer (B) and four fertility restorer (R) inbred lines of sunflower

Line	Heterotic group	Other names
HA89	B_B	OB-B and B_1
HA370	B_B	B_2
HA372	B_C	B_2
HA382	B_B	OB-B
HA383	B_C	OB-C
HA384	B_C	OB-C
HA385	Unassigned	None
HA390	Unassigned	None
HA821	B_C	OB-C and B_2
HA822	B_C	OB-C and B_2
HA850	Unassigned	None
HA851	Unassigned	None
RHA274	R_B	OR ad R_2
RHA373	R_B	OR and R_2
RHA377	R_A	OR and R_1
RHA801	R_A	OR and R_1

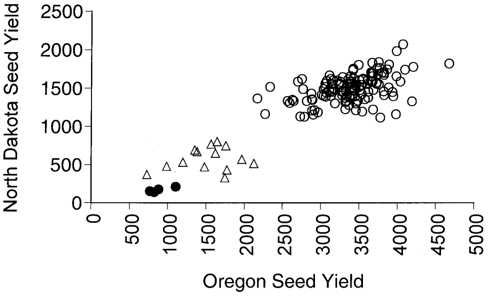

Fig. 1 Seed yields of R-lines (*solid circles*), B-lines (*open triangles*), and A × R and A × B single-cross hybrids (*open circles*) of sunflower tested at Corvallis, Ore., and Casselton, N.D., in 1996 and 1997

and contrasts between entry means and entry × location means were performed using *F*-statistics produced by PROC MIXED. Tests of significance for variance components were performed using *F*-statistics produced by the PROC GLM routine of SAS. This was necessary because PROC MIXED did not produce appropriate test statistics for random effects. PROC MIXED, however, did produce appropriate narrow prediction space statistics for fixed effects. Because stand counts were not uniform across the experiment, the number of plants per plot was used as a covariate for the analysis of seed yield differences (but not for days to flowering, plant height, or oil concentration). High-parent heterosis effects were estimated using differences between least square means across locations and years.

We performed analyses using the coancestry matrix (G_C) for the 18 parent lines (Cheres and Knapp 1998) and the Jacquard genetic distance matrix (G_D) for ten parent lines (HA89, 370, 372, 821, 822, and 852 and RHA274, 373, 377 and 801) (Hongtrakul et al. 1997). G_D was estimated from 360 amplified fragment length polymorphism (AFLP) markers (Hongtrakul et al. 1997). We had G_C estimates for all possible hybrids (123 total) among the 18 inbred lines and G_D estimates for 45 hybrids (Table 1). Analyses were performed using the heterotic groups proposed by Hongtrakul et al. (1997) and Cheres and Knapp (1998). Five B-lines (HA385, 390, 850, 851 and 853) have not been assigned to heterotic groups (Table 1). These were not fingerprinted by Hongtrakul et al. (1997) and could not be assigned to groups in the coancestry analysis (Cheres and Knapp 1998) because of incomplete pedigree records. We re-named the heterotic groups described by Hongtrakul et al. (1997) and Cheres and Knapp (1998) to create a single nomenclature. Our analysis was done on four A × R heterotic patterns ($B_B \times R_A$, $B_B \times R_B$, $B_C \times R_A$ and $B_C \times R_B$) and one A × B heterotic pattern ($B_B \times B_C$) among the four heterotic groups (B_B, B_C, R_A and R_B).

Simple correlation coefficients were estimated between G_C, G_D, seed yield, seed yield heterosis, plant height, plant height heterosis, seed oil concentration, and days to flowering for A × R and A × B hybrids. Observed seed yields for A x R hybrids were regressed on G_D estimates, and predicted and observed seed yields were compared for A × R hybrids.

Result and discussion

Hybrid performance and heterosis

There were significant differences ($P < 0.01$) between entries for all traits within and between locations. Entry by year and entry by location interaction effects were not significant for plant height, seed oil concentration, and days to flowering. Location and entry by location interaction effects were highly significant, while year and year by entry interaction effects were not significant for seed yield.

Seed yields ranged from 464 to 644 kg ha^{-1} for R-lines, 548 to 1278 kg ha^{-1} for B-lines, 1911 to 3253 kg ha^{-1} for A × R hybrids, and 1718 to 3038 kg ha^{-1} for A × B hybrids. Seed yields between locations were significantly correlated (Fig. 1) – rank and simple correlation coefficients were 0.86 ($P < 0.0001$) and 0.61 ($P < 0.0001$), respectively. The top nine A × R hybrids were ranked the same in both locations. Parent lines and hybrids produced significantly more seed and oil, flowered significantly later, and grew significantly shorter in Ore. than N.D. Most hybrids produced twice as much seed in Ore. as N.D. The seed yield of HA383 × RHA373, the highest yielding A × R hybrid in both locations, was 4743 kg ha^{-1} in Ore. and 1851 kg ha^{-1} in N.D.

A × R and A × B hybrids produced significantly more seed and were taller than B- and R-lines (Table 2). B-lines other than HA385 produced significantly more seed than R-lines. The seed yield of HA385 was not significantly different from the mean seed yield of the four R-lines (641 kg ha^{-1} versus 530 kg ha^{-1}). A × B hybrids had slightly greater oil concentrations than A × R hybrids, while B-lines had slightly greater oil concentrations than A × R hybrids (Table 2). A × R hybrids flowered later than R-lines. Several A × R hybrids produced less oil and flowered later than B-line parents (Table 2).

The mean seed yield for A × R hybrids was not significantly different from the mean seed yield for A × B hybrids (Table 2). Four of the five highest-yielding hybrids in both locations were A × B single-crosses. There were no significant differences in the seed yields of the top five hybrids in N.D., while the seed yield of the top hybrid (HA383 × RHA373) was significantly greater ($P \leq 0.0001$) than hybrids ranked two through five in Ore.

The correlation between B-line seed yield *per se* and hybrid seed yield ($r = 0.52$) was significant ($P = 0.0003$), whereas there was no correlation between R-line seed

Table 2 Tests of significance of contrasts between group least square means for seed yield (kg ha^{-1}), plant height (cm), seed oil concentration (g kg^{-1}), and days to flowering for A × R and A × B single-crosses and B- and R-lines tested at Corvallis, Ore., and Casselton, N.D., in 1996 and 1997

Contrast	Seed yield (kg ha^{-1})		Plant height (cm)		Seed oil concentration (g kg^{-1})		Flowering (days)	
	Effect	*Pr* > F	Effect	*Pr* > F	Effect	*Pr* > F	Effect	*Pr* > F
(A × B) vs (A × R)	11.7	0.98	5.2	0.002	30.2	0.05	1.0	0.17
(A × B) vs B	1398.9	0.03	29.0	0.0001	18.0	0.18	–1.0	0.08
(A × B) vs R	1937.8	0.01	24.6	0.0003	37.2	0.03	0.0	0.9
(A × R) vs B	1387.2	0.03	23.8	0.0001	–12.2	0.33	3.0	0.02
(A × R) vs R	1926.2	0.01	19.4	0.0008	7.1	0.57	1.0	0.23

Table 3 Least square means (mean), heterosis effects, and significance of heterosis effects (*Pr* > F) for seed yield (kg ha^{-1}), plant height (cm), seed oil concentration (g kg^{-1}), and days to flowering for ten A × R hybrids tested at Corvallis, Ore., and Casselton, N.D., in 1996 and 1997

Hybrid	Seed yield (kg ha^{-1})			Plant height (cm)			Seed oil concentration (g kg^{-1})			Days to flowering		
	Mean	Heterosis effect	*Pr* > F	Mean	Heterosis effect	*Pr* > F	Mean	Heterosis effect	*Pr* > F	Mean	Heterosis effect	*Pr* > F
HA383 × RHA373	3285.4	2068.5	0.0001	175.5	21.8	0.0001	410	7.0	0.64	73.9	–2.3	0.1
HA383 × RHA274	2896.6	1679.7	0.0001	178.3	24.6	0.0001	406	3.4	0.82	73.4	–3.0	0.03
HA372 × RHA377	2807.2	1568.6	0.0001	168.3	16.6	0.0012	433	10.1	0.51	74.4	–0.0	0.98
HA384 × RHA373	2782.3	1476.1	0.0001	175.0	24.7	0.0001	420	–44.7	0.003	73.9	–1.5	0.3
HA372 × RHA274	2779.8	1541.2	0.0001	177.1	25.4	0.0001	301	–31.5	0.003	74.5	–0.2	0.86
HA821 × RHA373	2700.3	1409.7	0.0001	170.9	25.5	0.0001	434	–16.8	0.26	72.8	–3.7	0.01
HA384 × RHA274	2593.5	1387.3	0.0001	169.2	18.9	0.0001	431	–33.5	0.03	73.9	–1.5	0.28
HA372 × RHA373	2648.3	1473.3	0.0001	177.9	26.3	0.0001	406	–16.2	0.28	76.5	1.9	0.18
HA852 × RHA373	2652.7	1461.8	0.0001	173.8	40.4	0.0001	417	3.9	0.81	73.5	1.4	0.4
HA89 × RHA373	2557.0	1498.9	0.0001	170.8	45.1	0.0001	417	–34.5	0.02	75.1	–1.6	0.26

yield *per se* and hybrid seed yield ($r = 0.01$). This difference can be attributed to branching differences. B-lines are unbranched, whereas R-lines are branched. The seed yield of a branched line is greatly affected by infloresence morphology and is a poor predictor of the genetic merit of the R-line as a parent in an unbranched hybrid.

Heterosis effects were significant for seed yield and plant height, but were not significant for seed oil concentration and days to flowering (Table 3). Heterosis was greatest for seed yield, and hybrid seed yield was significantly correlated ($r = 0.94$) with percent heterosis for seed yield. Heterosis for seed yield is usually significant in sunflower, whereas heterosis for seed oil concentration is seldom significant (Russell 1953; Gupta and Khanna 1982; Areco et al. 1985; Bedov 1985; Tersac et al. 1993; Fick and Miller 1997). Leon et al. (1995) showed that QTL effects for seed and kernel oil concentration were mostly additive in a confection by oilseed population and that most of the genetic variance for oil concentration was additive (two QTLs had dominant or incompletely dominant effects).

The performance of hybrids within and between heterotic groups

Genetic diversity within the B_C heterotic group and $B_B \times B_C$ heterotic pattern seems to be greater than within the B_B, R_A, and R_B heterotic groups (Table 4). Hybrids with HA383, HA384, and HA821 performed differently from hybrids with other B-lines from the B_C

Table 4 Least square means for seed yields (kg ha^{-1}) of hybrids within and between heterotic groups of sunflower

Heterotic group	Heterotic group			
	B_B	B_C	R_A	R_B
B_B	1968.4	2442.1	2233.1	2495.7
B_C		2516.7	2460.6	2674.3

heterotic group when crossed to the same testers; hence, although originally assigned to the B_C heterotic group (Table 1), HA383, HA384 and HA821 may comprise a separate heterotic group. Certain A × B hybrids were heterotic and outperformed or performed as well as A × R hybrids, whereas hybrids between closely related B-lines, as expected, performed more poorly than A × R hybrids.

The outstanding performance of several within-heterotic-group hybrids suggests that the heterotic groups are genetically diverse. The mean seed yield of $B_C \times B_C$ hybrids was not significantly different from the mean seed yields of $B_B \times B_C$, $B_B \times R_B$ and $B_C \times R_A$ hybrids. $B_C \times B_C$ hybrids produced significantly more seed than $B_B \times R_A$ hybrids and significantly less seed than $B_C \times R_B$ hybrids (Table 4). $B_B \times B_B$ hybrids produced significantly lower seed yields than hybrids from other heterotic patterns, but still produced significantly more seed than B-lines (1968 kg ha^{-1} for $B_B \times B_B$ hybrids versus 1044 kg ha^{-1} for B-lines) (Table 4).

The proposed heterotic groups for sunflower, in contrast to corn, are not strictly composed of very closely related lines (Godshalk et al. 1990; Melchinger et al. 1990; Smith et al. 1990; Dudley et al. 1991; Smith and Smith 1992). The mean genetic distances within heterotic groups could be decreased by splitting lines into additional groups, but statistically significant subgroups were not found (the distances between lines were not great enough to justify additional groups or clusters) (Hongtrakul et al. 1997; Cheres and Knapp 1998). DNA fingerprints and pedigrees did not separate lines into groups beyond those shown (Table 1). Despite this, the seed yields of within-group hybrids show that significant genetic diversity is present within groups.

HA383 and HA384 from the B_C heterotic group and hybrids from the $B_C \times R_B$ heterotic pattern had the highest yields in this study. Hybrids from the $B_C \times B_C$ heterotic pattern were a close second. Splitting the B_C heterotic group into two groups seems warranted. Specifically, we are proposing to assign HA383, HA384 and HA821 to a third oilseed B-line heterotic group called B_E.

Genetic distance as a predictor of heterosis and hybrid performance

G_D was significantly correlated with the seed yield and plant height of A × R and A × B hybrids and the percent heterosis for the seed yield of A × B hybrids (Table 5).

Table 5 Correlations between genetic distances (G_C or G_D) and least square means (LSMs) and heterosis effects for seed yield (kg ha^{-1}) and plant height (cm) for 22 A × R and 13 A × B hybrids tested in field trials at Corvallis, Ore., and Casselton, N.D., in 1996 and 1997

Variable	A × R		A × B	
	G_D	G_C	G_D	G_C
	Seed yield (kg ha^{-1})			
LSM	0.63*	–0.02	0.79*	0.54
Heterosis effect	0.21	0.15	0.76*	0.56
	Plant height (cm)			
LSM	0.47*	0.14	0.70*	0.50
Heterosis effect	–0.40	0.23	0.45	0.59

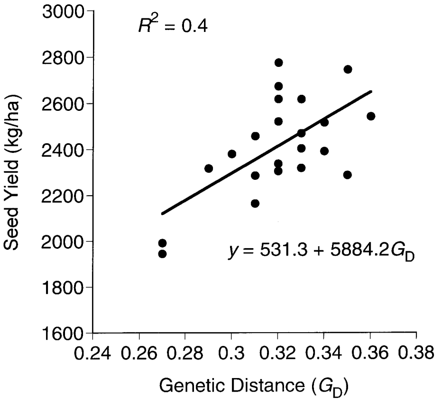

Fig. 2 Simple linear regression of seed yields (kg ha^{-1}) on genetic distances (G_D) for 22 A × R hybrids of sunflower tested at Corvallis, Ore., and Casselton, N.D., in 1996 and 1997

G_C was not correlated with seed yield or plant height or the percent heterosis for seed yield or the plant height of A × R or A × B hybrids (Table 5). G_D was significantly correlated with the seed yields and plant heights of A × R (0.63) and A × B (0.79) hybrids, whereas G_C was not significantly correlated with the seed yields or plant heights of either (Table 5). G_D, although correlated with seed yield, was a poor predictor of hybrid performance (seed yield) (Fig. 2). Hybrids with $G_D > 0.34$ were ranked 2, 6, and 19 out of 22 for seed yield (Fig. 2). Similarly, hybrids with $G_D = 0.32$ were ranked 1, 3, 4, 7, 14, and 17 out of 22 for seed yield; thus, hybrid performance varied tremendously among hybrids with similar genetic distances. This result was expected and was consistent with results reported in other crop species (Lee et al. 1989; Godshalk et al. 1990; Melchinger et al. 1990; Dudley et al. 1991; Smith and Smith 1992; Martin et al. 1995; Zhang et al. 1995 a; Diers et al 1996).

Although genetic distance *per se* is a poor predictor of cross or hybrid performance (Smith et al. 1990; Charcosset et al. 1991; Dudley et al. 1991; Bernardo 1992; Smith and Smith 1992), promising methods have been developed for predicting hybrid performance from genetic distances (Bernardo 1996; Charcosset et al.

1998). Bernardo (1996) proposed using best linear unbiased prediction (BLUP) to predict the performance of untested hybrids and showed that BLUP accurately predicted hybrid performance within the limits imposed by non-genetic variances. BLUP and other methods (Bernardo 1996; Charcosset et al. 1998) should be powerful tools for choosing potentially promising hybrids in sunflower, something that cannot be confidently done using genetic distances alone.

Acknowledgements Oregon Agric. Exp. Stn. Technical Paper No. 11399. This research was funded by a grant (95–37300–1573) to S.J. Knapp from the USDA National Research Initiative Competitive Grants Program (NRIGCP).

References

Areco CM, Alvarez D, Ljubich A (1985) Diallelic analysis of grain yield and oil content in six sunflower cultivars. In: Proc 11th Int Sunflower Conf, Mar del Plata, Buenos Aires, Argentina, Assoc Argentina Girasol, pp 755–759

Bedov S (1985) A study of combining ability for oil and protein contents in seed of different sunflower inbreds.. In: Proc 11th Int Sunflower Conf, Mar del Plata, Buenos Aires, Argentina, Assoc Argentina Girasol, pp 675–682

Bernardo R (1992) Relationship between single-cross performance and molecular markers in maize. Theor Appl Genet 85: 1055–1062

Bernardo R (1996) Best linear unbiased prediction of maize single-cross performance. Crop Sci 36:50–56

Berry ST, Allen RJ, Barnes SR, Caligari PDS (1994) Molecular-marker analysis of *Helianthus annuus* L. 1. Restriction fragment length polymorphism between inbred lines of cultivated sunflower. Theor Appl Genet 89:435–441

Charcosset AM, Lefort-Buson M, Gallais A (1991) Relationship between heterosis and heterozygosity at marker loci: a theoretical computation. Theor Appl Genet 81:571–575

Charcosset AM, Bonnisseau B, Touchebeuf O, Burstin J, Dubreuil P, Barriere Y, Gallais A, Denis JB (1998) Prediction of maize hybrid silage performance using marker data: comparison of several models for specific combining ability. Crop Sci 38: 38–44

Cheres MT, Knapp SJ (1998) Ancestral origins and genetic diversity of cultivated sunflower: analysis of the pedigrees of public germplasm. Crop Sci 38:1476–1482

Diers BW, Macvetty PBE, Osborn TC (1996) Relationship between heterosis and genetic distance based on restriction fragment length polymorphism markers in oilseed rape (*Brassica napus* L.). Crop Sci 36:79–83

Dudley JW, Shaghai Maroof MA, Rufener GK (1991) Molecular markers and grouping of parents in a maize breeding program. Crop Sci 31:718–723

Fick GN, Miller JF (1997) Sunflower breeding. In: Sunflower technology and production. Crop Sci Soc America, Madison, Wisconsin, pp 395–439

Gentzbittel L, Zhang Y-X, Vear F, Griveau B (1994) RFLP studies of genetic relationships among inbred lines of the cultivated sunflower, *Helianthus annuus* L.: evidence for distinct restorer and maintainer germ plasm pools. Theor Appl Genet 89:419–425

Gerdes JT, Tracy WF (1994) Diversity of historically important sweet corn inbreds as estimated by RFLPs, morphology, isozymes, and pedigree. Crop Sci 34:26–33

Godshalk EB, Lee M, Lamkey KR (1990) Relationship of restriction fragment length polymorphisms to single-cross hybrid performance in maize. Theor Appl Genet 80:273–280

Gupta KK, Khanna KR (1982) Gene action and heterosis for oil yield and component characters in sunflower. Indian J Genet Plant Breed 42: 265–271

Hongktrakul V, Huestis GM, Knapp SJ (1997) Amplified fragment length polymorphisms as a tool for DNA fingerprinting sunflower germ plasm: genetic diversity among oilseed inbred lines. Theor Appl Genet 95:400–407

Lee M, Godshalk EB, Lamkey KR, Woodman WW (1989) Association of restriction fragment length polymorphisms among maize inbreds with agronomic performance of their crosses. Crop Sci 29:1067–1071

Leon AJ, Lee M, Rufener GK, Berry ST, Mowers RP (1995) Use of RFLP markers for genetic linkage analysis of oil percentage in sunflower seed. Crop Sci 35:558–564

Martin JM, Talbort LE, Lanning SP, Blake NK (1995) Hybrid performance in wheat as related to parental diversity. Crop Sci 35:104–108

Melchinger AE, Lee M, Lamkey KR, Woodman WW (1990) Genetic diversity for restriction fragment length polymorphisms: relation to genetic effects in maize inbreds. Crop Sci 30: 1033–1040

Mumm RH, Dudley JW (1994) A classification of 148 U.S. maize inbreds. I. Cluster analysis based on RFLPs. Crop Sci 34: 842–851

Mumm RH, Hubert LJ, Dudley JW (1994) A classification of 148 U.S. maize inbreds. II. Validation of cluster analysis based on RFLPs. Crop Sci 34:852–869

Robertson JA, Morrison WH (1979) Analysis of oil content in sunflower by wide-line NMR. J Am Oil S°C 56:961–964

Russell WA (1953) A study of inter-relationships of seed yield, oil content, and other agronomic characters with sunflower inbred lines and their topcrosses. Can J Agric Sci 3:291–314

Schneiter AA, Miller JF (1981) Description of sunflower growth stages. Crop Sci 21:901–903

Smith JSC, Smith OS, Bowen SL, Tenborg RA, Wall SJ (1991) The description and assessment of distances between lines of maize. III. A revised scheme for the testing of distinctiveness between inbred lines utilizing DNA RFLPs. Maydica 36: 213–226

Smith JSC, Smith OS, Wright S, Wall SJ, Walton M (1993) Diversity of U.S. hybrid maize germplasm as revealed by restriction fragment length polymorphisms. Crop Sci 32:598–604

Smith OS, Smith JSC (1992) Measurement of genetic diversity among maize inbreds; a comparison of isozymic, RFLP, pedigree, and heterosis data. Maydica 37:53–60

Smith OS, Smith JSC, Bowen SL, Tegborg RA, Wall SJ (1990) Similarities among a group of elite maize inbreds as measured by pedigree, F_1 heterosis, and RFLPs. Theor Appl Genet 80: 833–840

Tersac M, Vares D, Vincourt P (1993) Combining groups in cultivated sunflower populations (*Helianthus annuus* L.) and their relationship with country of origin. Theor Appl Genet 87: 603–608

Tersac M, Blanchard P, Brunel D, Vancourt P (1994) Relations between heterosis and enzymatic polymorphisms in populations of cultivated sunflower (*Helianthus annuus* L.). Theor Appl Genet 88:49–55

Zhang Q, Gao YJ, Saghai Maroof MA, Yang SH, Li JX (1995 a) Molecular divergence and hybrid performance in rice. Mol Breed 1:133–142

Zhang YX, Gentzbittel L, Vear F, Nicholas P (1995 b) Assessment of inter- and intra-inbred line variability in sunflower (*Helianthus annuus* L.) by RFLPs. Genome 38:1040–1048