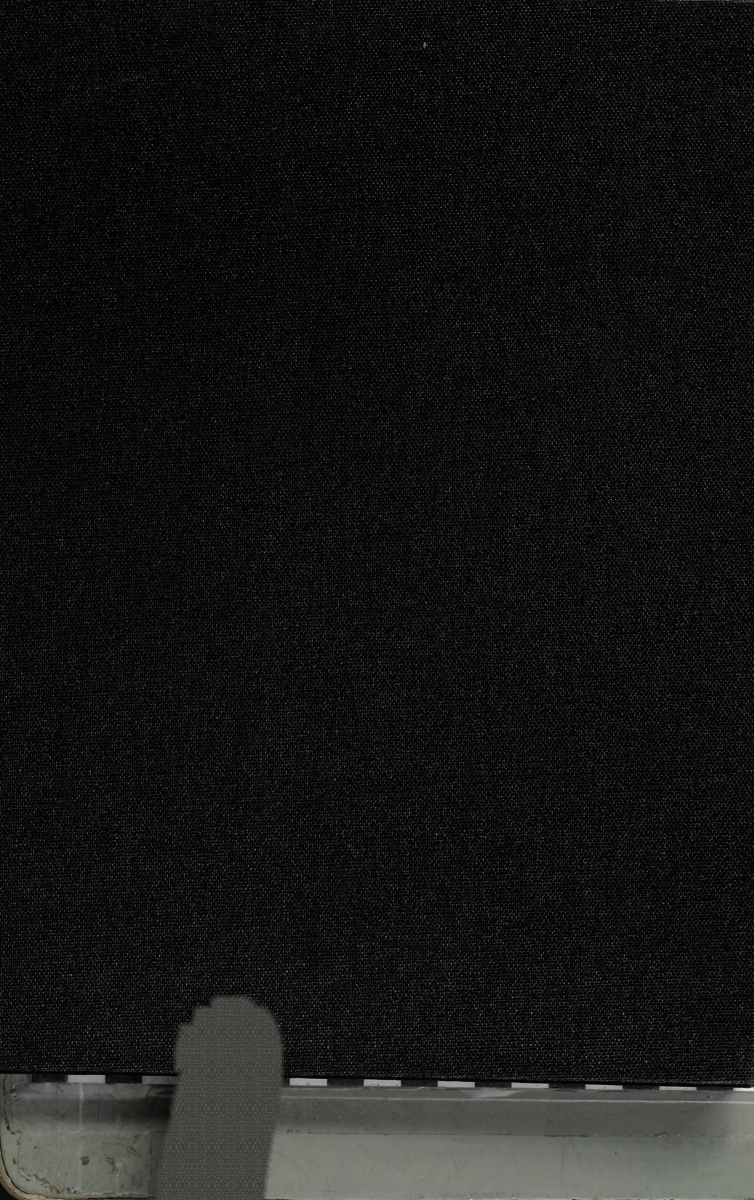

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Muhammad Ali

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MULTIVARIATE ANALYSIS AND HETEROTIC EFFECT STUDIES IN CANOLA (*Brassica napus* L.)

By

Muhammad Ali

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ABSTRACT

MULTIVARIATE ANALYSIS AND HETEROTIC EFFECTS IN CANOLA (Brassica napus L.)

By

Muhammad Ali

Thirty winter canola cultivars (Brassica napus L.) from various sources were analyzed and clustered/grouped based upon their morphological traits, yield and yield component data. Cultivars were placed in three distinct clusters. Genetic distance between all of the thirty cultivars was also estimated. Two cultivars from each group were selected as parents and fifteen partial diallel inter- and intra-cluster crosses were made between the six selected parents. These crosses, along with their parents, were evaluated at two locations: East lansing and Clarksville in Michigan in 1991. The heterotic response for all of the fifteen crosses was calculated as a percent of the mid-parent performance.

All of the fifteen crosses exceeded the mid-parent value for yield, pods per plant and seeds per pod at both locations. The correlation between parental distance and heterotic effects for these traits was positive and highly significant. No significant correlation was observed between genetic distance and heterotic effect for morphological traits like, crown diameter, leaf length, leaf width and branches per

plant. A lack of genetic variation and genotype x environmental interaction was evident in these traits. Dominance genetic variance was observed in favor of early flowering in all crosses. Clustering based on yield and yield component traits demonstrated that inter-cluster heterosis was shown to be greater than intra-cluster heterosis in the majority of cases.

Dedicated to my loving parents

to whom I stand in debt for my education and knowledge

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INTRODUCTION

During the last two decades rapeseed has developed into a major cash crop in Canada and is also beginning a parallel development in the United States. In 1987, 2,671,000 hectares were seeded in Canada with a production of 1,442 kilograms per hectare (FAO Production Yearbook 1987).

The development of new cultivars with improved oil quality has been a major focus around the world, including Canada. In 1968, the first low erucic acid (5 percent or less) cultivar produced in Canada, was Midas (*Brassica napus*). Span and Torch are other examples of low erucic acid rapeseed cultivars from *Brassica campestris* that were grown in Canada (Daun 1983). Between 1972 and 1977, the erucic acid content of Canadian rapeseed oil was further reduced through genetic improvement to 2 percent or less.

The new commodity 'canola' (Canadian Oil low acid) was adopted by Canola Crushers Association of Canada to distinguish the new rapeseed with low erucic acid content in the oil (2 percent or less) and low glucosinolate content in the defatted meal (30μ mol/g or less) from the old or common rapeseed.

Importation of canola oil into the United States has grown considerably in the last few years and demand is increasing very rapidly. Only 12,000 metric tons of oil were

imported into the United States in 1985, compared to an estimated 205,000 metric tons in 1989 and 400,000 in 1993. Prior to 1985, there was less than 20,000 hectares of rapeseed and canola cultivated annually in the United States. In 1985, the U.S. Food and Drug Administration (FDA) granted GRAS (generally recognized as safe) status to low erucic acid rapeseed (canola) oil (National Archives and Records 1985). Since the fatty acid composition of canola oil has been increasingly recognized by nutritionists as beneficial in human diets, the consumption of imported canola oil in U.S. has increased (Foreign Agricultural Service 1989).

It is expected that the development of hybrid rapeseed cultivars might lead not only to increased seed yields, but also to improvement in quality components such as oil constituents. The successful development of hybrid canola cultivars requires three components: an acceptable level of heterosis that offsets the increased cost of hybrid seed, an efficient mechanism of pollination, and sufficient pollen transfer to seed parents to produce enough hybrid seed economically.

Historically, the development of hybrid cultivars of corn, sunflower, sorghum and many horticultural species has led to significant increases in seed yield due to the phenomenon of heterosis or hybrid vigor (Duvick 1984, Furgala et al.1979, Miller & Kebede 1984). The yield potential of single cross oilseed rape hybrids (Brassica napus L.) has

attracted considerable interest from oilseed breeders, seed producers and growers around the world.

It is a common belief among plant breeders that heterosis, measured as the superiority of hybrids over their mid-parent, is proportional to genetic distance between their respective parents (Ghaderi et al. 1979; Murty et al. 1965; and Ramanujam et al 1974). Genetic distance between populations can be defined either on the basis of known relationships or their genetic composition (Jacquard 1974). Moll et al. (1962; 1965) reported that within a restricted range of diversity, distant populations of corn (Zea mays L.), as judged from their ancestral relationship and geographical separation, produced higher levels of heterosis for yield in their hybrid progenies compared to that of F_1's from closely related genotypes.

However, there should be an optimum degree of genetic divergence for maximum expression of heterosis (Moll et al. 1965). This optimum occurs within a range of divergence that is narrow enough so that incompatibility barriers such as those caused by cytological irregularities are not present.

The objectives of this research were:

1. To use multivariate statistics to investigate the genetic relationships and distance among a set of 30 canola genotypes and cluster genotypes based on genetic distance.
2. To select parents from these clusters and make crosses within and between the groups and compare the resulting

heterosis of the crosses.

3. To study the level of heterosis for a set of agronomic traits.

REVIEW OF LITERATURE

2.1 Rapeseed vs. Canola

The word "rapeseed" is derived from a Latin word "rapum", which means turnip. All of the oilseed rape species belong to the family Brassicaceae. Unlike most of the other oilseeds, rapeseed originates from the various species belonging to the genus *Brassica*. These species are *B. napus*, *B. campestris* and *B. junceae*. All of these species are similar in their phenotypic appearance but differ in chromosome and ploidy levels. *B. napus* is an allotetraploid with a chromosome number of 2n = 38, where as *B. campestris* (2n = 10) and *B. olearaceae* (2n = 9) are the basic diploid species from which *B. napus* was derived. These species have been defined with only slight differences in various parts of the world. In Canada and Europe the seeds of rape and turnip rape are named rapeseed, whereas in India, leaf mustard and turnip leaf is considered rapeseed.

All traditional rapeseed cultivars contain high erucic acid rapeseed oil (HEAR), ranging from 22 to 60 percent. Such a high amount of erucic acid decreases the nutritional value of the oil, while another chemical compound, glucosinolates, limits the feeding value of the meal. These problems were eliminated by the Canadian researchers who genetically modified the traditional rapeseed cultivars by lowering the

amount of erucic acid to 2 percent or less and by reducing the glucosinolate content in the meal to less than 30 μ mol glucosinolates / g or less of meal.

Since genetically modified cultivars of rapeseed have a very low amount of erucic acid and glucosinolate content, they have been designated officially named by the Canadians as "canola" for Canadian oil with low acid. To better exploit the high quality oil of canola, there is an interest in developing high yielding hybrids. In *Brassica* the exploitation of heterosis for oil content and yield productivity has not reached the same commercial level as in corn, so efforts are being made all over the world to utilize the heterozygous advantage of the F_1 hybrids (Shiga, 1976, Anand & Mishra, 1984). In order to formulate a successful hybrid program it is essential to estimate the extent of heterosis for seed and oil yield in this crop.

Various efforts are currently underway to develop cytoplasmic male sterility CMS and genetic restorer systems for the production of hybrid cultivars. Ogura (1968) found a male sterility inducing cytoplasm in radish (*Raphanus sativus L.*). Bannerot et al. (1977) transferred the nucleus of *B. napus* into the radish cytoplasm using intergeneric crossing followed by a series of backcrosses. Fu (1981) discovered male sterile plants from the seed of the cultivar Polima (*B. napus*) and this male sterile cytoplasm was designated as Pol by Fan and Stefansson (1986). Shiga et al. (1983) studied the nap CMS

types of some European *B. napus* cultivars and their ability to restore male fertility in nap CMS lines. They also found that a few cultivars could act as "maintainers" of the nap cytoplasm since they possessed a male fertile cytoplasm but had no male fertility restoration genes.

2.2 Genetic Distance

Genetic diversity plays a very crucial role in improving plants to meet different human needs. Modern crop species were selected from the vast array of species in the plant kingdom and farmers have further selected among existing diverse genotypes to improve these species. Later, plant breeders began crossing different genotypes to create additional diversity by recombining the genes of one parent with those of the other parent. It is assumed that a cross will generate successful progeny if both parents possess different genes (i.e. exhibit adequate genetic distance between them). Furthermore, plant breeders make the crosses with the aim of creating new and improved genotypes for a specific trait, which requires that the parents are at least genetically distant for the trait to be improved.

The amount of genetic variability is very important in a population and is a parameter which can be easily measured since it is influenced by the genetic distance between the parents (Cowen & Frey, 1987 a). The second parameter of significant importance is the amount of mid-parent heterosis,

exhibited by the hybrid population (Falconer, 1981).

Genetic distance between parents varies with the method of estimation. One means of estimation is to compare the parents on the basis of various heritable traits and attempt to measure the genetic distance through differences in phenotype. Such an approach has been used by various researchers both for the quantitative (e.g., morphological traits), as well as qualitative traits. Another approach is based on examining the pedigree data under a set of assumptions concerning ancestral genealogy, ancestral genotypes and unrestricted genetic transmission between the parents and offsprings. These approaches, specifically for quantitative traits and their application in breeding are discussed below with the type of data that is used to determine the genetic distance. Attempts have been made here only to review the methods of estimating genetic distance and research where the quantified genetic distances between parents are related to some form of breeding behavior in the hybrid population.

2.2.1 Estimation of Genetic Distance

Morphological data can be used for estimating the relationship between two populations. This is achieved by obtaining a reliable estimate of the phenotype of the population for univariate or multivariate traits and comparing them statistically. This approach gives a statistical distance

between the population and any inferences about the genetic distances are made with the assumption that the phenotypic differences reveal underlying genotypic differences. Generally speaking, a large phenotypic difference results in a large genetic distance, regardless of the extent of underlying genetic differences. More precise inferences are possible, especially for highly heritable traits through the examination of more traits, since this assays genetic differences at more loci.

Several statistical methods have been used to estimate the genetic distance between two populations with phenotypic data. One of the commonly used approaches is to calculate the Euclidian distance (ED) between populations (Goodman, 1972) where the distance between the i^{th} and j^{th} population is

$$ED_{ij} = [\sum_{k=1}^{n} (X_{ik} - X_{jk})^2]^{1/2}$$

X_{ik}, X_{jk} = mean of the k_{th} of n traits for the i^{th} and j^{th} population, respectively that have been standardized by dividing by the standard deviation of the k^{th} trait.

Each population could be visualized as a point in 'n' dimensions corresponding to 'n' traits where the mean for the k^{th} trait for the population coordinates that point along the k^{th} axis. ED_{ij} is actually the distance between the i^{th} and the j^{th} points in this multidimensional space, ED_{ij} is also equivalent to the distance between the principal components

derived from an analysis of the correlation matrix between the traits (Goodman, 1972) where

$$ED_{ij} = [\sum_{K=1}^{n} (Y_{ik} - Y_{jk})^2]^{1/2}$$

Y_{ik}, Y_{jk} = Coordinates of the k-th of 'n' principal components for the i-th and j-th population respectively.

In case of principal component analysis, the original 'n' axes corresponding to each trait under study are rotated in space to correspond to new variates that are uncorrelated to each other. Although the population points remain at the same positions, their location in the new dimensional space are now defined by the coordinates of the new axes. These new coordinates for the i^{th} population are called its principal components score. The Euclidean distances such as Pearson's (1926) coefficients or racial likeness or Sokal's (1961) distance could be used generally when all the measured traits are uncorrelated (Goodman, 1972). This would seem to be an unlikely scenario, especially when a large number of traits are compared, and ignoring the correlation may result in an exaggerated genetic distance, especially when the correlation has a genetic basis. This would be comparable to giving some gene differences more weight than others in the distance measured.

Another method used first by Mahalanobis (1936) addressed the problems of the intercorrelated traits by calculating a generalized distance (D) where the euclidean

distance is adjusted within the population correlation matrix in such a way that the distance between i^{th} and j^{th} population is

$$D_{ij} = [(X_i - X_j)\ R^{-1}\ (X_i - X_j)]^{1/2}$$

$$D_{ij} = [\sum_{k=1}^{n} \{(Y_{ik} - Y_{jk})^2 / \ _k\}]^{1/2}$$

X_i, X_j = vector of the standardized means of the 'n' traits for the i_{th} and j_{th} populations.

R^{-1} = inverse of the correlation matrix of the 'n' traits.

$_k$ = eigenvalue of the kth principal components.

D is the multivariate generalization of the students 't' test (Hotteling, 1954)and is commonly used for equality testing of the two means and the D^2 could be used for calculating the Hotteling's 't^2' test of the similarity of two mean vectors in conjunction with a multivariate analysis of variance. All the eigenvalues equal unity when the measured traits are not correlated and 'D' then becomes equal to euclidean distance(ED). The problem with the 'D' is that the principal components which are with very small eigenvalues and which accounts for very little of the overall variability may not be biologically significant, and could have an inflated contribution from more important principal components (Goodman,1972).

An alternative would be to include only some of these standardized principal components in the distance (Goodman,

1972). This approach projects the population point in a space with the fewest but hopefully more biologically significant dimensions. Goodman (1972) suggested using the k-th principal components in the distance estimate only when the $\lambda K >= K$, whereas a less conservative approach could be to use all the principal components where $\lambda K > = 1$.

Calculations and interpretations on the distances becomes more complex when there is heterogeneity between the covariance matrices of the population being compared, since this may result in D_{ij} differing from D_{ji} (Atchley et al. 1982). The heterogeneity of the covariance matrices reflects different types of relationships of the traits within different populations. This could be due to the biological differences brought about by genetic and developmental differences and the interaction of these factors with the environment where the traits are measured.

When a plant breeder wants to make improvement for a particular trait by crossing parents with high means for that trait, the parents should not show excessive phenotypic variability for that trait. In such case, the plant breeder should measure the phenotypic variability for a substitute morphological trait and hope that it is predictive of genetic variability for the desired trait. Populations with a narrow genetic base, normally do not have adequate variability for other morphological traits for a successful application of this method, particularly when the other traits are

correlated to the trait under improvement. The use of quantitative traits has a great potential to assay genetic distance at many loci because there are probably several hundreds of gene differences between two populations at the extreme ends of the expression range with multiple morphological traits. However, it seems unlikely that this type of extreme range would exist in an elite breeding population.

Although genetic distances are pairwise comparisons between populations, they could also be used to show a broader relationship which might exist among all genotypes. This may be achieved by coupling the resulting distance matrix with a clustering technique. This is a very common technique in taxonomy and classification work, which could also be applied to parental breeding populations.

Many reports exist of the use of quantitative trait distance techniques in taxonomy, classification and evolution studies. However, relatively few studies have related parental distances to any form of breeding behavior exhibited by a hybrid population. The morphological distance between parents has been positively correlated to the mid-parent heterosis for grain yield of hybrids of rapeseeds (Brassica napus L.) (Lefort-Buson et al. 1987), soybean (*Glycine max* L. Merr.) (Chauhan and Singh, 1982), wheat (*Triticum aestivum* L.) (Shamsuddin 1985, Cox & Murphy, 1990), dry beans (*Phaseolus vulgaris* L.) (Ghaderi et al. 1984), peanut (*Arachis hypogaea*

L.) (Arunachalam, 1984; Isleib & Wynne, 1983), maize (*Zea mays* L.) (Prasad & Singh, 1986) and tomato (*Lycopersicum esculentum* Mill.) (Maluf et al., 1983). No relationship was found in faba bean (*vicia faba* L.) (Ghaderi et al., 1984) or oat (*Avena sativa* L) (Cowen & Frey; 1987 a),however, Cox & Murphy (1990) reported that the value of their morphological data in predicting heterosis in a F_2 wheat population depended on the environment in which the data was collected.

There are a few studies relating distance based on morphological data to genetic variance and the number of transgressive segregants in segregating populations despite the importance of these parameters in plant breeding. The Euclidean distance between oat parents based on morphological data was reported to be negatively correlated with the number of transgressive segregants and the generalized variance (Cowen & Frey, 1987 a) which is a measure of all measured traits (Sokal, 1965; Goodman 1968).

It has now become a major concern of gene bank managers and plant breeders that desirable material cannot be evaluated effectively in large collections (Holden, 1984). Only a relatively small portion of the germplasm on hand has been fully described for agronomically useful characters (Duvick 1984). Many of the desirable characters are quantitative, so multivariate statistical techniques have been suggested and utilized to a limited extent to measure genetic and phenotypic divergence among entries and genotypes to aid in planing

crosses among genotypes belonging to different clusters (Bhatt, 1970: Goodman 1973; Sneath, 1976; Camussi et al. 1983). Studies on several crops have indicated that a large amount of variation occurs in these collections (i.e. Ashri, 1973; Narayan & Macefield, 1976; Hussaini et al; 1977; Camussi, 1979; Tolbert et al., 1979).

Ariyo (1987) conducted multivariate analysis studies for 30 genotypes of Okra of diverse ecogeographical origin. He used D^2 analysis technique to measure the genetic divergence among these genotypes based on 14 different characters. He identified five different clusters/groups and observed no relationship between genetic divergence and ecogeographical distribution. Cluster #1 contained the most geographically diverse genotypes, including those from Nigeria, Ghana, Turkey, and Zambia. Duddley & Davis (1966), Bhatt (1970), Chedda & Fatokun (1982), and Dasgupta and Dass (1984), working with cultivars of alfalfa, wheat, okra, and black gram, respectively, noted that the cultivars clustered into different groups irrespective of their countries of origin.

Peters et al. (1989) did cluster analysis to classify entries from barley germplasm collections obtained from AFRC - IPSR, based on both qualitative and quantitative descriptors including disease resistance. They concluded that more relatedness between entries exists within a given country gene pool than between country gene pools. They also suggested that cluster analysis could be a useful tool for the management of

the variation in germplasm collections. Results from crosses of material between country gene pools were found to produce more segregation than that from within the gene pools.

Dorothea et al. (1986) sampled the cultivars of sesame from 20 countries for their morphological variability, and used factor, cluster, and principal component analysis to establish the patterns of similarities and generate the grouping taxa. The results indicated that eight major groups can be discerned, and they concluded that genetic variation in sesame can be used to identify the source of genetic material for crop improvement.

Hillig et al. (1988) evaluated individuals in a sour cherry germplasm collections from Eastern Europe for their morphological traits by using principal component analysis. They observed that families of cold hardy Russian cultivars generally show a greater morphological resemblance to ground cherry than did families of less-cold hardy cultivars. They also reported a gradual range of diversity rather than two distinct groups of sour cherry based on morphological variation.

Buson et al. (1987) studied different types of rapeseed hybrids from similar and different geographic origins in Asia, Europe and, mixed locations. They conducted the experiments over two years at two locations and found that mixed group F_1 hybrids were taller and more productive in seed yield than both European and Asiatic groups alone. They did not conduct

any multivariate analysis to cluster or group the genotypes involved in crossing through any genetic distance measuring technique but assumed that genetic distance was predictable on the basis of the origin of the cultivar, i.e. Europe and Asia. Grant et al. (1985) conducted 6x6 diallel cross in spring oilseed rape and reported positive heterosis for seed yield of up to 72 percent over the high yielding parent in the hybrid cross. Heterosis for seed weight, percent oil, plant height, and lodging resistance was not significant. They also observed negative heterosis for percent protein in some hybrids.

Shamsuddin (1985) performed multivariate analysis of ten cultivars of spring wheat and grouped them according to genetic diversity. During the correlation studies of genetic diversity and heterosis, he found that the parents of most of the best hybrids belonged to two divergent groups, which indicates the positive relationship between genetic divergence of parents and their hybrid performance. He also found that the correlation between heterosis for grain yield of hybrids and genetic diversity between parents was positive and significant ($r = 0.45$, $P = 0.01$). Bhatt (1970) measured the genetic distance quantitatively for 40 genotypes of wheat from different ecogeographic regions of Australia, using D^2 statistics analysis technique. The results supported the findings of Moll, Salhuana & Robinson (1962), Timothy (1963) and Murty and Arunchalam (1966) who could not find any relationship between geographic distribution and genetic

divergence. In this study he observed that the genotypes from different regions had clustered together in seven out of twelve cases. Conversely, genotypes of the same origin were distributed in three different clusters.

Bhatt (1973) compared four different systems to select parents for hybridization in wheat based on: (a) the conventional method (b) the random method (c) the multivariate analysis method, and (d) ecogeographic diversity. He found the multivariate analysis to be more efficient in selecting parents than that based on ecogeographic diversity. Genetic drift and selection in different environments could cause greater diversity than that caused by geographical distance (Murty & Arunchalam, 1966). Moreover, multivariate analysis is a sound statistical technique for objective assessment of parental diversity compared to other methods. The conventional and random methods were found to be less efficient. Spagnoletti et al. (1985) assessed morphological and genetic distances among six durum wheat lines, two from Algeria, two from Italy and two from Ethiopia. Morphophysiological characters were analyzed and multivariate statistics analysis conducted to ascertain phenotypic and genotypic similarities among entries. They found large variation among lines of different origin compared with that found within origin. They also observed a close relation between phenotypic and genetic values, suggesting that diversity based upon phenotypic analysis of morphological characters may be a reasonably good

indication of the choice of breeding material.

Balasch et al. (1984) conducted multivariate analysis studies on 60 tomato cultivars of different origin and based their analysis on twenty characteristics. They used two different methods: the principal coordinate technique, and Mahalanobis (D^2) distance method to group cultivars based on their genetic similarities. Large similarities of association between both analytical methods were observed. They also observed that the genetic divergence of the cultivars was in no way influenced by geographic distribution, since they found variation in the same geographic group. Rajana et al. (1977) studied 21 F_1 hybrids of tomato derived by crossing 21 cultivars with a common female parent 'A 142' to observe heterozygote advantage as a function of genetic divergence. Genetic distance was calculated by Mahalanobis D^2 method. They observed low yielding hybrids resulting from crossing closely related or genetically less divergent parents. The poorest F_1 hybrid 'A 142' x 'Gamed' had the smallest genetic distance between parents (D^2 = 223.83) with a negative heterosis over the control parent when compared to the high performance of F_1 hybrid 'A142' x 'Sioux' (D^2 = 2197.17) with a significant positive heterosis of 71.6 percent over the control parent.

Peter et al. (1978) studied heterosis in relation to genetic distance in an F_1 diallel set of ten homozygous cultivars of tomato. They reported a 5.87 kg yield in an F_1 hybrid Mobaci x EPH7 compared to 2.72 kg in Pusa Ruby, the

check parent. They noted the same type of results for most of the crosses but did not find any clear correspondence between the extent of the genetic divergence and the heterosis for yield. The reason they explained could be due to the highly domesticated and selected nature of the cultivars used in the hybridization program.

Khanna et al. (1977) reported greater inter-cluster heterosis than intra-cluster heterosis in the majority of the cases in an experiment conducted on 50 cultivars of tomatoes. Cultivars were grouped into clusters based on seven traits. They pointed out that with some exceptions it was not possible to correlate the percentage of the heterosis exactly with the cluster distances. Such a situation would not be unexpected considering the complex nature of the expression of the heterosis for any character and a relatively simple model of statistical distance.

Moll et al. (1962) speculated that genetic differences among cultivars have probably arisen through geographical isolation accompanied by a combination of genetic drift selection in a different environment. They did not use any statistical analysis to determine genetic distance between maize cultivars. In this study they chose six cultivars of maize, two from each of the three geographical regions, i.e. midwestern United States, southeastern United States, and Puerto Rico. They observed that greater genetic diversity based on the geographical separation of the parental cultivars

was associated with greater heterosis. They also suggested that divergent material may have potential utility in yield improvement in spite of poor local adaptation of cultivars from distant sources.

2.2.2 Heterosis

Heterosis has been reported among parents of diverse origins (Sprague, 1966; Brown, 1967 and Heidrich-Sobrinho). Beal (1880) was the first scientist to conduct experiments in maize (Zea mays L.) that are analogous to present day methods used for maize hybridization. It was not until later that the modern concept of heterosis was established by Shull (1908). He used the word heterosis to describe the yield stimulation resulting from increased heterozygosity. He demonstrated that certain lines when recombined produced F_1 yields that exceeded those of the parental cultivars. The commercial use of F_1 hybrids did not materialize until the 1930s (Lamkey & Hallauer, 1984).

Earlier work with maize conducted by East and Hayes (1912), East (1936), Hayes & Johnson (1939), Johnson & Hayes (1940), and Wu (1939) suggested that greater heterosis is observed as a result of the crosses made between the more distantly related parents, compared to those which are closely related. This may not be true for an entire range of genetic diversity encountered in all species.

Niehaus et al. (1966) performed combining ability

analysis in sorghum crosses and reported that genetic diversity could be the key to maximize hybrid vigor. They also reported that geographically diverse parents, which presumably were also genetically diverse, produced the highest yielding hybrid. In a similar study in corn, Kinman and Sprague (1945) suggested that the range in combining ability among the inbred parents could indicate the value of parents in a synthetic variety.

Ashton (1946) in a survey of many self pollinated crops reported evidence that interspecific crosses showed better heterosis compared to intraspecific crosses. Heterosis or hybrid vigor has been defined by many researchers, such as Hayman, 1957; Burton, 1980; Mather & Jinks, 1982; Mukherjee & Saha 1982, Jinks, 1983. Shull (1952) defined it as "the interpretation of increased vigor, size, fruitfulness, speed of development, resistance to disease and to insect pests, manifested by crossbred organisms compared with corresponding inbreds, as the specific results of unlikeness in constitution of the uniting parental gametes."

The term heterosis, is used to refer to either an increase in performance over the better parent or an increase over the mid-parent performance of a cross. Patterson and Blitzer (1966) defined this term as the improvement of the heterozygote over the better parent in a cross. Paterniani (1973) and Burton (1980) suggested that hybrid vigor is of practical importance only when the offspring exceeds the

better parent.

2.2.3 Gene Action in Heterosis

There are many theories, which explain the mechanism of heterosis, and it might be quite possible that different mechanisms operate in different organisms. Since hybrid vigor was utilized first in corn, its success stimulated interest in searching for the genetic basis for heterosis. Two main hypotheses have been proposed (Jones, 1917; Brieger, 1950; Hayman, 1957; Burton, 1980, Hallauer and Miranda, 1981):

1. Dominance Hypothesis

Davenport (1908) reported that hybrid vigor results from the action and interaction of the favorable dominant genes. This hypothesis has been challenged because the evidence does not substantiate the proposed model (Burton, 1980). Jones (1917) proposed that heterosis occurs as a result of the dominance of linked factors. Dobzhansky (1941) and others have proposed that during the evolutionary process, deleterious recessive genes become accumulated in many species and reduce the efficiency of the organism, whereas the deleterious recessive genes effect is masked by their dominant alleles when the genes are present in heterozygous form. Crow (1952) discussed inbreeding depression and explained its recovery on crossing. He suggested that this recovery is the result of loci where the favorable allele is dominant and the recessive

allele is present at a low frequency.

2. Overdominance Hypothesis

Much of the early work on heterosis was done in maize, which is a cross pollinated crop. In most of the cases, the crosses, which involved inbred lines, showed heterosis, which was associated with heterozygosity. As a result of this investigation, the theory of overdominance was developed by Shull (1908) who reported that heterozygotes were more vigorous than either homozygotes. Hull (1952) presented the same evidence by using the regression of progenies on parents to show the overdominance in diallel crosses of maize. Mather (1956) suggested that the genetic advantage of heterozygosity lies in providing flexibility and greater stability. Robertson and Reeve (1952), and Haldane (1954) proposed that heterosis probably results from the physiological advantages of heterozygotes.

Green and Green (1940) reported that the unit of specific physiological action may not be one locus but a complex of loci which are tightly linked together. Many investigators believe that these complex loci produce the specific effects of heterosis. Lerner (1954) concluded that overdominance is widespread and quite important with respect to the characters, which are closely connected with fitness. Mather (1955) explained that overdominance in plants can be attributed to epistasis. Rambaugh & Lonquist (1959) also reported that most

genetic effects were additive with a few examples of overdominance from their studies of diallel crosses in maize.

The overdominance effects, especially in complex traits like yield, could be due to the multiplicative action of the components. This was explained in (*Phaseolus vulgaris* L.) by Adams and Duarte (1961) who found heterosis in a complex trait, namely total leaf area in beans. They believed this was because of the multiplicative relationship that prevailed between the two components which were leaf area and leaflet number.

Different planting methods and environments could also influence heterosis. Santiago et al. (1968) found a higher level of heterosis in 'hill' than in drill-planted winter wheat. Pfahler (1966), in his experiments with rye, *Secale cereale* found that the heterosis was dependent on the genotype and environmental interactions. Sprague (1952) also confirmed this fact in maize. Pawlisch and van Dijk (1965) reported heterosis in four F_1 barley hybrids both for forage and grain yield. Immer (1941) and Suneson (1962) also reported heterosis for grain yield in barley.

Interest in the possibility of developing hybrid rape cultivars with the potential for substantially higher seed yield was stimulated by reports of cytoplasmic male sterility. Shiga and Baba (1973) and Thompson (1972) discovered a cytoplasm that induced male sterility in naturally occurring *Brassica napus*. Seed yield in F_1 hybrids was 40 to 60 percent

greater than parental cultivars in oilseed forms of *Brassica napus* and/or *Brassica campestris*. Shiga (1976) and Buson 1980) noted significant heterosis for seed yield in F_1 *Brassica napus* hybrids. Hutcheson et al. (1981) discovered a naturally occurring hybrid between *Brassica campestris* ssp. Sarson Prain. Cultivar R-500 and Brassica campestris L. var oleifera metzg which yielded 146 percent of the *Brassica campestris* var oleifera cv. Candle. Sernyk and Stefansson (1983) found that certain rapeseed (*Brassica napus*) cultivars in crosses with cultivar 'Regent' produced progeny that exhibited 38 to 43 percent more seed yield than Regent.

Populations that are widely differentiated through adaptation to local conditions may fail to show heterosis and may suffer a reduction of fitness in the F_2 generation as has been shown in studies of Drosophila populations (Wallace and Vetukhiv, 1955).

Heterosis, like inbreeding depression, depends for its occurrence on dominance 'd'. The amount of heterosis following a cross between two particular lines or populations depends on the square of the difference of gene frequency (y) between the populations (Falconer 1982). If the populations crossed do not differ in gene frequency, there will be no heterosis, and the heterosis will be greatest when one allele is fixed in one population and the other allele in the other population. Thus heterosis in F_1 can be calculated as $H_{F1} = \Sigma dy^2$.

Genetic distances based on the genetic composition of

populations can be expressed either on the basis of the frequency of different genotypes (genotypic distance) or the frequency of the various alleles at a given locus (genic distance). It is the later definition of the genetic distance that is associated positively with heterosis (Cress 1966; Falconer 1960). The association of genetic distance and heterosis has been investigated in several crops species (Moll et al. 1965, Murty et al. 1965, Ramanujam et al. 1974). Heterotic responses have been reported to range from significantly positive to significantly negative values. Cress (1966), presented evidence that even in the absence of epistasis, multiple alleles at a given locus could lead to either positive or negative heterosis. Hutchinson et al. (1930) concluded that not only dominance but epistasis or interallelic gene actions may also be involved in heterosis.

MATERIALS AND METHODS

3.1 Development of Experimental Material

Thirty cultivars and/or breeding lines of winter canola (*Brassica napus* L.) from different origins and breeding programs were used for this study. The list is given in Table 1. (Actual pedigree are unknown since this is proprietary information.)

These cultivars were first planted on September 7, 1988 at Agronomy Farm of the Crop and Soil Sciences Department in East Lansing Michigan in a randomized complete block design with four replications. The plot size used in all experiments was 6 m X 0.75 m (4.5 m^2). There were five rows and row width was 15 cm apart. The same thirty cultivars were planted the following year in 1989 at two locations. One location was on Botany Research farm on College Road at Michigan State University, East Lansing. The planting date was September 5, 1989 and the statistical design used was randomized complete block design with four replications. The second location was the Horticultural Research Farm at Clarksville, Michigan. Planting date was September 23, 1989 in a randomized complete block design.

Since the duration of the crop is about 10 to 11 months, the data on yield components was recorded on the 1988 crop while data on morphological traits was recorded on the crop

planted in 1989 at two locations. The reason for recording yield component data on the 1988 crop, was to complete the multivariate analysis and allow selection of the parents prior to the crossing, which had to be completed by May 1990. Details of the data taken on morphological traits and yield components are shown below.

Harvest Dates and Methods

Harvest date was July 15, 1990 in East Lansing and July 20, 1990 at Clarksville. A Hege Combine, 1.2 m wide with a cylinder speed of 600 revolutions per minute was used for this purpose at both locations. The harvest area was the same as planting area, i.e. 4.5 m^2.

Data Collected

1. Crown Diameter

Crown diameter was recorded in millimeters with the help of a Vernier Calliper one month after the emergence of plants at both locations.

2. Leaf Length

Leaf length in centimeters was recorded in three different stages at both locations. First, leaf length was recorded from the base of the leaf (which is attached to the stem) up to the first node. The second length was noted from the base up to the second node, and the third and final length

was recorded from the base of the leaf up to the tip.

3. Leaf Width

Leaf width was also recorded at both sites. It was measured from the center of the leaf to get the maximum width.

4. Number of Branches

Eight plants per cultivar at each location were selected randomly and the data on the number of branches were recorded. Two plants per replication were selected in four replications for this purpose.

5. Number of Pods

The same randomly selected eight plants were used to collect data on pod numbers per plant.

6. Number of Seeds per Pod

Number of seeds per pod were also recorded for all of the thirty genotypes used for this study. The same eight randomly selected plants were used for this purpose.

7. Hundred Seed Weight

One hundred seed weight (in grams) was recorded for the same randomly selected plants for all the thirty genotypes.

3.2 Multivariate Analysis

Based on the morphological traits and yield components, this multivariate data set, consisting of the thirty genotypes of different origins as discussed above was analyzed using the principal component and clustering techniques.

3.2.1 Analysis of Variance

Proc Anova procedure of the SAS program was used to determine whether there was a significant difference among the genotypes under evaluation. The result showed a significant difference, which permitted clustering analysis in order to group cultivars.

3.2.2 Principal Component Analysis

Principal component analysis was performed using the PRINCOMP procedure of the SAS statistical package.

3.2.3 Clustering Analysis

The purpose of the clustering analysis was to determine if these thirty genotypes fell into different clusters. Clusters are made in such a way that the genotypes in a given cluster tended to be similar to each other while the genotypes placed in different clusters, tended to be dissimilar. Initially, nine traits including four yield component and five morphological traits were used to make the clusters. However, four morphological traits out of a total of nine were dropped.

These remaining included four yield components and only one morphological trait, which was crown diameter. These five traits finally contributed towards making three distinct clusters.

PROC CLUSTER procedure of the SAS program was used for this purpose. Only two genotypes, LD-9430 and Cascade were placed in cluster No.1 and two genotypes, Cobra and Winfield, were placed in cluster No.2. The rest of the twenty six genotypes were placed in cluster No.3.

3.2.4 Euclidean Distance

Euclidean Distance among the parents used for the crossing program was calculated using SAS. The distance among the parents was estimated to allow correlation with the level of heterosis observed from crossing the six selected parents in this study.

3.3 Selection of the Parents

Based on the clustering analysis procedures, two genotypes, LD-9430 and Cascade were placed in cluster No.1 and selected as parents for use in crossing program. These genotypes belonged to the Calgene and Cargill groups respectively and exhibited a nonsignificant difference from each other, so they were placed in the same group/cluster.

Cluster No.2 had also only two genotypes out of thirty which were analyzed. These two genotypes were also selected as

parents to be used in the crossing program. These genotypes, namely Cobra and Winfield exhibited a nonsignificant difference from each other. Both of the genotypes belonged to Calgene Inc. group.

Cluster No.3 comprised the rest of the twenty-six genotypes out of thirty. Non of these genotypes were significantly different from each other, since the actual differences in morphological traits and yield components for these 26 genotypes were very small. Thus, all were placed in one cluster. The two genotypes, Ceres and CC-4, from Calgene and Cargill, respectively were most similar to each other and were selected as parents from this cluster. The distance found between these genotypes through clustering analysis was almost equal to the distance found among the parents selected from the other two clusters. In order to make the selection uniform, these parents were identified and selected from the third cluster on the almost equal distance criteria as stated above.

3.4 Crossing Program

Six parents representing two genotypes from each cluster were then used in the crossing program. Cultivars used as parents were as follows:

1. LD-9430 ¦
2. Cascade ¦ Cluster No.1

3. Cobra ¦
4. Winfield ¦ Cluster No.2

5. Ceres ¦
6. CC-4 ¦ Cluster No.3

A half diallel crossing scheme was conducted between the six parents using the formula n(n-1)/2 which is equal to 6(6-1)/2=15 crosses. In this way these crosses were made within and between the clusters.

3.4.1 Floral Morphology

The flower of Brassica napus L. has six stamens, the outer ones are distinctly shorter than the inner four, which surround the stigma. The anthers are shorter than the stigma at an early bud stage but prior to flower opening the filament elongates and carries the anthers upward so that they become as high as the stigma. The flower begins to open before 8 a.m. and continues to open until about noon. The flower remains open three to four days, after which the sepals and petals are shed.

3.4.2 Crossing Technique

Crossing work was started on May 4, 1990 and continued through May 13, 1990 in the Botany Research Farm at Michigan State University in East Lansing. It involved the following

steps:

1. Bagging the inflorescence approximately one day prior to the bud opening.

2. Emasculation of buds was completed the following day after bagging the plants.

3. Dusting the male parent pollen and covering it with a butter paper bag until pod development started. This was done to avoid contamination from any foreign pollen.

Five plants from each parent in each replication were randomly selected for the crossing program. Unwanted or matured flowering buds from the covered inflorescence were clipped off before crossing with the help of scissors to avoid any selfing. Such types of buds were clipped off and removed and were not used in crossing. Forceps were used to emasculate the buds by opening them and taking out the anthers. All possible care was taken not to injure the stigma and ovary after emasculation. Again the emasculated buds were covered with butter paper bags until the mature pollen from the desired plants was available for crossing purposes.

Most of the crossing was done at about 10 to 11 a.m. in the field when the fresh flowers were in full bloom, and the pollen dehiscence was at a maximum. Ten to fifteen buds were emasculated and pollinated with one inflorescence of the male plant. Two to three inflorescenses were used on one plant to produce the maximum amount of seed. Details of the crosses made are given in Table 2.

3.5 Evaluation of Crosses

3.5.1 Data Recording

Data on morphological traits and yield components were recorded (Table 3). All of the 15 crosses, along with their six parents were planted at East Lansing, Michigan on August 25 and, Clarksville on September 3, 1990. Harvesting of these crosses and their parents was done in East Lansing on July 24, 1991 and Clarksville on July 22, 1991.

3.5.2 Data Analysis

3.5.2.1 Analysis of Variance

Analysis of variance for each character listed above was performed for significance by MSTAT.

3.5.2.2 Correlation Studies

Correlation coefficients were calculated to establish the relationship among the characters noted for all cultivars/crosses under study. The MSTAT program was used for this analysis.

3.6 Estimation of Heterosis

Heterosis estimation which was the major part of the study was also done. The heterosis for each character under study was measured.

Mid-Parent Heterosis

This measurement was taken by comparing the performance of F_1 with the average performance of its parents. The Spread Sheet program of LOTUS 123 was used for this study and following formula used to calculate the heterosis:

Mid-parent heterosis (%) = (F_1 - MP) / MP x 100

where F_1 = performance of hybrid.

MP = average performance of parent per se

(parent No.1 + parent No.2 / 2)

3.7 Chemical Analysis

3.7.1 Oil Content

Seed samples (5 grams each) were collected after the harvest of the crop at a moisture level between eight to nine percent. Samples were taken from all three replications at East Lansing and Clarksville. After packing and labeling the samples were sent to the American Pedigreed Seeds for analysis.

3.7.2 Determination of Oil Content by NMR

Oil content of seed samples was determined by Nuclear Magnetic Resonance (NMR) using 1.2 gram of clean, whole and unbroken seeds for each sample dried in aluminum cups for two hours at 130°C. After drying, the seed samples were immediately transferred to plastic NMR vials to bring them to equilibrium with NMR's room temperature. The NMR analyzer was

calibrated using samples containing 0, 50, 100 percent oil. Oil content of all the seed samples was determined individually.

Table 1. Cultivars and origin of 30 winter canola (*Brassica napus* L.) genotypes

Cultivar	Source
1. TH-101	Canola, Inc. 8910 Purdue Rd. Indianapolis, IN 46268
2. TH-102	
3. TH-103	
4. Liraborn	
5. Glacier	Bonis & Co. Ltd., P.O. Box 317 Lindsay, Ont., Canada, K9V5Z4
6. Crystal	"
7. SV0220	"
8. SV0238	"
9. SV0253	"
10. SV0255	"
11. SV0261	"
12. 88-A	Ameri-Can (Calgene) Pedigreed Seed 7664 Moore Rd., Memphis, TN 38120
13. 88-B	"
14. 88-C	"
15. 88-D	"
16. LD-9430	"
17. LD-9431	"
18. Allstar	"
19. Ceres	"

20. Cobra	Ameri-Can (Calgene) Pedigreed Seed
21. Diadem	7664 Moore Rd., Memphis, TN 38120
22. Winfield	Cargill Hybrid Seeds, 2600
23. CC-001	W. Galena Blvd., Aurora, IL 60506
24. CC-007	"
25. CC-1	"
26. CC-2	"
27. CC-4	"
28. Cascade	"
29. Libraska	"
30. Libravo	"

Table 2. List of 15 canola (Brassica napus L.) crosses made by Using six selected parents from three different clusters

1. LD-9430 X Cascade
2. LD-9430 X Cobra
3. LD-9430 X Winfield
4. LD-9430 X Ceres
5. LD-9430 X CC-4
6. Cascade X Cobra
7. Cascade X Winfield
8. Cascade X Ceres
9. Cascade X CC-4
10. Cobra X Winfield
11. Cobra X Ceres
12. Cobra X CC-4
13. Winfield X Ceres
14. Winfield X CC-4
15. Ceres X CC-4

Table 3. List of morphological traits and yield components selected for data recording

Abbreviations	Traits
1. DE	Days to emergence
2. Cwn Dia	Crown diameter in mm
3. Lf L 1.nd	Leaf length (up to 1st node) in cm
4. Lf L 2.nd	Leaf length (up to 2nd node) in cm
5. Lf L full	Leaf length full (up to the tip) in cm
6. Lf Wd	Leaf width in cm
7. DOF	Days of flowering
8. DTM	Days to maturity
9. Br/Plt	Branches per plant
10. Pd/Plt	Pods per plant
11. Sd/Pod	Seeds per pod
12. 100 Sd/Wt	One hundred seed weight in grams
13. Yld Kg/ha	Seed yield in kilograms per hectare
14. Oil %	Percent oil content

RESULTS

4.1 Analysis of Variance

Analysis of variance and mean separation tests were performed to measure the effects of different parents and crosses on various morphological and yield component traits (Tables 1 to 9).

Days to Emergence

No significant difference was detected between the crosses and parents for this character at either East Lansing or Clarksville, even when data was analyzed separately for both locations.

Crown Diameter

Differences between the parents and crosses showed significant effects on crown diameter using the combined analysis for both locations. The same trend was observed when analysis was performed separately for both locations.

The crosses LD-9430 x Ceres and Ceres x CC-4 shared the highest mean value of 4.10 mm for each cross in a combined analysis (Table 4a), whereas in East Lansing, Ceres x CC-4 had the highest mean value of 5.13 mm, followed by the parent Ceres with a mean value of 5.06 mm (Table 5a). In Clarksville the cross LD-9430 x Cascade and Cascade as a parent shared the

first position with a mean value of 3.23 mm (Table 6a).

Leaf Length (1st, 2nd, & 3rd node)

This character, recorded at three different stages, i.e., first observation up to first node, then up to second node, and finally up to the tip of the leaf (third node), starting from the basal attachment of the leaf with the stem, was significantly affected by the difference between parents and crosses, when a combined analysis for both locations was performed. Similar results were observed when separate analyses were conducted separately for both locations. It is interesting to note that based on mean values the parent Ceres exhibited the largest leaf length observations at three nodes (Table 4a) in a combined analysis. The same trend also persisted for the East Lansing location for this parent (Table 5a). However, LD-9430 at Clarksville had the largest value for this character analyzed (Table 6a).

Leaf Width

Significant differences for leaf width occurred between the parents and the crosses for both combined and separate analyses. The cross Ceres x CC-4 had the highest mean value of 6.18 cm, followed by one of its parents, CC-4, with a mean value of 6.15 cm in combined analysis (Table 4a). In East Lansing the parent CC-4 had the highest mean value of 7.56 cm followed by the cross Ceres x CC-4 with a mean value of 7.36

cm (Table 5a). However, LD-9430 had the highest leaf width with a mean value of 5.23 cm followed by the cross LD-9430 x Cascade with a value of 5.2 cm in Clarksville (Table 6a).

Days to Flower

Days to flower varied significantly between the crosses and the parents in combined analysis. The cross Cascade x CC-4 was the earliest cross to flower with a mean value of 233 days from planting, followed by Cascade x Cobra with a mean value of 235 days (Table 4a). In East Lansing, the parent Cascade was the earliest to flower with a mean value of 230 days, followed by Cobra x CC-4 with a value of 231 days (Table 5a). In Clarksville no significant differences in flowering date were found between Cascade, LD-9430 x Winfield, Cascade x Winfield and Cobra x CC-4, all of which shared the highest common mean value of 240 days (Table 6a).

Days to Maturity

The combined analysis of variance revealed a significant difference at 0.05 alpha level between the parents and the crosses for days to maturity. The cross Cobra x Ceres exhibited the earliest maturity with an average value of 282 days, followed by CC-4 with a value of 290 days (Table 4b). In East Lansing, Cascade x CC-4 exhibited the earliest maturity with a mean value of 288 days, followed by CC-4 with a value of 289 days (Table 5b). In Clarksville CC-4 was the

earliest maturing cultivar with a mean value of 291 days followed by Cascade x CC-4 with a value of 293 days (Table 6b).

Branches per Plant

The combined analysis of number of branches per plant revealed significant differences between the parents and crosses. LD-9430 had the highest number of branches per plant with an average of 8.4 branches, followed by LD-9430 x Winfield with an average number of 8.4 branches per plant (Table 4b). In East Lansing LD-9430 and the cross LD-9430 x Winfield both had a value of 8.3 branches per plant (Table 5b). In Clarksville LD-9430 and LD-9430 x Winfield again had the largest value, both with the highest common value of 8.5 branches per plant (Table 6b).

Pods per Plant

Significant differences were found between the parents and crosses using combined analysis of variance for both locations. The cross Cobra x CC-4 had the highest number of pods with a mean value of 231 followed by Ceres x CC-4 with a mean value of 221 (Table 4b). In East Lansing, Cobra x CC-4, exhibited the highest number of pods with a mean value of 230, followed by Winfield x CC-4 with a value of 226 (Table 5b). However, in Clarksville, Cobra x CC-4 had the highest value with an average of 233 pods per plant, followed by Cascade x

CC-4 with a mean value of 225 (Table 6b).

Seeds Per Pod

Significant differences were found between the crosses and their parents in the combined analysis. The cross Cobra x Ceres had the highest mean value of 32.8, which was followed by the cross Cobra x CC-4 with an average of 32.3 seeds per pod. In East Lansing, again the cross Cobra x Ceres had the highest mean value of 34.0 seeds per pod. This was followed by the cross Ceres x CC-4 with an average of 32.6. In Clarksville, the cross Cascade x CC-4 was the highest with an average of 32.6, which was followed by the cross Cobra x CC-4 with a mean value of 32.3.

One Hundred Seed Weight

Significant differences occurred between the parents and crosses both for combined and separate analyses at both locations. In the combined analysis, the cross Cascade x Cobra had the highest one hundred seed weight with an average value of 0.52 gms, followed by Cascade with a mean value of 0.51 gms (Table 4b). In East Lansing and Clarksville, the same trend was observed, i.e. both crosses maintained their respective positions with the highest and second highest average one hundred seed weight at both locations separately (Tables 5b & 6b).

Yield (kg/ha)

Highly significant differences were found between the crosses and parents for yield in the combined analysis. Significant differences were also found when separate analysis for both locations were performed. In the combined analysis, the cross Cobra x Ceres had the highest mean yield of 3314 kg/ha followed by Cascade x CC-4 with 3258 kg/ha (Table 4b). In East Lansing, Cobra x Ceres also produced the highest yield at 3616 kg/ha followed by LD-9430 x Ceres at 3510 kg/ha (Table 5b). In Clarksville, Cascade x CC-4 gave the highest average yield of 3258 kg/ha followed by Cobra x Ceres at 3012 kg/ha (Table 6b).

Percent Oil Content

Significant differences between the parents and crosses were observed when a combined analysis as well as separate analyses of this trait for both locations were performed. The cross Winfield x Ceres had the highest oil content in combined analysis with a mean value of 45.1 percent followed by Winfield x CC-4 at 44.2 percent oil content (Table 4b). In East Lansing and Clarksville exactly the same trend for all of these crosses occurred as for combined analysis (Tables 5b & 6b).

Table 4.a Means for seven traits of 21 entries/crosses of canola combined for both locations, East Lansing and Clarksville, MI 1991

Entries/Crosses	DE*	Cwn Dia	Lf L 1.nd	Lf L 2.nd	Lf L full	Lf Wd	DOF
1.LD-9430	10	3.83	5.35	7.10	11.03	5.81	246
2.Cascade	8	3.78	5.88	7.16	11.53	5.63	235
3.Cobra	9	3.70	5.40	6.96	11.93	5.56	241
4.Winfield	9	3.23	5.75	7.75	12.26	5.58	242
5.Ceres	10	4.03	6.28	8.00	13.93	5.80	246
6.CC-4	8	4.00	5.66	7.43	12.21	6.15	236
7.LD-9430xCasc.	9	3.95	5.60	7.13	11.50	5.83	237
8.LD-9430x Cobra	9	3.88	5.25	6.96	11.41	5.81	240
9.LD-9430xWin.	9	3.48	5.35	7.48	11.60	5.78	241
10.LD-9430xCeres	10	4.10	6.15	7.55	11.53	5.91	247
11.LD-9430xCC-4	9	3.96	5.76	7.16	11.75	5.80	238
12.Casc.xCobra	8	3.86	5.56	6.93	11.80	5.61	235
13.Casc.xWinf.	9	3.43	5.75	7.36	12.01	5.63	237
14.Casc.xCeres	9	3.91	6.26	7.50	12.88	5.86	241
15.Casc.xCC-4	8	3.86	5.73	7.23	11.78	5.93	233
16.CobraxWinf.	9	3.40	5.50	7.26	12.15	5.95	237
17.CobraxCeres	9	4.00	5.76	7.50	13.11	5.90	243
18.CobraxCC-4	8	3.80	5.51	7.00	12.13	5.93	235
19.Winf.xCeres	10	3.73	5.93	7.95	13.26	5.73	243
20.Winf.xCC-4	8	3.51	5.58	7.60	12.11	5.60	236
21.CeresxCC-4	10	4.10	4.70	7.68	13.21	6.18	242
Grand mean	9	3.79	5.65	7.36	12.15	5.81	240
LSD (0.05)	ns	0.18	0.19	0.16	0.19	0.17	1.9

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 4.b Means for seven traits in 15 canola crosses combined for both locations, East Lansing and Clarksville, MI 1991

Entries/Crosses	DTM*	Br/ Plt	Pd/ Plt	Sd/ Pod	100 Sd/Wt	Yld kg/ha	Oil %
1.LD-9430	305	8.4	140	17.6	.47	2130	40.0
2.Cascade	292	7.2	136	20.8	.51	2246	41.3
3.Cobra	301	6.7	172	26.0	.49	2512	40.7
4.Winfield	301	7.8	158	21.8	.42	2253	42.3
5.Ceres	298	6.7	184	29.1	.38	2829	40.6
6.CC-4	290	6.8	205	27.8	.37	2634	41.6
7.LD9430xCas.	300	7.9	152	20.8	.48	2465	42.6
8.LD9430xCob.	302	7.7	186	25.5	.48	2816	42.4
9.LD9430xWin.	302	8.4	170	22.1	.43	2548	42.8
10.LD9430xCer.	300	7.6	207	29.6	.40	3240	40.9
11.LD9430xCC-4	295	7.5	212	27.5	.40	3022	41.3
12.Cas.xCob.	297	6.9	180	26.5	.52	2756	41.0
13.Cas.xWin.	298	7.4	164	23.8	.46	2558	42.7
14.Cas.xCer	294	7.1	197	30.1	.42	3178	42.2
15.Cas.xCC-4	290	6.8	217	31.0	.44	3258	40.8
16.Cob.xWin.	299	7.7	181	26.6	.42	2698	40.6
17.Cob.xCer.	282	6.9	217	32.8	.42	3314	42.7
18.Cob.xCC-4	293	6.6	231	32.3	.45	3181	42.8
19.Win.xCer.	297	7.6	197	30.6	.42	2932	45.1
20.Win.xCC-4	295	7.3	221	29.0	.43	2976	44.2
21.Cer.xCC-4	294	6.7	221	31.6	.40	3061	43.5
Grand mean	296	7.3	188	26.8	.44	2790	42.1
LSD (0.05)	14.9	0.67	30	7.2	ns	387	2.5

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 5.a Means for seven traits of 21 entries/crosses of canola grown in East Lansing, MI 1991

Entries/Crosses	DE*	Cwn Dia	Lf L 1.nd	Lf L 2.nd	Lf L full	Lf Wd	DOF
1.LD-9430	9	4.70	5.90	8.20	13.60	6.40	242
2.Cascade	7	4.33	7.46	8.80	14.80	6.40	230
3.Cobra	8	4.63	7.36	9.50	16.03	6.40	235
4.Winfield	8	3.93	7.10	10.20	16.40	6.00	239
5.Ceres	9	5.06	8.30	10.75	19.83	7.06	243
6.CC-4	7	4.80	7.46	9.93	16.50	7.56	232
7.LD-9430xCasc.	8	4.60	6.53	8.40	14.70	6.46	233
8.LD-9430xCobra	8	4.80	6.40	8.53	14.76	6.60	237
9.LD-9430xWin.	9	4.10	6.20	9.23	14.86	6.16	242
10.LD-9430xCeres	9	5.00	7.86	9.50	14.76	6.86	243
11.LD-9430xCC-4	8	4.76	7.13	8.93	15.10	6.40	233
12.Casc.xCobra	7	4.50	7.46	9.10	15.67	6.33	229
13.Casc.xWinf.	8	4.03	7.20	9.43	15.80	6.23	233
14.Casc.xCeres	8	4.90	8.00	9.56	17.63	6.86	237
15.Casc.xCC-4	7	4.63	7.43	9.23	15.43	7.10	229
16.CobraxWinf.	8	4.20	7.20	9.70	16.40	6.90	233
17.CobraxCeres	8	5.06	7.76	10.26	18.30	6.73	240
18.CobraxCC-4	7	4.66	7.36	9.50	16.13	6.93	231
19.Winf.xCeres	9	4.60	7.60	10.60	18.40	6.46	240
20.Winf.xCC-4	7	4.23	7.20	10.20	16.13	6.33	231
21.CeresxCC-4	9	5.13	5.06	10.16	18.43	7.36	240
Grand mean	8	4.60	7.14	9.51	16.17	6.48	236
LSD (0.05)	ns	0.22	0.19	0.17	0.19	0.19	2.1

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 5.b Means for seven traits in 21 entries/crosses of canola grown in East Lansing, Mi 1991

Entries/Crosses	DTM*	Br/ Plt	Pd/ Plt	Sd/ Pod	100 Sd/Wt	Yld kg/ha	Oil %
1.LD-9430	301	8.3	146	18.3	.47	2256	40.2
2.Cascade	290	7.2	142	21.6	.51	2411	41.3
3.Cobra	297	6.8	175	26.6	.49	2712	41.0
4.Winfield	296	7.8	162	21.6	.42	2435	42.3
5.Ceres	295	6.8	187	30.3	.38	3096	39.5
6.CC-4	289	6.7	205	28.0	.37	2858	41.4
7.LD9430xCas.	294	7.8	159	21.6	.50	2625	42.7
8.LD9430xCob.	299	7.7	190	26.3	.50	3002	42.4
9.LD9430xWin.	297	8.3	180	23.0	.45	2781	42.6
10.LD9430xCer.	298	7.5	212	31.0	.41	3510	41.6
11.LD9430xCC-4	291	7.5	219	28.3	.40	3302	41.4
12.Cas.xCob.	294	7.0	188	27.6	.52	2987	41.2
13.Cas.xWin.	294	7.5	171	24.3	.47	2804	42.8
14.Cas.xCer	291	7.0	206	31.3	.43	3459	42.2
15.Cas.xCC-4	288	6.8	209	29.3	.44	3258	40.9
16.Cob.xWin.	294	7.7	179	26.6	.44	2877	40.8
17.Cob.xCer.	295	6.8	221	34.0	.44	3616	42.9
18.Cob.xCC-4	290	6.7	230	32.3	.46	3405	42.9
19.Win.xCer.	293	7.5	201	29.0	.43	3146	45.2
20.Win.xCC-4	292	7.3	226	29.0	.44	3203	44.5
21.Cer.xCC-4	292	6.8	222	32.6	.40	3318	43.7
Grand mean	294	7.3	192	27.4	.44	3002	42.1
LSD (0.05)	2.2	0.83	33	6.3	ns	343.6	2.6

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 6.a Means for seven traits of 21 entries/crosses of canola grown in Clarksville, MI 1991

Entries/Crosses	DE*	Cwn Dia	Lf L 1.nd	Lf L 2.nd	Lf L full	Lf Wd	DOF
1.LD-9430	12	2.96	4.80	6.00	8.46	5.23	251
2.Cascade	9	3.23	4.30	4.53	8.26	4.86	240
3.Cobra	10	2.76	3.43	4.43	7.83	4.73	247
4.Winfield	10	2.53	4.40	5.30	8.13	5.16	245
5.Ceres	11	3.00	4.26	5.23	8.03	4.53	250
6.CC-4	10	3.20	3.86	4.93	7.93	4.73	240
7.LD-9430xCasc.	10	3.30	4.66	5.86	8.30	5.20	242
8.LD-9430xCobra	11	2.96	4.10	5.40	8.06	5.03	243
9.LD-9430xWin.	10	2.86	4.50	5.73	8.33	5.40	240
10.LD-9430xCeres	12	3.20	4.43	5.60	8.30	4.96	251
11.LD-9430xCC-4	10	3.16	4.40	5.40	8.40	5.20	242
12.Casc.xCobra	10	3.23	3.66	4.76	8.03	4.90	240
13.Casc.xWinf.	10	2.83	4.30	5.30	8.23	5.03	240
14.Casc.xCeres	11	2.93	4.53	5.43	8.13	4.86	244
15.Casc.xCC-4	9	3.10	4.03	5.23	8.13	4.76	237
16.CobraxWinf.	10	2.60	3.80	4.83	7.90	5.00	242
17.CobraxCeres	11	2.93	3.76	4.73	7.93	5.06	247
18.CobraxCC-4	10	2.93	3.66	4.50	8.13	4.93	240
19.Winf.xCeres	11	2.86	4.26	5.30	8.13	5.00	247
20.Winf.xCC-4	10	2.80	3.96	5.00	8.10	4.86	241
21.CeresxCC-4	11	3.06	4.33	5.20	8.00	5.00	245
Grand mean	10	2.97	4.16	5.22	8.13	4.97	244
LSD (0.05)	ns	0.14	0.20	0.20	0.20	0.16	1.8

* Abbreviations & units of the characters are explained in table 3,p. 42

Table 6.b Means for seven traits in 21 entries/crosses of canola grown in Clarksville, MI 1991

Entries/Crosses	DTM*	Br/ Plt	Pd/ Plt	Sd/ Pod	100 Sd/Wt	Yld kg/ha	Oil %
1.LD-9430	310	8.5	135	17.0	.47	2004	39.9
2.Cascade	295	7.2	130	20.0	.51	2081	41.3
3.Cobra	306	6.7	170	25.3	.49	2313	40.5
4.Winfield	306	7.8	155	22.0	.42	2072	42.3
5.Ceres	301	6.7	181	28.0	.38	2562	41.7
6.CC-4	291	7.0	205	27.6	.37	2416	41.7
7.LD9430xCas.	306	8.0	146	20.0	.47	2304	42.5
8.LD9430xCob.	305	7.8	182	24.6	.47	2631	42.4
9.LD9430xWin.	307	8.5	161	21.3	.41	2315	42.9
10.LD9430xCer.	301	7.7	203	28.3	.40	2971	40.3
11.LD9430xCC-4	300	7.5	206	26.6	.41	2745	41.3
12.Cas.xCob.	300	6.8	172	25.3	.52	2526	40.8
13.Cas.xWin.	302	7.3	157	23.3	.44	2311	42.6
14.Cas.xCer.	297	7.2	188	29.0	.41	2900	42.1
15.Cas.xCC-4	293	6.8	225	32.6	.44	3258	40.8
16.Cob.xWin.	305	7.8	183	26.6	.40	2520	40.7
17.Cob.xCer.	268	7.0	213	31.6	.40	3012	42.5
18.Cob.xCC-4	296	6.7	233	32.3	.44	2958	42.8
19.Win.xCer.	301	7.7	193	29.0	.40	2719	45.0
20.Win.xCC-4	299	7.3	215	29.0	.42	2748	43.9
21.Cer.xCC-4	297	6.7	221	30.6	.40	2803	43.3
Grand mean	299	7.36	184	26.2	.43	2579	41.9
LSD (0.05)	21.2	0.50	27.3	8.2	ns	437	2.5

* Abbreviations & units of the characters are explained in table 3, p. 42

Heterosis

Heterosis was calculated as a percent increase or decrease over the mid-parent performance for yield and a series of morphological traits and yield components as explained in materials and methods. The negative heterosis value describes the decrease in trait performance while the positive value indicates the greater heterosis compared to its mid-parent value.

Days to Emergence

A range of negative to positive percent heterosis was observed among the crosses for this trait for both combined as well as separately for each location. The cross Ceres x CC-4 showed the highest percent increase with a mean value of 8.11 percent followed by Cascade x Winfield with a mean of 5.88 percent increase when calculated combined for both locations (Table 7a).

In East Lansing, the same crosses maintained their respective positions (Table 8a), whereas in Clarksville, Cascade x Ceres showed the highest performance with an increase of 10 percent over the mid-parent value followed by Cascade x Cobra and Cascade x Winfield, both with a common increase of 5.26 percent (Table 9a).

Crown Diameter

The cross LD-9430 x Ceres showed the highest heterosis with a 4.73 percent increase over mid-parent yield, calculated across both locations. It was followed by Cobra x Ceres with 3.9 percent increase (Table 7a).

In East Lansing, Cobra x Ceres exhibited an increase of 4.4 percent followed by Ceres x CC-4 with 4.06 percent increase (Table 8a). In Clarksville, Cascade x Cobra was found with the largest increase of 7.85 percent followed by LD-9430 x Ceres with a 7.38 percent increase (Table 9a).

Leaf Length (1st, 2nd & 3rd node)

The cross LD-9430 x Ceres exhibited the largest percent increase with a 10.76 percent value, followed by LD-9430 x CC-4 with an increase of 6.74 percent for the leaf length up to fist node, when combined for both locations. For leaf length up to second node, Winfield x CC-4 was the best with a 1.34 percent increase, followed by Cobra x Ceres with an increase of 1.28 percent. The cross LD-9430 x Cascade proved to be the best with an increase of 3.52 percent (Table 7a) for leaf length up to the third node (full leaf length).

In East Lansing, the highest percent increase for the leaf length up to the first node occurred for the cross LD-9430 x Ceres with an increase of 10.76 percent. In the same location, Winfield x CC-4 exhibited the largest leaf length up to the second node with 1.34 percent increase. For the final

leaf length (up to the 3rd node) LD-9430 x Cascade had the largest 3.52 percent increase (Table 8a).

In Clarksville the cross Ceres x CC-4 had the largest percent increase for the leaf length up to the first node with 6.65 percent, whereas LD-9430 x Cobra was next for leaf length up to the 2nd node with 3.55 percent increase and for full leaf length (up to the 3rd node) Cobra x CC-4 had the highest percent increase of 3.17 Percent over the mid-parent value (Table 9a).

Leaf Width

The cross Cobra x Winfield exhibited the largest increase of 5.78 percent heterosis combined for both locations (Table 7a), whereas in East Lansing, it exhibited the largest increase of 15.17 percent (Table 8a). In Clarksville the cross Cobra x Ceres had the highest increase of 9.29 percent (Table 9a).

Days to Flower

The cross Cobra x Winfield was the earliest maturing, with a decrease of -1.76 percent, when heterosis was calculated across both locations. This was followed by LD-9430 x Cobra with -1.61 percent decrease (Table 7a).

In East Lansing, the cross Winfield X CC-4 was the earliest maturing with -1.91 percent decrease, followed by Cobra x Winfield with a -1.69 percent decrease (Table 8a). In

Clarksville, the Cross LD-9430 x Winfield was the earliest maturing with a decrease of -3.22 percent, followed by LD-9430 X Cobra with -2.60 percent decrease (Table 9a).

Days to Maturity

When calculated across locations, the cross Cobra x Ceres was the earliest maturing of all others with a decrease of -5.95 percent, followed by Cobra x CC-4 with a decrease of -0.87 percent (Table 7b). When calculated for East Lansing, the cross LD-9430 x CC-4 was found the earliest maturing with a decrease of -1.36 percent followed by Cobra x CC-4 with -0.85 percent decrease (Table 8b). In Clarksville the cross Cobra x Ceres was the earliest with -11.58 percent increase followed by LD-9430 x Ceres with a decrease of -1.42 percent (Table 9b).

Branches per Plant

The Cross Cobra x Winfield had the highest number of branches per plant with 6.31 percent increase over the mid-parent, followed by Winfield x Ceres, with a 3.98 percent increase across both locations (Table 7b).

In East Lansing, Cobra x Winfield, again had the highest number of branches with an increase of 4.50 percent. This was followed by LD-9430 x Winfield with an increase of 3.09 percent (Table 8b).

In Clarksville, the same cross Cobra x Winfield

maintained its first position, with the highest percent increase of 8.07 percent followed by Winfield x Ceres with a 5.73 percent increase (Table 9b).

Pods per Plant

The Cross LD-9430 x Ceres had the highest number of pods per plant with 27.90 percent increase, followed by Cascade x CC-4 with a 27.34 percent increase across both locations (Table 7b).

In East Lansing, LD-9430 x Ceres had the highest number of pods per plant with a 27.47 percent increase, followed by LD-9430 x CC-4 which had the highest number of pods per plant, with an increase of 25.04 percent (Table 8b). In Clarksville, Cascade x CC-4 had the highest number of pods with an increase of 34.59 percent, was followed by LD-9430 x Ceres with an increase of 28.35 percent (Table 9b).

Seeds per Pod

The cross Cascade x CC-4 had the largest number of seeds per pod with an increase of 27.41 percent. This was followed by LD-9430 x Ceres with a 26.67 percent increase combined for both locations (Table 7b).

In East Lansing, LD-9430 x Ceres had the largest number of seeds per pod with an increase of 27.41 percent followed by LD-9430 x CC-4 with a 22.30 percent increase (Table 8b). In Clarksville, the cross Cascade x CC-4 was the largest with a

37.05 percent increase followed by LD-9430 x Ceres with an increase of 25.91 percent (Table 9b).

One Hundred Seed Weight

The cross Winfield x CC-4 exhibited the highest one hundred seed weight with an increase of 8.86 percent followed by Ceres x CC-4 with a 8.11 percent increase across both locations (Table 7b).

In East Lansing, the cross Winfield x CC-4 had the largest percent increase of 11.39, followed by Winfield x Ceres, with an increase of 7.50 percent (Table 8b). In Clarksville, Ceres x CC-4 had the highest mean seed weight, value with a 6.67 percent increase followed by Winfield x CC-4 with a 6.33 percent increase (Table 9b).

Yield (kg/ha)

When calculated across locations Cascade x CC-4 had the highest yield increase of 33.46 percent. It was followed by LD-9430 x Ceres with a 30.69 percent increase (Table 7b).

LD-9430 x Ceres showed the greatest heterosis with a 31.18 percent yield increase at East Lansing, was followed by LD-9430 x CC-4 with a 29.12 percent increase in yield (Table 8b). In Clarksville, Cascade x CC-4 had the best yielding cross, with a 44.94 percent increase. It was followed by LD-9430 x Ceres with an increase of 30.13 percent (Table 9b). Heterosis ranged from 12.0 to 33.5 percent across locations.

Percent Oil Content

When the heterosis was calculated across both locations, the cross Winfield x Ceres had the highest oil content with a 8.81 percent increase, followed by Ceres x CC-4 with a 5.90 percent increase. At East Lansing, Winfield x Ceres had a 10.47 percent increase in oil content, followed by Ceres x CC-4 with a 8.07 percent increase (Table 8b). In Clarksville, the cross Winfield x Ceres showed the highest oil content with a 7.18 percent increase followed by LD-9430 x Cobra with a 5.64 percent increase (Table 9b).

4.2 Cultivar Analysis

The first three PCs of the cultivar data accounted for the largest amount of variation, which was 76 percent of the total variance for crown diameter and yield components among the cultivar means; PC_1, PC_2 and PC_3, accounted for 32 percent, 23 percent and 21 percent of the variance, respectively (Table 11). No significant correlation between the 12 traits of the thirty canola cultivars occurred except that between pods per plant and seed per pod ($r = 0.43$) (Table 12).

4.3 Genetic Distance

The genetic distance between the six parents used in the crossing program was based upon their morphological and yield component traits. The distance between the parents ranged from 1.104 to 7.497 (Table 10). The minimum distance was between

Cobra and Winfield which belong to the second cluster. In the first cluster comprised of LD-9430 and Cascade with genetic distance of 2.128. In the third cluster the distance between the two parents was 2.501. This was compared with a maximum distance of 7.497 between the parents of two different clusters. One parent, LD-9430, belonged to cluster number one, whereas the other parent, Ceres, belonged to cluster number three.

Table 7.a Percent mid-parent heterosis for 15 canola crosses combined for both locations, East Lansing and Clarksville, MI 1991

Crosses	DE*	Cwn Dia	Lf L 1.nd	Lf L 2.nd	Lf L full	Lf Wd	DOF
1.LD-9430xCasc.	-2.70	3.81	-0.27	0.00	1.95	1.92	-1.42
2.LD-9430xCobra	-2.56	3.05	-2.33	-1.00	-0.61	1.22	-1.61
3.LD-9430xWin.	-2.56	-1.42	-3.60	0.74	-0.39	1.49	-1.36
4.LD-9430xCeres	2.44	4.73	5.76	0.00	-7.61	1.81	0.07
5.LD-9430xCC-4	-5.26	1.15	4.63	-1.45	1.12	-3.01	-1.48
6.Casc.xCobra	0.00	3.21	-1.42	-1.84	0.60	0.27	-1.33
7.Casc.xWinf.	5.88	-2.14	-1.12	-1.27	0.97	0.45	-0.73
8.Casc.xCeres	5.56	0.51	2.96	-1.06	1.18	2.54	-0.03
9.Casc.xCC-4	-3.03	-0.77	-0.69	-0.89	-0.76	0.68	-1.13
10.CobraxWinf.	0.00	-1.88	-1.35	-1.29	0.45	5.78	-1.76
11.CobraxCeres	0.00	3.90	-1.37	0.27	1.39	2.88	-0.10
12.CobraxCC-4	-2.86	-1.30	-0.36	-2.71	0.50	0.34	-1.33
13.Winf.xCeres	5.26	3.18	-1.41	0.95	1.26	0.70	-0.41
14.Winf.xCC-4	-2.86	-2.90	-2.19	0.13	-1.02	-4.52	-1.29
15.CeresxCC-4	8.11	2.50	-1.27	-0.45	1.07	3.43	0.45
Mean	0.36	1.04	0.26	-0.62	0.01	1.06	-0.90

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 7.b Percent mid-parent heterosis for seven traits in 15 canola crosses combined for both locations, East Lansing and Clarksville, MI 1991

Crosses	DTM*	Br/ Plt	Pd/ Plt	Sd/ Pod	100 Sd/Wt	Yld	Oil %
1.LD-9430xCasc.	0.42	1.54	10.18	8.21	-2.04	12.66	4.72
2.LD-9430xCobra	-0.55	2.18	18.72	16.78	0.00	21.33	5.09
3.LD-9430xWin.	-0.47	3.51	14.14	12.20	-3.37	16.27	3.96
4.LD-9430xCeres	-0.66	-0.07	27.90	26.67	-5.88	30.69	1.45
5.LD-9430xCC-4	-0.87	-1.64	23.08	20.88	-4.76	26.85	1.40
6.Casc.xCobra	-0.03	-0.65	16.66	13.18	4.00	24.32	-0.09
7.Casc.xWinf.	0.45	-1.13	11.13	11.72	-1.08	13.70	2.18
8.Casc.xCeres	-0.42	1.80	22.91	20.66	-5.62	25.28	2.92
9.Casc.xCC-4	-0.23	-2.36	27.34	27.41	0.00	33.46	-1.42
10.CobraxWinf.	-0.58	6.31	9.41	11.52	-7.69	13.27	-1.82
11.CobraxCeres	-5.95	2.37	21.74	19.04	-3.45	24.10	4.89
12.CobraxCC-4	-0.87	-1.91	22.63	20.12	4.65	23.56	4.07
13.Winf.xCeres	-0.86	3.98	15.14	20.26	5.00	15.41	8.81
14.Winf.xCC-4	0.00	0.00	21.38	16.79	8.86	21.70	5.34
15.CeresxCC-4	0.09	-0.59	13.81	11.14	8.11	12.01	5.90
Mean	-0.70	0.89	18.41	17.11	-0.22	20.97	3.16

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 8.a Percent mid-parent heterosis for seven traits in 15 canola crosses grown in East Lansing, MI 1991

Crosses	DE*	Cwn Dia	Lf L 1.nd	Lf L 2.nd	Lf L full	Lf Wd	DOF
1.LD-9430xCasc.	0.00	1.88	-2.45	-1.18	3.52	7.40	-1.27
2.LD-9430xCobra	-5.88	2.89	-3.47	-3.62	-0.37	10.37	-0.56
3.LD-9430xWin.	5.88	-4.98	-4.62	0.33	-0.93	2.84	0.55
4.LD-9430xCeres	0.00	2.46	10.76	0.21	-11.70	12.46	0.07
5.LD-9430xCC-4	0.00	0.21	6.74	-1.49	0.33	1.99	-1.48
6.Casc.xCobra	-6.67	0.45	0.67	-0.55	0.94	5.85	-1.29
7.Casc.xWinf.	6.67	-2.42	-1.10	-0.74	1.28	4.01	-0.43
8.Casc.xCeres	0.00	32.61	1.52	-2.25	1.82	12.46	0.21
9.Casc.xCC-4	0.00	1.42	-0.40	-1.44	-1.41	13.15	-0.94
10.CobraxWinf.	0.00	-1.87	-0.41	-1.52	1.14	15.19	-1.69
11.CobraxCeres	-5.88	4.44	-0.89	1.28	2.06	10.33	0.35
12.CobraxCC-4	-6.67	-1.17	-0.67	-2.21	-0.83	10.44	-1.01
13.Winf.xCeres	-5.88	2.34	-1.30	1.15	1.57	9.49	-0.48
14.Winf.xCC-4	-6.67	-3.09	-1.10	1.34	-1.95	4.20	-1.91
15.CeresxCC-4	8.11	4.06	-5.79	-1.79	1.46	11.43	0.98
Mean	-1.13	2.62	-0.17	-0.83	-0.26	8.77	-0.59

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 8.b Percent mid-parent heterosis for seven traits in 15 canola crosses grown in East Lansing, MI 1991

Crosses	DTM*	Br/ Plt	Pd/ Plt	Sd/ Pod	100 Sd/Wt	Yld	Oil %
1.LD-9430xCasc.	-0.40	1.10	10.16	8.33	2.04	12.51	4.75
2.LD-9430xCobra	0.06	1.06	18.26	17.05	4.17	20.85	4.55
3.LD-9430xWin.	-0.56	3.09	16.63	15.03	1.12	18.59	3.38
4.LD-9430xCeres	0.11	-1.06	27.47	27.41	-3.53	31.18	4.47
5.LD-9430xCC-4	-1.36	0.07	25.04	22.30	-4.76	29.12	1.43
6.Casc.xCobra	0.11	0.07	18.40	14.49	4.00	16.61	0.19
7.Casc.xWinf.	0.28	0.07	12.01	12.33	1.08	15.76	2.46
8.Casc.xCeres	-0.51	0.07	24.93	20.52	-3.37	25.60	4.49
9.Casc.xCC-4	-0.40	-1.16	20.12	18.12	0.00	23.68	-1.09
10.CobraxWinf.	-0.84	4.50	5.92	10.35	-3.30	11.85	-1.97
11.CobraxCeres	-0.17	0.00	22.13	19.32	1.15	24.57	6.54
12.CobraxCC-4	-0.85	-1.33	21.02	18.29	6.98	22.26	4.13
13.Winf.xCeres	-0.79	2.32	15.13	11.56	7.50	13.79	10.47
14.Winf.xCC-4	-0.11	1.10	23.01	16.79	11.39	21.03	6.26
15.CeresxCC-4	0.00	1.19	12.98	11.98	6.67	11.49	8.07
Mean	-0.36	0.74	18.21	16.26	2.08	19.93	3.87

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 9.a Percent mid-parent heterosis for seven traits in 15 canola crosses grown in Clarksville, MI 1991

Crosses	DE*	Cwn Dia	Lf L 1.nd	Lf L 2.nd	Lf L full	Lf Wd	DOF
1.LD-9430xCasc.	-4.76	6.62	2.42	1.65	-0.72	3.07	-1.56
2.LD-9430xCobra	0.00	3.50	-0.36	3.55	-1.04	1.00	-2.60
3.LD-9430xWin.	-9.09	4.19	-2.17	1.42	0.42	3.95	-3.22
4.LD-9430xCeres	4.35	7.38	-2.21	-0.27	0.67	1.64	0.07
5.LD-9430xCC-4	-9.09	2.60	1.62	-1.19	2.50	4.42	-1.49
6.Casc.xCobra	5.26	7.85	-5.34	-4.42	-0.19	2.19	-1.37
7.Casc.xWinf.	5.26	-1.74	-1.15	-2.12	0.43	0.40	-1.03
8.Casc.xCeres	10.00	-5.94	5.84	0.93	-0.18	3.51	-0.27
9.Casc.xCC-4	-5.26	-3.58	-1.23	0.00	0.43	-0.73	-1.32
10.CobraxWinf.	0.00	-1.70	-2.94	-0.72	-1.00	1.11	-1.82
11.CobraxCeres	4.76	1.74	-2.21	-2.07	0.00	9.29	-0.67
12.CobraxCC-4	0.00	-1.68	0.41	-3.85	3.17	4.23	-1.57
13.Winf.xCeres	4.76	3.44	-1.62	0.66	0.62	3.20	-0.33
14.Winf.xCC-4	0.00	-2.27	-4.12	-2.25	0.87	-1.72	-0.69
15.CeresxCC-4	4.76	-1.29	6.65	2.36	0.25	7.99	-0.20
Mean	0.73	1.27	-0.43	-0.42	0.42	2.90	-1.20

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 9.b Percent mid-parent heterosis for seven traits in 15 canola crosses grown in Clarksville, MI 1991

Crosses	DTM*	Br/ Plt	Pd/ Plt	Sd/ Pod	100 Sd/Wt	Yld	Oil %
1.LD-9430xCasc.	1.21	2.17	10.19	8.11	-4.08	12.83	4.73
2.LD-9430xCobra	-1.13	3.30	19.22	16.51	-2.08	21.88	5.64
3.LD-9430xWin.	-0.38	4.10	11.49	9.31	-7.87	13.61	4.54
4.LD-9430xCeres	-1.42	1.06	28.35	25.91	-5.88	30.13	-1.25
5.LD-9430xCC-4	-0.39	-3.23	21.06	19.39	-2.38	24.23	1.35
6.Casc.xCobra	-0.17	-1.16	14.76	11.76	4.00	14.97	-0.33
7.Casc.xWinf.	0.61	-2.20	10.18	11.10	-5.38	11.29	1.88
8.Casc.xCeres	-0.34	3.62	20.77	20.83	-7.87	24.89	1.37
9.Casc.xCC-4	-0.06	-3.53	34.59	37.05	0.00	44.94	-1.76
10.CobraxWinf.	-0.33	8.07	12.70	12.66	-12.09	14.93	-1.69
11.CobraxCeres	-11.58	5.11	21.33	18.73	-8.05	23.54	3.30
12.CobraxCC-4	-0.89	-2.49	24.05	22.02	2.33	25.09	4.03
13.Winf.xCeres	-0.93	5.73	15.16	16.00	0.00	17.35	7.18
14.Winf.xCC-4	0.11	-1.15	19.70	16.79	6.33	22.49	4.42
15.CeresxCC-4	0.17	-2.49	14.65	10.17	6.67	12.63	3.76
Mean	-1.03	1.13	18.55	17.09	2.42	20.98	2.48

* Abbreviations & units of the characters are explained in table 3, p. 42

Table 10. Genetic distance between six parents calculated based on their morphological and yield components traits*

	Cluster No.1		Cluster No.2		Cluster No.3	
	LD-9430	Cascade	Cobra	Winfield	Ceres	CC-4
LD-9430	-	-	-	-	-	-
Cascade	2.128	-	-	-	-	-
Cobra	3.576	2.402	-	-	-	-
Winfield	4.266	2.927	1.104	-	-	-
Ceres	7.497	6.180	4.592	4.376	-	-
CC-4	5.610	4.785	3.341	3.545	2.501	-

* Five traits including four yield components and one morphological trait (crown diameter) were used to make three clusters.

Table 11. Eigenvalues of the five PC axes from PC analysis of thirty canola cultivars, with the proportion of total variance accounted for by each axis

Principal Component	Eigenvalue	Proportion of Variance	Cumulative Variance
1	1.609	0.322	0.322
2	1.169	0.234	0.555
3	1.056	0.211	0.767
4	0.774	0.154	0.922
5	0.390	0.078	1.000

Table 12. Correlation coefficients between five traits for thirty canola cultivars

	Br/ Plt*	Pd/ Plt	Sd/ Pod	100 Sd/Wt
Cwn Dia	-0.040	0.184	-0.002	0.119
Br/ Plt	_	0.290	-0.065	0.063
Pd/ Plt	_	_	0.435	-0.213
Sd/ Pod	_	_	_	-0.190

* Abbreviations & units of the characters are explained in table 3, p. 42

DISCUSSION

The heterotic response was calculated as a percent of the mid-parent performance for yield, yield components and other morphological traits. The data reveals that all of the fifteen hybrids exceeded the mid-parent value for seed yield at both locations during 1991. Twelve out of fifteen crosses showed higher performance than their mid-parent value for oil content. Likewise, all the 15 crosses exhibited higher performance compared to their mid-parent value for pods per plant and seeds per pod.

All of the fifteen crosses exceeded the high parent value for seed yield which is an important trait and major focus of the study. High parent heterosis ranged from 3-23 percent compared to mid-parent heterosis which showed a range of 13-33 percent. Since high parent heterosis was demonstrated, however, the value of the low parent does not appear to negatively effect dominance genetic variance contributing to yield. The low parent might be used for combining some other important qualitative traits like disease resistance and oil content with the yield.

The data agrees with findings of other researchers. Paterniani (1973) observed that 61 out of 63, or 97 percent of the crosses exceeded their mid-parental value for yield in maize. Upadhaya (1967) observed that in 28 barley crosses, 14

exceeded the corresponding mid-parent value significantly for yield, 7 out of 28 exceeded the mid-parent for kernel weight, 11 for kernels per head and 5 out of 28 exceeded mid-parent for heads per plant.

The correlation between heterotic effects for seed yield and parental distance as estimated by the Euclidean distance method was positive and highly significant ($r = 0.70$) for combined analysis at both individual and combined locations. The correlation coefficient $r = 0.86$ was estimated for the East Lansing location and $r = 0.60$, for the Clarksville location. This positive and significant correlation supports the strong association of seed yield heterosis with genetic distance between parents. These data agree with earlier reports by Khanna et al. (1977) in tomato, Moll et al. (1962) in maize and Shamsuddin (1985) in wheat. In a study of genetic diversity in relation to heterosis and combining ability in spring wheat, Shamsuddin (1985) observed a significant positive correlation for genetic diversity between the parents with heterosis for grain yield of hybrids ($r = 0.45$).

Estimated heterosis for the number of pods per plant and seeds per pod was also highly significant and positively correlated with genetic distance. The correlation for number of pods per plant calculated for both locations was $r = 0.79$, which was positive and highly significant for both East Lansing at $r = 0.71$ and Clarksville at $r = 0.63$. Likewise, the correlation for number of seeds per pod for combined analysis

at both locations highly significant and positive at r = 0.80. It was also positive and highly significant for each location separately. Values for East Lansing were r = 0.86 and r = 0.61 for Clarksville. From individual and combined locations it is concluded that both pods per plant and seeds per pod have a strong association with the genetic distance. This association is therefore, an indication that there was a positive association between seed yield as deduced from the number of pods per plant, seeds per pod and the genetic distance. This supports the findings of other researchers in several crops (Moll et al. 1962, Grant et al. 1985, Hutcheson et al. 1981, Khanna et al. 1977) in maize, rapeseed and tomato respectively. In a similar study in dry beans Ghaderi et al. (1984) found a positive correlation between genetic distance and number of pods per plant, seeds per pod, and seed yield. However, they did not find any correlation for seed yield and number of seeds per pod with the genetic distance in faba bean. They presumed that this could be due to the complete additivity of genes and the common genes shared by the parents.

Relatively little variation occurred between the crosses for traits like crown diameter, leaf length, leaf width and branches per plant. The data for crown diameter deviated from mid-point values for all the fifteen crosses from -0.11 to 0.14, for leaf length -0.95 to 0.23, for leaf width it ranged from -0.27 to 0.38, and -0.17 to 0.29 for branches per plant.

No significant correlation occurred between mid-parent heterosis for these traits and the estimates of genetic distance. The data suggests that the observed variation was due to environmental effects rather than genetic effects.

Falconer (1982) showed the occurrence of heterosis (H) in the F_1 generation for a given quantitatively inherited trait depends on the following:

$$H = \Sigma\ dy^2$$

where "d" is the deviation of the heterozygote from the mean of the homozygote parents and "y" is the difference of gene frequency between the two intermated populations. The positive association between the above-mentioned characters under the study could be attributed to the following:

Two possible factors could be contributing to a positive association between the genetic distance and heterosis in a set of crosses. 1) Either dominance has to exist, which should increase in magnitude and proportion directly with an increase in distance of the parental population and/or 2) the parental populations should be different in gene frequencies which are controlling these characters and this difference should also have to increase as the distance among the parents becomes greater. For characters such as yield, numbers of pods, and seeds per pod which are inherited quantitatively in canola, the heterotic effect depends on the number of

contrasting loci and their dominance effects.

As discussed earlier, almost all of the morphological and phenological characters except yield and yield components showed no correlation with the genetic distance estimates. This could be explained by the complete additivity of genes controlling these characters, i.e. (d = 0) and/or the parental populations involved in crossing shared the same genes and thus lacked adequate genetic variation for these traits (y^2 = 0). A second possible reason for lack of association could be due to an unpredictable and random expression of the heterosis. The data indicates that certain crosses have zero heterotic effects, perhaps because of the cancellation of positive and negative dominance effects, which occurs in both directions. Moreover, the interallelic interactions or epistasis may also produce certain kinds of specific effects which may lead to the lack of association between the heterosis and genetic distance.

A lack of genetic variation in the morphological traits in the parental material used for this study is apparent. For a successful hybridization program some long term strategies are needed to maximize the genetic diversity in the material. New germplasm could be obtained from geographically diverse origins and international germplasm centers. This would enhance the genetic diversity and broaden the genetic base of the material, which should lead towards the maximum heterosis and ultimately improvement in both yield and specific useful

morphological traits.

For phenological traits such as days to flower and days to maturity, there was no significant correlation occurred between heterosis and genetic distance. Thus, is based on combined and separate analysis for both locations, almost all of the crosses had negative heterosis. These results are also consistent with those of Khanna et al. (1977) who observed maturity as an earliness character with negative heterosis in a similar study conducted with tomatoes. This kind of heterosis implies dominance of genes favoring early flowering which would give a negative "d". Based on this assumption, it may be concluded that as the parents became more distantly related, their hybrid's performance moved towards the dominant early flowering parents due to dominance genetic variance.

Since the average seed yield of canola is rather low, selection for larger seed size could be an important consideration for increasing the seed yield. The task of a canola breeder should be to improve the genetic capacity for maximum yield while maintaining a desirable oil and meal quality. The major emphasis in a rapeseed breeding program should be on improving the agronomic performance of the crop to get the maximum yield, which our data indicates, could be achieved by making hybrids. In various hybridization programs, high levels of heterosis for seed yield, both in spring and winter forms of *B. napus* have been found (Sernyk & Stefansson, 1983; Lefort-Buson and Dattee, 1982). The mid-parent heterosis

was up to 40 percent for yield in summer rape and 60 to 70 percent for winter forms of Brassica. The average heterosis found was 10 to 20 percent, a level which would justify the efforts directed towards the production of hybrid cultivars.

In order to maximize genetic diversity, the crossability of rapeseed and mustard could be important for the breeder because of the excellent possibilities to transfer the economically important traits from the related species to the commercial crop. Another major breeding objective for canola is to obtain higher levels of oil with improved nutritional value for human consumption and industrial use. Brassica oil with low erucic acid is good for human consumption, whereas high erucic acid oil is used for industrial purposes. High erucic acid, which is fractioned from the oil, is first converted to an amide for use in plastic products as a slip agent. This is done to avoid any sticking problem of plastic products with each other. High yielding cultivars developed through hybridization are required to serve both edible and industrial markets. Our data showed a small increase in the percent oil content for the crosses ranging from -1.82 to 8.81 percent. This could be due to limited genetic variation in the parental material for this trait. However, considering the importance of oil content in this crop, the parents with a wider genetic range for this trait could be selected in future hybridization to improve oil content.

In this study, as in the majority of other studies, the

inter-cluster heterosis was shown to be greater than the intra-cluster heterosis. These results support the findings of other researchers, i.e. Khanna et al. (1977), Moll et al. (1962) in other crops like tomatoes and maize.

Since the association between heterosis and genetic distance observed in this study for a series of morphological traits, yield, and yield components was variable, one should not always expect a significant correlation between genetic distance and heterosis. Such situations could be expected by considering the complex genetic nature of expression of heterosis for a given character.

Since pods per plant and seeds per pod showed a highly significant positive correlation with yield in this study, more importance should be given to these components when selecting the parents for hybridization, provided adequate variability exists for both traits.

Calculating the genetic distance between the parents based upon morphological traits, yield, and yield components is one approach to determine the relationship between the parental material prior to hybridization. However, genetic distance could also be estimated by using the allele frequency data from simply inherited polymorphic traits. Suitable data in this regard could be derived from isozyme, RFLP and RAPD markers. A general approach to calculating genetic distance from marker loci data is to determine the frequency of different marker loci alleles in the parental population and

compare these marker loci profiles using the same distance equation.

Some researchers using isozymes (Hunter & Kannenberg, 1971; Hadjinov et al. 1982) and RFLPs (Godshalk et al., 1990) in maize have found insignificant correlation between hybrid yield and parental distance. Frei et al. (1986) found the marker loci distance between maize parents to be predictive of hybrid performance only when there was a known pedigree relationship between the parents. Despite some limitations, the marker loci comparison could also give useful additional insight into the genetic relationship between the parental material.

The highly significant correlation of genetic distance with yield demonstrated that the greater the genetic distance between the parents, the higher would be the yield potential. Thus, multivariate analysis and clustering techniques play a very crucial role in the selection of parents. Based on the results of this study, it could be recommended that multivariate statistics and clustering procedures could be adopted to determine the genetic distance among the cultivars. This provides the breeder with objective information to help narrow down the initial parental selection for a successful hybridization program. While measuring the genetic distance between the cultivars only those traits should be included in the clustering procedure, which are useful in forming distinct clusters. In this study, yield components like branches per

plant, pods per plant, seeds per pod and one hundred seed weight are the examples of the traits which placed the cultivars in distinct clusters prior to parental selection. Other traits did not have any significant impact in cluster formation. This suggests that yield components in particular are very important traits to be utilized in clustering procedure if yield is the ultimate objective within the breeding program.

Up to 33 percent heterosis for yield in this study justifies the effort to develop a successful system like cytoplasmic male sterility for production of hybrid cultivars in such an important crop. Several attempts in this regard are still underway and some male sterility, inducing cytoplasms for *B. napus* have already been found. For example the previously described Pol CMS cytoplasm could be used to prevent self pollination of the female parent of the cross, and the restorer genes could be incorporated to restore the male fertility of the F_1 hybrid. In other systems self incompatibility could also be investigated, since some self incompatible plants have been found in *B. napus*. Thompson (1983) proposed a scheme for the production of a self compatible three way cross hybrid of *B. napus* utilizing self incompatibility. A major drawback of this scheme is the difficulty of producing commercial quantities of selfed seed on the self incompatible parent lines. Despite these difficulties, efforts could still be made to find efficient

large-scale methods of producing the hybrid seed in order to minimize the cost of the hybrid seed to the farmer and thus permit the exploitation of heterosis demonstrated in the crop.

APPENDIX

ANALYSIS OF VARIANCE TABLES

Table A1. Analysis of variance for 14 traits in 21 entries crosses of canola in East Lansing, MI 1991

Name of Trait	ms
Days of emergence	ns
Crown diameter	**
Leaf length (1st node)	**
leaf length (2nd node)	**
Leaf length full (up to tip)	**
Leaf width	**
Days to flower	**
Days to maturity	**
Branches/plant	**
Pods/plant	**
Seeds/pod	**
100 seed weight	ns
Yield in Kg/ha	**
oil content (%)	*

*, ** Indicate significance at 0.05 and 0.01 level of probability respectively according to the F-test

Table A2. Analysis of variance for 14 traits in 21 entries/crosses of canola in Clarksville, MI 1991

Name of Trait	ms
Days of emergence	ns
Crown diameter	**
Leaf length (1st node)	**
leaf length (2nd node)	**
Leaf length full (up to tip)	**
Leaf width	**
Days to flower	**
Days to maturity	**
Branches/plant	**
Pods/plant	**
Seeds/pod	**
100 seed weight	ns
Yield in Kg/ha	**
oil content (%)	*

*, ** Indicate significance at 0.05 and 0.01 level of probability respectively according to the F-test

Table A3. Analysis of variance for 14 traits in 21 entries/crosses of canola combined for both locations, East Lansing and Clarksville, MI 1991

Name of Trait	ms
Days of emergence	ns
Crown diameter	**
Leaf length (1st node)	**
leaf length (2nd node)	**
Leaf length full (up to tip)	**
Leaf width	**
Days to flower	**
Days to maturity	**
Branches/plant	**
Pods/plant	**
Seeds/pod	**
100 seed weight	ns
Yield in Kg/ha	**
oil content (%)	*

*, ** Indicate significance at 0.05 and 0.01 level of probability respectively according to the F-test

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