Theor Appl Genet (2007) 115:27–34
DOI 10.1007/s00122-007-0537-x

ORIGINAL PAPER

Heterotic patterns in rapeseed (*Brassica napus* L.): I. Crosses between spring and Chinese semi-winter lines

W. Qian · O. Sass · J. Meng · M. Li ·
M. Frauen · C. Jung

Received: 1 August 2006 / Accepted: 10 March 2007 / Published online: 24 April 2007

Abstract Chinese semi-winter rapeseed is genetically diverse from Canadian and European spring rapeseed. This study was conducted to evaluate the potential of semi-winter rapeseed for spring rapeseed hybrid breeding, to assess the genetic effects involved, and to estimate the correlation of parental genetic distance (GD) with hybrid performance, heterosis, general combining ability (GCA) and specific combining ability (SCA) in crosses between spring and semi-winter rapeseed lines. Four spring male sterile lines from Germany and Canada as testers were crossed with 13 Chinese semi-winter rapeseed lines to develop 52 hybrids, which were evaluated together with their parents and commercial hybrids for seed yield and oil content in three sets of field trials with 8 environments in Canada and Europe. The Chinese parental lines were not adapted to local environmental conditions as demonstrated by poor seed yields per se. However, the hybrids between the Chinese parents and the adapted spring rapeseed lines exhibited high heterosis for seed yield. The average mid-parent heterosis was 15% and ca. 50% of the hybrids were superior to the respective hybrid control across three sets of field trials. Additive gene effects mainly contributed to hybrid performance since the mean squares of GCA were higher as compared to SCA. The correlation between parental GD and hybrid performance and heterosis was found to be low whereas the correlation between $GCA_{(f+m)}$ and hybrid performance was high and significant in each set of field trials, with an average of $r = 0.87$ for seed yield and $r = 0.89$ for oil content, indicating that hybrid performance can be predicted by $GCA_{(f+m)}$. These results demonstrate that Chinese semi-winter rapeseed germplasm has a great potential to increase seed yield in spring rapeseed hybrid breeding programs in Canada and Europe.

Introduction

Rapeseed (*Brassica napus* L., AACC), originating from spontaneous hybridisations between *B. rapa* (AA) and *B. oleracea* (CC) in Europe (U N 1935), is an important oilseed crop due to the high nutritional quality of its oil and meal. Recently, attention has been given to its potential as a renewable resource for biofuel production.

However, the genetic basis of commonly used rapeseed is quite narrow which is limiting the breeding progress for this species (Gómez-Campo 1999). One reason for this could be the short history of cultivation in comparison to its

---

Communicated by T. Lübberstedt.

W. Qian · C. Jung (✉)
Plant Breeding Institute, Christian-Albrechts-University of Kiel,
Kiel 24118, Germany
e-mail: c.jung@plantbreeding.uni-kiel.de

W. Qian · O. Sass · M. Frauen
Norddeutsche Pflanzenzucht Hans-Georg Lembke KG,
Hohenlieth 24363, Germany

W. Qian · J. Meng
National Key Laboratory of Crop Genetic Improvement
and National Center of Crop Molecular Breeding, Huazhong
Agricultural University, Wuhan 430070, China

W. Qian
School of Agronomy and Life Science, South West University,
Chongqing 400716, China

M. Li
School of Life Science and Technology, Huazhong University
of Science and Technology, Wuhan 430070, China

two parental species (Becker et al. 1995). In practical breeding, locally adapted varieties are preferred as crossing partners although substantial genetic diversity exists among spring lines from Europe and Canada, winter lines from Europe and semi-winter lines from China (Becker et al. 1995; Diers and Osborn 1994; Ma et al. 2000). Two strategies can be adapted to widen the genetic diversity. One strategy is to introgress genome components from the two parental species or other relative species. During evolution and domestication of the genus of rapeseed the structure of its 'A' and 'C' genomes became much different from its related Brassica species (Song et al. 1988b, 1995). In terms of the 'A'-genome, it is known that Asian *B. rapa* differs from European *B. rapa* which is believed to be one parent of modern rapeseed (Song et al. 1988a; Qian et al. 2003; Zhao et al. 2005). More recent studies have found that the introgression of Asian *B. rapa* can widen the genetic diversity of rapeseed (Qian et al. 2006). Based on the differences between Brassica genomes, a concept of ''subgenomic heterosis'' was proposed to increase heterosis for biomass and seed yield, according to which hybrids were developed between current rapeseed cultivars and ''new type'' rapeseed lines carrying the genomic components of other species, such as the 'A' genome from *B. rapa* and the 'C' genome from *B. carinata* (Qian et al. 2003, 2005; Li et al. 2006).

The other strategy is to use non-adapted germplasm from other geographical regions. Such material may contain favourable alleles not present in adapted germplasm. Butruille et al. (1999) and Quijada et al. (2004) found that the introgression of winter germplasm could increase the yield of spring rapeseed hybrids. Lefort-Buson et al. (1987) observed high heterosis for seed yield between European winter and Asian rapeseed cultivars, which had been adapted to European environments. Udall et al. (2006) identified alleles in Asian semi-winter germplasm contributing to the increase in seed yield of spring rapeseed hybrids.

Heterotic pattern is a term to describe a group of related or unrelated genotypes from the same or different populations, which display similar combining ability and heterotic response when crossed with genotypes from other genetically distinct germplasm groups (Melchinger and Gumber 1998). Heterotic patterns have been widely used in hybrid breeding programs, such as maize and sunflower (Beck et al. 1991; Cheres et al. 2000; Crossa et al. 1990; Reif et al. 2003; Vasal et al. 1992a, b, c).

High heterosis has been observed in crosses between Chinese semi-winter and winter rapeseed (Lefort-Buson et al. 1987) and between Chinese semi-winter and spring rapeseed (Udall et al. 2004). Since these germplasm are highly divergent, heterotic pattern can be anticipated between Chinese semi-winter rapeseed and spring rapeseed, and between Chinese semi-winter rapeseed and true winter rapeseed germplasm.

Positive correlation between heterosis and parental genetic diversity was demonstrated for hybrid combinations within the same ecotype group like spring by spring (Diers et al. 1996; Riaz et al. 2001), winter by winter (Ali et al. 1995) and semi-winter by semi-winter rapeseed hybrids (Yu et al. 2005). However, little is known about the relationship between heterosis and parental genetic distance when parents from different ecotypes are used. In this study, Chinese ''normal'' lines and new rapeseed lines carrying introgressions from Chinese *B. rapa* were crossed with spring rapeseed lines from Europe and Canada, and these hybrids were evaluated across eight environments in Europe and Canada in two years with the following objectives: (1) to evaluate the potential of Chinese semi-winter rapeseed as parents for spring rapeseed hybrid breeding, (2) to assess the genetic effects involved, and (3) to estimate the correlation of parental genetic distance (GD) with hybrid performance, heterosis, general combining ability (GCA) and specific combining ability (SCA) among combinations between Chinese semi-winter and spring rapeseed.

Materials and methods

Plant materials and genetic distances

Thirteen semi-winter type accessions from China were used as pollinators: nine high yielding new type rapeseed lines with introgressions from Chinese *B. rapa* as determined by molecular marker analysis, three F_6 lines derived from crosses between Chinese *B. napus* and Chinese *B. rapa*, three BC_1F_6 lines derived from crosses (Chinese *B. napus* × Chinese *B. rapa*) × Chinese *B. rapa* (Qian et al. 2005), three new type F_4 lines derived from crosses Chinese *B. napus* × (*B. carinata* × Chinese *B. rapa*) (Li et al. 2005), and four normal rapeseed types (without known alien introgressions) which had been used as parents to develop the new type lines listed above. Four male sterile spring lines (MSL) of the seed company Norddeutsche Pflanzenzucht Hans-Georg Lembke KG were used as females, MSL 04 and MSL 05 from Germany and MSL 06 and MSL 07 from Canada. A total of 52 hybrid combinations were developed using NC design II (Comstock and Robinson 1952). The genetic distances (GD) between these accessions based on AFLP had been previously reported (Qian et al. 2006). For calculation of GD the method of Nei and Li (1979) had been used. The average genetic distance was 0.431 ± 0.058 between the two parent groups, 0.400 ± 0.087 among the males and 0.171 ± 0.027 among the females. Four commercial hybrid varieties were used as controls: Siesta, PF 7615, Terra and PF8293, which had been produced by using the four female lines (see above) as parents. This allows to compare the hybrid combinations sharing the same female.

Field evaluation

The hybrid combinations were evaluated in three sets of field trials with 8 environments: in the first set of field trials, the 26 hybrids derived from two Canadian MSL lines were tested at Morden and Thornhill (Canada) in 2005; in the second set of field trials, the 26 hybrids derived from two European MSL lines were planted in three environments in Germany, Hohenlieth in 2004, Moosburg and Hovedissen in 2005; in the third set of field trials, all 52 combinations were evaluated in three environments, two of these at Odder (Denmark) in 2004 and 2005, and the third one at Hohenlieth in 2005. In order to decrease the influence of edge effects from heterosis, the plot block was split into two subplot blocks. The hybrids were sown in one subplot block together with the control, and Chinese male lines and the maintainer lines of MSL females were sown in the other subplot block, in a randomized complete design in each subplot block with two replications. The size of the plots ranged from 10 to 13.1 m^2 depending on the amount of seeds and the local field practice, with a density of 50 seeds/m^2. The data were collected and adjusted for seed yield (dt/ha), and oil content (%) with 9% humidity.

Data analysis

General combining ability (GCA) among parents and specific combining ability (SCA) among combinations were calculated separately for each environment using the following statistical model:

$$X_{ijk} = u + g_i + g_j + s_{ij} + b_k + e_{ijk},$$

where X_{ijk} is the observed value of the combination between ith and jth parent in the kth replication; u is the mean of all observation values; g_i and g_j are the GCA values of the ith and jth parents, respectively; S_{ij} is the SCA for the cross involving ith and jth parent; b_k is the replication effect and e_{ijk} is the error. Significance of GCA values was determined by using the t-test. The mean squares of GCA from the female and male group ($\sigma^2_{\mathrm{GCA(f\,+\,m)}}$) and of SCA ($\sigma^2_{\mathrm{SCA}}$) were estimated in order to determine the importance of genetic effects using the ratio, $(\sigma^2_{\mathrm{GCA(f\,+\,m)}})/(\sigma^2_{\mathrm{GCA(f\,+\,m)}} + \sigma^2_{\mathrm{SCA}})$ (Gao 1986).

Analysis of variance (ANOVA) was done among hybrid combinations across all environments with the GLM procedure using the Statistical Analysis System (SAS) (SAS Institute 1992). Pearson's simple correlation coefficients among traits of interest were calculated, and significance of comparisons between groups of hybrids was tested by the F test. Relative hybrid performance (in %) in comparison with the mean of both parents (mid-parent heterosis, MPH) and in comparison with the hybrid control (over-control, OC) were calculated as follows: MPH = 100 × (F1 – MP)/MP and OC = 100 × (F1 - CK)/CK, where F1 = hybrid performance, MP = mean performance of both parents, and CK = performance of the commercial hybrid control.

Results

Parental genetic diversity and hybrid performance

The two parental groups exhibited great differences in their flowering times and in some morphological characters such as leaf size and colour, whereas their hybrids showed intermediate characters. Chinese rapeseed parents were poorly adapted to spring growing environments. They were inferior to the locally adapted spring parents for seed yield by 17.9% across 8 environments. In contrast, hybrids between Chinese and adapted spring parents exhibited high heterosis and high yield performance in three sets of field trials (Table 1). For seed yield, ca. 50% of the hybrids were superior to the respective controls. On average, mid-parent heterosis was 15% for seed yield across three sets of field trials (Table 1). In general the hybrid combinations had better yield performance in European environments than in Canadian environments, and in comparison with oil content, seed yield exhibited wider variation for MPH (Table 1).

Significant differences between genotypes were detected for seed yield and oil content (Table 2). Moreover, significant genotype × environment interactions were found for both traits ($P \leq 0.01$). The interactions between females and males were found to be not significantly different from zero for both traits. However, highly significant differences were observed between males for both traits and between females for seed yield ($P \leq 0.01$). These results indicate that additive gene effects play an important role in hybrid performance. No significant differences were found between the combinations derived from the new type rapeseed and those from the Chinese normal cultivars across 8 environments ($P = 0.72$ for seed yield, $P = 0.27$ for oil content), and between combinations derived from European MSL and those from Canadian MSL parents for seed yield ($P = 0.85$), all of which were evaluated in the third set of field trial.

The importance of additive effects of genes was further supported by combining ability analysis. The ratios of mean squares $(\sigma^2_{\mathrm{GCA(f\,+\,m)}})/(\sigma^2_{\mathrm{GCA(f\,+\,m)}} + \sigma^2_{\mathrm{SCA}})$, were rather high for both traits in all sets of field trials (Table 3). The average ratio was 0.96 for seed yield and 0.93 for oil

Table 1 Hybrid performance (HP) between Chinese semi-winter and spring rapeseed lines grown in 3 sets of field trials (FT) with 8 different environments for seed yield and oil content

Field trials[a]	HP[b]	MPH	OC
	Seed yield (dt/ha)		
FT1	18.08 (12.45, 21.70)	5.21 (–27.57, 26.24)	10.30 (–44.05, 76.96)
FT2	33.80 (30.10, 35.90)	17.15 (4.31, 24.43)	–8.77 (–29.23, 7.84)
FT3	34.80 (31.54, 38.89)	21.82 (10.42, 36.14)	–0.24 (–33.08, 36.90)
Mean	28.90 (12.45, 38.89)	14.73 (–27.57, 36.14)	0.43 (–44.05, 76.96)
	Oil content (%)		
FT1	42.73 (41.53, 44.33)	3.53 (0.61, 7.39)	–4.21 (–11.47, 2.38)
FT2	43.44 (42.27, 44.62)	–1.94 (–4.59, 0.72)	–4.45 (–13.12, 3.77)
FT3	45.11 (43.52, 46.65)	0.50 (–3.04, 3.94)	–4.08 (–11.69, 5.97)
Mean	43.76 (41.53, 46.65)	0.70 (–4.59, 7.39)	–4.25 (–13.12, 5.97)

Mid-parent heterosis (MPH) and relative performance as compared to the commercial hybrid control (OC) were calculated

[a] FT1 = a set of 26 hybrid combinations derived from two Canadian MSLs were grown in 2005 across two Canadian environments, Morden and Thornhill; FT2 = a set of 26 hybrids derived from two European MSLs were grown across three Germany environments, Hohenlieth in 2004, Moosburg and Hovedissen in 2005; FT3 = a set of 52 hybrids were grown across three European environments, Hohenlieth in 2005, and Odder in 2004 and 2005, Denmark

[b] Mean (min, max)

Table 2 ANOVA from a field test with 52 hybrid combinations between Chinese semi-winter and spring rapeseed lines across 8 environments

Source	*df*	Mean squares	
		Seed yield	Oil content
Environment	7	3686.32**	109.42**
Genotype	51	18.05**	4.83**
Female	3	81.70**	2.61
Male	12	39.44**	16.55**
Female × male	36	5.55	1.26
Genotype × environment	226	9.44**	1.37**

*,** Significant at $P = 0.05$ and 0.01

content, respectively. This indicates that both, additive and non-additive effects contributed to seed yield and oil content, but additive effects were much more important than non-additive effects.

General combining abilities were calculated for each of sets of field trials (Table 3). A number of male lines exhibited significant GCA under different sets of field trials, e.g. HAU 01, HAU 02 and HAU 03 had significant positive GCA, while HAU 09 and HAU 12 exhibited significant negative GCA for oil content in 2 sets of field trials. Significant positive GCA effects were found for HAU 14 in 2 sets of field trials for seed yield.

Correlation between genetic distances, hybrid performance, heterosis and combining ability

Parental GD positively correlated with mid-parent heterosis for both traits in all sets of field trials, with correlations ranging from 0.28 to 0.64 for seed yield and from 0.42 to 0.48 for oil content (Table 4). In contrast, correlation was generally found to be low between parent GD and hybrid performance, $GCA_{(f+m)}$ and SCA. However, a high and significant correlation between $GCA_{(f+m)}$ effects and hybrid performance was found in each sets of field trials, with an average of $r = 0.87$ for seed yield and $r = 0.89$ for oil content. It is interesting that high correlation of GCA from males with hybrid performance was detected across three sets of field trials ($r = 0.79$ for seed yield and $r = 0.86$ for oil content on average).

Discussion

Heterosis prediction

Predicting heterosis is of utmost importance in hybrid breeding. Since genetic distances can be easily determined by molecular markers predicting heterosis by the relatedness of the parents is a challenge. Positive correlations between heterosis and parental GD based on morphological characters and molecular markers have been reported for Brassica (Teklewold and Becker 2006; Yu et al. 2005). More reports have been published for maize (Smith et al. 1990) and rice (Liu and Wu 1998; Zhang et al. 1994, 1996), but the extent of correlation varied widely from one trait to another and from one dataset to another. From data of different crop species, Melchinger (1999) reported that the association between parental GD and mid-parent heterosis decreased from crosses between related lines to intra-group and inter-group crosses. This was supported by

Table 3 General combining ability (GCA) for seed yield (dt/ha) and oil content (%) from a field test with 52 hybrid combinations in 3 sets of field trials with 8 environments

Parent	Seed yield			Oil content		
	FT1	FT2	FT3	FT1	FT2	FT3
Female						
MSL 04		–0.13	0.43		0.09	0.04
MSL 05		0.13	–0.54		–0.09	0.27
MSL 06	–0.46		–1.21*	0.20		–0.27
MSL 07	0.46		1.32**	–0.20		–0.04
SE	0.52	0.27	0.27	0.14	0.11	0.11
Male						
HAU 01	0.04	1.16	0.13	1.14	0.70*	1.11**
HAU 02	0.31	–2.39**	1.41*	0.32	1.12**	0.95**
HAU 03	0.63	–1.29	–0.63	0.14	0.74*	0.78**
HAU 04	1.06	0.71	0.50	–0.04	–0.86**	–0.40
HAU 05	–1.15	–0.63	–1.40*	–0.74	–0.52	–0.58*
HAU 06	0.19	0.77	1.70**	–0.14	0.73*	0.17
HAU 08	–0.95	–0.43	–0.26	0.36	–0.50	–0.87**
HAU 09	1.09	1.85*	–0.12	0.16	–0.76*	–1.21**
HAU 10	0.85	–0.47	–0.28	0.02	–0.54	–0.92**
HAU 11	1.40	1.23	–1.49**	–0.14	0.08	0.77**
HAU 12	–5.36**	–0.75	–0.98	–0.72	–0.62*	–0.60*
HAU 13	–1.30	–0.88	–0.18	–0.34	0.36	0.41
HAU 14	3.18*	1.12	1.60**	–0.01	0.07	0.40
SE	1.32	0.69	0.49	0.37	0.28	0.21
Ratio	1	0.99	0.88	1	0.93	0.87

The ratio of $(\sigma^2_{GCA(f+m)})/(\sigma^2_{GCA(f+m)} + \sigma^2_{SCA})$ was calculated for two traits in three sets of field trials. The parents were four male sterile lines (MSL 04–MSL 07), nine new type pollinator lines with introgressions from *B. carinata* and Chinese *B. rapa* (HAU 01–HAU 10 except HAU 07) and four Chinese normal type pollinator lines (HAU 11–HAU 14). Field trials (FT1–FT3) are explained in Table 1

*, ** Significant at $P = 0.05$ and 0.01

the data of our study, which showed that the parental GD weakly correlated with mid-parent heterosis because the parents came from two far distinct gene pools, Chinese semi-winter and spring rapeseed. Thus, it seems to be difficult to predict hybrid performance and/or heterosis in crosses between Chinese semi-winter and spring rapeseed by their parental GD.

Interestingly, in our study a high positive correlation of hybrid performance with the total of parental GCA effects and GCA effects from males was found. Hence it was possible to predict hybrid performance from GCA effects. This can be explained by the main contribution of additive effects to hybrid performance. This is consistent with results published by Dhillon et al. (1990), who found that promising hybrid combinations can be identified mainly by their parental GCA effects in inter-group maize hybrids between European flint and dent lines, with predominance of σ^2_{GCA} over σ^2_{SCA}.

Table 4 Correlations between parental genetic distance (GD) and four different parameters calculated for seed yield and oil content from three sets of field trials with eight environments

Field trials	GD				HP		
	HP	SCA	GCA	MPH	SCA	GCA	MPH
Seed yield							
FT1	0.12	0.04	0.11	0.28	0.44*	0.90**	0.64**
FT2	0.18	–0.11	0.27	0.50**	0.49*	0.87**	0.42*
FT3	0.08	0.02	0.09	0.64**	0.55**	0.83**	0.24**
Mean	0.13	–0.02	0.16	0.47	0.49	0.87	0.43
Oil content							
FT1	0.05	0.09	0.01	0.42*	0.46*	0.89**	0.55**
FT2	–0.24	0.02	–0.28	0.46*	0.41*	0.91**	0.16
FT3	–0.34*	0.07	–0.43**	0.48*	0.47**	0.88**	0.32*
Mean	–0.18	0.06	–0.23	0.45	0.45	0.89	0.34

HP hybrid performance, *MPH* mid-parent heterosis, *GCA* total general combining ability of both parents, *SCA* specific combining ability

*, ** Significant at $p = 0.05$ and 0.01

Heterotic pattern between spring and Chinese semi-winter lines

It is an obvious advantage of heterotic pattern to predetermine to a large extent the type of germplasm used in a hybrid-breeding program (Melchinger and Gumber 1998). Theoretical and experimental investigations suggest that grouping of germplasm into divergent heterotic groups can reduce the variance of SCA and increase the variance of GCA, and prediction of heterosis at an early stage of the breeding program becomes more efficient if based on GCA effects (Melchinger 1999; Reif et al. 2006). In this study, high heterosis and predominance of σ^2_{GCA} over σ^2_{SCA} were detected among hybrid combinations between Chinese semi-winter and spring rapeseed. Thus, spring and Chinese semi-winter rapeseed are suggested to constitute heterotic pattern, which may be used in spring rapeseed hybrid breeding programs.

However, this heterotic pattern should be further optimized by improving adaptation of the Chinese paternal lines to spring rapeseed environments. The Chinese lines used in this study had been selected without consideration of adaptation to spring rapeseed-growing conditions. In most cases they flowered much later than spring lines, some semi-winter lines could not even be harvested due to very late ripening (data not shown). In our original mating design 14 Chinese semi-winter lines were included as male parents, but later one line was discarded due to its very late flowering. Moreover, high susceptibility to blackleg (*Leptosphaeria maculans*) excludes direct use of semi-winter rapeseed lines for hybrid breeding in Canada.

It should be noted that genetic diversity within the Chinese semi-winter rapeseed group was high (Qian et al. 2006), and that additive genetic effects mainly contributed to hybrid performance. Further selection among Chinese semi-winter rapeseed for superior combining ability is possible. Although substantial genetic diversity among Canadian and European spring rapeseed as females was found, the smaller genetic diversity in comparison with males and similar combining ability effects for seed yield within Canadian and European spring rapeseed indicate low genetic variation within and between these two groups of accessions, which is in accordance with previous results (Grant and Beversdorf 1985; Brandle and McVetty 1990). In conclusion, there is a demand for increasing the genetic diversity of spring rapeseed in Canada and Europe.

Subgenomic heterosis in rapeseed

Previous studies have shown that gene introgressions from related species can widen the genetic diversity of rapeseed, and result in subgenomic heterosis for biomass and seed yield (Qian et al. 2003, 2005, 2006; Li et al. 2006). In this study, the new type rapeseed lines (for example, HAU 04 and HAU 06) exhibited stronger heterotic potential in comparison with their parental *B. napus* (HAU 12 and HAU 13) (Table 3), but no general rule was found for hybrid combinations from new type rapeseed and Chinese normal cultivars. There are two explanations for lack of significant differences between new type and normal rapeseed. First, gene introgression into new rapeseed lines was not properly identified. Qian et al. (2005) identified some DNA segments from *B. rapa* with positive and negative effects on seed yield and yield components demonstrating that genome introgressions can have opposite effects. Similar studies on introgressions from exotic germplasm were reported for rice (Septiningsih et al. 2003), wheat (Huang et al. 2003) and tomato (Frary et al. 2004). Another explanation is that only parts of the genomes from Chinese *B. rapa* and *B. carinata* were introduced into new type rapeseed lines (Qian et al. 2005; Li et al. 2005). Thus, there is a need for further characterization of genome introgressions from related Brassica species. A program was initiated to produce a series of recombinant inbred lines with alien genome introgressions for mapping of QTL responsible for heterosis in rapeseed.

Acknowledgments This work was supported by the ''Forschungs- und Entwicklungsfonds Raps''. We sincerely acknowledge the help of Dr. V. Marwede, Mr. F.H. Jensen for running the field trials in Canada and Denmark. We thank Prof. Dr. M. Hühn and Dr. A.E. Müller for critically reading the manuscript.

References

Ali M, Copeland LO, Elias SG, Kelley JD (1995) Relationship between genetic distance and heterosis for yield and morphological traits in winter canola (*Brassica napus* L.). Theor Appl Genet 91:118–121

Beck DL, Vasal SK, Crossa J (1991) Heterosis and combining ability among subtropical and temperate intermediate-maturity maize germplasm. Crop Sci 31:68–73

Becker HC, Engqvist GM, Karlsson B (1995) Comparison of rapeseed cultivars and resynthesized lines based on allozyme and RFLP markers. Theor Appl Genet 91:62–67

Brandle JE, McVetty PBE (1990) Geographical diversity, parental selection and heterosis in oilseed rape. Can J Plant Sci 70:935–940

Butruille DV, Guries RP, Osborn TC (1999) Increasing yield of spring oilseed rape hybrids through introgression of winter germplasm. Crop Sci 39:1491–1496

Cheres MT, Miller JF, Crane JM, Knapp SJ (2000) Genetic distance as a predictor of heterosis and hybrid performance within and between heterotic groups in sunflower. Theor Appl Genet 100:889–894

Comstock RE, Robinson HF (1952) Estimation of the average dominance of genes. In: Gowen JW (ed) Heterosis. The Iowa State College Press, Ames, pp 494–516

Crossa J, Vasal SK, Beck DL (1990) Combining ability estimates of CIMMYT tropical late yellow maize germplasm. Maydica 35:273–278

Dhillon BS, Gurrath PA, Zimmer E, Wermke M, Pollmer WG, Klein D (1990) Analysis of diallel crosses of maize for variation and covariation in agronomic traits at silage and grain harvests. Maydica 35:297–302

Diers BW, Osborn TC (1994) Genetic diversity of oilseed *Brassica napus* germ plasm based on restriction fragment length polymorphism. Theor Appl Genet 88:662–668

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

Frary A, Fulton TM, Zamir D, Tanksley SD (2004) Advanced backcross QTL analysis of a *Lycopersicon esculentum* × *L. pennellii* cross and identification of possible orthologs in the Solanaceae. Theor Appl Genet 108:485–496

Gao ZR (1986) Quantitative genetics. Sichuan University Press, Chengdu, pp 414–433

Gómez-Campo C (1999) Biology of *Brassica* coenospecies. Elsevier Press, Netherlands, pp 33–58

Grant I, Beversdorf WD (1985) Heterosis and combining ability estimates in spring oilseed rape (*Brassica napus* L.). Can J Genet Cytol 27:472–478

Huang XQ, Coster H, Ganal MW, Roder MS (2003) Advanced backcross QTL analysis for the identification of quantitative trait loci alleles from wild relatives of wheat (*Triticum aestivum* L.). Theor Appl Genet 106:1379–1389

Lefort-Buson M, Guillot-Lemoine B, Dattee Y (1987) Heterosis and genetic distance in rapeseed (*Brassica napus* L.): crosses between European and Asiatic selfed lines. Genome 29:413–418

Li MT, Li ZY, Zhang CY, Qian W, Meng JL (2005) Reproduction and cytogenetic characterization of interspecific hybrids derived from cross between *Brassica carinata* and *B. rapa*. Theor Appl Genet 110:1284–1289

Li M, Chen X, Meng J (2006) Intersubgenomic heterosis in rapeseed production with a partial new-typed *Brassica napus* containing subgenome A^r from *B. rapa* and C^c from *Brassica carinata*. Crop Sci 46:234–242

Liu XC, Wu JL (1998) SSR heterogenic patterns of parents for marking and predicting heterosis in rice breeding. Mol Breed 3:263–268

Ma C, Kimura Y, Fujimoto H, Sakai T, Imamura J, Fu T (2000) Genetic diversity of Chinese and Japanese rapeseed (*Brassica napus* L.) varieties detected by RAPD markers. Breeding Sci 50:257–265

Melchinger AE (1999) Genetic diversity and heterosis. In: Coors CG, Pandey S (eds) Genetic and exploitation of heterosis in crops. American Society of Agronomy, Madison, pp 99–118

Melchinger AE, Gumber RK (1998) Overview of heterosis and heterotic groups in agronomic crops. In: Lamkey KR, Staub JE (eds) Concepts and breeding of heterosis in crop plants. CSSA, Madison, pp 29–44

Nei M, Li WH (1979) Mathematical model for studying genetic variation in terms of restriction endouncleases. PNAS 76:5269–5273

Qian W, Liu R, Meng J (2003) Genetic effects on biomass yield in interspecific hybrids between *Brassica napus* and *B. rapa*. Euphytica 134:9–15

Qian W, Chen X, Fu D, Zou J, Meng J (2005) Intersubgenomic heterosis in seed yield potential observed in a new type of *Brassica napus* introgressed with partial *Brassica rapa* genome. Theor Appl Genet 110:1187–1194

Qian W, Meng J, Li M, Frauen M, Sass O, Noack J, Jung C (2006) Introgression of genomic components from Chinese *Brassica rapa* contributes to widening the genetic diversity in rapeseed (*B. napus* L.), with emphasis on the evolution of Chinese rapeseed. Theor Appl Genet 113:49–54

Quijada PA, Udall JA, Polewicz H, Vogelzang RD, Osborn TC (2004) Phenotypic effects of introgressing French winter germplasm into hybrid spring canola. Crop Sci 44:1982–1989

Reif JC, Melchinger AE, Xia XC, Warburton ML, Hoisington DA, Vasal SK, Beck D, Bohn M, Frisch M (2003) Use of SSRs for establishing heterotic groups in subtropical maize. Theor Appl Genet 107:947–957

Reif JC, Maurer HP, Kömle S, Schön CC (2006) Theortical and experimental investigations on optimum exploitation of heterosis utilizing the concept of heterotic patterns in hybrid breeding. In: International symposium: heterosis in plants, Potsdam-Golm, Germany May 18–20

Riaz A, Li Q, Quresh Z, Swati MS, Quiros CF (2001) Genetic diversity of oilseed *Brassica napus* inbred lines on sequence-related amplified polymorphism and its relation to hybrid performance. Plant Breeding 120:411–415

SAS Institute Inc. (1992) SAS Technical Report. SAS statistics Software: changes and enhancements. Release 6.07. SAS Institute Inc., Cary, North Carolina

Septiningsih EM, Prasetiyono J, Lubis E, Tai TH, Tjubaryat T, Moeljopawiro S, McCouch SR (2003) Identification of quantitative trait loci for yield and yield components in an advanced backcross population derived from the *Oryza sativa* variety IR64 and the wild relative *O. rufipogon*. Theor Appl Genet 107:1419–1432

Smith OS, Smith JSC, Bowen SL, Tenborg RA, Wall SJ (1990) Similarities among a group of elite maize inbreds as measured by pedigree, F1 grain yield, grain yield heterosis, and RFLPs. Theor Appl Genet 80:833–840

Song KM, Lu P, Tang K, Osborn TC (1995) Rapid genome change in synthetic polyploids of Brassica and its implication for polyploid evolution. PNAS 92:7719–7723

Song KM, Osborn TC, Williams PH (1988a) *Brassica* taxonomy based on nuclear restriction fragment length polymorphism (RFLP) 2. Preliminary analysis of subspecies within *B. rapa*. Theor Appl Genet 76:593–600

Song KM, Osborn TC, Williams PH (1988b) *Brassica* taxonomy based on nuclear restriction fragment length polymorphism (RFLP) 1.Genome evolution of diploid and amphidiploid species. Theor Appl Genet 75:784–794

Teklewold A, Becker HC (2006) Comparison of phenotypic and molecular distance to predict heterosis and F1 performance in Ethiopian mustard (*Brassica carinata* A. Braum). Theor Appl Genet 112:752–759

U N (1935) Genomic analysis in *Brassica* with specific reference to the experimental formation of *B.* napus and peculiar mode of ferilization. Jpn J Bot 7:389–452

Udall JA, Quijada PA, Polewicz H, Vogelzang R, Osborn TC (2004) Phenotypic effects of introducing unadapted germplasm into a spring canola hybrid. Crop Sci 44:1990–1996

Udall JA, Quijada PA, Lambert B, Osborn TC (2006) Quantitative trait analysis of seed yield and other complex traits in hybrid spring rapeseed (*Brassica napus* L.): 2. identification of alleles from unadapted germplasm. Theor Appl Genet 113:597–609

Vasal SK, Srinivasan G, Crossa J, Beck DL (1992a) Heterosis and combining ability of CIMMYT's subtropical and temperate early maturity maize germplasm. Crop Sci 32:884–890

Vasal SK, Srinivasan G, Beck DL, Crossa J, Pandey S, Leon C de (1992b) Heterosis and combining ability of CIMMYT's tropical late white maize germplasm. Maydica 37:217–223

Vasal SK, Srinivasan G, Gonzalez F, Han GC, Pandey S, Beck DL, Crossa J (1992c) Heterosis and combining ability of CIMMYT's tropical × subtropical maize germplasm. Crop Sci 32:1483–1489

Yu C, Hu SW, Zhao HX, Guo AG, Sun GL (2005) Genetic distances revealed by morphological characters, isozymes, proteins and RAPD markers and their relationships with hybrid performance in oilseed rape (*Brassica napus* L.). Theor Appl Genet 110:511–518

Zhang Q, Gao YJ, Yang SH, Ragab RA, Saghai Maroof MA, Li ZB (1994) A half-diallel analysis of heterosis in elite hybrid rice based on RFLP and microsatellites. Theor Appl Genet 89:185–192

Zhang Q, Zhou ZQ, Yang GP, Xu CG, Liu KD, Saghai Maroof MA (1996) Molecular marker heterozygosity and hybrid performance in indica and japonica rice. Theor Appl Genet 93:1218–1224

Zhao J, Wang X, Deng B, Lou P, Wu J, Sun R, Xu Z, Vromans J, Koornneef M, Bonnema G (2005) Genetic relationship within *Brassica rapa* as inferred from AFLP fingerprints. Theor Appl Genet 110:1301–1314