

**INHERITANCE OF SEED YIELD, OIL CONTENT,
CHARACTERS RELATED TO OIL QUALITY AND
AGRONOMIC CHARACTERS, AND ASSOCIATIONS
AMONG THE CHARACTERS IN RAPESEED
(*Brassica napus* L.)**

Zesu Huang

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การถ่ายทอดลักษณะของผลผลิต เปอร์เซ็นต์น้ำมัน ลักษณะที่เกี่ยวข้องกับ
คุณภาพน้ำมัน และลักษณะทางพืชไร่ และความสัมพันธ์ระหว่างลักษณะ
ในเรปซีด (*Brassica napus* L.)

นางชื้อชู หวง

วิทยานิพนธ์นี้สำหรับการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
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Suranaree University of Technology has approved this thesis submitted in
fulfillment of the requirements for the Degree of Doctor of Philosophy.

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เรปซีด (*Brassica napus* L.) เป็นพืชน้ำมันที่มีความสำคัญพืชชนิดหนึ่งของโลก ใช้น้ำมัน
เพื่อบริโภค และใช้ในอุตสาหกรรมหลายชนิด และกากยังใช้ในอุตสาหกรรมอาหารสัตว์ ดังนั้น
การปรับปรุงพันธุ์เพื่อเพิ่มผลผลิต รวมถึงคุณภาพของน้ำมัน และกาก จึงเป็นเป้าหมายหลักใน
โครงการปรับปรุงพันธุ์เรปซีด แต่ลักษณะดังกล่าวเป็นลักษณะปริมาณ ดังนั้นการศึกษาลักษณะนี้มี
วัตถุประสงค์ เพื่อศึกษาการถ่ายทอดของลักษณะผลผลิต องค์ประกอบผลผลิต เปอร์เซ็นต์น้ำมัน
และลักษณะที่เกี่ยวข้องกับผลผลิต และเปอร์เซ็นต์น้ำมัน และหาความสัมพันธ์ระหว่างลักษณะ
เหล่านี้ของเรปซีด ซึ่งแบ่งเป็น 3 การทดลอง ดังนี้

การทดลองที่ 1 ศึกษาการแสดงออกของยีน และอัตราพันธุกรรมของลักษณะต่าง ๆ โดยวิธี
วิเคราะห์ค่าเฉลี่ยของประชากร พร้อมทั้งหาความสัมพันธ์ระหว่างลักษณะต่าง ๆ ของเรปซีด โดยทำ
การผสมพันธุ์ระหว่างเรปซีด 4 สายพันธุ์ จำนวน 2 คู่ผสม (III174 × Zi20, III38 × III142) พร้อมทั้ง
ผลิตลูก F_2 , BC_1 และ BC_2 ของคู่ผสมเหล่านี้ ดังนั้นแต่ละคู่ผสมจะมี 6 ประชากร คือ P_1 , P_2 , F_1 , F_2 ,
 BC_1 และ BC_2 นำประชากรทั้งหมดมาปลูกทดสอบในแปลง จากนั้นวัดลักษณะเปอร์เซ็นต์น้ำมัน
เปอร์เซ็นต์โปรตีน ปริมาณ erucic acid, oleic acid และ glucosinolate ในคู่ผสมที่ 1 ส่วนคู่ผสมที่ 2
วัดลักษณะเปอร์เซ็นต์น้ำมัน เปอร์เซ็นต์โปรตีน อายุออกดอก และอายุเก็บเกี่ยว โดยวัดเป็นรายต้น
จากการทดลองพบว่า หลายลักษณะควบคุมโดยยีนหลายคู่ ยกเว้นลักษณะเปอร์เซ็นต์โปรตีนใน
คู่ผสมที่ 2 ที่ไม่เป็นไปตามกฎการข้าม-บวก ซึ่งอาจมีการแสดงออกของยีนเป็นแบบข่มข้ามคู่ และ
คู่ผสมที่ 1 พบว่าลักษณะปริมาณ erucic acid, oleic acid และ glucosinolate มีอัตราพันธุกรรมสูง
โดยลักษณะ erucic acid และ oleic acid ต่างถูกควบคุมโดยยีน 2 คู่ ส่วนปริมาณ glucosinolate ถูก
ควบคุมโดยยีนหลัก 3 คู่

การทดลองที่ 2 ศึกษาการถ่ายทอดลักษณะต่าง ๆ ของสายพันธุ์ที่ดอกตัวผู้เป็นหมันของ
Brassica napus L. และหาความสัมพันธ์ระหว่างลักษณะ โดยนำสายพันธุ์ที่ควบคุมการเป็นหมันโดย
ยีนด้อย (RGMS) จำนวน 10 สายพันธุ์มาผสมกันแบบพบกันหมด และใช้เฉพาะลูกผสมตรง 45
คู่ผสม นำมาปลูกทดสอบร่วมกับพันธุ์พ่อ-แม่ 10 สายพันธุ์ พบว่าทั้งสมรรถนะการรวมตัวทั่วไป
(GCA) และสมรรถนะการรวมตัวจำเพาะ (SCA) มีความสำคัญในทุกลักษณะที่ศึกษา และการ

แสดงออกของยีนแบบบวกรมิตีอิทธิพลมากกว่า และยังพบว่า สายพันธุ์ Qianyou 8AB และ You 2894AB มี GCA สูงในลักษณะผลผลิต สายพันธุ์ You 2894AB, QH 303-4AB และ You 157AB และ You 2431AB พบว่าลักษณะเปอร์เซ็นต์น้ำมัน มี GCA สูง คู่ผสม Qianyou 3A × Qianyou 8B, Qianyou 8A × Qianyou 2894B, You 2894A × Qianyou 6B, Qianyou 8A × QH303-4B และ Qianyou 8A × Qianyou 6B มี SCA ของลักษณะผลผลิตสูง พบความดีเด่นของลูกผสมในทุกลักษณะ นอกจากนี้จำนวนฝักต่อต้น เมล็ดต่อฝัก น้ำหนัก 1,000 เมล็ด และความสูงต้นมีอิทธิพลทางตรงต่อผลผลิตสูง

การทดลองที่ 3 ทำการศึกษาทดสอบการแสดงออกของลูกผสม โดยการผสมระหว่างสายพันธุ์ที่มีปริมาณ erucic acid และ glucosinolate ต่ำ และเพื่อประเมินสมรรถนะการรวมตัว และวัดความดีเด่นของ 4 ลักษณะ โดยนำสายพันธุ์เรปซิด 9 สายพันธุ์ เป็นพันธุ์พ่อผสมพันธุ์กับพันธุ์แม่ RGMS จำนวน 5 สายพันธุ์ โดยใช้แผนการผสมพันธุ์แบบ NC II ได้ลูกผสม 45 คู่ผสม นำลูกผสมทั้งหมดมาปลูกทดสอบร่วมกับพ่อ-แม่พันธุ์ใน 2 สถานที่ ผลการทดสอบพบว่า ลักษณะผลผลิตเปอร์เซ็นต์น้ำมัน อายุออกดอก อายุเก็บเกี่ยว มีการแสดงออกของยีนในทั้งแบบบวกร และไม่เป็นแบบบวกร แต่พบว่าแบบบวกรมีความสำคัญมากกว่า และพบว่า คู่ผสม Qianyou 8A × q034, QH303-4A × III224, Qianyou 3A × 2365, QH303-4A × 1190 และ 24A × III153 มีค่า SCA ของลักษณะผลผลิต เป็นบวกร และพบว่าลูกผสมให้ความดีเด่นในลักษณะผลผลิตเหนือพ่อ-แม่ ที่ให้ผลผลิตสูง และเหนือพันธุ์มาตรฐานสูง

สาขาวิชาเทคโนโลยีการผลิตพืช

ปีการศึกษา 2552

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ZESU HUANG : INHERITANCE OF SEED YIELD, OIL CONTENT,
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IN RAPESEED (*Brassica napus* L.). THESIS ADVISOR : PROF. PAISAN
LAOSUWAN, Ph.D., 159 PP.

INHERITANCE/ASSOCIATIONS/SEED YIELD/OIL CONTENT/RAPESEED

Rapeseed is an important oilcrop of the world. Its oil is used for human consumption and industries, and the meal can be used as animal feed. Improvement of yield, oil content, and quality of oil and meal are important objectives of rapeseed breeding programs. Most or all of these characters inherit quantitatively. This research was aimed to study the inheritance of yield, yield components, oil content and characters related to yield and oil content in rapeseed and associations among these characters. Three sets of experiments were conducted in this study.

The first experiment was carried out to study gene actions and heritabilities of characters by using generation mean analysis, and to identify the relationships between characters. Two crosses (Cross I: III174 $\times$ Zi20; Cross II: III38 $\times$ III142) were made, and their F₂, BC₁ and BC₂ were produced. Six populations including P₁, P₂, F₁, F₂, BC₁ and BC₂ were evaluated. Characters including oil, protein, erucic acid, oleic acid and glucosinolate contents in Cross I, oil and protein contents, days to flowering, and days to maturity in Cross II were recorded on individual plants. It was found that the effects of genes controlling the characters studied, except protein content in Cross II, did not follow the additive-dominance model. This indicates that epistatic gene effects were also important for these characters. High broad sense

heritabilities were obtained for erucic acid, oleic acid and glucosinolate contents in Cross I. Two major gene pairs were found to control the expression of erucic acid and oleic acid contents, while three major gene pairs were detected to control glucosinolate content in Cross I. Significant, negative or positive correlations were found between certain characters.

The second experiment was conducted to evaluate the inheritance of many characters of male sterile lines in *Brassica napus* L., and to find the correlation between characters. Ten RGMS lines were used as parents to cross among them in a half diallel cross method. Forty five crosses and their 10 parents were evaluated in a randomized complete block design. It was found that both GCA and SCA effects were important for all characters studied, but additive gene effects were more predominant than others. Lines Qianyou 8AB and You 2894AB showed highly significant GCA effects for seed yield. Lines You 2894AB, QH303-4AB, You 157AB, and You 2431AB had highly significant GCA effects for oil content. The crosses between lines Qianyou 3A $\times$ Qianyou 8B, Qianyou 8A $\times$ You 2894B, You 2894A $\times$ Qianyou 6B, Qianyou 8A $\times$ QH303-4B and Qianyou 8A $\times$ Qingyou 6B gave high SCA effects for seed yield. Percentages of heterosis were found for all characters studied. Pods per plant, seeds per pod, 1,000-seed weight, and plant height showed high direct contributions to seed yield.

The third experiment was conducted to test performance of hybrids obtained by crossing between lines developed to have low erucic acid and glucosinolate content and to estimate combining ability effects and heterosis for four characters. Nine inbred lines of rapeseed used as male were crossed with five RGMS lines used

as female in a NCII design manner to produce 45 single crosses. The crosses, their parents and a check hybrid were tested at two locations. The results showed that both additive and non-additive gene effects were important for yield, oil content, days to flowering, and days to maturity, but additive gene effects were more important for these traits. Both GCA and SCA effects were significantly positive and negative for different characters. The crosses of females $\times$ males Qianyou 8A $\times$ q034, QH303-4A $\times$ III224, Qianyou 3A $\times$ 2365, QH303-4A $\times$ 1190 and 24A $\times$ III153 had significantly positive SCA effects for seed yield. Heterosis, heterobeltiosis and standard heterosis were found high for seed yield.

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LIST OF ABBREVIATIONS

CMS	=	Cytoplasmic male sterile
RGMS	=	Recessive genetic male sterile
GCA	=	General combining ability
SCA	=	Specific combining ability
df	=	Degree of freedom
OC	=	Oil content
PC	=	Protein content
OAC	=	Oleic acid content
EAC	=	Erucic acid content
GC	=	Glucosinolate content
DF	=	Days to flowering
DM	=	Days to maturity
P/P	=	Pods per plant
S/P	=	Seeds per pod
TSW	=	1,000-seed weight
B/P	=	Branches per plant
PH	=	Plant height

CHAPTER I

INTRODUCTION

1.1 Rationale of the Study

Rapeseed is the second important oilseed crop of the world after soybean, providing about 13% of the world's oilseed supply. It is widely cultivated in temperate region of the world for the production of animal feed, vegetable oil for human consumption, lubricant, biodiesel and other uses (Weiss, 1983; Tong, 2004; Wang, 2007). The planting area for this crop reached 30 million hectares in 2006-2007 (FAO Statistical Yearbook, 2008). Leading producers of rapeseed in 2007 were China, Canada, India, Germany, and France. According to the United States Department of Agriculture, rapeseed was the third leading source of vegetable oil of the world in 2004, after soybean and oil palm, and also the world's second leading source of protein meal after soybean (USDA, 2005). World production of rapeseed is increasing rapidly. The FAO reported that 36 million tonnes of rapeseed were produced in 2003-2004, and increased to 49 million tonnes in 2006-2007 (FAO Statistical Yearbook, 2008).

Rapeseed is grown mainly for seeds. However, rapeseed's leaves and stems are edible, similar to those of the related kales. Some varieties of rapeseed are sold as green vegetable, primarily in Asian groceries (SAAS, 1964; Weiss, 1983; Wang et al., 2001; Sun et al., 2003; Tong, 2004). They are also used as forage for animal feed (SAAS, 1964; Zhao et al., 1997). The crop is also grown as a winter-cover crop. It

provides good coverage of the soil in the winter and reduces the nitrogen run-off (Fu et al., 2006; Wang et al., 2009).

Rapeseed contains about 40% oil and 25% protein. Rapeseed oil has a long history using as edible purposes in Asia, but it was used as lubricant in Europe. Its use as an edible vegetable oil in Western countries is very recently (Shahidi, 1990).

Rapeseed oil is obtained from the seeds of several species of *Brassica*, and the oil from different species is not distinguishable in the market, since all have similar properties. The oil is separated either by solvent extraction or by cold or hot pressing. Usually the pressed oil is used for edible purposes, and by-product rapeseed meal is used for animal feed or fertilizer (Shahidi, 1990; Tong, 2004).

Traditional rapeseed oil contains erucic acid, oleic acid, linoleic acid and linolenic acid which constitute of about 90% of total fatty acid. Erucic acid is not beneficial to human as oleic acid and linoleic acid (Ackman, 1990). However, high erucic acid oil is good as lubricant. Rapeseed meal contains glucosinolate and protein. Glucosinolate is harmful to animal while protein is beneficial (Downey and Bell, 1990). Therefore, breeding of rapeseed for desired oil and protein quality are important breeding objectives. Of course, the yield improvement is the most important objective in most rapeseed breeding programs.

Up to now, rapeseed breeding has made the great progress in improving oil content, yield and quality characters related to oil and meal. However, in China, characters such as oil content, yield, erucic acid, glucosinolate and oleic acid contents and other characters are still needed to be improved (Wang, 2002; 2004; 2005). For example, oil content of Chinese cultivars averaged from 202 samples was 37.7%, but that were 42.6, 42.4, 44.3 and 41.4% for Canada, Australia, France, and USA,

respectively (Li et al., 2004). However, erucic acid and glucosinolate contents of rapeseed in China were much higher than that in those countries. According to the FAO reports, the yield of rapeseed in China is much lower than that in European countries. The average yield in 2007 was 1,472 kg ha⁻¹ for China, but that were 2,888, 3,440 and 3,095 kg ha⁻¹ for France, Germany and England, respectively (FAO Statistical Yearbook, 2008).

Therefore, these characters including yield, oil content, erucic acid content, glucosinolate content, and other characters of Chinese varieties should be improved. Thus, the inheritance studies of such characters are required.

1.2 Research Objectives

1.2.1 To study the inheritance of seed yield, oil content, characters associated with oil quality and other agronomic characters of different groups of rapeseed.

1.2.2 To determine the associations among characters, characters related to seed yield and oil content.

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CHAPTER II

REVIEW OF THE LITERATURE

2.1 General Information of Rapeseed

Rapeseed, also known as rape, oilseed rape, rapa, rapaseed and double-low rapeseed called canola (low erucic acid and glucosinolate contents rapeseed), belongs to the species of *Brassica*, members of Cruciferae. The name rape derived from the Latin *rapum* meaning turnip (Weiss, 1983). There are three basic species: *B. nigra*, *B. oleracea*, and *B. campestris*. By hybridization and chromosome doubling, the three species: *B. carinata*, *B. juncea*, and *B. napus* L. were synthesized. The botanical relationships among these species are illustrated by the “U triangle” (Figure 2.1) which was proposed by a Japanese scientist, named U, in 1935 (U, 1935).

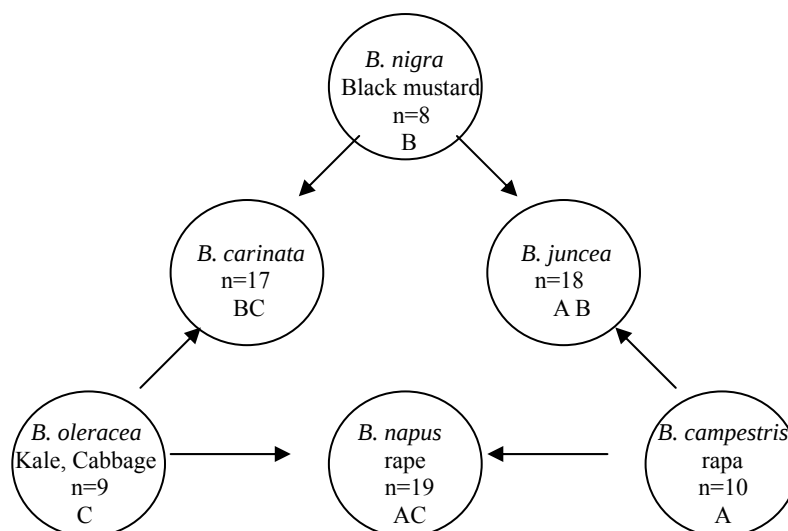


Figure 2.1 Relationships among important *Brassica* species shown by the triangle of U (1935).

Now *B. napus*, *B. campestris*, and *B. juncea* are the main species planted in the world. *B. juncea* has natural outcrossing rate below than 10 percent. However, some varieties may have more than 40 percent outcrossing in certain areas. *B. napus* L. has natural outcrossing rate of 10 to 30 percent in general, whereas *B. campestris* has 85 to 90 percent (Rakow and Woods, 1987; Li, 1999). Their flower colors are bright yellow, sometimes orange yellow or pale yellow. Seed-coat colors of rapeseed are different from species. In general, they are dark-brown to black. We can find pure yellow seed in *B. campestris* and *B. juncea*, but not in *B. napus*. It was found that yellow-seeded rapeseed could have more oil and protein contents and lower fibre than brown and black rapeseed (Weiss, 1983; Liu, 1992). Yellow seed in *B. napus* L. was first found in artificially synthesized rapeseed in Sweden (Olsson, 1960).

Rapeseed can be divided according to vernalization requirements into two types including winter and spring types (Wang et al., 2007). Winter varieties of *B. napus* L. are grown predominantly in most of Europe, China, and the eastern United States, whereas spring varieties predominate in Canada, northern Europe, northwest of China. *B. rapa* has a shorter growing season than *B. napus* L. and this trait makes the spring varieties of this species suitable for the more severe climates. Spring type *B. rapa* occupies approximately 50% of the Canadian rapeseed area and is also grown in northern Europe, China, and India. Winter type *B. rapa* has largely been replaced by more productive winter type *B. napus*. *B. juncea* is the leading *Brassica* oilseed in India and also produced in Canada, Europe, and China (Sovero, 1993).

2.2 Rapeseed Production in China

China is the world's largest rapeseed producer and consumer. The grown area

and total production of rapeseed in China are about 7 million hectares and 11 million tonnes, respectively (Zhou and Fu, 2007). Rapeseed production in China was about 22.45% of the total oil crops yield, after soybean and peanut. The consumption of rapeseed oil was 4.84 million tonnes, about 23.46% of total consumption of vegetable oil in China in 2005, just after soybean oil (Wang, 2005).

Rapeseed production area in China is divided into two regions, winter region and spring region (Figure 2.2). The winter rape is grown in more than 90% of the total rapeseed planting area, while spring rape accounts for about 10% (Wang et al., 2007).

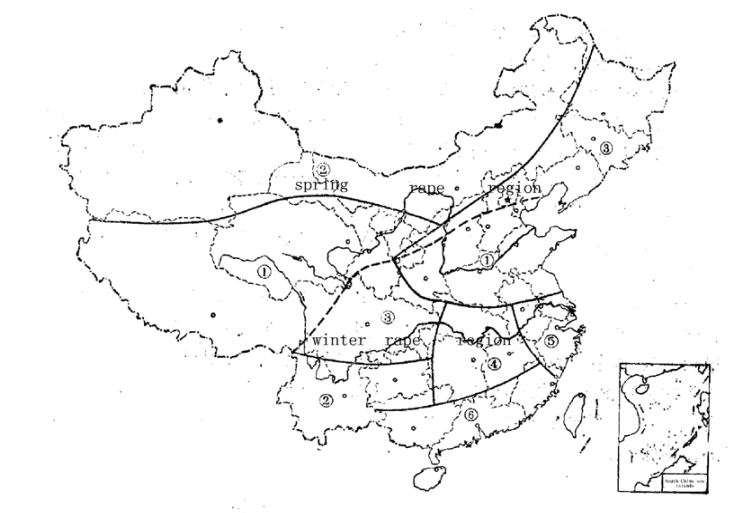


Figure 2.2 Rapeseed production sub-areas in China.

Three main species of rapeseed, *B. napus*, *B. campestris*, and *B. juncea* are planted in China. Among them, *B. campestris* and *B. juncea* were mainly cultivated before 1940s. *B. napus* L. was introduced into China in 1940s. After middle 1950s, *B. napus* L. began to widely spread in China. At present, it has reached about 95% of the

total rapeseed area, while *B. campestris* area is about 4% and *B. juncea* about 1% (Wang et al., 2007).

2.3 Rapeseed Breeding

Traditional rapeseed breeding began in Germany, Sweden, Japan, India and some other countries in 1920s, and in China in 1930s. At the very beginning, cytogenetics of rapeseed was studied and the triangle of U had provided a good basis on the derivation and evolution of rapeseed. Germany, Sweden and Japan were leading in rapeseed breeding during 1940s to 1950s, and some valuable cultivars in *B. napus* L. were bred in these countries. China began to breed rapeseed cultivars in 1950s. Some varieties of *B. napus* L. replaced traditional *B. campestris* and *B. juncea* during 1960s to 1970s, and China became the world's most important rapeseed producer after 1980. Canada began to plant rapeseed in 1942, but the area of production has spread very quickly, and taken the leading role in rapeseed trade since 1970s, after quality rapeseed were produced (Liu, 1993).

Quality rapeseed breeding has been an important objective of most rapeseed breeders. Stefansson et al. (1961) in Canada identified the first low erucic acid rapeseed from “Liho” which was a German forage rapeseed and the first low erucic acid rapeseed variety named “Oro” (*B. napus*) was developed in 1968. The first low glucosinolate rapeseed, Bronowski (*B. napus*), a Polish cultivar, was identified in 1967 (Finlayson et al., 1973), and was introduced into Canada. In 1974, Stefansson and Kondra (1975) developed the first double low rapeseed variety named “Tower” by crossing and backcrossing between Bronowski and a low erucic acid germplasm. After 1968, many European countries introduced varieties Oro and Bronowski and

began quality rapeseed breeding. After that, many canola cultivars were developed such as Regent, Altex, Andor, Tobin, Wichita, Flint, Athena, etc. For other characters, rapeseed breeders have paid attention to the improvement of other fatty acids, other than low erucic acid content, such as high erucic acid, high oleic acid and low linolenic acid (McVetty et al., 2007; Guan et al., 2007; Nath et al., 2007).

Hybrid breeding results in a higher productivity of field crops such as maize and rice. This can be economically made by using male sterility. Rapeseed is a largely autogamous crop (Rakow and Woods, 1987; Li, 1999). It is difficult to produce hybrid seeds by emasculation of female parents. Thus, the first step for breeding hybrid rapeseed is the development of male sterile line. Ogura (1968), in Japan, discovered male sterile gene in radish and this sterile system was transferred into rapeseed by repeated backcrossing (Barnrot et al., 1974) and was called Ogu CMS (cytoplasmic male sterility). It expresses very stable sterility, but restorer genes had not been found in rapeseed. Shiga and Baba (1971, 1973) and Thompson (1972) found nap CMS with restorer genes but its sterility is not stable. Fu (1981) reported the discovery of Pol CMS in 1972. It has restorer genes that can be used in the production of hybrid. The Pol CMS system was spread in China in 1973 and internationally in 1981 (Fu et al., 1995). Subsequently, many other types of male sterility including cytoplasmic male sterility (CMS), genetic male sterility (GMS), ecotype sensitive male sterility or environment sensitive male sterility (EMS), gametocide (GC) and self-incompatible (SI) system were developed and used in the production of hybrids (reviewed by Yu and Hu, 2007). Many hybrid varieties were produced by using CMS including Qinyou 2 (1985), Huaza 2 (1992), and Chuanyou 12 (1992) in China, Hyola 40 (1989) and Hyola 401 (1991) in Canada. These

varieties had played very important roles in increasing rapeseed yield (Fu et al., 1995). Now hybrid breeding is the major method of cultivars development in this crop in China and worldwide.

2.4 Rapeseed Breeding in China

China began hybrid breeding of rapeseed after the discovery of Pol CMS in 1972 (Fu et al., 1995), and began quality breeding around 1980 after varieties Oro and Tower were introduced from Canada (Fu et al., 2003). Hybrid cultivar “Qinyou 2”, released in 1985, was high in erucic acid and glucosinolate contents, and was the first hybrid of rapeseed used in commercial production in the world (Fu et al., 1989). Recently, China rapeseed breeding program attempts to develop hybrid varieties by using different male sterile systems. Among these, the CMS systems are widely used. However, some of these CMS are not completely sterile under low temperature (Fu, 1995). Genetic male sterility (GMS) systems are also widely used. These include two types, one is recessive genetic male sterility (RGMS), the other is dominant genetic male sterility (DGMS). The disadvantage of these systems is that 50% of the plants are fertile and must be removed in the seed production (Fu, 1995).

Up to 2005, 191 quality hybrid cultivars were registered in China. They were produced by different male sterility systems. CMS system was the most popular one and shared about 63% of total varieties developed during 2000-2005, followed by GMS system which taking part 28% of the total, the others were GC 2% and EMS 7% (Zhou and Fu, 2007).

Up to now, hybrid and quality breeding in China have made great progress in increasing yield and lowering erucic acid and glucosinolate contents, but still lack

behind other countries (Wang, 2004; 2005). For example, oil content of rapeseed in China is much lower than that in Canada, Australia, etc. Li et al. (2004) reported that oil content of Chinese varieties averaged from 202 samples was 37.7%, but that were 42.6, 42.4, 44.3 and 41.4% for Canada, Australia, France and USA, respectively. However, erucic acid and glucosinolate contents of rapeseed in China were much higher than that in those countries.

2.5 Heterosis

The term heterosis was coined by Shull (1914) as a descriptive synonym for hybrid vigor. This is a phenomenon in which the performance of an F_1 hybrids produced from a cross between genetically distant parents is superior to their mid-parent value. Shull's definition of heterosis was concerned with size, yield, vigor, speed of development, and resistance to diseases and pest, etc. Powers (1944) and Stern (1948) extended the concept to include negative heterosis; and a special term, heterobeltiosis, has been suggested to describe increased performance of the hybrid over the better parent (Fonseca and Patterson, 1968). Breeders of autogamous crops often have to employ a third measure, i. e., superiority of the F_1 over the best pure line variety, that is generally referred to as standard heterosis. Heterosis is a phenotypic measure and as such not an absolute measure (Mackay, 1976). Direction, extent, degree, and reproducibility of heterosis depend not only on the method of measurement, but also on the environmental and genetic background.

Explaining heterosis in terms of gene action, Agrawal (1998) explained if the gene action is purely additive, there would be no heterotic response as the average would be equal to the mid-parent values. If the gene action is dominant and /or

epistatic any then can a heterotic response be expected, either because of the coming together of a greater number of dominant alleles and/or complementary interaction of favourable dominant alleles and interallelic interaction.

Heterosis has been recognized in nearly every crop where experiments have been designed to measure it. This includes self-pollinated as well as cross-pollinated crops (Briggs and Knowles, 1967). Heterosis was reported by Beal (1876-1882) among maize varieties. The best combinations yielded 50% more than the mean of the parents (quoted by Bains et al., 1999). Heterosis was first reported in wheat when Freeman (1919) found that F_1 plants were generally taller than the tall parent. This phenomenon was first reported in rice by Jones (1926) who observed that some F_1 rice hybrids had more culms and yielded higher than their parents. However, the first report about heterosis in *Brassica* was much later (Sun, 1943) which was reported that significant heterosis of yield was found in the cross between *B. campestris* and *B. juncea*. After this first report, many researchers in many countries had studied heterosis in rapeseed for different characters they need, but put more concentration on seed yield. Now heterosis in rapeseed is well documented (Sernyk and Stefansson, 1983; Grant and Beversdorf, 1985; Lefort-Buson et al., 1987; Brandle and McVetty, 1989; Anand, 1987; Prajapati et al., 2007; Shen et al., 2002; Teklewold and Becker, 2005; Hu and Liu, 1989). However, the rates of heterosis for different characters in rapeseed varied according to populations. For example, Brandle and McVetty (1989) reported that heterosis of seed yield varied between hybrids being 20.3 to 120% over high yielding parents, while Sernyk and Stefansson (1983) reported that heterosis of seed yield ranged from 7 to 64% over mid-parent in their rapeseed populations. Hu and Liu (1989) and Wang (1992) reported that the ranges of heterosis for oil content

were -1.26 to 4.374% and -11.16 to 15.95% in their populations, respectively.

2.6 Oil Content

Oil content is the character related closely with oil yield in rapeseed. It is known as a heritable character with different heritability levels depending on populations (Grami et al. 1977; Han, 1990; Hu, 1987; Wu et al., 2006; Zhang et al., 2006). Many inheritance studies in this character found that it is a quantitative trait, and gene action follows additive-dominant model (cited by Tu and Fu, 2001; Gao, 1984; Hu and Liu, 1989; Han, 1990). However, the proportion of gene action was different depending on genetic materials used in the study. Grami and Stefansson (1977) and Shen et al. (2002) reported that oil content was controlled by additive gene effect and dominant gene effect was not significant. Some reports showed that both additive and non-additive gene effects were important for this character (Dong et al., 2007; Delourme et al., 2006). Many investigators showed that oil content was influenced by both gene effects and genotype $\times$ environment (GE) interaction (Brandle and McVetty, 1988; Wu et al., 2006; Shafii et al., 1992).

2.7 Characters Related to Quality of Rapeseed Oil and Meal

Erucic acid and oleic acid are characters related to quality of oil in rapeseed. High erucic acid is not beneficial, while high oleic acid is beneficial to human health. However, high erucic acid is good for lubricant manufacture. Erucic acid content in *Brassica* is known as a highly heritable character with different rates of heritability (Liu D. and Liu H., 1990a; Qi et al., 2001; Wang et al., 2006). In their study, Harvey and Downey (1964) found in *B. napus* L. that the inheritance of erucic acid was controlled by two gene pairs with additive effect. Similar results were found in *B.*

napus L. and *B. juncea* by many investigators (Zhou and Liu, 1987a; Huang et al., 1999; Siebel and Pauls, 1989; Chen and Beversdorf, 1990). However, Liu, D. and Liu, H. (1990a) found that inheritance of erucic acid followed additive-dominant model of two gene pairs with additive effect was more important than dominant effect. Qi et al. (2001) also found that two major gene pairs were responsible for erucic acid with additive effect, but other types of gene effects were also found in controlling the character.

Oleic acid content in *B. napus* L. was found to be highly heritable (Schierhoft and Becker, 2001; Zhang et al., 2004; Wang et al., 2006) and was controlled by both additive and dominance gene effects (Krzymanski and Downey, 1969; Liu, D. and Liu, H., 1990b; Wang et al., 2006). However, the importance of the types of gene effects depends on the population used in the study. Some researchers reported that, in their materials, additive gene effect was important (Dong et al., 2007; Zhou and Liu, 1987a). Chen and Beversdorf (1990) and Schierhoft et al. (2001) found that oleic acid content was controlled by two gene pairs, while Schierhoft et al. (2001) and Velasco et al. (2003) found that it was controlled by one gene pair in some plant materials. Radovan et al. (2007) reported that non-additive gene effect was predominant. Zhang et al. (2004) reported that oleic acid content of rapeseed was simultaneously controlled by different kinds of genetic gene actions as well as their GE interaction effects.

Glucosinolate and protein are main factors affecting quality of rapeseed meal. Glucosinolate is harmful to animal, while protein is beneficial. Glucosinolate of rapeseed has been proved to be a highly heritable character (Pietka et al., 2007; Dong et al., 2007). Inheritance of glucosinolate content was reported by many workers, but

the results were different. It was shown that total glucosinolate was controlled by a number of gene pairs (2-6 pairs) with both additive and non-additive gene effects (Krzymanski, 1970; Zhou and Liu, 1987b; Mou and Liu, 1990; Chauhan et al., 2007). High glucosinolate content was partially dominant over low content (Krzymanski, 1970; Mou and Liu, 1990). However, Hu and Liu (1989) and Pietka et al. (2007) reported that inheritance of glucosinolate was of mainly additive and a trace of dominant effect.

Dong et al. (2007) reported that the heritability of protein content in rapeseed (*B. napus* L.) was 74.21% for broad sense and 8.98% for narrow sense heritabilities. Grami et al. (1977) reported that the broad sense heritability of protein content for summer rape was 24.5%. The inheritance of protein content in *B. napus* L. was reported by many workers to be controlled mostly by non-additive gene effects, while additive gene effects played a little role (Hu and Liu, 1989; Dong et al., 2007), while Grami and Stefansson (1977) reported protein content was governed by additive gene effects, while dominant gene effects was not significant.

2.8 Study on Gene Action in Rapeseed

Information on inheritance and types of gene actions is important in designing efficient methods for improvement of crop characters. Many statistical methods were developed suitable to different types of populations for evaluation types and amount of gene actions.

2.8.1 Generation Mean

In 1960, Falconer developed the basis for gene study that heterosis at one locus is a function of both dominance and the square of the difference of gene

frequency between two strains at that locus (Falconer, 1960). With multiple loci reaction of dominance type of epistasis also were involved. Hayman (1958) developed a model to separate additive, dominance, and epistatic effects. With his model, various gene effects are equated to means of F_1 , F_2 , backcrosses and other generations derived from two inbred lines. Gamble (1962) used method similar to those described by Hayman (1958) to obtained parameters for various gene effects for yield of maize. Cavali (1952) developed a method named as a joint scaling test that can estimates parameters for gene action. Sprague et al. (1962) produced all possible single and three way crosses among six inbred lines of maize. The mean of three single crosses (1×2 , 1×3 and 2×3) were then compared with the mean of three 3-way crosses involving the same inbred lines [$(1 \times 2) \times 3$, $(1 \times 3) \times 2$, $(2 \times 3) \times 1$]. Significant differences in average performance indicated epistasis arising due to interaction of gene action.

This method has been widely used in rapeseed for studying the inheritance of characters including agronomic characters such as number of days to flower initiation and days to maturity (Sachan and Singh, 1987); quality characters such as erucic acid content and oleic acid content (Qi et al., 2001; Velasco et al., 2003); resistance to disease such as white rust resistance in *B. juncea* (Kumar and Thakral, 2007). In these experiments, different populations and testing methods were employed, and at least six populations [P_1 , P_2 , F_1 , F_2 , B_1 ($F_1 \times P_1$), and B_2 ($F_1 \times P_2$)] were involved. Genetic models of characters, number of genes controlling characters and heritability of characters were estimated from data of these experiments.

2.8.2 Diallel Mating Design

Sprague and Tatum (1942) used the diallel mating method to obtain estimates of general and specific combining ability variances in maize, which they related to types of gene action. They defined general combining ability as the average performance of a line in hybrid combinations and specific combining ability as the deviation of certain cross from the average performance of the lines. The theory of diallel mating design was later developed by Jinks and Hayman (1953), Hayman (1954a, 1954b and 1957). Hayman's approach was extended to estimate comparison of gene action (Absel and Johnson, 1963). Griffing (1956) developed different methods to analyze the diallel mating design. Four mating methods were used, depending on whether the parents and reciprocal crosses were included or excluded. Griffing (1956) had shown that, for homozygous parents, the genetic variance, σ_g^2 , could be expressed as $\sigma_g^2 = 2\sigma_{gca}^2 + \sigma_{sca}^2$, where σ_{gca}^2 and σ_{sca}^2 were variances for general and specific combining ability, respectively.

Diallel mating design was employed very widely in all crops including rapeseed, and Griffing's approaches were used even more frequently. By using diallel mating design with different parents, oil content, glucosinolate content, protein content, fresh biomass yield, dry matter content, dry biomass yield, some agronomic characters, yield, and oil yield of rapeseed were studied for gene effects, combining ability, heterosis, and heritability (Hu and Liu, 1989; Han, 1990; Wang, 1992; Teklewold and Becker, 2005; Ofori and Becker, 2007).

2.8.3 NCII Design

Comstock and Robinson (1948) and Comstock et al. (1949) developed three designs known as North Carolina Designs I, II, and III, respectively. Among

these three designs, NCII Design or factorial design was used more frequently. Basic features of NCII design and diallel mating designs are quite different, but the genetic information obtained from the two designs is similar. For the diallel design the same parents are used as males and females, whereas different sets of parents are used as males and females in design II. So for a fixed number of experimental units, approximately twice as many parents can be used in the experiment in design II. This is an advantage of design II, particularly if one wishes to estimate the genetic parameters of a reference population. The expectations of males and females for design II were equivalent to GCA, and the male $\times$ female source is equivalent to SCA of the diallel analysis. Because we have two sets of parents in design II, we have two independent estimates of GCA (Hallauer and Miranda, 1988).

NCII design was used as widely as diallel mating design. It could be used to study genetic effects, combining ability and heterosis for all characters in rapeseed. By using this method, some agronomic characters, oil content, yield, quality characters related to oil and meal, and other characters in rapeseed were studied for gene effects, combining ability, heterosis, and heritability (Tian et al., 2005; Shen et al., 2002; Wang, J. et al., 2007).

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CHAPTER III

INHERITANCE OF OIL, ERUCIC ACID, GLUCOSINOLATE CONTENTS, AND OTHER CHARACTERS AND ASSOCIATIONS AMONG CERTAIN CHARACTERS OF RAPESEED

3.1 Abstract

Many characters of rapeseed are inherent quantitatively. This study was conducted to verify the inheritance of certain characters of rapeseed including oil content, erucic acid content, etc. by using generation mean analysis. Two crosses of rapeseed including the crosses of lines III174 $\times$ Zi20 (Cross I) and III38 $\times$ III142 (Cross II), their F_2 , BC_1 ($F_1 \times P_1$), BC_2 ($F_1 \times P_2$), and their parents (P_1 and P_2) were evaluated in the field. Data were measured on individual plants for oil, protein, oleic acid, erucic acid, and glucosinolate contents in Cross I and for oil and protein contents, days to flowering, and days to maturity in Cross II. Transgressive variations in F_2 populations were observed for oil, protein, and oleic acid contents in Cross I and oil and protein contents, days to flowering, and days to maturity in Cross II, indicating that dominance and recessive genes distributed in both parents. Scaling test indicated that the effects of genes controlling these characters, except protein content in Cross II, did not follow the additive-dominance model. The data for all characters were analyzed using six parameter model and found that one or more types of

epistatic gene effects were important for each character except erucic acid content in Cross I and protein content in Cross II. High broad sense heritabilities were obtained for erucic acid, oleic acid, and glucosinolate contents in Cross I with the respective values of 98.97, 93.68, and 86.17%, while moderately heritabilities were found for the other characters in both crosses. Two major gene pairs were found to control the expression of erucic acid and oleic acid contents, while three major gene pairs were detected to control glucosinolate content in Cross I. At least one major gene pair was found in determining days to flowering in Cross II. Significant and negative correlations were found between oil and protein contents in both crosses (-0.66 in Cross I and -0.77 in Cross II), between oleic acid and erucic acid contents (-0.93), and between oleic acid and glucosinolate contents (-0.20) in Cross I. Significant and positive correlation was found between days to flowering and days to maturity (0.40) in Cross II.

3.2 Introduction

The improvement of oil content is one of the most important objectives for rapeseed breeding programs in China. After the discovery the source of low erucic acid and low glucosinolate contents in this crop, rapeseed breeding for quality improvement has been quite progressive. The best quality of rapeseed oil for human consumption is low in erucic acid and high in polyunsaturated fatty acid, especially oleic acid content. After oil extraction, rapeseed meal has been used quite extensively as the source of protein in animal feed. Therefore, the modifications erucic acid, oleic acid, glucosinolate, and protein contents in rapeseed become important objectives of many rapeseed breeding programs.

Previous studies made by a number of workers found that oil content (Grami et al., 1977; Han, 1990; Hu, 1987; Wu et al., 2006), erucic acid content (Liu D. and Liu H., 1990; Qi et al., 2001; Wang et al., 2006), oleic acid content (Schierhoft and Becker, 2001; Zhang et al., 2004; Wang et al., 2006), glucosinolate content (Pietka et al., 2007; Dong et al., 2007), and protein content (Dong et al., 2007; Wang and Qiu, 1990) in rapeseed (*B. napus* L.) were heritable characters with different kinds of gene actions and levels of heritabilities depending on the materials used in their studies. For example, inheritance studies on oil content showed that it followed additive-dominance model (Hu and Liu, 1989; Han, 1990), but Grami and Stefansson (1977) reported that oil content in this crop was governed by additive gene effect, while dominance gene effect was not important.

The relationship between characters can be used for indirect selection for low heritable characters. Although most of the previous studies found strong negative correlation between oil and protein contents (Grami et al., 1977; Zhou and Liu, 1989), but Li et al. (1990) found significant positive correlation between these characters in their population. Strong negative correlation between erucic acid and oleic acid contents was also found by most researchers (Jonsson and Persson, 1983; Stefansson, 1983; Siebel and Pauls, 1989; Chen and Beversdorf, 1990). Significantly negative correlations between oleic acid and glucosinolate contents and between erucic acid and protein contents were found by Shi et al. (2006) and Zhu et al. (2007). Therefore, the correlations between characters might be useful to increase one character as the expense of another which we want to decrease.

Breeding of rapeseed for oil content and oil quality in China has made great progress in increasing oil content, lowering erucic acid and glucosinolate contents. In

2004, the contents of oil, erucic acid, and glucosinolate of Chinese varieties has reached 39.1%, 3.1%, and $35.76 \mu\text{mol g}^{-1}$, respectively, but still lack behind other countries (Wang, 2005). For example, oil content of rapeseed in China is much lower than that in Canada, Australia, etc. However, erucic acid and glucosinolate contents of rapeseed in China were much higher than that in those countries.

For improving above characters, information concerning the inheritance of the characters of plant materials to be used in the breeding program should be studied and accumulated. This is the information on the amount and types of gene actions. The applications of diallel cross and factorial cross to evaluate gene actions sometimes inadequate and inclusive as the epistatic effects are negligible. The objectives of this study were to study the gene actions and heritabilities of characters which need to be improved, and to find the relationships between characters in our rapeseed population by using generation mean analysis.

3.3 Materials and Methods

3.3.1 Plant Materials

Four inbred lines of rapeseed (*Brassica napus* L.) were chosen to make two pairs of crosses including III174 $\times$ Zi20 (Cross I) and III38 $\times$ III142 (Cross II). III174 was an inbred line of low erucic acid, glucosinolate, and protein contents, but has relatively high oleic acid and oil contents. It was developed from the cross of lines 325 $\times$ 9003. Zi20 was developed from an interspecific cross of [Youyan 2 (*B. napus*) $\times$ Hong youcai (*B. campestris*)], and has purple-red leaf, high erucic acid and glucosinolate contents, and relatively high protein content, but low in oleic acid and oil contents. Purple-red leaf is a visible marker in rapeseed. It can be used to identify

the purity of hybrids when it is used as the male parent to cross with the green leaf female parent. Therefore, as marker, Zi20 was selected to improve for erucic acid, glucosinolate, oil, and oleic acid contents. III38, an early flowering and early maturity line, was an inbred line derived from 90089. III142 was an inbred line with late flowering and late maturity, introduced from Xian, Shanxi province (Northwest of China). III142 had restorer gene for CMS, but it was late in Guizhou. It was chosen for improving early flowering and early maturity.

Four parents were planted in Sept., 2005, and two crosses (III174 $\times$ Zi20 and III38 $\times$ III142) were made in spring 2006 at Guiyang, Guizhou, China. Then two F_1 crosses with their parents were planted in Sept. 2006, and F_2 , BC_1 , and BC_2 of the two crosses were made in spring 2007 at Guiyang. At flowering, two F_1 crosses (III174 $\times$ Zi20 and III38 $\times$ III142), two BC_1 crosses [(III174 $\times$ Zi20) $\times$ III174 and (III38 $\times$ III142) $\times$ III38], and two BC_2 crosses [(III174 $\times$ Zi20) $\times$ Zi20 and (III38 $\times$ III142) $\times$ III142] were made in the way as follows: unopened flower buds in the inflorescence of plants using as female parents were emasculated by hand carefully after bloomed flowers and young buds were cut away. The pollinations were done immediately after emasculation by using fresh pollen collected from male parents, then the pollinated buds were covered with paper bags for protecting from other pollens. Four to five inflorescences with about 10 buds each were used for making cross. Seeds from each cross were bulked for planting in the next season. Two F_2 s and their parents (III174, Zi20, III38 and III142) were obtained by selfing F_1 [(III174 $\times$ Zi20) and (III38 $\times$ III142)] plants and their parents, respectively. Six generations including P_1 , P_2 , F_1 , F_2 , BC_1 , and BC_2 for each cross were made in this experiment.

3.3.2 Field Experiment

Experiments were conducted at Guiyang, Guizhou, China, from Sept. 2007 through May 2008. All six generations of the two crosses were planted in nursery plots to produce seedlings on 13 Sept., 2007. Before planting, the seedbed was prepared carefully and a small amount of N, P and K fertilizers were applied in the soil. After planting, the seedbed was watered for ensuring the germination of seeds. All generations were transplanted with two plants per hill on 17 Oct., 2007. Each plot consisted of different number of rows of 5-m in length with 45-cm inter-row and 33.3-cm intra-row spacings. The number of rows varied according to populations, but at least 150 plants for P_1 , P_2 , BC_1 and BC_2 (except III142), 180 plants for F_1 , and 270 plants for F_2 were obtained. After the seedlings were transplanted, 600 kg ha⁻¹ N, P and K fertilizers and 15 kg ha⁻¹ borax were applied by putting in hills. The field was then watered for ensuring the recovery of seedlings. During the growing period, 450 kg ha⁻¹ urea and 300 kg ha⁻¹ N, P and K fertilizers were applied. Pesticide was used for two times when insect incidence occurred. Weeding was done for three times. Supplement irrigations was done twice due to less rainfall.

3.3.3 Data Collection

Data for each character were recorded on individual plants. For Cross I (III174 × Zi20), four to five inflorescences from each plant in randomly chosen rows were covered with white paper bags one by one and self-pollinated to collect seeds for quality analysis in each generation. Numbers of plants self-pollinated were different according to populations, but at least 50 plants for P_1 , P_2 and F_1 , 80 plants for BC_1 and BC_2 , 140 plants for F_2 were selfed. Data were collected for oil, erucic acid, oleic acid, protein, and glucosinolate contents in Cross I. For Cross II (III38 × III142), days to

In this study, the NIRS was used to analyse for oil and protein contents, and the fatty acid composition as the technique is nondestructive, fast, cost-effective and permits the simultaneous analysis of many traits in a single measurement.

3.3.4 Statistical Analysis

Scaling test outlined by Mather (1949) was used to test if the variation followed the additive–dominant model. Six parameters according to Gamble (1962) were calculated and tested for significance. Broad sense and narrow sense heritabilities were estimated using the method outlined by Warner (1952), and number of genes was estimated using the method developed by Sinnot et al. (1950), Weber (1950), and Burton (1951). Phenotypic and genotypic correlation coefficients in the F₂ generation between characters were calculated by the method suggested by Stuber (1970). Path coefficient analysis was made using method shown by Singh and Chaudhary (1979). The followings were statistical procedures used for analyses of means and variances:

(1) Scaling test: A, B and C values and their respective variances were calculated as follows:

$$A = 2\overline{BC_1} - \overline{P_1} - \overline{F_1}$$

$$B = 2\overline{BC_2} - \overline{P_2} - \overline{F_1}$$

$$C = 4\overline{F_2} - 2\overline{F_1} - \overline{P_1} - \overline{P_2}$$

$$V_A = 4V(\overline{BC_1}) + V(\overline{P_1}) + V(\overline{F_1})$$

$$V_B = 4V(\overline{BC_2}) + V(\overline{P_2}) + V(\overline{F_1})$$

$$V_C = 16V(\overline{F_2}) + 4V(\overline{F_1}) + V(\overline{P_1}) + V(\overline{P_2})$$

Significance of values was evaluated by using following t-statistics:

$$t_{(A)} = A / \sqrt{V_A}$$

$$t_{(B)} = B / \sqrt{V_B}$$

$$t_{(C)} = C / \sqrt{V_C}$$

where $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$, $\bar{F}_2$, $\overline{BC_1}$ and $\overline{BC_2}$ were means of P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 , respectively. $V(\bar{P}_1)$, $V(\bar{P}_2)$, $V(\bar{F}_1)$, $V(\bar{F}_2)$, $V(\overline{BC_1})$ and $V(\overline{BC_2})$ were variances of mean in populations P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 , respectively.

(2) Components of generation means

The means of all populations were analyzed by the method outlined by Gamble (1962) to determine types and amounts of various gene actions. The six populations can be described in terms of the F_2 mean (m), additive gene effects (a), dominance gene effects (d), additive $\times$ additive epistatic gene effects (aa), additive $\times$ dominance epistatic gene effects (ad), and dominance $\times$ dominance epistatic gene effects (dd). The equations are as follows:

$$\begin{aligned} m &= \bar{F}_2 \\ a &= \overline{BC_1} - \overline{BC_2} \\ d &= -\frac{1}{2}\bar{P}_1 - \frac{1}{2}\bar{P}_2 + \bar{F}_1 - 4\bar{F}_2 + 2\overline{BC_1} + 2\overline{BC_2} \\ aa &= -4\bar{F}_2 + 2\overline{BC_1} + 2\overline{BC_2} \\ ad &= -\frac{1}{2}\bar{P}_1 + \frac{1}{2}\bar{P}_2 + \overline{BC_1} - \overline{BC_2} \\ dd &= \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\overline{BC_1} - 4\overline{BC_2} \end{aligned}$$

The variances of these estimates and “t” values were obtained in the usual manner, for example:

$$V_{(D)} = \frac{1}{4}V(\overline{P_1}) + \frac{1}{4}V(\overline{P_2}) + V(\overline{F_1}) + 16V(\overline{F_2}) + 4V(\overline{BC_1}) + 4V(\overline{BC_2})$$

and t-test was used to determine importance of gene effects,

$$t_{(d)} = d / \sqrt{V_{(D)}}$$

(3) Heritability

Broad-sense heritability (h_b^2) and narrow-sense heritability (h_n^2) estimates were computed as below (Warner 1952):

$$h_b^2 = \frac{V_{F_2} - (V_{P_1} + V_{P_2} + V_{F_1})/3}{V_{F_2}} \times 100$$

$$h_n^2 = \frac{2V_{F_2} - (V_{BC_1} + V_{BC_2})}{V_{F_2}} \times 100$$

where V_{P_1} , V_{P_2} , V_{F_1} , V_{F_2} , V_{BC_1} and V_{BC_2} were the variances of P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 , respectively.

(4) Number of effective factors

Different formulas were used to estimate number of effective factors (or genes) of different characters as follows:

$$(a) \quad k_1 = \frac{(\bar{P}_1 - \bar{P}_2)^2}{8(\sigma_{F_2}^2 - \sigma_{F_1}^2)} \quad (\text{Sinnot et al., 1950})$$

$$(b) \quad k_2 = \frac{(\bar{P}_1 - \bar{P}_2)^2}{8[(\sigma_{F_2}^2 - (\sigma_{P_1}^2 + \sigma_{F_1}^2 + \sigma_{P_2}^2))/3]} \quad (\text{Weber, 1950})$$

$$(c) \quad k_3 = \frac{[1/4(3/4 - h + h^2)(\bar{P}_1 - \bar{P}_2)^2]}{\sigma_{F_2}^2 - \sigma_{F_1}^2} \quad (\text{Burton, 1951})$$

where k is number of genes, $h = \frac{\bar{F}_1 - \bar{P}_1}{\bar{P}_2 - \bar{P}_1}$. $\bar{P}_1$, $\bar{P}_2$ and $\bar{F}_1$ are actual means of P_1 , P_2 and F_1 , respectively. $\sigma_{P_1}^2$, $\sigma_{P_2}^2$, $\sigma_{F_1}^2$ and $\sigma_{F_2}^2$ represent the variances of respective generations.

(5) Phenotypic and genetic correlation coefficients

Phenotypic and genetic correlation coefficients were calculated as follow:

$$r_{ph(xy)} = \frac{\text{Cov}_{(xy)} F_2}{\sqrt{[V_{(x)} F_2][V_{(y)} F_2]}}$$

$$r_{g(xy)} = \frac{\text{Cov}_{(xy)} F_2 - \text{Cov}_{(xy)E}}{\sqrt{[V_{(x)} F_2 - V_{(x)E}][V_{(y)} F_2 - V_{(y)E}]}} \quad (\text{Stuber, 1970})$$

where $\text{Cov}_{(xy)} F_2$ = phenotypic covariance between X and Y in F_2 .

$$\text{Cov}_{(xy)E} = \frac{\text{Cov}_{(xy)} P_1 + \text{Cov}_{(xy)} F_1 + \text{Cov}_{(xy)} P_2}{3}$$

$V_{(x)} F_2, V_{(y)} F_2$ = var. x, var. y in F_2

$$V_{(x)E} = \frac{V_x P_1 + V_x F_1 + V_x P_2}{3}$$

$$V_{(y)E} = \frac{V_y P_1 + V_y F_1 + V_y P_2}{3}$$

(6) Path coefficient

It can be calculated by following equations:

$$P_{y.x_i} = \frac{\sigma_{x_i}}{\sigma_y} \quad (\text{Singh and Chaudhary, 1979})$$

where $P_{y.x_i}$ can be obtained from these equations by inversion of matrix:

$$\begin{aligned} r_{x_1y} &= P_1 + P_2 r_{x_1x_2} + P_3 r_{x_1x_3} + \dots + P_n r_{x_1x_n} \\ r_{x_2y} &= P_1 r_{x_2x_1} + P_2 + P_3 r_{x_2x_3} + \dots + P_n r_{x_2x_n} \\ r_{x_3y} &= P_1 r_{x_3x_1} + P_2 r_{x_3x_2} + P_3 + \dots + P_n r_{x_3x_n} \end{aligned}$$

where $P_{y.x_i}$ was the path coefficient from x_i to y ; σ_{x_i} was the standard deviation of the effect due to x_i ; σ_y was the total standard deviation of the effect y ; r is coefficient of correlation between two characters.

3.4 Results and Discussion

3.4.1 Growing Condition

Growing condition was rather adverse for rapeseed during the years of 2007-2008. At Guiyang, early in the winter there was a lack of rain, and late winter was quite cold with long ice rain period during Jan. 12 through Feb. 4, 2008

(Appendix: Attached figure 1 and 2). The ice rain damaged early buds. Spring in 2008 was late. The flowering and maturity periods of rapeseed were delayed and later than usual due to the cold weather.

3.4.2 Variations and Generation Means of Characters

(1) Cross I

The distributions and means of Cross I are presented in Tables 3.1 through 3.5. There were some plants in F_2 exceeded the P_1 and P_2 distributions in the lower and upper parts for oil, protein and oleic acid contents, indicating that low and high effective factors distributed in both parents which make difficult to obtain desirable hybrids for these characters. This may be remedied by selecting new parents from the topmost of transgressive variation. For erucic acid and glucosinolate contents none of the plants in F_2 exceeded the P_1 and P_2 distributions in the lower and upper parts. It was apparent that the effective factors conditioning high erucic acid and glucosinolate contents came from P_1 and the other from P_2 . For such characters as erucic acid and glucosinolate, it also indicated that the number of factors was not large since the parental types were recovered.

The mean of F_1 for oil content was equal to low oil content parent, indicating the negative dominance of this trait. Mean protein content in F_1 was almost equal to the mid-parent, indicating that additive effects influenced this character. The F_1 mean of oleic acid content was lower than mid-parent, indicating partially negative dominance of this character. The mean F_1 values of erucic acid and glucosinolate contents were higher than their mid-parent values. This indicated that partially positive dominance existed for these characters.

The variances of all populations of all characters in Cross I are shown

flowering and days to maturity were recorded on individual plants except the extreme plants in each generation. Self-pollinated seeds for quality analysis were obtained in the same way as in Cross I. Open pollinated plants which were recorded for days to flowering and days to maturity were harvested randomly for quality analysis seeds. Characters including oil and protein contents were analyzed in Cross II. Data for characters in this experiment were recorded as follows:

Days to flowering (no.): Days from sowing until the first flower bloomed.

Days to maturity (no.): Days from sowing until 90% of the pods matured.

Oleic acid content (%): Proportion of oleic acid content from dried seeds determined by Near-infrared reflectance spectroscopy (NIRS).

Protein content (%): Proportion of protein content from dried seeds determined by NIRS.

Oil content (for Cross I) (%): Was analyzed by using the method in GB/T17376-1998. This work was done at Institute of Industrial Crops, Jiangsu Academy of Agricultural Science.

Oil content (for Cross II) (%): Proportion of oil content from dried seeds determined by NIRS.

Erucic acid content (%): Was analyzed with Agilent 6890N GC by using the method reported by Gao et al. (2008). This work was done at Institute of Industrial Crops, Jiangsu Academy of Agricultural Science.

Glucosinolate content ($\mu\text{mol/g}$): Was analyzed by using glucosidase and peroxidase method reported by Qi et al. (1991), and this work was done at Institute of Industrial Crops, Jiangsu Academy of Agricultural Science.

in Tables 3.1 through 3.5. For most characters except glucosinolate, the magnitudes of variance of populations agreed with theoretical expectations which the variances of segregating populations were higher than that of pure lines and F_1 hybrid, and variances of F_2 genetically higher than those of BC_1 and BC_2 . For glucosinolate content, variances of P_1 and F_1 were high probably parental materials were not genetically homozygous.

Table 3.1 Distributions for oil content of populations in Cross I.

Oil content %	Populations/ No. of plants					
	$P_1^\dagger$	P_2	F_1	F_2	BC_1	BC_2
< 30				3		2
31				1		0
32				0		2
33				1	1	3
34		1		4	0	3
35		2	2	10	5	5
36		4	3	9	1	8
37		7	5	16	7	4
38		6	6	13	3	7
39	2	1	5	21	5	7
40	4		3	13	2	4
41	2		1	9	8	1
42	8			13	3	
43	4			1	4	
44	2			1		
45				1		
n	22	21	25	116	39	46
Mean	41.06	37.35	37.36	37.76	38.44	35.88
Variance	1.99	1.57	2.42	8.12	7.30	7.45

$^\dagger P_1 = \text{III174}, P_2 = \text{Zi 20}$

Table 3.2 Distributions for protein content of populations in Cross I.

Protein content %	Populations/No. of plants					
	P ₁ [†]	P ₂	F ₁	F ₂	BC ₁	BC ₂
26.0						1
26.5		1		3		2
27.0		1		3		2
27.5		2	1	3		5
28.0		6	1	14	1	8
28.5		11	4	14	2	6
29.0		7	5	20	6	7
29.5	2	9	6	29	7	5
30.0	9	5	9	17	7	5
30.5	7		6	11	13	3
31.0	6		3	12	14	2
31.5	3		2	5	8	
32.0	2		1	3	10	
32.5				3	0	
33.0				1	2	
33.5				1	1	
n	29	42	38	139	71	46
Mean	30.32	28.59	29.56	29.27	30.41	28.42
Variance	0.54	0.79	0.89	1.67	1.28	1.56

[†] P₁ = Zi 20, P₂ = III174

Table 3.3 Distributions for oleic acid content of populations in Cross I.

Oleic acid content %	Populations/No. of plants					
	P ₁ [†]	P ₂	F ₁	F ₂	BC ₁	BC ₂
32				2		
34				5		
36		2		7		5
38		4		5		9
40		12		13		9
42		9	2	11	1	13
44		2	8	18	1	13
46			17	16	5	7
48			10	12	2	8
50				14	7	2
52				12	3	3
54				7	7	1
56				5	1	1
58				0	2	
60				3	5	
62				5	1	
64	6			3	4	
66	6			1	5	
68	18				1	
70	11					
72	1				1	
n	42	29	37	139	46	71
Mean	66.79	39.32	45.06	45.67	54.38	42.52
Variance	4.28	3.44	2.78	55.38	54.56	30.76

[†] P₁ = III174, P₂ = Zi 20

Table 3.4 Distributions for erucic acid content of populations in Cross I.

Erucic acid content	Populations/No. of plants					
	$P_1^\dagger$	P_2	F_1	F_2	BC_1	BC_2
< 1		22		5		11
5						
10				2		4
15				11		6
20				8		9
25			1	16	1	4
30			22	24	8	5
35			2	20	4	
40				12	14	
45	15			10	12	
50	6			8	7	
n	21	22	25	116	46	39
Mean	44.39	0.23	27.78	27.72	37.97	12.83
Variance	1.40	0.00	2.68	132.88	48.38	86.33

$^\dagger P_1 = Zi\ 20, P_2 = III174$

Table 3.5 Distributions for glucosinolate content of populations in Cross I.

Glucosinolate content μ mol/g	Populations/No. of plants					
	$P_1^\dagger$	P_2	F_1	F_2	BC_1	BC_2
< 20		2				
25		17		3		1
30		3		0		3
35				5		1
40				6		3
45				4		6
50				9		2
55				6		4
60			3	9		4
65			1	15	1	1
70			8	12	3	4
75			2	11	3	2
80			4	11	8	3
85			5	8	3	3
90	3		1	5	4	1
95	3		1	1	7	1
100	5			5	4	
105	2			3	3	
110	5			1	5	
115	2			1	2	
120	1			1	2	
125					1	
n	21	22	25	116	46	39
Mean	100.73	22.71	73.05	65.5	90.35	55.78
Variance	79.47	5.45	80.46	398.52	231.29	366.23

$^\dagger P_1 = \text{Zi 20}, P_2 = \text{III174}$

(2) Cross II

The distributions, means and variances of all populations in Cross II are presented in Tables 3.6 through 3.9. The distributions of all characters in F_2 exceeded both lower and higher parts of P_1 and P_2 distributions. This indicated that low and high effective factors distributed in both parents. The modifications of the breeding procedure were required to improve these characters.

The F_1 mean for oil content was lower than the mean of low parent, indicating the negative dominance of this trait. Mean protein content in F_1 was higher than the mean of high parent, indicating the existence positive dominance effects of this trait. F_1 mean values for days to flowering and days to maturity were almost equal to the mid-parent. This indicated that additive effects were important for these characters.

The variances of all populations for all characters agreed with theoretical expectations which variances of segregating populations were higher than those of pure lines and F_1 hybrid.

Table 3.6 Distributions for oil content of populations in Cross II.

Oil content %	Populations/No. of plants					
	$P_1^\dagger$	P_2	F_1	F_2	BC_1	BC_2
28				1		1
29				1		2
30				3	1	2
31			1	3	2	7
32			2	2	1	2
33			3	6	8	5
34		1	5	13	2	8
35		5	2	19	7	9
36	4	5	13	12	10	4
37	2	4	5	17	9	9
38	3	4	5	8	12	9
39	7	1	4	16	10	5
40	2		4	7	9	
41	6			2	8	
42	2			2	2	
43				2		
n	26	20	44	114	81	63
Mean	38.52	35.96	35.81	35.76	37.68	34.35
Variance	3.74	1.72	4.85	8.68	7.95	8.61

$^\dagger P_1 = \text{III38}, P_2 = \text{III142}$

Table 3.7 Distributions for protein content of populations in Cross II.

Protein content %	Populations/No. of plants					
	P ₁ [†]	P ₂	F ₁	F ₂	BC ₁	BC ₂
25.5				1		
26.0				1		2
26.5		2		5	3	3
27.0		1		6	0	3
27.5	1	4	2	9	2	7
28.0	1	4	2	10	3	5
28.5	1	6	3	12	7	7
29.0	2	2	6	16	10	14
29.5	6	3	9	15	8	16
30.0	4	2	6	18	9	10
30.5	4	2	4	7	5	5
31.0	0		5	7	6	6
31.5	1		6	3	4	1
32.0			0	1	3	0
32.5			1	2	0	0
33.0				1	2	1
33.5					1	1
n	20	26	44	114	63	81
Mean	29.38	28.25	29.63	28.86	29.52	28.89
Variance	0.83	1.24	1.44	2.20	2.31	1.95

[†] P₁ = III142, P₂ = III38

Table 3.8 Distributions for days to flowering of populations in Cross II.

Days to flowering no.	Populations/No. of plants					
	P ₁ [†]	P ₂	F ₁	F ₂	BC ₁	BC ₂
171				1	2	1
173				1	3	3
175		5		2	6	5
177		11	9	6	9	10
179		16	12	9	7	8
181		43	16	37	15	22
183	4	17	23	40	17	22
185	8	13	45	45	40	29
187	21	6	32	42	21	26
189	25		22	18	17	3
191	10		11	14	4	
193	8			7		
195	6			5		
197	2			4		
n	84	111	170	231	141	129
Mean	188.6	180.6	184.3	184.6	183.1	182.2
Variance	10.25	7.77	12.84	19.87	20.05	16.25

[†] P₁ = III142, P₂ = III38

Table 3.9 Distributions for days to maturity of populations in Cross II.

Days to maturity no.	Populations/No. of plants					
	P ₁ [†]	P ₂	F ₁	F ₂	BC ₁	BC ₂
237						2
238			1		3	3
239		8	6	16	4	13
240		0	2	2	1	0
241		5	14	5	6	8
242	11	52	33	24	20	34
243	5	23	17	9	19	14
244	8	9	22	21	7	5
245	15	12	37	40	31	12
246	16		17	20	15	11
247	15		7	28	15	5
248	4		5	8	4	9
249			1	12	2	5
250				10		1
251				7		
n	74	109	162	202	127	122
Mean	245.1	242.4	243.7	245.0	244.1	243.3
Variance	3.26	2.06	4.64	9.33	5.68	9.06

[†] P₁ = III142, P₂ = III38

3.4.3 Genetic Analysis of Characters

Scaling tests, as outlined by Mather (1949), were used to assess the adequacy of the simple additive-dominance model in explaining observed differences among generation means. The calculated values of A, B and C for characters in both crosses are presented in Table 3.10. The “t” values of A, B and C showed at least one of them was significant ($P < 0.05$) for each character. However, a joint scaling test,

Table 3.10 A, B, C and “t” values for scaling test of characters in Cross I and Cross II.

Cross I (III174 × Zi20)										
	OC		PC		OAC		EAC		GC	
	Value	t value	Value	t value	Value	t value	Value	t value	Value	t value
A	-1.54	-1.59	0.95	2.81*	-3.08	-1.39	3.76	1.80	6.93	1.33
B	-2.95	-3.26**	-1.32	-3.12**	0.67	0.48	-2.36	-0.79	15.81	2.47*
C	-2.10	-1.62	-0.94	-1.65	-13.54	-5.16**	10.67	2.46*	-7.55	-0.89

Table 3.10 Continued

Cross II (III38 × III142)								
	OC		PC		DF		DM	
	Value	t value	Value	t value	Value	t value	Value	t value
A	1.03	1.28	0.04	0.08	-6.60	-7.54**	-0.57	-1.13
B	-3.06	-3.55**	-1.10	-0.24	-0.41	-0.51	0.45	0.77
C	-3.04	-2.21*	-1.46	-2.00*	0.54	0.40	5.17	5.39**

*,** significant at 0.05 and 0.01 levels of probability, respectively.

outlined by Cavali (1952), was used to test for additive-dominance model, and found it was adequate for protein content in Cross II, while it was inadequate for other characters in both crosses (Table 3.11). These revealed that all characters in both crosses except protein content in Cross II did not follow the additive-dominance model, and indicated the presence of epistatic effects for these characters.

Table 3.11 Chi-square values (χ^2) of joint scaling test of characters for additive-dominance model.

Character	Cross I (III174 × Zi20)					Cross II (III38 × III142)			
	OC [‡]	PC	OAC	EAC	GC	OC	PC	DF	DM
χ^2	12.58**	25.00**	28.72**	9.74*	9.50*	20.10**	4.81	61.54**	34.57**

*,** significant at 0.05 and 0.01 levels of probability, respectively.

‡ OC = oil content; PC = protein content; OAC = oleic acid content; EAC = erucic acid content; GC = glucosinolate content; DF = days to flowering; DM = days to maturity.

Estimates of six genetic parameters of each character in both crosses are displayed in Table 3.12. The contribution of each parameter to these characters was indicated by relative magnitude of each parameter to the mean.

Table 3.12 Estimates for genetic parameters of characters in Cross I and Cross II.

Parameters	Cross I (III174 × Zi20)				
	OC	PC	OAC	EAC	GC
m	37.76 **	29.27 **	45.67 **	27.71 **	65.50 **
a	2.56 **	2.00 **	11.86 **	25.14 **	34.57 **
d	-4.23 **	0.68	3.13	-3.79	41.60 **
aa	-2.39	0.57	11.12 **	-9.27	30.28 **
ad	0.71	1.13 **	-1.87	3.06	-4.44
dd	6.88 **	-0.20	-8.71	7.87	-53.01 **

Table 3.12 Continued

Parameters	Cross II (III38 × III142)			
	OC [‡]	PC	DF	DM
m	35.76 **	28.86 **	184.55 **	245.01 **
a	3.32 **	0.64 **	0.90	0.82 *
d	-0.42	2.20 **	-7.89 **	-5.37 **
aa	1.01	1.39	-7.56 **	-5.28 **
ad	2.04 **	0.07	-3.09 **	-0.51
dd	1.03	-1.33	14.57 **	5.40 **

*,** significant at 0.05 and 0.01 levels of probability, respectively.

‡ OC = oil content; PC = protein content; OAC = oleic acid content; EAC = erucic acid content; GC = glucosinolate content; DF = days to flowering; DM = days to maturity.

(1) Cross I

The “t” test for all six parameters showed that additive gene effects of all characters were positively significant. This indicated that additive gene effects were important in controlling these characters. The magnitudes of additive effects (a) were high relative to dominance effects for almost all characters except oil and glucosinolate contents. This indicated that additive gene effects provided a major contribution to the inheritance of these characters. Significant negative contribution of dominance effect was found for oil content while significant positive contribution of dominance effect was found for glucosinolate content. The importance of dominance gene effect was indicated not only by significant and relative magnitude but also by its significant positive and negative values. Positive and negative dominance gene effects suggest its enhancing and diminishing effects on the performance of characters. Additive $\times$ additive gene effects were positively significant for oleic acid and glucosinolate contents. This gene effects gave considerable contributions to the inheritance of these characters. Additive $\times$ dominance gene effect was found to give positive significant contribution to protein content. Significant positive contribution of dominance $\times$ dominance effect was found for oil content while significant negative contribution of dominance $\times$ dominance effect was found for glucosinolate content.

(2) Cross II

The “t” test for all six parameters showed that additive gene effects of all characters except days to flowering were positively significant. This indicated that additive gene effects were important in controlling these characters. Significant positive contribution of dominance was found for protein content while significant negative contributions were found for days to flowering and days to maturity. For

these characters, dominance gene effects were relatively high. This indicated that dominance gene effects were more important than additive effects. Significant additive $\times$ additive gene effects were found for days to flowering and days to maturity, but both were negative. This indicated that they were in the direction of early blooming and early maturity. Oil content and days to flowering had significantly positive and negative additive $\times$ dominance gene effects, respectively. Dominance $\times$ dominance gene effects showed significantly positive contributions to days to flowering and days to maturity.

It was shown in Cross I that all characters did not follow the additive – dominance model. This indicated the presence of epistatic effects for these characters. That is both additive and non-additive gene effects influenced these characters. However, non-additive gene effects were not important for erucic acid and oleic acid contents, while additive, including additive $\times$ additive, gene effects were important for these two characters. Similar result for erucic acid was reported by Qi et al. (2001) that additive effect was more important for this character than others, but other types of gene effects were also found to control erucic acid content. The magnitude of heritable effects in the form of additive (a), additive $\times$ additive (aa) for these two characters provided the potential for improvement of these traits through selection.

For glucosinolate content, many researchers (Krzymanski, 1970; Zhou and Liu, 1987; Mou and Liu, 1990) reported that it was controlled by both additive and non-additive gene effects. Our result for this character was consistent with that. In this study, the high negative value of dominance $\times$ dominance was higher than all other gene effects. The inheritance of this character was complicated by enhancing and diminishing effects of all types of gene action.

The results for Cross II showed both additive and non-additive gene effects for days to flowering and days to maturity. These two characters had very similar gene actions. Significantly negative dominant gene effects expressed by these characters indicated that early flowering and early maturity were dominant over the late flowering and late maturity. This type of gene action is useful to develop early variety, and the significantly negative additive $\times$ additive effect is useful to improve these characters.

For protein content, the results from Cross I and Cross II were different. In this study, protein content was found to be controlled by additive and non-additive gene effects in Cross I, while it was found to be controlled by additive and dominance gene effects with both additive and dominance effects were important in Cross II. This was not agreed with the reports by some researchers (Grami and Stefansson, 1977; Hu and Liu, 1989; Dong et al., 2007) who reported that additive gene effect was important. However, the result from Cross II was consistent with that of Wang and Qiu (1990).

For oil content, it was found in both crosses that both additive and non-additive gene effects were important for this character. Similar results were found by other researchers (Dong et al., 2007; Delourme et al., 2006). However, many other reports gave different results on the inheritance of oil content. Some found that the inheritance of this character followed additive-dominance model (Hu and Liu, 1989; Han, 1990), but Grami and Stefansson (1977) reported that oil content was governed by additive gene effect and dominant gene effect was not important. The significantly negative dominant effect for oil content in Cross I might make difficult in the selection for high oil content.

3.4.4 Heritability

Heritability estimates were obtained for all characters in both crosses and are presented in Table 3.13. Broad sense heritabilities were generally higher than narrow sense ones for all characters. This difference demonstrated the influence of non-additive gene actions. Moderate broad sense heritabilities and low narrow sense heritabilities for oil and protein contents in both crosses were observed (Table 3.13).

Table 3.13 Estimates of heritability for characters in Cross I and Cross II.

	Cross I (III174 × Zi20) (%)				
	OC [‡]	PC	OAC	EAC	GC
h_b^2 [†]	75.47	55.81	93.68	98.97	86.17
h_n^2	18.37	29.89	45.94	98.62	50.06

Table 3.13 Continued

	Cross II (III38 × III142) (%)			
	OC	PC	DF	DM
h_b^2	60.39	46.80	48.23	64.38
h_n^2	9.21	6.19	17.25	40.04

[†] h_b^2 = broad sense heritability; h_n^2 = narrow sense heritability.

[‡] OC = oil content; PC = protein content; OAC = oleic acid content; EAC = erucic acid content; GC = glucosinolate content; DF = days to flowering; DM = days to maturity.

(1) Cross I

The highest broad sense and narrow sense heritabilities of 98.97 and 98.62%, respectively, were obtained for erucic acid content. These values indicated that erucic acid content was highly heritable and was predominantly influenced by additive genetic effect.

High broad sense heritability (93.68%) was obtained for oleic acid content while its narrow sense heritability was moderate (45.95%). This indicated for this character that non-additive gene effects were more important than additive gene effects.

Glucosinolate content gave relatively high heritabilities with the values of 86.17 and 50.06% for broad sense and narrow sense, respectively (Table 3.13). The results indicated the substantial contribution of non-additive gene effects to this character.

(2) Cross II

Moderate broad sense heritability (48.23%) and low narrow sense heritability (17.25%) for days to flowering were found. Moderate broad sense and narrow sense heritabilities were found for days to maturity (Table 3.13).

High broad sense and narrow sense heritabilities of 98.97 and 98.62% were obtained for erucic acid in this study. This agreed with the report of Liu D. and Liu H (1990) who found that both broad and narrow sense heritabilities were high for this character. The high value indicated that early generation selection methods should be effective for improving this trait. High broad sense (93.68%) and moderate narrow sense (45.94%) heritabilities were obtained in this study for oleic acid content which were different from other reports which showed that the both broad and narrow sense

heritabilities were higher than 86% (Wang et al., 2006; Schierholt and Becker, 2001) and broad and narrow sense heritabilities of 75.65% and 66.75% (Dong et al., 2007). However, the heritability of glucosinolate content in this study was found to be lower than that reported by some researchers (Dong et al., 2007; Pietka et al., 2007). The heritabilities of oil content were very similar to the report of Dong et al. (2007) who found that heritabilities of oil content were 79.68% and 13.93% for broad sense and narrow sense, respectively, but were higher than that reported by Grami et al. (1977) and lower than that reported by Han (1990) and Hu (1987). The small narrow sense heritability of protein content was very similar to the report of Dong et al. (2007) who found that narrow heritability of protein content was 8.98%, but broad heritability (74.21%) was higher than that found in this study. In this study, moderate heritabilities for oil and protein contents in both crosses, days to flowering and days to maturity in Cross II, indicating that these characters were influenced by both environment and gene effects.

3.4.5 Minimum Number of Genes

The estimates of number of genes conditioning all characters in both crosses are presented in Table 3.14. Similar results were obtained from three formulas used in this study. Many estimates were very low, even lower than one, indicating that low number of genes controlling these characters. In Cross I, the estimates for oleic acid and erucic acid contents indicated that the minimum of 2 gene pairs controlling parental difference of these characters, and the number of genes controlling glucosinolate content was three pairs. In Cross II, the range of 0.83 to 1.14 gene pairs was found for days to flowering indicating that at least 1 major gene pair controlled this character. Many characters gave very low estimates for number of genes, even

less than 1 gene pair. This was due to the distribution of genes in both parents which was reflexed by transgressive distribution in segregating populations.

Table 3.14 Estimates for number of gene pairs of characters in Cross I and Cross II.

Gene pair	Cross I (III174 × Zi20)				
	OC	PC	OAC	EAC	GC
k ₁	0.30	0.48	1.80	1.87	2.39
k ₂	0.28	0.40	1.82	1.85	2.22
k ₃	0.45	0.48	2.10	1.93	2.49

Table 3.14 Continued

Gene pair	Cross II (III38 × III142)			
	OC	PC	DF	DM
k ₁	0.21	0.21	1.13	0.19
k ₂	0.16	0.16	0.83	0.15
k ₃	0.35	0.43	1.14	0.19

In this study, the results of two major gene pairs controlling oleic acid and erucic acid content were consistent with many other reports (Chen and Beversdorf, 1990; Schierhoft et al., 2001; Huang et al., 1999; Siebel and Pauls, 1989), and three major gene pairs controlling glucosinolate was also consistent with the reports by other researchers (Zhou and Liu, 1987; Mou and Liu, 1990), but different from the result of Chauhan et al. (2007) who found that glucosinolate content was controlled by at least 4-5 gene pairs. Small number of gene pairs for oil content,

protein content, and days to flowering were found in this study. Similar result for oil content was found by Grami et al. (1977).

3.4.6 Correlations Between Characters in Two Crosses

The estimates of coefficient of correlation between characters in both crosses are displayed in Table 3.15.

Table 3.15 Coefficients of correlations between characters in Cross I and Cross II.

Character		Cross I (III174 × Zi20)				Character		Cross II (III38 × III142)		
		PC	OAC	EAC	GC			PC	DF	DM
OC [‡]	r _{ph} [†]	-0.66**	-0.07	-0.08	-0.01	OC	r _{ph}	-0.77**	0.23	0.20
	r _g	-0.81	-0.07	-0.08	0.01		r _g	-0.93	0.60	0.47
PC	r _{ph}		0.02	0.10	0.07	PC	r _{ph}		-0.12	-0.06
	r _g		-0.02	0.10	0.08		r _g		-0.43	-0.18
OAC	r _{ph}			-0.93**	-0.20*	DF	r _{ph}			0.40**
	r _g			-0.97	-0.32		r _g			0.39
EAC	r _{ph}				0.15					
	r _g				0.16					

*,** significant at 0.05 and 0.01 levels of probability, respectively.

† r_{ph} = phenotypic coefficient of correlation; r_g = genetic coefficient of correlation.

‡ OC = oil content; PC = protein content; OAC = oleic acid content; EAC = erucic acid content; GC = glucosinolate content; DF = days to flowering; DM = days to maturity.

(1) Cross I

Highly significant negative phenotypic correlations were found between oil and protein contents, oleic acid and erucic acid contents with the

coefficients of -0.66^{**} and -0.93^{**} , respectively, and they also resulted in high negative genetic coefficients of -0.81 and -0.97 . Significantly negative correlation of -0.20^{*} was found between oleic acid and glucosinolate contents. Small positive correlations were detected between erucic acid and protein contents, erucic acid and glucosinolate contents.

(2) Cross II

Phenotypic correlation between oil and protein contents was found to be negative and highly significant (-0.77^{**}). This also resulted in high negative genetic correlation (-0.93). Significantly positive correlation of 0.40^{*} was found between days to flowering and days to maturity. Positive but not significant correlations were found between oil content and days to flowering and oil content and days to maturity. However, relatively higher values of genetic coefficient of correlation were found between these characters.

Correlations among characters were partitioned into direct and indirect effects which contributed to oil content of rapeseed, and are presented in Table 3.16. In Cross I, path analysis revealed that all characters had negative direct contributions to oil content (Table 3.16). Although the direct effect of oleic acid content to oil content was negative (-3.083), the indirect contribution of this character to oil content through erucic acid was high (2.855). The direct effect of erucic acid to oil content also was negative (-2.943), the indirect contribution to oil content through oleic acid content was high (2.991). In Cross II, protein content gave negatively direct contribution to oil content, while days to flowering and days to maturity gave small positive direct contributions to oil content.

Table 3.16 Direct (diagonal) and indirect effects of quality characters on oil content.

Character	Cross I (III174 × Zi20)				
	PC	OAC	EAC	GC	GCC [†]
PC	-0.540	0.062	-0.294	-0.037	-0.810
OAC	0.011	-3.083	2.855	0.148	-0.070
EAC	-0.054	2.991	-2.943	-0.074	-0.080
GC	-0.043	0.987	-0.471	-0.463	0.010

Table 3.16 Continued

Character	Cross II (III38 × III142)			
	PC	DF	DM	GCC
PC	-0.820	-0.062	-0.048	-0.93
DF	0.353	0.143	0.104	0.60
DM	0.148	0.056	0.266	0.47

[†] GCC = genotypic correlation coefficients with oil content.

The negative and highly significant correlation between oil and protein contents in both crosses was agreed with results found by many researchers (Grami et al., 1977; Mahmood et al., 2006; Alemayehu and Becker, 2002; Singh et al., 2007; Zhu et al., 2007). The negative and highly significant correlation between oleic acid and erucic acid content was found in Cross I. Similar results were also detected by other researchers (Chen and Beversdorf, 1990; Shi et al., 2006; Zhu et al., 2007). The correlation between oleic acid and glucosinolate contents in Cross I was found to be

significantly negative and agreed with result of Shi et al. (2006) and Zhu et al. (2007), but not consistent with the result found by Zhou and Liu (1989) who found small positive correlation between these characters. Significantly positive correlation was found between days to flowering and days to maturity in this study. This was in agreement with that of Alemayehu and Becker (2002), and indicates that selection for early days to flowering can result in early days to maturity.

3.5 Conclusion

Two crosses of rapeseed (Cross I: III174 $\times$ Zi20; Cross II: III38 $\times$ III142) were made, their F_2 , BC_1 ($F_1 \times P_1$) and BC_2 ($F_1 \times P_2$) were produced. These generations and their parents were evaluated by generation mean analysis. The distributions of F_2 populations of certain characters showed transgressive variations, indicates that dominant and recessive genes controlling these characters distributed in both parents. The accumulation of favorable genes in one parent should be made for the improvement of these characters.

Results from genetic analysis using six parameter model for all characters showed that protein content in Cross II followed additive–dominance model with both additive and dominance effects were important. Other characters in both crosses were controlled by both additive and non-additive gene effects. However, non-additive gene effects were not important for erucic acid and oleic acid contents, while additive (including additive $\times$ additive) gene effects played predominantly roles for these two characters.

In this study, high broad sense and narrow sense heritabilities of 98.97 and 98.62% were obtained for erucic acid in Cross I. This indicates that additive gene

effects controlled this character and also indicates early generation selection methods should be effective for improving this trait. High broad sense heritabilities and moderate narrow sense heritabilities for oleic acid and glucosinolate contents indicated that these characters were controlled mainly by genetic effects, and both additive and non-additive gene effects were important.

Estimates for minimum number of genes showed that two major gene pairs controlled erucic acid and oleic acid contents in Cross I, three major gene pairs and at least one major gene pair controlled glucosinolate content in Cross I and days to flowering in Cross II, respectively. However, small number of gene pair was found for other characters studied. This was due to the distribution of genes in both parents which reflexed by transgressive variation in segregating generations. However, at least one gene pair controlled these characters.

The correlation analysis showed that relationships between oil and protein, erucic acid and oleic acid, oleic acid and glucosinolate contents were negative. Thus made difficult to improve both oil and protein contents together. Positive correlation was found between days to flowering and days to maturity, and indicates that selection for early days to flowering can result in early days to maturity. Correlations between other characters were weak.

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CHAPTER IV

ANALYSIS OF COMBINING ABILITY AND ASSOCIATIONS FOR CHARACTERS OF MALE STERILE LINES IN RAPESEED (*Brassica napus* L.)

4.1 Abstract

The male sterile line is very important in the hybrid breeding program of rapeseed. This study was conducted to evaluate the inheritance of many characters of male sterile lines in *Brassica napus* L. Ten recessive genetic male sterile (RGMS) lines were used as parents to cross in a half diallel cross method to produce 45 single cross hybrids. These forty five crosses and their 10 parents were evaluated at Guiyang during 2007-2008. The results showed that mean squares for parents and hybrids were significant for all characters. Both GCA and SCA effects were important for all characters, but additive gene effects were more predominant than non-additive gene effects. Line 5 (Qianyou 8AB) and line 6 (You 2894AB) gave respective highly significant GCA effects of 230.94 and 127.65 kg ha⁻¹ for seed yield. Lines 6, 8, 9 and 10 (You 2894AB, QH303-4AB, You 157AB and You 2341AB) gave highly significant GCA effects for oil content of 0.99, 1.62, 1.20 and 1.53%, respectively. The crosses between lines 2 × 5, 5 × 6, 6 × 7, 5 × 8 and 5 × 7 (Qianyou 3A × Qianyou 8B, Qianyou 8A × You 2894B, You 2894A × Qianyou 6B, Qianyou 8A × QH303-4B and Qianyou 8A × Qianyou 6B) gave high SCA effects of 616.29, 398.71, 356.48, 394.24 and 303.79 kg ha⁻¹ for seed yield, respectively. All these crosses also gave

high seed yield indicating that these crosses can be used for the breeding program. Percentages of heterosis were found for all characters studied. The highest heterosis and heterobeltiosis for seed yield were found in the cross between lines 2 × 5 (Qianyou 3A × Qianyou 8B) with the values of 78 and 59%, respectively. Seed yield gave significantly positive correlations with plant height (0.644), pods per plant (0.583), days to flowering (0.281) and days to maturity (0.341). Highly significant and negative correlation was observed between seed per plant and seed size (-0.533). Pods per plant, seeds per pod, 1,000-seed weight, and plant height showed high direct contributions to seed yield.

4.2 Introduction

Rapeseed (*Brassica napus* L.) is a widely grown oil seed crop in China. The area grown to this crop was 7 million hectares with the yield over 10 million tonnes in 2006-2007 (FAO Statistical Yearbook, 2008). China is the largest producer in both the planting area and total production of rapeseed. Among three main species of rapeseed, *Brassica napus* L. accounts for about 95% of total planting area in China (Wang et al., 2007). The seed was extracted for oil and the meal can be used as animal feed. Prior to 1985, pure lines were grown on a commercial scale. Until recently, more than 70% of planted areas are grown to hybrids (Zhou and Fu, 2007). Many research institutes in China have been working on the development of hybrid varieties to replace pure line cultivars.

In the breeding for hybrid varieties, sufficient information on inheritance of characters of plant materials to be used in the breeding program should be accumulated. These are general combining ability (GCA), specific combining ability

(SCA) and heterosis. Sprague and Tatum (1942) defined the term “general combining ability” (GCA) as the average performance of a line in hybrid combinations and the term “specific combining ability” (SCA) as the deviation of certain combinations which are either better or worse than would be expected on the average performance of the parent inbred lines involved. Variance due to GCA, estimates additive gene effect, includes additive genetic variance and additive $\times$ additive interaction variance, whereas, SCA is assumed to include non-additive genetic variance arising from dominance and epistatic deviations. Studies on combining ability in rapeseed have been made by many workers (Becker, 1999; Alizadeh, 2007; Ofori and Becker 2007).

Heterosis is generally due to non-additive gene action. This term was coined by Shull (1914) as a descriptive synonym for hybrid vigor. This is a phenomenon in which the performance of an F_1 hybrids produced from a cross between genetically distant parents is superior to their mid-parent value. It had been extended to include negative heterosis (Powers, 1944; Stern, 1948) and heterosis over high parent (Fonseca and Patterson, 1968). Heterosis for various characters in rapeseed has been reported by many workers (Sernyk and Stefansson, 1983; Grant and Beversdorf, 1985; Lefort-Buson et al., 1987; Brandle and McVetty, 1989; Anand, 1987; Shen et al., 2002; Prajapati et al., 2007; Starmer et al., 1998). However, the rates of heterosis for characters in rapeseed varied according to populations. Brandle and McVetty (1989) reported that heterosis of seed yield varied between hybrids being 20.3 to 120% over high yielding parents, while Sernyk and Stefansson (1983) reported in their rapeseed populations that heterosis of seed yield ranged from 7 to 64% over mid-parent. Shen et al. (2002) reported that mid-parent heterosis for oil content, pods per plant and 1,000 seed weight ranged from 1.55 to 7.44%, from -4.14 to 36.99% and from -16.37

to 10.34%, respectively.

For breeding of hybrid varieties in rapeseed, one of the most important materials is male sterile lines. This is because rapeseed is largely self-pollinated and androgynous crop (Rakow and Woods, 1987; Li, 1999) and it is difficult to obtain hybrid by emasculation. Therefore, use of male sterile system is the most practical method in the production rapeseed hybrid seeds. Male sterile line could be found in nature or may be induced by mutation. It can be transferred from one species or one cultivar to another by backcrossing. For example, Ogu CMS in rapeseed was transferred from a male sterile radish (Barnnrot et al., 1974). Pol CMS was found in a rapeseed variety named Polima (Fu et al., 1995). After the CMS system was found, several other systems of male sterility such as genetic male sterile (GMS), ecotype sensitive male sterile or environment sensitive male sterile (EMS), gametocide (GC) and self-incompatible (SI) systems were developed or reported (Yu and Hu, 2007).

Now male sterile system is widely used in the production of hybrid in rapeseed. The CMS system is the most popular system. However, in Guizhou province, China, genetic male sterile system (GMS) is more popular than cytoplasmic male sterile (CMS) system. The GMS lines used are of two types, recessive genetic male sterile (RGMS) and dominant genetic male sterile (DGMS). RGMS is more widely used than DGMS because RGMS has extensive restorers. Therefore, it is necessary that the inheritance of RGMS lines have to be thoroughly evaluated.

The objectives of this study were to evaluate the combining ability and heterosis of the RGMS lines of rapeseed (*Brassica napus* L.) for oil content, seed yield and other characters related to them and to find the correlations between characters.

4.3 Materials and Methods

4.3.1 Plant Materials

Plant materials used in this study consisted of ten recessive genetic male sterile lines (RGMS) with low erucic acid and glucosinolate contents and varied oil contents. These lines are shown with basic information in Table 4.1. These parents were planted in Sept. 2006 and crossed in a half diallel (Griffing, method 2) in spring 2007. At flowering, both male sterile and male fertile plants were identified and

Table 4.1 Designations, names and origins of rapeseed lines used producing single cross hybrids.

No.	Name	Prominent character	Origins
Line 1	IIAB	Medium flowering	Introduced from Sinan county, Guizhou province.
Line 2	Qianyou 3AB	Early flowering and maturity	Introduced from Yunan province.
Line 3	Qianyou 5AB	Low oil content and medium maturity	Introduced from Sinan county, Guizhou province.
Line 4	Qianyou 7AB	Medium maturity	Derived from a hybrid combination named youyan no. 7. in Guizhou.
Line 5	Qianyou 8AB	Yellow seedcoat, late flowering and maturity	Derived from a hybrid combination named You 1162 in Guizhou province
Line 6	You 2894AB	High oil content with yellow seed coat	Derived from a hybrid combination named Youyan no. 10 in Guizhou province
Line 7	Qianyou 6AB	Medium oil content and maturity	Derived from a hybrid variety named Shuza no. 6 in Shichuan province
Line 8	QH303-4AB	High oil content with yellow seedcoat	A mutation from a open-pollinated variety Youyan no.6
Line 9	You 157AB	High oil content	Derived from a hybrid combination named You 157 in Guizhou province
Line 10	You 2341AB	High oil content with yellow seedcoat and late maturity	Derived from a hybrid combination named You 2341 in Guizhou province

tagged. Flower buds of tagged plants were covered with white paper bags after bloomed flowers were cut away. Flowers of male sterile plants covered were pollinated with fresh pollen of male plants manually within three days after blooming and immature buds at the top of inflorescence were cut away. For each cross, plants with male sterile were pollinated by male fertile plants in all combinations including selfing. The pollinated flowers were covered back after pollination, and the paper bags were removed after 15 days. Four to five plants were pollinated for each cross. According to Griffing's method 2, forty five F_1 crosses and ten parents were obtained. Seeds were obtained by bulking of 4-5 plants in each cross.

4.3.2 Field Experiment

Experiment was carried out in a randomized complete block design with three replications at Guiyang, Guizhou, China, during Sept., 2007 to May, 2008. Plots consisted of two rows of 5-m in length with 45-cm inter-row and 33.3-cm intra-row spacings. Before planting, plots were prepared carefully and 600 kg ha⁻¹ N, P and K fertilizers and 15 kg ha⁻¹ borax were applied in hills. All the 45 crosses and 10 parents were planted in hills on 27 Sept., 2007, and thinned to two plants per hill within 45 days after planting. Each plot contained 60 plants. During growing period, the total amount of 375 kg ha⁻¹ urea was used by applying in hills for two times. Pesticide application was done three times, and weeding was made twice. Supplement irrigations were made as needed. The experiment was harvested from May 7 through May 19, 2008.

4.3.3 Data Collection

After blooming, ten plants, five male sterile and five male fertile, were selected randomly for each plot and tagged. At maturity, these ten tagged plants were

measured for plant height, branches per plant, pods per plant and seeds per pod. Means of these characters were used for analysis. One thousand seed weight was measured by using a bulk of seed from each plot. Days to flowering, days to maturity, and yield were based on plot observation. Oil content was analyzed by using open pollinated bulked seeds. Data for characters were recorded as follows:

Days to flowering (DF): Days from sowing until 50% of the plants flowered.

Days to maturity (DM): Days from sowing until 90% of the pods matured.

Branches per plant (B/P): Productive branches originating from the main stem.

Pods per plant (P/P): Productive pods borne on all branches of a plant.

Plant height (PH): Main stem length measured from the cotyledonary node to the top of the plant.

Seeds per pod (S/P): Seeds of twelve individual pods per plant, four each from bottom-, middle-, and top-borne branches.

1,000-seed weight (TSW): Weight of 1,000 seeds taken randomly, average of three samples.

$$\text{Seed yield (Yield): } Y = \frac{100 - X}{100 - Y_s} \times \text{F.W.} \times \frac{10,000}{A}$$

where Y = yield in kg ha^{-1} , X = moisture content (measured), Y_s = standard moisture content (9%), F.W. = harvested yield in kg plot^{-1} , A = area harvested (m^2).

Percentage of oil content (OC): Proportion of oil content from dried seeds determined by NIRS.

4.3.4 Statistical Analysis

Diallel analysis method of Griffing's approach Method II Model I

(1956) was used to analyze for the combining abilities and other parameters of the 10 male sterile lines and their crosses.

The mathematical model for combining ability analysis is as follows:

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{bc} \sum_k \sum_l e_{ijkl}$$

$$i, j = 1, 2, \dots, p; p = 10$$

$$k = 1, 2, \dots, b; b = 3$$

$$l = 1, 2, \dots, c; c = 1$$

where u is the population mean, $g_i(g_j)$ is the GCA effect, s_{ij} is the SCA effect such that

$s_{ij} = s_{ji}$, and $\frac{1}{bc} \sum_k \sum_l e_{ijkl}$ is the error effect to the $ijkl^{\text{th}}$ observation. i, j are numbers

of parents, k is number of replication, and l is number of observation.

The general combining ability (GCA) and specific combining ability (SCA) effects and their respective standard errors were estimated as follows:

$$\hat{g}_i = \frac{1}{p+2} [x_{i.} + x_{.i} - \frac{2}{p} x_{..}]$$

$$\hat{s}_{ij} = x_{ij} - \frac{1}{p+2} [x_{i.} + x_{.i} + x_{j.} + x_{.j}] + \frac{2}{(p+1)(p+2)} x_{..}$$

$$S.E.\hat{g}_i = \sqrt{\frac{(p-1)}{p(p+2)}} \hat{\sigma}^2$$

$$S.E.\hat{s}_{ij} = \sqrt{\frac{p^2 + p + 2}{(p+1)(p+2)}} \hat{\sigma}^2 \quad (i \neq j)$$

where $\hat{g}_i$ is GCA effect of i^{th} parent, p is the number of parent; $x_{i.}$ is the sum of means

in crosses with the same i parent; x_{ii} is the mean of i^{th} parent; $x_{..}$ is the grand mean of experiment; $\hat{s}_{ij}$ is the SCA effect for cross between i^{th} and j^{th} parents; x_{ij} is the mean of cross ij^{th} ; $x_{.j}$ is the sum of means in crosses with the same j parent; x_{jj} is the mean of j^{th} parent; S.E. $\hat{g}_i$ is the standard error of GCA effects; S.E. $\hat{s}_{ij}$ is the standard error of SCA effects; $\hat{\sigma}^2$ is the variance of error.

To evaluate the relative importance of additive and non-additive genetic effects for each character, the ratio of MSgca/MSsca was used.

Heterosis and heterobeltiosis were estimated as follows:

$$\text{Heterosis (\%)} = \frac{F_1 - \text{MP}}{\text{MP}} \times 100 \quad (\text{Shull, 1914})$$

$$\text{Heterobeltiosis (\%)} = \frac{F_1 - \text{HP}}{\text{HP}} \times 100 \quad (\text{Fonseca and Patterson, 1968})$$

where MP is the mean of two parents and HP is the value of the high parent.

Phenotypic correlation coefficients were calculated as follow:

$$r_{\text{ph}(xy)} = \frac{\text{Cov}_{(xy)}}{\sqrt{[V_{(x)}][V_{(y)}]}} \quad (\text{Stuber, 1970})$$

Path coefficient: Path analysis was used to partition correlations between characters and yield into direct and indirect effects of component traits toward the expression of yield. It was calculated by following equations:

$$P_{y.x_i} = \frac{\sigma_{x_i}}{\sigma_y} \quad (\text{Singh and Chaudhary, 1979})$$

where $P_{y.x_i}$ can be obtained from these equations by inversion of matrix:

$$\begin{aligned} r_{x_1y} &= P_1 + P_2 r_{x_1x_2} + P_3 r_{x_1x_3} + \dots + P_n r_{x_1x_n} \\ r_{x_2y} &= P_1 r_{x_2x_1} + P_2 + P_3 r_{x_2x_3} + \dots + P_n r_{x_2x_n} \\ r_{x_3y} &= P_1 r_{x_3x_1} + P_2 r_{x_3x_2} + P_3 + \dots + P_n r_{x_3x_n} \end{aligned}$$

where $P_{y.x_i}$ is the path coefficient from x_i to y ; σ_{x_i} is the standard deviation of the effect due to x_i ; σ_y is the total standard deviation of the effect y ; r is coefficient of correlation between two characters.

The analysis of data for GCA and SCA effects were made by using DPS 9.50 data processing system that copyright belonging to Tang Qiyi, China.

4.4 Results and Discussion

4.4.1 Growing Condition

Growing conditions during 2007-2008 were quite unfavorable for rapeseed. Early winter at Guiyang was quite dry and late winter was quite cold with long ice rain period during Jan 12, 2008 - Feb 4, 2008. The ice rain damaged early buds. Spring in 2008 was late, but the temperature was good for rapeseed pollination (Appendix: Attached figure 1 and 2). Therefore, seed yield was not much affected. However, due to the cold weather, the flowering and maturity periods of rapeseed were longer than usual.

4.4.2 Analyses of Variance and Performance of Hybrids

The results from analyses of variance shown in Table 4.2 were highly significant among treatments for all characters. Means of seed yield and other

characters are given in Table 4.3. Seed yield of hybrids ranged from 1,841 to 2,951 kg ha⁻¹ with the mean of 2,294 kg ha⁻¹. The highest yield of 2,951 kg ha⁻¹ was recorded in the cross of lines 5 × 6, followed by the crosses of lines 6 × 7 and lines 2 × 5, which yielded 2,817 and 2,782 kg ha⁻¹, respectively (Table 4.3). All hybrids performed better than their means of parents. The difference between the mean of hybrids and the mean of parents was 553 kg ha⁻¹.

Table 4.2 Mean squares from analysis of variance for nine characters of diallel cross involving 10 lines of rapeseed.

Sources of variation	df	Mean squares				
		Yield	P/P	S/P	TSW	B/P
Replications	2	253,611	24,757 **	4.63	0.15	2.60 *
Treatments	54	340,346 **	6,339 **	5.21 **	0.25 **	1.47 *
Error	108	84,111	2,490	2.03	0.05	0.34

Table 4.2 Continued.

Sources of variation	df	Mean squares			
		PH	DF	DM	OC
Replications	2	116.10 *	1.82	1.35	1.08
Treatments	54	222.59 **	14.72 **	20.39 **	11.43 **
Error	108	37.31	1.31	1.92	0.94

*, ** significant at 0.05 and 0.01 levels of probability, respectively.

Table 4.3 Means of nine characters of single cross hybrids of rapeseed.

Single cross hybrid	Yield	P/P	S/P	TSW	B/P	PH	DF	DM	OC
	kg ha ⁻¹	no.	no.	g	no.	cm	no.	no.	%
Line 1×2	1,981	456	17.9	3.65	8.4	154.4	173.3	231.3	36.6
3	2,405	422	17.5	4.06	7.3	173.3	174.3	231.7	38.0
4	2,379	454	17.1	3.62	7.5	173.3	174.0	231.7	36.2
5	2,330	406	16.6	3.63	6.4	163.7	173.0	232.0	37.9
6	2,504	554	18.8	3.25	7.6	172.8	174.7	234.0	36.7
7	2,371	426	18.2	3.35	7.2	175.7	174.3	232.0	36.5
8	2,573	472	20.1	3.58	7.6	175.7	174.3	232.7	39.2
9	2,138	442	15.1	3.63	7.4	163.3	172.7	230.7	38.9
10	2,172	433	18.6	3.43	7.3	170.6	174.7	234.3	38.5
Line 2×3	1,928	444	19.7	2.88	8.3	153.2	172.0	227.0	37.3
4	1,841	447	17.1	3.36	9.0	153.3	168.3	225.3	36.7
5	2,782	540	19.6	3.10	8.1	164.0	173.7	230.0	37.7
6	2,324	498	19.6	2.92	8.2	170.4	170.7	229.0	39.6
7	2,050	462	19.5	2.94	8.4	164.6	173.0	227.7	38.5
8	2,191	441	19.9	3.14	8.3	169.9	171.7	231.3	39.8
9	2,313	483	18.9	3.00	7.9	155.4	168.7	225.0	39.1
10	2,104	491	18.6	3.06	8.2	168.6	171.7	228.7	39.5
Line 3×4	2,155	452	17.0	3.58	7.6	163.7	173.7	229.0	35.6
5	2,503	473	18.6	3.33	7.1	174.7	175.0	231.7	35.4
6	2,235	472	17.4	3.71	6.9	170.0	173.7	231.7	38.5
7	2,243	467	17.2	3.53	7.8	163.2	172.3	228.0	36.2
8	2,103	372	18.8	3.64	6.9	179.2	174.3	232.7	39.4
9	2,079	401	18.7	3.55	7.9	162.8	172.0	227.0	37.9
10	2,235	416	15.4	4.00	7.3	180.8	172.7	233.3	38.9
Line 4×5	2,137	468	17.8	3.17	7.6	170.0	174.7	232.7	34.8
6	2,495	483	18.9	3.15	7.9	171.7	174.0	228.7	37.7
7	2,324	453	18.2	3.50	7.9	173.1	174.7	229.0	38.9
8	2,139	476	18.3	3.42	8.4	160.5	175.3	232.3	37.1
9	2,251	495	16.5	3.47	8.1	174.0	173.0	230.3	37.5
10	1,899	496	17.3	3.30	7.6	170.5	173.7	233.0	38.4
Line 5×6	2,951	518	18.3	3.36	7.2	177.5	174.3	232.3	40.3
7	2,661	438	20.0	3.46	6.9	182.6	175.0	233.3	39.1
8	2,683	531	19.3	3.33	7.3	173.4	175.0	234.0	39.6
9	2,117	449	18.9	3.29	7.3	176.2	176.0	233.0	40.3
10	2,001	465	17.2	3.18	7.1	174.1	176.3	234.3	39.9
Line 6×7	2,817	548	20.1	2.93	8.9	173.3	172.3	229.0	40.4
8	2,155	395	18.9	3.61	8.3	158.4	170.3	230.0	42.3
9	2,452	508	15.3	3.59	7.9	175.9	174.3	231.7	40.9
10	2,518	462	17.2	3.58	8.1	174.5	174.3	233.0	42.2
Line 7×8	1,913	428	16.2	3.49	8.3	170.2	175.0	233.7	39.6
9	2,493	496	16.9	3.90	8.6	165.6	172.7	232.0	40.4
10	2,587	490	19.0	3.45	8.9	178.2	174.7	233.3	39.8
Line 8×9	2,259	496	19.3	2.94	8.1	171.7	174.7	230.7	42.4
10	2,151	488	17.8	3.34	8.3	165.8	173.0	233.0	42.5
Line 9×10	2,303	546	18.6	3.30	8.9	172.8	172.7	232.3	41.8
LSD 0.05	470	81	2.3	0.37	0.9	9.9	1.9	2.2	1.6
LSD 0.01	622	107	3.1	0.48	1.2	13.1	2.5	3.0	2.1
Mean of hybrids	2,294	468	18.1	3.39	7.8	169.5	173.4	231.1	38.8
Mean of parents	1,741	421	17.8	3.15	8.3	157.7	172.1	229.3	38.8

All yield component traits were highly significant (Table 4.2). Pods per plant of single crosses ranged from 372 to 554 pods with the mean of 468 pods. The highest pod number was found in the cross between line 1 $\times$ line 6 which produced 554 pods per plant, and followed by the crosses of line 6 $\times$ line 7 (548 P/P) and line 9 $\times$ line 10 (546 P/P) (Table 4.3). Difference between the mean of hybrids and the mean of parents was 47 pods per plant.

The range of seeds per pod for single crosses was found to be between 15.1 and 20.1 seeds pod⁻¹, and the mean was 18.1 seeds pod⁻¹. The highest seeds per pod was detected in the crosses of line 1 $\times$ line 8 and line 6 $\times$ line 7, both giving 20.1 seeds pod⁻¹ (Table 4.3). Seed size of single crosses as measured by 1,000-seed (TS) weight ranged from 2.92 to 4.06 g TS⁻¹ with the mean of 3.39 g TS⁻¹. The largest seed was found in the single cross of line 1 $\times$ line 3 which was 4.06 g TS⁻¹, and followed by the crosses of lines 3 $\times$ 10 and lines 7 $\times$ 9 which were 4.00 and 3.90 g TS⁻¹, respectively (Table 4.3). Branches per plant, an agronomic yield related trait, was found to range from 6.4 to 9.0 branches per plant with the mean was 7.8 branches per plant. The highest branches per plant was found in the cross of line 2 $\times$ line 4, followed by the crosses of line 6 $\times$ line 7 and line 7 $\times$ line 10 (Table 4.3).

Plant height of rapeseed is an important agronomic character related to seed yield. It was found that the range of single crosses for this character was from 153.2 to 182.6cm with the mean of 169.5cm. The highest plant height was measured in the cross of line 5 $\times$ line 7, followed by the crosses of line 3 $\times$ line 10 and line 3 $\times$ line 8. The lowest plant height was measured in the cross of line 2 $\times$ line 3, and followed by line 2 $\times$ line 4 and line 1 $\times$ line 2 crosses (Table 4.3).

Days to flowering and days to maturity, the indicators of early and late

maturity, are being important characters in our breeding program of rapeseed. It was found that the cross of line 5 $\times$ line 10 expressed the longest days to flowering (176.3 days), while the shortest was expressed by the cross of line 2 $\times$ line 4 (168.3 days). The range of days to maturity of 45 crosses was between 225 and 234.3 days, and the mean was 231.1 days. The longest days to maturity was recorded in the crosses of line 5 $\times$ line 10 and line 1 $\times$ line 10, followed by line 5 $\times$ line 8 cross. The shortest days to maturity expressed by the cross of line 2 $\times$ line 9, followed by line 2 $\times$ line 4 cross (Table 4.3).

Oil content, an important character related to rapeseed quality, ranged from 34.8 to 42.5% with the mean of 38.8% for single crosses. The highest oil content was found in the cross of line 8 $\times$ line 10, followed by the crosses of line 8 $\times$ line 9, line 6 $\times$ line 8 and line 6 $\times$ line 10, which gave oil content of 42.4, 42.3 and 42.2%, respectively (Table 4.3).

In this study, analyses of variance showed highly significant among treatments for all characters. This showed the existence of some degrees of diversity among hybrids and parents. The means of single crosses for all characters except branches per plant and oil content were higher than the respective means of parents indicating some degrees of heterosis for these characters. The difference in seed yield between the mean of hybrids and the mean of parents was larger, indicating the high degree of heterosis in this trait. The mean of branches per plant for hybrids was smaller than the mean of parents, indicating the negative heterosis of this trait.

In this study, the top five single crosses of lines 5 $\times$ 6, 6 $\times$ 7, 2 $\times$ 5, 5 $\times$ 8 and 5 $\times$ 7 gave high seed yield. The crosses of lines 8 $\times$ 10, 8 $\times$ 9, 6 $\times$ 8 and 6 $\times$ 10 gave high oil content. It was found that the highest yielder did not give high oil

content. This situation was also found by Shen et al. (2002) who reported that the F_1 hybrids of SI-1310 $\times$ Dunkecl, SI-1310 $\times$ SW9372561 and SI-1310 $\times$ Eagle gave high seed oil content, while F_1 hybrids SI-1300 $\times$ SW9372561, SI-1310 $\times$ SW9473754 and SI-1300 $\times$ SW9375645 gave high seed yield per plant. Therefore, the improvement of component lines of hybrid for seed yield and oil content should be made in separate breeding programs and these lines can be combined into a hybrid.

4.4.3 GCA Effects

The results for analyses of variance for general combining ability (GCA) and specific combining ability (SCA) are presented in Table 4.4. The analyses indicated that both GCA and SCA variances were highly significant ($P < 0.01$), which suggested that both additive and non-additive gene effects were important for the expression of all characters. The relative importance of GCA and SCA was judged from the ratio of mean squares GCA to SCA which helped to indicate the predominant presence of either additive or non-additive effects. The ratios showed that additive gene action was predominant for all characters. These ratios for seed yield (1.48), pods per plant (1.92), seeds per pod (2.25) and plant height (2.44) were quite low, but very high for certain characters such as oil content (20.70).

Table 4.4 Mean squares for general combining ability (GCA) effects and specific combining ability (SCA) effects of nine characters of diallel crosses of rapeseed involving 10 parents.

Sources of Variation	df [‡]	Mean squares				
		Yield	P/P	S/P	TSW	B/P
GCA	9	155,548 **	3,514**	3.24**	0.20**	1.78 **
SCA	45	105,029 **	1,833**	1.44*	0.06**	0.23 **
Error	108	28,037	830	0.68	0.02	0.11
MSgca/MSsca		1.48	1.92	2.25	3.33	7.74

Table 4.4 Continued

Sources of Variation	df	Mean squares			
		PH	DF	DM	OC
GCA	9	145.98 **	16.96**	27.67**	18.42**
SCA	45	59.84 **	2.50**	2.62**	0.89**
Error	108	12.44	0.44	0.64	0.31
MSgca/MSsca		2.44	6.78	10.56	20.70

*, ** significant at 0.05 and 0.01 levels of probability, respectively.

‡ df = degree of freedom; OC = oil content; P/P = pods per plant; S/P = seeds per pod; TSW = 1,000-seed weight; B/P = branches per plant; DF = days to flowering; DM = days to maturity; PH = plant height.

Table 4.5 Estimates of general combining ability (GCA) effects for nine characters of rapeseed lines.

Lines	Yield	OC	P/P	S/P	TSW
Line 1	-43.52	-1.01 **	-15.32	-0.22	0.141 **
Line 2	-155.97 **	-0.60 **	-0.77	0.82 **	-0.292 **
Line 3	-82.57	-1.35 **	-30.63 **	-0.27	0.183 **
Line 4	-74.10	-1.59 **	5.56	-0.55 *	0.020
Line 5	127.65 **	-0.83 **	-7.90	0.70 **	-0.091 *
Line 6	230.94 **	0.99 **	24.84 **	-0.07	-0.000
Line 7	35.50	0.05	-2.34	0.11	0.013
Line 8	-32.91	1.62 **	-9.51	0.38	-0.008
Line 9	52.94	1.20 **	16.46 *	-0.27	0.004
Line 10	-57.96	1.53 **	19.62 *	-0.77 **	0.030
LSD 0.05	90.98	0.30	15.65	0.45	0.071
LSD 0.01	120.40	0.40	20.72	0.59	0.094

Table 4.5 Continued.

Lines	B/P	PH	DF	DM
Line 1	-0.48 **	0.23	0.52 **	0.88 **
Line 2	0.59 **	-8.28 **	-2.46 **	-3.09 **
Line 3	-0.23 *	-1.78	-0.21	-1.09 **
Line 4	0.03	-0.08	0.35	-0.43
Line 5	-0.74 **	3.82 **	2.16 **	2.02 **
Line 6	0.09	1.94 *	-0.32	0.02
Line 7	0.09	0.61	0.24	-0.26
Line 8	0.23 *	-0.05	-0.51 **	0.82 **
Line 9	0.20 *	-0.71	-0.65 **	-0.76 **
Line 10	0.23 *	4.29 **	0.88 **	1.96 **
LSD 0.05	0.18	1.92	0.36	0.44
LSD 0.01	0.24	2.54	0.47	0.58

*, ** significant at 0.05 and 0.01 levels of probability, respectively.

Highly significant GCA effects for seed yield were found for three RGMS lines. They were lines 5 and 6 with positive GCA effects of 230.94 and 127.65 kg ha⁻¹, and line 2 with negative GCA effects (Table 4.5), respectively. Although other lines were not significant, positive GCA effects were found in lines 7 and 9. The GCA effects of the parents were found to associate with mean of crosses. These results indicated that line 5, line 6, and their crosses should give good yield performance, and, in contrast, line 2 and its crosses should give poor yield performance.

The highly significant GCA effects for oil content (OC) were found for all RGMS lines except line 7. Among them, lines 6, 8, 9 and 10 gave significantly positive GCA effects of 0.99, 1.62, 1.20 and 1.53% while lines 1, 2, 3, 4 and 5 gave significantly negative GCA effects (Table 4.5). The results showed that lines 6, 8, 9, 10 and their crosses should give good oil content.

Among the 10 RGMS lines, the significantly negative GCA effects for pods per plant (P/P) were found for line 3 and positive GCA effects for lines 6, 9 and 10, while no significant GCA effects were found for all other lines (Table 4.5). The results indicated that line 6, line 9, line 10 and their crosses gave more pods per plant.

Lines 2 and 5 gave significantly positive GCA effects for seeds per pod (S/P) at $P < 0.01$, while lines 4 and 10 gave significantly negative GCA effects for the same character at $P < 0.05$ and $P < 0.01$, respectively. Other lines were not significant for GCA effects for seeds per pod (Table 4.5).

For 1,000-seed weight, lines 1 and 3 showed significantly positive GCA effects at $P < 0.01$, while lines 2 and 5 gave significantly negative GCA effects at $P < 0.01$ and $P < 0.05$, respectively. No significant GCA effects were found for other lines (Table 4.5). The results indicated that lines 1, 3 and their crosses gave good

performance for 1,000-seed weight.

For branches per plant (B/P), significant GCA effects were found for all lines except lines 4, 6 and 7. Among them, lines 2, 8, 9 and 10 gave positive GCA effects, while lines 1, 3 and 5 gave negative GCA effects (Table 4.5). This indicated that lines 2, 8, 9, 10 and their crosses had more branches than others.

Significantly positive GCA effects for plant height were found for lines 5, 6 and 10, while significantly negative GCA effect was found for line 2. The results showed that line 2 should be good for breeding for short varieties, and lines 5, 6 and 10 were good for tall varieties.

Lines 1, 5 and 10 expressed significantly positive GCA effects for days to flowering (DF), while lines 2, 8 and 9 gave significantly negative GCA effects for this character. Similar results were found for days to maturity (DM). Lines 1, 5, 8 and 10 gave significantly positive GCA effects, while lines 2, 3 and 9 gave significantly negative GCA effects (Table 4.5). Significantly positive GCA effects for these two characters indicated that these lines were good for late flowering and maturity. On the other hand, significantly negative GCA effects were suitable for breeding for early flowering and maturity.

The analyses of variance for GCA and SCA indicated that both GCA and SCA were important for all characters studied in this experiment. However, the ratios of MS_{gca}/MS_{sca} indicated that additive gene effects are more important than non-additive gene effects. The small ratios of MS_{gca} to MS_{sca} for seed yield and pods per plant may indicate the high heterosis of these characters because heterosis relates proportionally to non-additive gene actions.

The analyses of GCA did not show that any single line was a high

general combiner for all characters simultaneously. Outstanding lines such as line 6 gave significant GCA estimates for seed yield, oil content, pods per plant and plant height should be favourable for any breeding program. Moreover, most of the crosses involving line 6 were good yielders. Therefore, it was the best choice for breeding of rapeseed hybrids. However, line 5 was a good combiner for seed yield. It gave significant GCA effects and some of its crosses expressed high yield. Though line 2 was not a good combiner for seed yield, it was good for short plant height, early flowering and early maturity, and its cross sometimes also could result in high yield as the cross lines 2×5 . It can be used in breeding program for short plant height and early maturity.

4.4.4 SCA Effects

Estimates of SCA effects for seed yield were positively significant in seven crosses as shown in Table 4.6. The large magnitude of SCA values indicated that lines used in these crosses were of more diverse in seed yield than other crosses, and may be developed to be candidate hybrid varieties. Crosses between lines 5×6 , 6×7 , 2×5 and 5×8 which gave significant SCA effects were also high yielders among other crosses.

Significantly positive SCA effects for oil content were found in six crosses (Table 4.6). The cross of lines 4×7 showed the highest positive SCA effect for this character; however, the mean oil content of this cross given in Table 4.3 was not the highest. However, this combination could be used for line improvement or in case that the level of seed yield is acceptable.

Table 4.6 Estimates of specific combining ability (SCA) effects for nine characters of rapeseed crosses.

Characters		Crosses								
		Line 2	Line 3	Line 4	Line 5	Line 6	Line 7	Line 8	Line 9	Line 10
Yield	Line 1	-12.95	337.04 *	303.03	52.47	123.22	185.66	455.73**	-64.92	79.58
	Line 2		-27.23	-122.32	616.29**	54.96	-22.73	186.59	222.24	124.18
	Line 3			117.69	264.03	-106.83	96.19	25.11	-84.67	181.94
	Line 4				-110.40	144.59	169.17	52.21	78.16	-162.96
	Line 5					398.71 *	303.79	394.24*	-257.75	-262.30
	Line 6	LSD 0.05	306.00				356.48 *	-237.19	-25.44	151.13
	Line 7	LSD 0.01	404.96					-283.12	210.60	415.65 **
	Line 8								44.91	48.67
	Line 9									114.14
Oil content	Line 1	-0.53	1.60**	0.02	1.02 *	-2.07 **	-1.30 *	-0.20	-0.04	-0.82
	Line 2		0.46	0.12	0.34	0.41	0.32	0.07	-0.29	-0.22
	Line 3			-0.24	-1.14 *	0.05	-1.22 *	0.42	-0.72	-0.06
	Line 4				-1.56**	-0.48	1.66 **	-1.67**	-0.92	-0.28
	Line 5					1.33 *	1.16 *	0.03	1.14*	0.42
	Line 6	LSD 0.05	1.02				0.55	0.98	-0.08	0.86
	Line 7	LSD 0.01	1.35					-0.79	0.43	-0.58
	Line 8								0.78	0.62
	Line 9									0.29
Pod plant ⁻¹	Line 1	12.46	8.26	4.13	-30.17	85.45 **	-15.34	37.80	-18.33	-30.29
	Line 2		15.77	-16.99	88.97**	14.97	5.91	-8.09	7.81	13.05
	Line 3			17.31	52.27	18.30	40.37	-47.53	-44.56	-32.12
	Line 4				11.05	-6.86	-9.35	20.62	13.65	11.03
	Line 5					41.37	-11.52	89.18**	-19.48	-6.21
	Line 6	LSD 0.05	52.65				65.57 *	-79.90**	6.94	-41.42
	Line 7	LSD 0.01	69.68					-19.12	22.02	13.66
	Line 8								29.85	18.03
	Line 9									50.60
Seed pod ⁻¹	Line 1	-0.75	-0.06	-0.23	-2.00**	0.89	0.27	1.89*	-2.44**	1.52 *
	Line 2		1.11	-1.26	-0.03	0.60	0.52	0.64	0.30	0.48
	Line 3			-0.25	0.05	-0.44	-0.76	0.59	1.20	-1.61 *
	Line 4				-0.46	1.27	0.53	0.44	-0.76	0.56
	Line 5					-0.52	1.12	0.15	0.42	-0.79
	Line 6	LSD 0.05	1.50				1.89 *	0.40	-2.62**	-0.20
	Line 7	LSD 0.01	1.99					-2.37**	-0.97	1.55 *
	Line 8								1.08	0.15
	Line 9									1.55 *

*, ** significant at 0.05 and 0.01 levels of probability, respectively.

Table 4.6 Continued

Characters		Crosses								
		Line 2	Line 3	Line 4	Line 5	Line 6	Line 7	Line 8	Line 9	Line 10
1000-seed weight	Line 1	0.45 **	0.39**	0.11	0.23	-0.24 *	-0.15	0.10	0.13	-0.09
	Line 2		-0.36**	0.28 *	0.13	-0.13	-0.13	0.09	-0.06	-0.03
	Line 3			0.03	-0.11	0.17	-0.01	0.12	0.01	0.43**
	Line 4				-0.11	-0.22	0.11	0.06	0.10	-0.10
	Line 5					0.10	0.19	0.08	0.02	-0.11
	Line 6	LSD 0.05	0.24				-0.44 **	0.26 *	0.24*	0.20
	Line 7	LSD 0.01	0.32					0.14	0.53**	0.06
	Line 8								-0.40**	-0.04
	Line 9									-0.08
Branches plant ⁻¹	Line 1	0.35	0.10	0.08	-0.32	0.05	-0.32	-0.06	-0.22	-0.32
	Line 2		0.00	0.51	0.38	-0.35	-0.15	-0.39	-0.79*	-0.53
	Line 3			-0.14	0.19	-0.83 **	0.06	-1.01**	0.02	-0.64*
	Line 4				0.44	-0.09	-0.10	0.27	-0.03	-0.60
	Line 5					-0.09	-0.33	-0.13	-0.10	-0.30
	Line 6	LSD 0.05	0.61				0.84 **	0.04	-0.33	-0.13
	Line 7	LSD 0.01	0.81					0.04	0.37	0.70 *
	Line 8								-0.24	-0.10
	Line 9									0.60
Plant height	Line 1	-4.85	7.48 *	5.78	-7.66	3.26	7.49 *	8.15 *	-3.59	-1.22
	Line 2		-4.04	-5.67	1.16	9.41 **	4.97	10.89**	-2.94	5.22
	Line 3			-1.74	5.35	2.54	-2.93	13.66**	-2.04	10.95**
	Line 4				-1.04	2.47	5.24	-6.67*	7.46*	-1.08
	Line 5					4.40	10.80 **	2.25	5.75	-1.38
	Line 6	LSD 0.05	6.44				3.45	-10.80**	7.30*	0.93
	Line 7	LSD 0.01	8.53					2.33	-1.67	5.96
	Line 8								5.16	-5.75
	Line 9									1.85
Days to flowering	Line 1	2.08*	0.83	-0.06	-2.87	1.27 *	0.38	1.13	-0.39	0.08
	Line 2		1.47 *	-2.76**	0.77	0.24	2.02 **	1.44*	-1.42*	0.05
	Line 3			0.33	-0.14	0.99	-0.89	1.86**	-0.34	-1.20
	Line 4				-1.03	0.77	0.88	2.30**	0.11	-0.76
	Line 5					-0.70	-0.59	0.16	1.30*	0.11
	Line 6	LSD 0.05	1.21				-0.78	-2.03**	2.11**	0.58
	Line 7	LSD 0.01	1.60					2.08**	-0.12	0.36
	Line 8								2.63**	-0.56
	Line 9									-0.76
Days to maturity	Line 1	2.78*	1.11	0.45	-1.66 *	2.34 *	0.61	0.20	-0.22	0.78
	Line 2		0.42	-1.91 *	0.31	1.31	0.25	2.84**	-1.91 *	-0.91
	Line 3			-0.25	-0.03	1.97 *	-1.41	2.17**	-1.91 *	1.75*
	Line 4				0.31	-1.69 *	-1.08	1.17	0.75	0.75
	Line 5					-0.47	0.81	0.39	0.97	-0.36
	Line 6	LSD 0.05	1.46				-1.53 *	-1.61 *	1.64*	0.31
	Line 7	LSD 0.01	1.93					2.34**	2.25**	0.92
	Line 8								-0.16	-0.50
	Line 9									0.42

*, ** significant at 0.05 and 0.01 levels of probability, respectively.

Significantly positive SCA effects were found for pods per plant in four crosses (Table 4.6). Crosses between lines 1×6 , 2×5 , 5×8 and 6×7 gave highly significant SCA effects. These crosses also gave high means of pods per plant (Table 4.3). This character is associated with seed yield; therefore it was usually found in high yield lines and crosses.

Significantly positive SCA effects of seeds per pod were found in five crosses. The highest SCA effect was found in the cross between lines 1×8 (Table 4.6) which also showed the highest seeds per pod (Table 4.3).

Estimates effects of SCA were found significant for seed size (TSW). Among 11 crosses, 7 showed positive values. The highest SCA effect was found in the cross between lines 7×9 (Table 4.6) which seed size was also significantly larger than others (Table 4.3).

Significantly positive SCA effects for branches per plant were found in two crosses. The highest SCA effect was found in the cross between lines 6×7 (Table 4.6) which also showed high branches per plants (Table 4.3).

For plant height, ten crosses gave significantly positive SCA effects and three crosses gave significantly negative SCA effects (Table 4.6). The highest positive value was found in the cross of lines 3×10 which also gave high plant height (Table 4.3). The maximum value of negative SCA effect was found in the cross between lines 6×8 which also gave relatively lower plant height. The results indicate that crosses with significantly positive and negative SCA effects were good for developing respective tall and short hybrids.

For days to flowering, eleven crosses gave significantly positive SCA effects, four crosses gave significantly negative SCA effects (Table 4.6). The highest

positive value was found in the cross of lines 8×9 . The maximum value of negative was found in the cross between lines 1×5 . For days to maturity, significantly positive SCA effects were detected in nine crosses, while significantly negative SCA effects were found in eight crosses (Table 4.6). The highest positive value was found in the cross of lines 2×8 . The maximum value of negative SCA effect was found in the cross between lines 4×6 . The results indicated that crosses with significantly positive SCA effects were good for developing late hybrids, while crosses with significantly negative SCA effects were good for developing early hybrids.

Analysis of specific combining ability in this study revealed that a number of crosses showed significant SCA effects for each character, but none showed the best SCA effects simultaneously. Cross lines 5×6 gave the highest seed yield and also gave significant SCA effect for this character which indicated that it should be the best hybrid for seed yield. Cross lines 2×5 gave the highest SCA effect, the yield was also high, should be the second choice for seed yield. The highest and positive SCA effect for oil content was found in the cross of lines 4×7 , which gave oil content of 38.9%. This indicates that the magnitude of SCA effect may not correspond to the expression of the character.

Most crosses with significant SCA effects for seed yield also showed significant SCA effects for yield related traits. For example, crosses lines 2×5 , 6×7 and 5×8 also showed significant SCA effects for pods per plant. Crosses lines 1×8 , 7×10 and 6×7 also showed significant SCA effects for seeds per pod. Cross lines 1×3 also showed significant SCA effects for 1,000-seed weight. These indicate that there are some relationships between the magnitude of SCA effects for seed yield and that of yield related traits.

Parents of some crosses with high SCA effects were both negative, or one negative and one positive, or both positive in GCA effects. These indicated that high SCA effects could be resulted from any parents with high or low GCA effects. This result was not agreed with the report of Sheikh et al. (1998) who found that high SCA effects of crosses in *Brassica juncea* were resulted from high GCA effects parents crossed with low GCA effects parents.

The crosses of lines 2×9 and 2×4 showed significantly negative SCA effects, and both crosses gave the shortest days to flowering and days to maturity. This indicates that these two crosses can be used for improving early flowering and early maturity lines.

4.4.5 Heterosis and Heterobeltiosis

Percentages heterosis and heterobeltiosis of single cross hybrids for all characters are presented in Tables 4.7 and 4.8, respectively. All single crosses gave better seed yield than the mean of their parents. This indicates the existence of dominance or non-additive gene actions. The heterosis for seed yield of single crosses ranged from 7 to 78% with the mean of 32.8% (Table 4.7). Out of 45 crosses, 26 crosses gave significantly positive heterosis. The highest heterosis for seed yield was found in the cross between lines 2×5 which also gave relatively high seed yield of 2,782 kg ha⁻¹ (Table 4.3) and the highest SCA effect for seed yield (Table 4.6). The heterobeltiosis of single crosses for seed yield ranged from -5 to 59% with the mean of 21.6% (Table 4.8). From these, eighteen out of 40 crosses showed significantly positive heterobeltiosis. The highest heterobeltiosis was expressed by the cross of lines 2×5 .

Table 4.7 Heterosis of single cross hybrids involving 10 lines of rapeseed.

Single cross hybrids	Yield	OC	P/P	S/P	TSW	B/P	PH	DF	DM
Line 1×2	44 *	-2.5	15.0	-3.2	25.4 **	-0.6	1.5	2.2 **	2.3 **
3	60 **	2.2	7.4	-2.0	24.0 **	-8.2	12.0 **	1.3 *	1.6 **
4	49 **	-3.7	6.8	-2.8	12.6 *	-0.7	6.6 *	0.3	0.7
5	49 **	3.0	10.0	-14.0 *	18.4 **	-7.9	0.6	-1.7 **	0.0
6	39 **	-5.8 **	29.0 **	5.3	-0.8	-3.8	8.0 *	1.5 **	2.0 **
7	62 **	-4.7 *	5.1	2.5	4.7	-2.7	13.0 **	1.1	1.3 **
8	63 **	-1.8	14.8	13.2 *	13.7 *	-7.9	10.5 *	2.3 **	1.5 **
9	20	-1.3	1.6	-17.9 **	15.4 **	-7.5	2.8	0.6	0.8
10	40 *	-3.3	-4.1	12.7	6.4	-10.4 *	3.8	0.1	1.4 **
Line 2×3	29	1.2	14.6	7.9	-4.5	-8.8	4.6	1.9 **	1.0 *
4	16	-1.5	6.6	-5.0	13.7	3.4	-0.6	-1.1 *	-0.7
5	78 **	3.4	48.6 **	-0.5	10.5	0.0	6.2	0.6	0.5
6	29 *	2.6	17.5	7.4	-3.2	-9.4 *	12.3 **	1.1 **	1.2 *
7	40 *	1.4	15.5	7.4	0.0	-1.8	11.8 **	2.3 **	0.8
8	39 *	0.6	8.8	9.6	8.7	-11.7 *	12.8 **	2.8 **	2.4 **
9	30 *	0.1	12.5	0.5	4.0	-13.7 **	3.3	0.2	-0.3
10	36 *	0.1	10.1	10.1	3.2	-11.8 *	8.1 *	0.3	0.3
Line 3×4	25	-3.5	8.7	-2.0	7.8	-7.3	4.3	0.6	0.1
5	48 **	-1.9	31.4 **	-2.4	5.0	-6.6	11.1 **	-0.1	0.4
6	16	0.7	12.2	-1.1	9.8	-19.3 **	10.1 **	1.4 **	1.5 **
7	41 **	-3.7	17.8	-1.7	6.8	-3.1	8.8 **	0.4	0.1
8	23	0.5	-7.5	7.4	11.8 *	-22.5 **	16.8 **	2.9 **	2.1 **
9	9	-2.1	-5.9	3.0	9.2	-8.7	6.2	0.7	-0.2
10	33 *	-0.5	-6.0	-5.2	20.1 **	-17.0 **	13.9 **	-0.6	1.5 **
Line 4×5	20	-4.7 *	19.4	-5.3	1.9	5.6	3.0	-1.0	0.0
6	24 *	-2.5	6.7	8.9	-5.1	-3.1	5.8	0.8	-0.7
7	38 **	2.4	5.7	5.5	7.9	3.3	9.7 **	1.0	-0.3
8	19	-6.3 **	9.7	6.1	7.0	-1.2	-0.4	2.6 **	1.1 *
9	13	-4.1 *	8.1	-7.8	8.8	-1.8	8.0 *	0.5	0.4
10	7	-2.8	4.5	8.1	0.9	-9.5	2.4	-0.8	0.5
Line 5×6	48 **	6.5 **	30.6 **	-3.9	6.0	-4.6	9.3 **	-0.5	0.1
7	61 **	5.1 *	17.6	5.5	11.8	-2.1	15.6 **	-0.3	0.7
8	52 **	2.1	40.5 **	1.8	9.4	-7.6	7.4 *	1.0	0.9 *
9	8	5.2 *	11.4	-3.6	8.2	-4.6	9.3 **	0.8	0.6
10	15	3.1	11.1	-2.8	1.9	-9.0	4.4	-0.7	0.2
Line 6×7	49 **	2.7	26.3 **	14.9 *	-11.3 *	11.3 *	11.7 **	0.4	-0.1
8	7	3.3	-9.9	8.0	10.9	-6.2	-0.2	0.5	0.3
9	11	1.1	9.8	-15.7 *	10.5	-8.1	11.0 **	2.1 **	1.2 *
10	27 *	3.3	-3.5	5.8	7.5	-7.4	6.4 *	0.4	0.7
Line 7×8	15	-1.7	3.3	-6.9	9.7	-0.6	10.4 **	3.0 **	2.1 **
9	34 **	1.5	13.1	-6.4	22.8 **	6.2	7.5 *	0.9	1.5 **
10	58 **	-1.0	7.7	17.6 *	6.0	7.9	11.8 **	0.4	1.1 *
Line 8×9	14	2.4	11.7	6.9	-5.9	-9.5 *	9.1 **	3.4 **	0.9
10	22	1.7	6.0	10.2	4.2	-8.8	1.8	0.7	0.9
Line 9×10	18	1.2	12.7	10.7	3.1	0.6	6.2 *	-0.3	0.7
Mean	32.8	0.0	11.4	1.9	7.5	-5.3	7.5	0.8	0.8

*, ** significant difference from mid-parent at 0.05 and 0.01 levels of probability.

Table 4.8 Heterobeltiosis of single cross hybrids involving 10 lines of rapeseed.

Single cross hybrids	Yield	OC	P/P	S/P	TSW	B/P	PH	DF	DM
Line 1×2	44 *	-3.4	13.4	-5.3	15.1 **	-12.5 **	-3.7	0.2	0.9
3	48 **	0.3	5.0	-3.3	20.1 **	-15.1 **	8.0 *	0.8	1.0
4	31 *	-4.5 *	1.3	-5.5	11.0	-3.8	5.2	0.0	1.0
5	33 *	0.0	1.0	-19.0 **	14.5 *	-12.3 *	-0.9	-3.4 **	-1.2 *
6	12	-8.2 **	21.2 *	3.9	-3.8	-10.6 *	7.7 *	1.0	1.9 **
7	53 **	-5.7 **	4.2	0.6	3.7	-4.0	9.5 **	0.8	1.2 *
8	44 **	-6.4 **	12.4	11.0	12.9 *	-17.4 **	9.5 **	0.8	1.5 **
9	-2	-4.9 *	-5.6	-19.3 **	14.5 *	-14.9 **	1.8	-0.2	0.6
10	25 *	-7.7 **	-13.6	2.8	4.6	-18.9 **	1.4	-0.8	0.6
Line 2×3	19	0.3	13.6	4.2	-14.8	-13.5 **	2.7	0.4	0.1
4	2	-1.6	-0.2	-9.5	3.1	-6.3	-7.0 *	-3.3 **	-2.3 **
5	59 **	1.3	38.1 **	-4.4	4.7	-15.6 **	-0.7	-3.0 **	-2.0 **
6	4	-1.0	9.0	3.7	-13.6 *	-14.6 **	6.7 *	-0.4	-0.3
7	32 *	-0.5	13.0	3.2	-9.0	-12.5 **	9.2 **	0.6	-0.5
8	23	-5.0 **	5.0	5.3	0.3	-13.5 **	7.8 *	2.4 **	1.0 *
9	6	-4.4 *	3.2	0.0	-3.8	-17.7 **	-1.2	-1.0	-1.4 **
10	21	-5.3 **	-2.0	-1.6	-6.7	-14.6 **	0.2	-2.5 **	-1.9 **
Line 3×4	19	-4.6 *	0.9	-3.4	5.9	-11.6 *	-0.7	-0.2	-0.7
5	43 **	-3.0	23.2 *	-9.3	-1.5	-17.4 **	5.8	-2.2 **	-1.3 **
6	0	-3.8	3.3	-1.1	9.8	-19.8 **	6.4 *	1.4 *	0.9
7	38 *	-6.5 **	14.2	-2.3	4.4	-9.3	8.3 *	0.2	-0.3
8	18	-6.0 **	-11.4	6.8	7.7	-25.0 **	13.7 **	1.8 **	1.6 **
9	-5	-7.3 **	-14.3	0.0	5.0	-9.2	3.5	0.4	-0.6
10	29 *	-6.7 **	-17.0 *	-12.5	18.3 **	-18.9 **	7.5 *	-1.9 **	0.1
Line 4×5	18	-6.7 **	4.5	-13.2 *	-2.8	-2.6	2.9	-2.4 **	-0.9
6	12	-5.7 **	5.7	7.4	-6.8	-7.1	4.2	0.0	-0.9
7	28 *	0.5	1.1	4.6	7.4	1.3	5.0	0.4	-0.7
8	18	-11.5 **	6.3	5.2	4.9	-8.7	-2.6	0.8	0.7
9	3	-8.3 **	5.8	-11.8	6.4	-6.9	5.6	-0.6	-0.2
10	5	-7.9 **	-1.0	1.2	0.6	-15.6 **	1.4	-1.3 *	0.0
Line 5×6	33 **	0.7	13.3	-10.7	-0.6	-15.3 **	7.4 *	-2.6 **	-1.0 *
7	52 **	1.0	7.1	-2.4	7.1	-8.0	10.5 **	-2.2 **	-0.6
8	50 **	-5.5 **	26.4 **	-5.9	6.4	-20.7 **	5.0	-2.2 **	-0.3
9	-3	-1.5	-4.3	-7.8	5.4	-16.1 **	6.7 *	-1.7 **	-0.7
10	14	-4.3 *	-7.2	-16.1 **	-3.0	-21.1 **	3.5	-1.5 **	-0.2
Line 6×7	27 *	1.0	19.7 *	14.2 *	-13.3 *	4.7	8.5 **	0.2	-0.3
8	-3	1.0	-13.6	7.4	6.8	-9.8 *	-0.8	-0.6	0.1
9	10	0.0	8.5	-18.2 **	6.2	-9.2	10.1 **	1.8 **	0.9
10	13	1.2	-7.8	-2.3	5.9	-10.0	3.7	-0.9	0.0
Line 7×8	7	-5.5 **	1.9	-6.9	8.0	-9.8 *	8.0 *	1.7 **	2.0 **
9	14	-1.2	6.0	-9.6	20.7 **	-1.1	5.3	0.4	1.4 **
10	49 **	-4.6 *	-2.2	9.2	5.2	-1.1	5.9 *	-0.8	0.1
Line 8×9	4	1.2	6.0	3.2	-6.1	-12.0 *	8.9 **	2.6 **	0.7
10	21	1.4	-2.6	2.3	1.8	-9.8 *	-1.4	-1.7 **	0.0
Line 9×10	6	0.2	9.0	-0.5	0.6	-1.1	2.7	-1.9 **	-0.3
Mean	21.6	-3.3	4.5	-2.3	3.6	-11.3	4.5	-0.5	0.0

*, ** significant difference from high parent at 0.05 and 0.01 levels of probability.

For oil content, heterosis ranged from -6.3 to 6.5%, and the mean of heterosis was 0% (Table 4.7). Twenty five out of 45 crosses gave positive heterosis, among them, three crosses gave significant values. The highest heterosis was found in the cross of lines 5×6 which gave relatively high oil content of 40.3% (Table 4.3). The heterobeltiosis ranged from -11.5 to 1.4% with the mean of -3.3% (Table 4.8). The three high-yielding hybrids gave positive heterobeltiosis for oil content and gave relatively high oil contents.

Heterosis of pods per plant ranged from -9.9 to 48.6% with the mean of 11.4% (Table 4.7). All the top four crosses for seed yield expressed significantly positive heterosis for this character. The highest value was found in the cross of lines 2×5 which also gave high pods per plant and seed yield (Table 4.3). The heterobeltiosis of pods per plant ranged from -17 to 38.1% with the mean of 4.5% (Table 4.8). The highest value was found in the same cross for heterosis for this character.

Heterosis for seeds per pod ranged from -17.9 to 17.6% with the mean of 1.9% (Table 4.7). The cross between lines 7×10 expressed the highest heterosis for this character. The heterobeltiosis for seeds per pod ranged from -19.3 to 14.2%, with the mean of -2.3% (Table 4.8). The cross of lines 6×7 gave significantly positive heterobeltiosis for seeds per pod.

Most crosses showed higher 1,000-seed weight than mid-parent. The heterosis ranged from -11.3 to 25.4%, and the mean heterosis was 7.5% for this character (Table 4.7). Out of 45 crosses, 39 crosses gave positive heterosis, and 9 crosses among them showed significant values. The cross between lines 1×2 showed the highest heterosis value. The heterobeltiosis of 1,000-seed weight ranged from

-14.8 to 20.7% with the mean of 3.6% (Table 4.8). From these crosses, 32 crosses out of 45 gave positive heterobeltiosis, and 7 crosses showed significant values. The cross between lines 7×9 showed the highest heterobeltiosis value. Among three high-yielding hybrids, two crosses (line $2 \times$ line 5 and line $5 \times$ line 6) showed positive heterosis, but the cross of line $6 \times$ line 7 failed to give positive heterosis for this character.

Most crosses had lower branches per plant than mid-parent. The heterosis ranged from -22.5 to 11.3% with the mean of -5.3% (Table 4.7). Out of 45 crosses, 7 crosses showed positive heterosis, but only the cross between lines 6×7 gave significant value. The heterobeltiosis for this character ranged from -25 to 4.7%, and the mean of heterobeltiosis was -11.3% (Table 4.8). Out of 45 crosses, only two crosses showed positive heterobeltiosis.

Heterosis for plant height ranged from -0.6 to 16.8%, and the mean was 7.5% (Table 4.7). Forty three out of 45 crosses showed positive heterosis, and 28 crosses gave significant values for this character. The highest value was found in the cross between lines 3×8 which ranked the third in plant height. The heterobeltiosis of plant height ranged from -7 to 13.7%, and the mean was 4.5% (Table 4.8). Thirty six out of 45 crosses showed positive heterobeltiosis. The highest significant value was found in the cross between lines 3×8 , while the lowest negative significant value was found in the cross between lines 2×4 which gave short plant height among single cross hybrids.

Heterosis ranged from -1.7 to 3.4% with the mean of 0.8% for days to flowering (Table 4.7). Out of 45 crosses, 10 crosses showed negative heterosis while 35 crosses showed positive values. The heterobeltiosis of days to flowering ranged

from -3.4 to 2.6%, and the mean was -0.5% (Table 4.8). From 45 crosses, 24 showed negative heterobeltiosis for this character. The lowest significantly negative heterosis and heterobeltiosis were found in the same cross between lines 1×5 , while the highest significantly positive values was found in the same cross between lines 8×9 .

Heterosis of days to maturity ranged from -0.7 to 2.4% with the mean of 0.8% (Table 4.7). Out of 45 crosses, 5 crosses showed negative heterosis, but none was significant. The highest positive and significant value was found in the cross between lines 2×8 . Heterobeltiosis of days to maturity ranged from -2.3 to 2% with the mean of 0% (Table 4.8). Out of 45 crosses, 22 showed negative heterobeltiosis, and 7 of them gave significant values. The lowest significant and negative heterobeltiosis was found in the cross between lines 2×4 , while the highest significant and positive heterobeltiosis were found in the cross between lines 7×8 .

The percentages for heterosis and heterobeltiosis for seed yield in some crosses were considerably high indicating the high degree genetic diversity among parents. The cross of lines 2×5 gave both highest heterosis and heterobeltiosis, besides giving high yield and the highest SCA effect for seed yield. It was found that percentages of heterosis and heterobeltiosis for seed yield were associated with those of yield related characters, especially pods per plant and seed size. For example, the lines 2×5 cross gave significant heterosis for seed yield and pods per plant, while the lines 1×3 cross gave significant heterosis for seed yield and seed size (TSW). It is also important to note that though these hybrids had maximum or high heterosis for different characters, not all of them showed the highest or high SCA effects.

Studies on the manifestations of heterosis and heterobeltiosis of yield and other characters were made by many workers. Our result on heterosis for seed

yield was high and impressive. This is similar to that found by Shen et al. (2002) who reported that heterosis for seed yield ranged from 5.5 to 64.11% with the mean of 29.41%. Other workers reported either higher or lower heterosis than this study (Brandle and McVetty, 1989; Radoev et al., 2007; Sernyk and Stefansson, 1983; Starmer et al., 1998). For oil content, the range of heterosis in this study was bigger. However, the mean of heterosis was smaller than those found by some researchers (Shen et al., 2002; Hu and Liu, 1989), but the range of heterosis was smaller than that found by Wang (1992). For other characters, similar or different results were found in many reports (Jorgensen et al., 1995; Fray et al., 1997; Shen et al., 2002; Pourdad and Sachan, 2003).

Percentages of heterosis and heterobeltiosis for oil content, days to flowering and days to maturity in all crosses were low, mostly negative and also their corresponding SCA effects. These suggested that additive gene effects were important for these characters.

4.4.6 Correlations Between Characters

Seed yield of rapeseed is the combined effects of many characters which included morphological and yield related traits. Therefore, it is important to evaluate the relationship between seed yield and these characters and among them. Phenotypic correlations among characters of crosses are shown in Table 4.9. The positive correlations of seed yield with plant height, pods per plant, days to flowering and days to maturity were significant. Their respective correlation coefficients (r) were 0.644**, 0.583**, 0.281* and 0.341*. Associations among these characters were also observed. Highly significantly positive correlations were found between days to flowering and days to maturity (0.793), days to flowering and plant height (0.643),

days to maturity and plant height (0.710), etc. Highly negative correlation were observed between seeds per plant and seed size (-0.533), branches per plant and seed size (-0.333), branches per plant and days to flowering (-0.566), etc.

Table 4.9 Coefficients of phenotypic correlation between characters of rapeseed in diallel crosses involving 10 lines.

Characters	S/P	TSW	B/P	DF	DM	PH	OC [‡]	Yield
P/P	0.045	-0.138	0.243	0.084	0.161	0.336*	0.269*	0.583**
S/P		-0.533**	0.008	-0.017	-0.110	0.023	-0.023	0.211
TSW			-0.333**	0.238	0.399**	0.331*	-0.007	0.262
B/P				-0.566**	-0.496**	-0.457**	0.308*	-0.193
DF					0.793**	0.643**	-0.115	0.281*
DM						0.710**	0.172	0.341*
PH							0.197	0.644**
OC								0.172

*,** significant at 0.05 and 0.01 levels of probability, respectively.

‡ OC = oil content; P/P = pods per plant; S/P = seeds per pod; TSW = 1,000-seed weight; B/P = branches per plant; DF = days to flowering; DM = days to maturity; PH = plant height.

Correlations between characters of rapeseed were studied by others (Quijada et al., 2006; Gabriele and Becker, 1993), and similar results were obtained. For example, positive correlations were observed between seed yield and pods per plant (Zhang and Zhou, 2006; Zhang et al., 2006; Li et al., 2001; Zhang et al., 2007),

seed yield and plant height (Quijada et al., 2006; Gabriele and Becker, 1993; Li et al., 2001; Zhang et al., 2007), and seed yield and seeds per pod (Zhang et al., 2006; Zhang and Zhou, 2006). Negative correlations were observed between 1,000-seed weight and seeds per pod (Gabriele and Becker, 1993; Zhang et al., 2006; Li et al., 2001), yield and branches per plant (Zhang and Zhou, 2006). In this study, positive and significant correlation between yield and days to flowering was obtained, but Quijada et al. (2006) reported negative correlation between these characters.

4.4.7 Path Coefficients

Correlations among characters were partitioned into direct and indirect effects which the characters contribute to seed yield of rapeseed. Path coefficients are presented in Table 4.10. Pods per plant gave the highest direct contribution (0.5562) and relatively small but positive contribution (0.1348) through plant height to seed yield. Seed size (TWS) was the second important characters in giving direct contribution (0.4813) to seed yield and relatively small contribution (0.1331) through plant height to seed yield, but its contribution was reduced through seeds per pod (-0.2172). Seeds per pod was the third important character in giving direct contribution (0.4074) to seed yield, but its contribution was reduced through seed size (-0.2566). Plant height also gave high direct contribution (0.4017) to seed yield, and gave some indirect contribution through pods per plant (0.1867) and seed size (0.1595). Days to flowering and oil content didn't show direct contribution to seed yield, but they gave some indirect contribution through plant height and pods per plant. Days to maturity (-0.2488) and branches per plant (-0.1216) gave negative direct contribution to seed yield, but they gave some positive indirect contribution through other characters.

Table 4.10 Direct (diagonal) and indirect effect of characters on yield of rapeseed in diallel crosses involving 10 lines.

Character	P/P	S/P	TSW	B/P	DF	DM	PH	OC [‡]	CC [†]
P/P	0.5562	0.0185	-0.0665	-0.0296	0.0001	-0.0401	0.1348	0.0097	0.5831
S/P	0.0253	0.4074	-0.2566	-0.0010	0.0000	0.0273	0.0092	-0.0008	0.2106
TSW	-0.0768	-0.2172	0.4813	0.0405	0.0002	-0.0992	0.1331	-0.0002	0.2617
B/P	0.1353	0.0034	-0.1605	-0.1216	-0.0005	0.1234	-0.1837	0.0111	-0.193
DF	0.0468	-0.0070	0.1145	0.0688	0.0008	-0.1973	0.2582	-0.0041	0.2807
DM	0.0897	-0.0447	0.1918	0.0603	0.0006	-0.2488	0.2853	0.0062	0.3406
PH	0.1867	0.0093	0.1595	0.0556	0.0005	-0.1767	0.4017	0.0071	0.6437
OC	0.1495	-0.0092	-0.0033	-0.0374	-0.0001	-0.0428	0.0789	0.0360	0.1716

† CC = correlation coefficients with seed yield

‡ OC = oil content; P/P = pods per plant; S/P = seeds per pod; TSW = 1,000-seed weight; B/P = branches per plant; DF = days to flowering; DM = days to maturity; PH = plant height.

In this study, pods per plant, seeds per pod, 1,000-seed weight and plant height were important characters contributing to seed yield. The first three characters are important component traits of field crops such as legumes and rapeseed. These results were somewhat different from those reported by some researchers (Li et al., 1990; Zhang et al., 2007; Wang, J. S. et al., 2007) who found that all three yield component traits gave high direct contributions to seed yield, but plant height gave small direct contribution to seed yield. Li et al. (1990) found that the direct effects to

seed yield of pods per plant, seeds per pod and 1,000-seed weight were 0.4630, 0.6321 and 0.4136, respectively, but the direct effect of plant height to seed yield was 0.1466.

4.5 Conclusion

Ten recessive genetic male sterile (RGMS) lines were crossed in a diallel manner to produce 45 single crosses. These crosses and their parents were evaluated for combining abilities and heterosis. Analyses of variance showed significant variations among parents and hybrids for seed yield, pods per plant, seeds per pod, seed size, branches per plant, plant height, days to flowering, days to maturity and oil content. Among 45 single crosses, the means for seed yield of five crosses including crosses between lines 5×6 , 6×7 , 2×5 , 5×8 and 5×7 were 2,951, 2,817, 2,782, 2,683 and 2,661 kg ha⁻¹, respectively. These crosses could be used in the breeding program.

Analysis of variance for gene effects showed that both general combining ability (GCA) and specific combining ability (SCA) were important for all characters, and GCA effects were more important than SCA effects in all traits. However, the magnitude of GCA effects for seed yield and pods per plant not very much higher than SCA effects as the ratios of MS_{gca}/MS_{sca} were 1.48 and 1.92, respectively. For other characters, especially oil content, the ratio of MS_{gca}/MS_{sca} was very high (20.70). The high magnitude of mean square GCA relative to SCA indicates that the diversity within the materials studied is not high and line improvement for these characters is effective.

Estimates of GCA effects revealed that only two lines, namely lines 5 and 6,

gave significant GCA effects for seed yield. Line 6 also gave significant GCA effects for oil content, pods per plant and plant height, indicating that it is a good general combiner for these characters and should be used in breeding program. Four lines, namely 6, 8, 9 and 10, gave significant and positive GCA effects for oil content which can be used to improve this character. Line 2 gave significant and negative GCA effects for plant height, days to flowering and days to maturity which indicate that it should be used to improve for short plant height and early maturity.

Analysis of specific combining ability in this study revealed that a number of crosses showed significant SCA effects for each character, but none showed the best SCA effect simultaneously. Many crosses showed significant SCA effects for seed yield. The top three cross manifesting SCA effects for seed yield were the crosses of lines 2×5 , 1×8 and 6×10 , but only lines 2×5 cross yielded correspondingly. This indicates that the magnitude of SCA effects may not correspond to the expression of characters as the characters is the sum of mean, GCA and SCA effects and environmental effect. Significant SCA effects were observed in a number of crosses for other characters. Most crosses with significant SCA effects for seed yield also showed significant SCA effects for yield related traits. These indicate that there are some relationships between the magnitude of SCA effects for seed yield and that of yield related traits. Parents of some crosses with high SCA effects were both negative, or one negative and one positive, or both positive in GCA effects. These indicate that high SCA effects can be resulted from any parents with high or low GCA effects. Positive and significant SCA effects for oil content were found in the crosses between lines 1×3 , 1×5 , 4×7 , 5×6 , 5×7 and 5×9 .

Both positive and negative heterosis and heterobeltiosis were found for all

characters in this study. The percentages for heterosis and heterobeltiosis for seed yield in some crosses were considerably high indicating the high degree genetic diversity among parents. It was found that percentages of heterosis and heterobeltiosis for seed yield were associated with those of yield related characters, especially pods per plant and seed size. It is also important to note that, though these hybrids gave maximum or high heterosis for different characters, not all of them gave high SCA effects.

The results from correlation and path analyses showed that pods per plant, seeds per pod, 1,000-seed weight and plant height gave positive correlations with seed yield and contributed high direct contributions to this character. Other characters including branches per plant, days to flowering, days to maturity and oil content provided either negative or very low direct effects to seed yield. Moreover, none of the indirect effects of these characters to seed yield were high. These indicate the low contributions of these characters to seed yield.

4.6 References

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CHAPTER V

EVALUATION FOR HETEROSIS, GENETIC EFFECT AND COMBINING ABILITY OF OIL CONTENT, SEED YIELD, DAYS TO FLOWERING AND DAYS TO MATURITY IN RAPESEED (*Brassica napus* L.)

5.1 Abstract

In breeding for improvement of quantitative characters in rapeseed, materials to be used should be thoroughly evaluated. Nine inbred lines of rapeseed (*Brassica napus* L.) used as male lines were crossed with five recessive genetic male sterile (RGMS) lines used as females to produce 45 single crosses. The crosses, their parents and a check hybrid were tested at two locations in 2007-2008, one at Guiyang and the other at Zunyi. The results showed that variations for seed yield, oil content, days to flowering and days to maturity were significant. Mean squares for hybrids were significant for all characters. Differences among hybrids were due to both GCA and SCA effects. Significantly positive and negative GCA and SCA effects were found for different characters in breeding materials used in this study. The crosses of females $\times$ males 5×8 , 1×7 , 3×2 , 1×9 and 2×3 (Qianyou 8A $\times$ q034, QH303-4A $\times$ III224, Qianyou 3A $\times$ 2365, QH303-4A $\times$ 1190 and 24A $\times$ III153) gave significant SCA effects of 434.6, 429.9, 427.8, 379.4 and 347.0 kg ha⁻¹ for seed yield, respectively. Heterosis, heterobeltiosis, and standard heterosis were found high for seed yield. The

highest heterosis and heterobeltiosis were found in the cross of female 1 $\times$ male 9 (QH303-4A $\times$ 1190). The highest standard heterosis was found in the cross of female 5 $\times$ male 8 (Qianyou 8A $\times$ q034). Both positive and negative heterosis of single crosses were detected for oil content. Small heterosis was found for both days to flowering and days to maturity. Eight favorable single cross hybrids were found to give positive GCA effects for both parents and positive SCA effects. All of them yielded high and expressed significant and positive standard heterosis.

5.2 Introduction

Rapeseed (*Brassica napus* L.) is one of the most important oilseed crops in China. The production area has been increasing rapidly since 1980s, especially during 1990s. Comparing to that in 1950-60s, the planting acreage and the annual average yield increased 3-4 times with the total yield increase more than 10 times (Zhou and Fu, 2007). The increase of yield was largely due to the increase of the annual average yield production and the expansion of planting area of the crop. The increase of yield per unit area was largely due to the exploitation of heterosis through the utilization of hybrids.

Up to date, hybrid varieties of rapeseed have played a significant role in the improvement of yielding potential and oil content in China, but both characters were still lower than those in Western varieties (Wang, 2004). For example, rapeseed oil content in China was much lower than that in Canada, Australia, etc. Li et al. (2004) reported that average oil content in 202 samples of rapeseed in China was 37.7%, but that were 42.6, 42.4, 44.3 and 41.4% in Canada, Australia, France and USA, respectively. The yield of rapeseed in China is much lower than that in European

countries. The yield of rapeseed in China in 2007 was 1,472 kg ha⁻¹, but that of France, Germany and England were 2,888, 3,440 and 3,095 kg ha⁻¹, respectively (FAO Statistical Yearbook. 2008). Yield and oil content of rapeseed are among the most important characters in most the rapeseed breeding programs. Therefore, most researchers have paid a great effort to improve these characters. Many authors reported studies on heterosis, combining ability and genetic effects of rapeseed for these two characters (Sernyk and Stefansson, 1983; Grant and Beversdorf, 1985; Lefort-Buson et al., 1987; Brandle and McVetty, 1989; Han, 1990; Wang, 1992; Hu, 1987). The results from different populations and groups of authors were varied. Seryk and stefansson (1983) reported that heterosis of yield ranged from 7 to 64% over mid-parent, while Brandle and McVetty (1989) reported that heterosis of seed yield varied between hybrids being 20.3 to 120% over high yielding parents. Hu and Liu (1989) and Wang (1992) reported that the ranges of heterosis for oil content were -1.26 to 4.374% and -11.16 to 15.95% in their populations, respectively.

Mating designs I, II and III proposed by Comstock and Robinson (1948) and Comstock et al. (1949) have been used to estimate the relative importance of genetic variation in specific populations. Among these, Design II has been used more frequently in crop plants. This design has been used extensively to determine combining ability and appropriate parents of a cross among intended lines. By using this method, Ouyang et al. (1999) estimated the genetic effects of parents in rice; Qian et al. (2007) and Shen et al. (2002) estimated the genetic effects and heterosis of seed yield and other characters such as pods per plant, seeds per pod, etc. in rapeseed.

The objectives of this study were (1) to evaluate the performance of hybrids obtained from crossing between female and male parents, (2) to estimate combining

ability effects for seed yield, oil content, days to flowering and days to maturity, and (3) to estimate amount of heterosis, heterobeltiosis, and standard heterosis expressed for these characters.

5.3 Materials and Methods

5.3.1 Plant Materials

Fourteen rapeseed lines which have low erucic acid and glucosinolate contents with different developing backgrounds were used in this study. Among them, five recessive genetic male sterile lines (RGMS) were used as females and nine inbred lines were used as males. These male and female lines are shown with basic information in Table 5.1. They were planted for crossing in a NCII design manner. Fourteen parents were planted in Sept. 2006, and crosses were made in spring, 2007. At the flowering stage, male sterile plants were identified and tagging were made on RGMS lines. Young buds in the inflorescence of plants in female and male parents were covered before blooming with white paper bag. Flowers of male sterile plants covered were pollinated manually with fresh pollen collected from male parents after immature buds at the top of inflorescence were cut away. The pollinated flowers were covered again after pollination, and the paper bag was taken after 15 days. Eight to ten plants were pollinated similarly as above for each cross. According to NCII design, 45 F_1 crosses were produced. Five RGMS lines were obtained by crossing male sterile with male fertile plants of the same line. Nine male lines were produced by self-pollination. Seeds of each cross or line were harvested, threshed and the bulk of 8-10 plants was made for testing.

Table 5.1 Descriptions of 14 parents, 5 females and 9 males, used in this study.

No.	Designation	Prominent character	Origin
Female 1	QH303-4AB	High oil content with yellow seed-coat	A mutation from a open-pollinated variety Youyan no.6.
Female 2	24AB	Low oil content	Introduced from Sinan county, Guizhou province.
Female 3	Qianyou 3AB	Early flowering and maturity	Introduced from Yunan province.
Female 4	Qianyou 6AB	Low oil content	Derived from a hybrid variety named Shuza no. 6 in Shichuan province
Female 5	Qianyou 8AB	Yellow seed-coat, late flowering	Derived from a hybrid combination named You 1162 in Guizhou province
Male 1	2313	High oil content with yellow seed-coat	A mutant from a open-pollinated variety Youyan no.2.
Male 2	2365	High oil content with yellow seed-coat	A progeny of cross 95III15 $\times$ III501
Male 3	III153	High oil content, early flowering	A progeny of cross 8909 $\times$ 9002
Male 4	III176	Early maturity	A progeny of cross 325 $\times$ 8907
Male 5	III188	High oil content, early flowering	A progeny of cross 210 $\times$ 207
Male 6	III199	High oil content	A progeny of cross 206 $\times$ 225
Male 7	III224	High oil content	A inbred line named 2236
Male 8	q034	High oil content, late maturity	A progeny of cross 95III20 $\times$ III507
Male 9	1190	Yellow seed-coat, late flowering	A progeny of cross R $\times$ 8904

5.3.2 Field Experiment

All 45 crosses and 14 parents plus 1 check, which is now a commercial hybrid cultivar, were tested at two locations. One was at Guiyang, and the other was at Zunyi, Guizhou, China, at the altitude of about 1,140 m and 900 m, respectively. Both locations are widely grown to rapeseed (*Brassica napus* L.). The experiment

was carried out in a randomized complete block design with three replications. Plots consisted of two rows of 5-m in length with 45-cm inter-row and 33.3-cm intra-row spacings. Each plot contained 60 plants. Traditional methods of planting were used for each location. At Guiyang, plots were prepared carefully, 600 kg ha⁻¹ N, P and K fertilizers and 15 kg ha⁻¹ borax were applied in hills before planting. All the 60 entries were planted in hill on Sept. 26, 2007 and thinned to two plants per hill within 45 days after planting. Throughout the growing period, the total amount of 375 kg ha⁻¹ urea was used by putting in the hills for two times. Pesticide application and weed control were done twice and the supplemented irrigations were made as needed. The experiment was harvested from May 7 through May 19, 2008. Similar cultural practices were used at Zunyi. All 60 entries were planted in seed bed to produce seedlings on Sept. 12, 2007, and were transplanted with two plants per hill on Oct 14, 2007. During growing period at this location, the total amount of 178 kg ha⁻¹ urea, 178 kg ha⁻¹ potassium chloride, 330 kg ha⁻¹ superphosphate, 440 kg ha⁻¹ N, P and K fertilizers and 20 kg ha⁻¹ borax were used. Pesticides were applied as needed and weed control was done once. The experiment was harvested from May 17 through May 25, 2008.

5.3.3 Data Collection

The following attributes were measured on plot at both locations:

Days to flowering: The number of days from planting until 50% of plants flowered.

Days to maturity: The number of days from planting until 90% of the plants matured.

Seed yield: The weight of seed in kilogram per hectare. The seeds were

harvested and seed yield was determined in the following manner:

$$\text{Seed yield } Y = \frac{100 - X}{100 - Y_s} \times F.W. \times \frac{10,000}{A}$$

where Y = yield in kg ha^{-1} , X = moisture content (measured), Y_s = standard moisture content (9%), $F.W.$ = harvested yield in kg plot^{-1} , A = area harvested (m^2).

Percentage of oil: Oil content was determined by NIRS.

5.3.4 Statistical Analysis

Fourteen parents, 45 hybrids and one commercial check were involved in the experiments. However, the commercial check was excluded when analysis of variance was done.

Data recorded for each character from individual location were first analyzed to determine the homogeneity of variances. They were then used to perform combined analysis of variance. The lines used as parents in this experiment were considered fixed and the locations in the experiments were conducted a random sample of locations in which rapeseed is grown in this area of Guizhou. The combined analysis of variance for each character was performed by using the following model:

$$Y_{ijk} = m + E_k + R_{(k)i} + V_j + (VE)_{jk} + e_{ijk}$$

where

Y_{ijk} = observed value of the ijk^{th} plot

m = grand mean

E_k = effect of the k^{th} environment

$R_{(k)i}$ = effect of replication i^{th} in environment k^{th}

V_j = effect of the j^{th} entry

$(VE)_{jk}$ = effect of interaction of the j^{th} entry with the k^{th} environment

e_{ijk} = the error associated with the ijk^{th} observation.

and where

$i = 1, 2, \dots, r$; $r = 3$ (r = number of replication)

$j = 1, 2, \dots, v$; $v = 59$ (v = number of entry)

$k = 1, 2, \dots, e$; $e = 2$ (e = number of environment)

The analysis of variance for the experiment were made by using DPS 9.50 data processing system that copyright belonging to Tang Qiyi, China.

In this experiment, the lines used as male and female parents were crossed in accordance with the pattern described for Design II by Comstock and Robinson (1948), the model was as follows:

$$Y_{ijkl} = m + E_l + R_{(l)k} + G_i + G_j + S_{ij} + (GE)_{il} + (GE)_{jl} + (SE)_{ijl} + e_{ijkl}$$

where

Y_{ijkl} = observed value of the ij^{th} hybrid in the kl^{th} plot

m = grand mean

E_l = effect of the l^{th} environment ($l = 1, 2$)

$R_{(l)k}$ = effect of k^{th} replication in the l^{th} environment

G_i = the average effect (GCA) of the i^{th} male parent on its cross

G_j = the average effect (GCA) of the j^{th} female parent on its cross

S_{ij} = the deviation average effect of the ij^{th} cross from expected performance based on the parents average effects (SCA)

$(GE)_{il}$, $(GE)_{jl}$, and $(SE)_{ijl}$ = the interactions with environments for the effects defined previously

e_{ijkl} = the error associated with the $ijkl^{\text{th}}$ observation.

and where

$i = 1, 2, \dots, m$; $m = 9$ (m = number of male)

$j = 1, 2, \dots, f$; $f = 5$ (f = number of female)

$k = 1, 2, \dots, r$; $r = 3$ (r = number of replication)

$l = 1, 2, \dots, e$; $e = 2$ (e = number of environment)

The partitions of sources, df and EMS are presented in Table 5.2 and Table 5.3, respectively.

Table 5.2 Form for combined analysis of variance of data across environments and expected mean squares.

Sources	df	EMS
Environments (Env.)	$e-1$	$\sigma_e^2 + v\sigma_R^2 + rv\sigma_E^2$
Replications/Env.	$e(r-1)$	$\sigma_e^2 + v\sigma_R^2$
Entries (V)	$v-1$	$\sigma_e^2 + r\sigma_{VE}^2 + reK_V^2$
Entries $\times$ Environments (V $\times$ Env.)	$(v-1)(e-1)$	$\sigma_e^2 + r\sigma_{VE}^2$
Pooled error (e)	$e(r-1)(v-1)$	σ_e^2
Total	$erv-1$	

Table 5.3 Expected mean squares for males and females.

Sources	df	EMS
GCA (males)	m-1	$\sigma_e^2 + rf\sigma_{g_{ie}}^2 + refK_{g_i}^2$
GCA (females)	f-1	$\sigma_e^2 + rm\sigma_{g_{je}}^2 + remK_{g_j}^2$
SCA	(m-1)(f-1)	$\sigma_e^2 + r\sigma_{s_{ije}}^2 + reK_{s_{ij}}^2$
GCA (males)×Env.	(m-1)(e-1)	$\sigma_e^2 + rf\sigma_{g_{ie}}^2$
GCA (females)×Env.	(f-1)(e-1)	$\sigma_e^2 + rm\sigma_{g_{je}}^2$
SCA × Env.	(m-1)(f-1)(e-1)	$\sigma_e^2 + r\sigma_{s_{ije}}^2$
Pooled error	e(m-1)(f-1)	σ_e^2

5.3.5 Analysis of Entry Means for Combining Ability Effects

The expected variation due to female and male parents corresponds to GCA, and that due to the female × male interaction corresponds to SCA (Hallauer and Miranda, 1988). For each character, the GCA estimates (g_i or g_j) for all parental lines and SCA estimates (s_{ij}) for all hybrid genotypes were calculated according to Beil and Atkins (1967) as follows:

$$g_i = (y_{i.} - y_{..})$$

$$g_j = (y_{.j} - y_{..})$$

$$s_{ij} = (y_{ij} - y_{i.} - y_{.j} + y_{..})$$

where y_{ij} is the mean of the hybrid of crossing the i^{th} female and the j^{th} male parents, $y_{i.}$ is the mean of all hybrids involving the i^{th} female parent, $y_{.j}$ is the mean of all hybrids involving the j^{th} male parent, and $y_{..}$ is the grand mean of hybrids.

Standard errors for g_i , g_j and s_{ij} estimates were calculated by using the respective mean squares as follows:

$$SE_{GCA} = \frac{MS_{fe}}{mre} \text{ (for females)}$$

$$SE_{GCA} = \frac{MS_{me}}{fre} \text{ (for males)}$$

$$SE_{SCA} = \frac{MS_{fme}}{re}$$

where MS_{fe} , MS_{me} and MS_{fme} are the respective females $\times$ environments, males $\times$ environments and females $\times$ males $\times$ environments mean squares. Two-tailed t tests were used to test the significance of the g_i or g_j and s_{ij} estimates deviated from zero.

To evaluate the relative importance of additive and non-additive genetic effects for each character, SS ratio was calculated as suggested by Pixley and Frey (1991) and Lee et al. (2005) as follows:

$$SS \text{ ratio} = \frac{SS_m + SS_f}{SS_{\text{hybrid}}}$$

where SS_m , SS_f , SS_{hybrid} are the respective males, females, and hybrids sum of squares. The closer the ratio is to unity, the greater the influence of additive genetic effects on the character.

Heterosis is a phenomenon in which the performance of an F_1 hybrids produced from a cross between genetically distant parents is superior to their mid-parent value (Shull, 1914). Powers (1944) and Stern (1948) extended the concept

to include negative heterosis. Heterobeltiosis (Fonseca and Patterson, 1968) has been suggested to describe increased performance of the hybrid over the better parent. The third measure was standard heterosis which was employed in autogamous crops over the best pure line variety, and was used over a commercial hybrid check in this study. They were calculated as follows:

$$\text{Heterosis (\%)} = \frac{F_1 - \text{MP}}{\text{MP}} \times 100 \quad (\text{Shull, 1914})$$

$$\text{Heterobeltiosis (\%)} = \frac{F_1 - \text{HP}}{\text{HP}} \times 100 \quad (\text{Fonseca and Patterson, 1968})$$

$$\text{Standard heterosis (\%)} = \frac{F_1 - \overline{\text{CK}}}{\overline{\text{CK}}} \times 100$$

where F_1 is the mean of F_1 hybrids, MP is the mean of two parents, HP is the value of the high parent and $\overline{\text{CK}}$ is the mean performance of commercial check. The tests of significance were made by using t-test.

5.4 Results and Discussion

5.4.1 Growing Condition

Growing conditions during 2007-2008 were quite unfavorable for rapeseed. Early winter at Guiyang was quite dry and late winter at both locations was quite cold with long ice-rain period during Jan 12, 2008 - Feb 4, 2008. The ice rain caused early buds damage. Spring 2008 was late, but the temperature was good for rapeseed pollination (Appendix: Attached figure 1 and 2). Therefore, seed yield were not much affected. However, due to the cold weather, the flowering and maturity periods of rapeseed were longer than usual.

5.4.2 Analysis of Variance and Means

Mean squares from the analyses of variance combined over two environments for seed yield, oil content, days to flowering and days to maturity are shown in Table 5.4. Location to location difference was significant ($P < 0.01$) for all traits. Highly significant differences among entries were also obtained for all characters except days to maturity which was significant at 0.05 level. The mean squares obtained by partitioning the entries sum of squares were tested against their analogous interaction mean squares. F-test for parents vs. hybrids mean square was significantly different for seed yield but not other characters. This test can be interpreted as a measure of the extent of heterosis. Highly significant difference for entries $\times$ environments was shown for each character. Variations among parents and hybrids were highly significant for all characters except for days to maturity which was not significant for parents and significantly different at 0.05 for hybrids. Highly significant differences for parents $\times$ environments and hybrids $\times$ environments were found for all characters.

Means of hybrids averaged over two locations for seed yield, oil content, days to flowering and days to maturity are presented in Table 5.5. Seed yield of hybrids ranged from a low of 1,513 kg ha⁻¹ for the female 2 $\times$ male 2 (24A $\times$ 2365) cross to a high of 3,090 kg ha⁻¹ for the female 5 $\times$ male 8 (Qianyou 8A $\times$ q034) cross. The environment for seed yield at Zunyi was more favorable than at Guiyang. Therefore, the higher seed yield of crosses and check were obtained at this location. The range of means for oil content of 45 crosses was from 37.33 to 43.38%. The highest oil content was obtained in the female 1 $\times$ male 7 (QH303-4A $\times$ III224) cross, followed by the female 1 $\times$ male 9 (QH303-4A $\times$ 1190) cross. For days to flowering,

means of 45 crosses ranged from 164.7 to 179 days. The means for days to maturity ranged from 237.5 to 244.5 days. The cross of female 3 $\times$ male 1 (Qianyou 3A $\times$ 2313) was the earliest and the cross of female 5 $\times$ male 2 (Qianyou 8A $\times$ 2365) was the latest.

Table 5.4 Analysis of variance for yield, oil content, days to flowering and days to maturity combined over two environments.

Sources	df	Mean squares			
		Yield	OC [‡]	DF	DM
Environments(Env.)	1	2780055 **	450.53 **	56949.44 **	41199.89 **
Replications/Env.	4	37434	1.88	0.50	4.41
Entries	58	1391261 **	14.26 **	59.52 **	15.74 *
Parents vs. Hybrids	1	28555221 *	8.95	0.96	0.00
Parents	13	470121 **	16.43 **	63.46 **	15.84
Hybrids	44	1046054 **	13.75 **	59.68 **	16.07 *
Entries $\times$ Env.	58	242110 **	1.92 **	5.26 **	9.83 **
Parents vs hybrids $\times$ Env.	1	142352 *	4.76 **	32.21 **	1.50
Parents $\times$ Env.	13	73585 **	3.16 **	9.46 **	13.66 **
Hybrids $\times$ Env.	44	294168 **	1.50 **	3.41 **	8.89 **
Pooled error	232	30918	0.81	0.31	2.01

*,** significant at 0.05 and 0.01 levels of probability, respectively.

‡ OC = oil content; DF = days to flowering; DM = days to maturity.

Table 5.5 Means for seed yield, oil content, days to flowering and days to maturity in hybrids grown in two environments.

Characters	Yield			Oil content			Days to flowering			Days to maturity		
	Guiy. [‡]	Zuny.	Ave.	Guiy	Zuny.	Ave.	Guiy	Zuny.	Ave.	Guiy.	Zuny.	Ave.
	kg ha ⁻¹			%			no.			no.		
Female 1× male 1	2,710	2,313	2,512	43.26	40.68	41.97	159.0	183.3	171.2	229.3	250.3	239.8
male 2	2,235	1,394	1,814	42.86	40.07	41.46	163.3	187.3	175.3	233.7	254.3	244.0
male 3	2,046	1,776	1,911	41.96	40.71	41.34	159.0	183.3	171.2	230.7	253.7	242.2
male 4	2,058	1,667	1,863	42.75	42.06	42.41	157.3	185.3	171.3	228.0	249.0	238.5
male 5	2,089	2,512	2,301	40.59	40.96	40.77	156.3	183.3	169.8	232.7	253.3	243.0
male 6	1,784	1,462	1,623	42.92	41.46	42.19	159.3	186.3	172.8	231.3	253.3	242.3
male 7	2,562	3,205	2,884	44.13	42.62	43.38	159.0	184.0	171.5	230.7	252.0	241.3
male 8	2,128	2,365	2,246	42.62	40.63	41.63	158.3	185.3	171.8	230.3	252.0	241.2
male 9	2,527	2,779	2,653	43.54	41.72	42.63	163.0	188.0	175.5	233.0	252.7	242.8
Female 2× male 1	2,628	2,944	2,786	40.18	38.52	39.35	161.7	189.0	175.3	229.7	252.7	241.2
male 2	1,800	1,226	1,513	41.84	37.94	39.89	163.7	189.0	176.3	234.3	253.7	244.0
male 3	2,229	2,698	2,464	41.66	39.66	40.66	161.7	185.3	173.5	233.0	251.3	242.2
male 4	2,238	2,251	2,244	39.76	37.80	38.78	162.0	188.7	175.3	229.7	249.3	239.5
male 5	2,503	3,075	2,789	38.23	37.41	37.82	158.3	184.3	171.3	231.3	251.0	241.2
male 6	2,155	1,800	1,977	40.84	38.29	39.57	163.7	190.0	176.8	233.3	251.3	242.3
male 7	2,553	2,373	2,463	41.82	38.47	40.15	161.0	187.0	174.0	230.7	252.7	241.7
male 8	2,701	2,539	2,620	40.48	38.44	39.46	164.0	190.0	177.0	233.3	249.7	241.5
male 9	2,314	1,852	2,083	38.62	36.97	37.80	163.7	190.0	176.8	232.3	254.0	243.2
Female 3× male 1	2,064	1,275	1,669	39.38	35.53	37.46	156.7	181.3	169.0	223.0	252.0	237.5
male 2	2,216	1,437	1,827	39.77	38.15	38.96	162.7	185.3	174.0	230.0	254.3	242.2
male 3	1,829	1,367	1,598	40.16	37.29	38.73	155.3	183.7	169.5	229.0	252.0	240.5
male 4	1,830	1,211	1,521	39.55	36.88	38.22	157.0	183.0	170.0	226.7	250.7	238.7
male 5	2,610	1,936	2,273	38.3	36.36	37.33	151.0	178.3	164.7	229.7	253.0	241.3
male 6	2,034	1,416	1,725	40.16	36.85	38.51	159.0	182.7	170.8	229.3	254.0	241.7
male 7	2,190	1,581	1,886	39.73	37.62	38.68	158.3	184.3	171.3	224.0	251.3	237.7
male 8	1,878	1,916	1,897	39.62	37.49	38.56	157.3	182.3	169.8	227.7	251.7	239.7
male 9	2,087	1,591	1,839	39.69	36.49	38.09	161.7	188.0	174.8	227.7	253.0	240.3
Female 4× male 1	2,406	2,737	2,572	40.92	39.19	40.05	159.0	187.0	173.0	229.3	250.0	239.7
male 2	2,434	1,771	2,069	41.57	39.60	40.59	163.7	189.3	176.5	230.7	254.0	242.3
male 3	2,366	1,723	2,045	38.96	37.32	38.14	155.7	180.0	167.8	230.7	252.7	241.7
male 4	2,130	1,999	2,064	42.86	39.44	41.15	160.3	183.3	171.8	229.7	250.0	239.8
male 5	2,398	2,530	2,464	37.97	37.96	37.96	156.3	180.7	168.5	231.7	252.3	242.0
male 6	2,321	2,116	2,219	38.01	37.52	37.77	159.7	183.0	171.3	229.0	251.0	240.0
male 7	2,481	2,941	2,711	41.95	39.48	40.72	161.0	187.0	174.0	228.3	252.3	240.3
male 8	2,758	3,347	3,052	40.39	39.52	39.96	162.7	187.0	174.8	231.7	250.3	241.0
male 9	2,430	2,047	2,238	42.45	39.07	40.76	162.7	191.0	176.8	231.7	254.0	242.8
Female 5× male 1	2,522	1,667	2,095	39.68	36.85	38.27	162.7	189.3	176.0	230.0	251.0	240.5
male 2	1,906	1,508	1,707	41.44	37.41	39.42	167.0	191.0	179.0	234.3	254.7	244.5
male 3	2,061	1,781	1,921	40.06	38.25	39.16	161.7	189.0	175.3	232.3	250.7	241.5
male 4	2,293	1,760	2,027	40.55	38.76	39.65	162.0	189.0	175.5	231.3	251.7	241.5
male 5	2,768	2,729	2,782	39.52	37.72	38.62	160.3	184.0	172.2	233.7	253.7	243.7
male 6	2,250	1,758	2,004	40.82	37.95	39.39	164.3	192.0	178.2	233.0	254.0	243.5
male 7	2,552	2,068	2,310	40.11	37.28	38.70	163.7	190.3	177.0	233.0	252.7	242.8
male 8	2,778	3,401	3,090	40.98	37.90	39.44	163.0	188.7	175.8	231.7	250.7	241.2
male 9	2,526	2,555	2,541	40.01	38.69	39.35	164.7	190.0	177.3	233.0	253.0	243.0
Mean of hybrids	2,297	2,098	2,198	40.73	38.60	39.66	160.5	186.2	173.4	230.7	252.2	241.4
Check	2,216	2,428	2,322	38.51	38.54	38.53	159.7	187.3	173.5	230.3	250.7	240.5
LSD 0.05			200			1.02			0.6			1.6
LSD 0.01			264			1.35			0.8			2.1

‡ Guiy. = Guiyang; Zuny. = Zunyi; Ave. = average over two locations

Table 5.6 shows the means of crosses with one parent in common and the means of common parents for all characters measured. The means of single cross hybrids with one parent in common were significantly different and ranged from 1,786 to 2,581 kg ha⁻¹, from 38.28 to 41.98%, from 170.4 to 176.3 days and from 239.6 to 245.5 days for seed yield, oil content, days to flowering and days to maturity, respectively. The significant differences between the means of common parents of each character were also identified. The means of common parents ranged from 1,132 to 1,970 kg ha⁻¹, from 36.73 to 41.80%, from 169.3 to 179.3 days and from 238.2 to 243.7 days for seed yield, oil content, days to flowering and days to maturity, respectively. These results showed that three lines namely male 5 (III188), male 7 (III224) and male 8 (q034) gave consistently high seed yield performance indicating that these three lines might have high general combining ability for seed yield. For oil content, male 2 (2365), male 7 (III224) and female 1 (QH303-4AB) gave high oil content for both means of single cross hybrids with one parent in common and the common parents indicating that these three lines might have high combining ability for this character. Male 5 (III188) gave the earliest days to flowering for both means of single cross hybrids and common parent indicating that early crosses might result from this line. The longest days to flowering was found in male 9 (1190) for both means of single cross hybrids and the common parent indicating that late crosses could be found from the crosses involving this line.

Table 5.6 Means of single cross hybrids with one parent in common and the means of common parents for four characters.

Common parent	Yield		Oil content		Days to flowering		Days to maturity	
	Hybrid	Parent	Hybrid	Parent	Hybrid	Parent	Hybrid	Parent
	kg ha ⁻¹		%		no.		no.	
Male 1	2,327	1,511	39.42	40.17	172.9	175.8	239.7	239.5
Male 2	1,786	1,377	40.06	41.80	176.2	174.3	243.4	242.7
Male 3	1,988	1,215	39.60	40.54	171.5	170.7	241.6	242.0
Male 4	1,944	1,132	40.04	38.35	172.8	174.2	239.6	238.2
Male 5	2,522	1,836	38.50	40.47	169.3	169.3	242.2	243.0
Male 6	1,909	1,321	39.48	39.59	174.0	173.5	242.0	241.5
Male 7	2,451	1,793	40.32	40.05	173.6	176.2	240.8	242.3
Male 8	2,581	1,857	39.81	40.80	173.9	177.5	240.9	243.7
Male 9	2,271	1,353	39.73	39.66	176.3	179.3	242.4	242.3
LSD 0.05	99	132	0.46	1.18	0.3	0.7	0.7	1.6
LSD 0.01	131	178	0.60	1.59	0.4	0.9	1.0	2.2
Female 1	2,201	1,465	41.98	40.37	172.3	170.8	241.7	240.8
Female 2	2,327	1,793	39.27	36.78	175.2	170.3	241.9	241.3
Female 3	1,804	1,186	38.28	37.72	170.4	169.5	239.9	238.8
Female 4	2,382	1,611	39.68	36.73	172.7	171.0	241.1	242.7
Female 5	2,275	1,970	39.11	37.05	176.3	176.5	242.5	240.8
LSD 0.05	74	146	0.34	0.94	0.2	0.8	0.5	1.7
LSD 0.01	98	202	0.45	1.29	0.3	1.0	0.7	2.4

Analysis of variance combined over two environments showed that the F-test for parents vs. hybrids mean square was significantly different for seed yield but not for other characters in this study indicating that heterosis in seed yield was more important than others.

Many means for seed yield of individual hybrids tested at two locations were higher than the standard check indicating that these crosses were favorable. Eleven single cross hybrids yielded high and were significantly different from check. Among them, ten crosses gave higher oil content than check. Therefore, these crosses may be used in future breeding program, especially those with high oil content. Two crosses including female 3 $\times$ male 7 (Qianyou 3 $\times$ III224) and female 3 $\times$ male 1 (Qianyou 3A $\times$ 2313) expressed early maturity, but their average yield over two locations were not favorable. However these two crosses yielded moderately for seed yield, higher oil content than check, and were 5.7 days and 6.7 days earlier than check at Guiyang. Therefore, these crosses can be used as candidate varieties for early hybrids at Guiyang.

5.4.3 Combining Ability Analysis of Variance

Combining ability mean squares for data combined over two environments for seed yield, oil content, days to flowering and days to maturity of single cross hybrids are presented in Table 5.7. Differences among hybrids were significant for all traits. The mean squares attributable to male and female parents of hybrids provide a measure of GCA effects of the two parental groups, respectively.

Table 5.7 Analysis of variance for combining ability of yield, oil content, days to flowering and days to maturity combined over two environments.

Sources	df	Mean squares			
		Yield	OC [‡]	DF	DM
Hybrids	44	1046054 **	13.75 **	59.68 **	16.07 *
GCA(Males)	8	2585316 *	8.28 *	142.52 **	47.97 **
GCA(Females)	4	2867803	104.18 **	293.26 **	49.14
SCA(Male×Female)	32	433520 **	3.81 **	9.78 **	3.96
Hybrids×Env.	44	294168 **	1.50 **	3.41 **	8.89 **
Male×Env.	8	554313 **	2.39 **	2.54 **	6.93 **
Female×Env.	4	654358 **	2.97 **	1.27 **	59.60 **
Male×female×Env.	32	184109 **	1.09	3.90 **	3.04 *
Pooled error	232	30918	0.81	0.31	2.01
SS ratio		0.70	0.80	0.88	0.82

*,** significant at 0.05% and 0.01% levels of probability, respectively.

‡ OC = oil content; DF = days to flowering; DM = days to maturity.

The data indicated that GCA effects were significant for all characters for male and female, but seed yield and days to maturity for female were not significant. The interaction between male and female effects is the estimate of SCA effects. The SCA effects were significant for seed yield, oil content and days to flowering, but not days to maturity. The interaction between hybrids and environments was significant ($P<0.01$) for all characters. Male × environment and

female $\times$ environment interaction mean squares were highly significant for all characters. The male $\times$ female $\times$ environment mean squares were significant for all characters except oil content.

Partitioning of hybrid sum of squares into variation due to males, females and female $\times$ male, showed that GCA effects accounted for over 70% of hybrids sum of squares for all traits (Table 5.7). The SS ratios were 0.70, 0.80, 0.88 and 0.82 for seed yield, oil content, days to flowering and days to maturity, respectively.

In this study, the general combining ability accounted for 70% (SS ratio was 0.70) of the variability for seed yield. This indicated that both additive and non-additive gene effects were important for seed yield. Similar result of SS ratio for seed yield in rapeseed was reported by Shen et al. (2002). However, Brandle and McVetty (1990) reported that GCA accounted for 44% of gene effects controlling seed yield in rapeseed. The SS ratios of oil content and days to flowering were 0.80 and 0.88, respectively, but both GCA and SCA effects were significant, indicating that additive effects were more important than non-additive gene effects for these two characters. Similar SS ratio for oil content in rapeseed was reported by Brandle and McVetty (1990) who reported GCA accounted for 75% of hybrids sum of squares. However, Shen et al. (2002) reported that genetic effect for oil content was all additive as they found that SCA was not significant. The SS ratio for days to maturity was 0.82, but SCA effect for this trait was not significant, indicating that additive effects were predominant for this trait. Therefore, the performance of single cross hybrids may be adequately predicted on the basis of GCA effects, and the best hybrids should be obtained from crosses between parents having high GCA effects.

The results from the analysis of variance for combining ability shown in Table 5.7 demonstrated that both GCA and SCA effects were important for most characters. The mean squares for GCA (female) tended to be larger than GCA (male) for each character, indicating a greater genetic diversity among the female than the male parents for each trait. The relative importance of GCA and SCA effects for each trait as examining by the ratio of GCA sum of squares to hybrids sum of squares showed that, for all characters, GCA effects were more important than SCA effects. This may indicate that this group of males and females may be originated from the same group and possessed low diversity among them. However, SCA effects were significant in the expression of seed yield, oil content and days to flowering indicating that non-additive gene effects also contributed to the variation observed for these traits.

5.4.4 Estimates of GCA and SCA Effects

Estimates of general combining ability of each parent for both parental groups when combined into single cross hybrids are presented for all characters in Table 5.8. The GCA effects are numerical values assigned to parents according to their average performance in hybrid combinations. Males 5 (III188), 7 (III224) and 8 (q034) gave large positive effects for seed yield among male parents. Their respective GCA effects were 317.6, 253.1 and 383.5 kg ha⁻¹ (Table 5.8). This showed that these males were good combiners for seed yield and should be used as parents in a breeding program to improve seed yield. This was partly confirmed by the high yielding potential in the crosses of female 5 × male 8 (Qianyou 8A × q034), female 4 × male 8 (Qianyou 6A × q034), female 1 × male 7 (QH303-4A × III224) and female 2 × male 5 (24A × III188) (Table 5.5). The means of single cross hybrids with these lines in

common also gave good yield (Table 5.6).

Table 5.8 Estimates of general combining ability (GCA) effects for four characters of rapeseed lines.

Lines	Yield	Oil content	Days to flowering	Days to maturity
	kg ha ⁻¹	%	no.	no.
Male 1	129.1	-0.24	-0.48	-1.67 **
Male 2	-404.8 **	0.40	2.86 **	2.00 **
Male 3	-209.9	-0.06	-1.91 **	0.20
Male 4	-253.8	0.38	-0.58 *	-1.80 **
Male 5	317.6 *	-1.16 **	-4.08 **	0.83
Male 6	-288.1 *	-0.18	0.62 *	0.56
Male 7	253.1	0.66 *	0.19	-0.64
Male 8	383.5 **	0.14	0.49	-0.50
Male 9	73.3	0.06	2.89 **	1.03 *
LSD 0.05 (m)	266.6	0.55	0.57	0.94
LSD 0.01 (m)	350.7	0.73	0.75	1.24
Female 1	3.2	2.31 **	-1.10 **	0.28
Female 2	129.0	-0.39	1.79 **	0.45
Female 3	-393.8 **	-1.38 **	-2.93 **	-1.46
Female 4	187.7	0.01	-0.64 **	-0.33
Female 5	73.9	-0.55 *	2.88 **	1.06
LSD 0.05 (f)	215.8	0.46	0.30	2.06
LSD 0.01 (f)	284.0	0.60	0.40	2.71

*, ** significant difference from zero at 0.05 and 0.01 levels of probability, respectively.

Significant differences existed among males and females for oil content (Table 5.7). However, this significance was corresponded by negative GCA effects of many male and female parents. Significant positive GCA effects were detected for male 7 (III224) and female 1 (QH303-4AB) of which the respective GCA effects were 0.66 and 2.31% (Table 5.8). These parents should be good combiners for oil content. This was confirmed by the highest oil content in the female 1 $\times$ male 7 (QH303-4A $\times$ III224) cross among 45 hybrids (Table 5.5). Mean for oil content of hybrids which involved female 1 (QH303-4A) was also found to be the highest among 14 parents (Table 5.6).

Significant GCA effects were found for 6 males and all 5 females in days to flowering. Significant and positive GCA effects were expressed by males 2 (2365), 6 (III199), 9 (1190) and female 2 (24AB), 5 (Qainyou 8AB) with the GCA effect values of 2.86, 0.62, 2.89, 1.79 and 2.88 days, respectively. These parents should be good combiners for late flowering. Males 3 (III153), 4 (III176), 5 (III188), females 1 (QH303-4AB), 3 (Qianyou 3AB) and 4 (Qianyou 5AB) gave significant and negative GCA effects of -1.91, -0.58, -4.08, -1.10, -2.93 and -0.64 days, respectively (Table 5.8). These parents should be good combiners for early flowering.

Four male lines were found to show significant GCA effects for days to maturity. Among them, male 2 (2365) and male 9 (1190) showed significant and positive GCA effects with the values of 2.00 and 1.03 days; male 1 (2313) and male 4 (III176) showed significant and negative GCA effects with the values of -1.67 and -1.80 days. These results indicated that days to maturity of crosses involving male 2 (2365) and male 9 (1190) were relatively longer, and days to maturity of crosses involving male 1 (2313) and male 4 (III176) were relatively shorter than other

crosses.

Significant specific combining ability effects of crosses are shown in Table 5.7 for all traits except days to maturity. The estimates for these effects are shown in Table 5.9 for seed yield, oil content, days to flowering and days to maturity. Significant SCA effects for seed yield were found in 6 crosses. Among them, 5 crosses gave positive SCA effects. The highest positive SCA effects was found in the cross of female 5 $\times$ male 8 (Qianyou 8A $\times$ q034) with the value of 434.6 kg ha⁻¹, followed by crosses female 1 $\times$ male 7 (QH303-4A $\times$ III224), female 3 $\times$ male 2 (Qianyou 3A $\times$ 2365), female 1 $\times$ male 9 (QH303-4A $\times$ 1190), and female 2 $\times$ male 3 (24A $\times$ III153) with the SCA effects of 429.9, 427.8, 379.4, and 347.0 kg ha⁻¹, respectively. These results indicate that these crosses should be considered in the production of hybrids for high seed yield in a breeding program.

Among 45 crosses, significant SCA effects were found in 9 crosses for oil content. Among them, 3 crosses gave positive SCA effects. The highest positive SCA effect was found in the cross of female 2 $\times$ male 3 (24A $\times$ III153) with the value of 1.45%, followed by crosses female 4 $\times$ male 4 (Qianyou 6A $\times$ III176) and female 4 $\times$ male 9 (Qianyou 6A $\times$ 1190) which had the SCA effects of 1.09 and 1.02%, respectively. These crosses should be included in a breeding program for rapeseed to improve oil content.

Significant SCA effects were found for 7 crosses out of 45 for days to flowering. Among them, 2 crosses gave positive SCA effects while 5 crosses gave negative SCA effects. The maximum positive value of SCA effect was found in the cross of female 1 $\times$ male 5 (QH303-4A $\times$ III188) with the value of 1.63 days, followed by cross female 4 $\times$ male 8 (Qianyou 6A $\times$ q034) with the value of 1.60

Table 5.9 Estimates of specific combining ability (SCA) effects for four characters of rapeseed crosses.

Characters		Crosses								
Yield		Male 1	Male 2	Male 3	Male 4	Male 5	Male 6	Male 7	Male 8	Male 9
	Female 1	181.9	18.5	-80.1	-84.2	-217.6	-289.6	429.9*	-338.0	379.4*
	Female 2	330.2	-408.6*	347.0*	171.5	144.8	-61.3	-116.6	-90.1	-316.8
	Female 3	-263.5	427.8*	4.2	-29.4	151.5	209.0	-171.1	-290.1	-38.3
	Female 4	57.3	121.9	-130.9	-67.1	-238.5	121.5	72.3	283.6	-220.2
	Female 5	-305.8	-159.6	-140.2	9.1	159.8	20.4	-214.5	434.6*	196.0
		LSD 0.05=343.3			LSD 0.01=451.9					
Oil content		Male 1	Male 2	Male 3	Male 4	Male 5	Male 6	Male 7	Male 8	Male 9
	Female 1	0.24	-0.91*	-0.58	0.05	-0.04	0.40	0.74	-0.49	0.59
	Female 2	0.32	0.21	1.45**	-0.87*	-0.29	0.47	0.21	0.04	-1.54**
	Female 3	-0.58	0.28	0.51	-0.44	0.21	0.41	-0.26	0.13	-0.25
	Female 4	0.62	0.51	-1.48**	1.09*	-0.55	-1.73**	0.38	0.14	1.02*
	Female 5	-0.60	-0.09	0.11	0.17	0.67	0.46	-1.07*	0.18	0.18
		LSD 0.05=0.83			LSD 0.01=1.10					
Days to flowering		Male 1	Male 2	Male 3	Male 4	Male 5	Male 6	Male 7	Male 8	Male 9
	Female 1	-0.63	0.20	0.80	-0.37	1.63*	-0.07	-0.97	-0.93	0.33
	Female 2	0.64	-1.69*	0.24	0.74	0.24	1.04	-1.36	1.34	-1.22
	Female 3	-0.97	0.70	0.97	0.13	-1.70*	-0.23	0.70	-1.10	1.50
	Female 4	0.74	0.90	-3.00**	-0.33	-0.16	-2.03*	1.07	1.60*	1.20
	Female 5	0.22	-0.11	0.99	-0.18	-0.01	1.29	0.55	-0.91	-1.81*
		LSD 0.05=1.58			LSD 0.01=2.08					
Days to maturity		Male 1	Male 2	Male 3	Male 4	Male 5	Male 6	Male 7	Male 8	Male 9
	Female 1	-0.18	0.32	0.29	-1.38	0.49	0.09	0.29	-0.01	0.12
	Female 2	0.99	0.15	0.12	-0.55	-1.51*	-0.08	0.45	0.15	0.29
	Female 3	-0.77	0.23	0.36	0.53	0.56	1.16	-1.64*	0.23	-0.64
	Female 4	0.26	-0.74	0.40	0.56	0.10	-1.64*	-0.10	0.43	0.73
	Female 5	-0.29	0.04	-1.16	0.84	0.37	0.47	1.01	-0.79	-0.49
		LSD 0.05=1.40			LSD 0.01=1.84					

*, ** significant difference from zero at 0.05 and 0.01 levels of probability, respectively.

days. The maximum negative value of SCA effect was found in the cross of female 4 $\times$ male 3 (Qianyou 6A $\times$ III153) with the value of -3.00 days, followed by crosses female 4 $\times$ male 6 (Qianyou 6A $\times$ III199), female 5 $\times$ male 9 (Qianyou 8A $\times$ 1190), female 3 $\times$ male 5 (Qianyou 3A $\times$ III188) and female 2 $\times$ male 2 (24A $\times$ 2365) with the SCA effects values of -2.03, -1.81, -1.70 and -1.69 days, respectively.

Significant negative SCA effects of days to maturity were found for 3 crosses out of 45. The maximum negative value of SCA effect was found in the crosses of female 3 $\times$ male 7 (Qianyou 3A $\times$ III224) and female 4 $\times$ male 6 (Qianyou 6A $\times$ III199) with the value of -1.64 days, followed by cross female 2 $\times$ male 5 (24A $\times$ III188) with the SCA value of -1.51 days. These crosses should be considered in breeding for early maturity.

This study indicated that high SCA cross could be obtained from crossing between any high or low GCA effect parents. For example, the cross of female 3 $\times$ male 2 (Qianyou 3A $\times$ 2365) gave significantly positive SCA effect for seed yield, but both parents gave negative and significant GCA effects for this trait. On the other hand, the high SCA cross of a character might not correspond to the mean performance of cross for the character. For example, the cross of female 2 $\times$ male 3 (24A $\times$ III153) gave the highest significant SCA value for oil content, but the mean oil content of this cross was 39.89%, lower than the highest oil content of 43.38% in the cross of female 1 $\times$ male 7 (QH303-4A $\times$ III224).

For individual male parents, males 1, 5, 7 and 8 (2313, III188, III224 and q034) gave high seed yield in their cross combinations. Their high yielding potential was associated with high GCA effects (Table 5.8). These lines should be useful in future breeding program. For female parents, high mean square of GCA

effects for seed yield was associated with negative GCA effects of certain parent, four females gave positive GCA effects but none of them were significant. However, the yield expression shown in Table 5.6 suggested that females 2 and 4 (24AB and Qianyou 6AB) were quite good combiners.

From the present study, it may be suggested that males 8, 5 and 7 (q034, III188 and III224) should be good combiners and be used extensively in a breeding program aiming at developing breeding materials to improve yield as they gave high GCA effects. Males 8 and 7 (q034 and III224) were one of the parents in the cross combinations with high SCA effects for seed yield (Table 5.9). Male 7 (III224) also gave high GCA effect for oil content. None of the females gave significant and positive GCA effects for seed yield, but female 2 and female 4 (24AB and Qianyou 6AB) were outstanding without regard to GCA effects. The crosses of female 5 $\times$ male 8 (Qianyou 8A $\times$ q034), female 4 $\times$ male 8 (Qianyou 6A $\times$ q034) and female 1 $\times$ male 7 (QH303-4A $\times$ III224) were promising for high yield.

Comparison of means of the parents and hybrids (Table 5.6) showed that males 1 and 4 (2313 and III176) and their hybrids expressed early maturity. The early maturity is related to negative GCA effects of days to maturity. Both males 1 and 4 (2313 and III176) gave significant and negative GCA effects indicating that these two lines should be useful in future breeding program for earliness.

5.4.5 Heterosis, Heterobeltiosis and Standard Heterosis

The heterosis, heterobeltiosis and standard heterosis of single cross hybrids are presented in Table 5.10 for four characters. Yield improvement is the ultimate goal in a rapeseed breeding program. High yield is always the main objective, therefore, positive heterosis is desirable for seed yield. Both high positive heterosis

Table 5.10 Heterosis, heterobeltiosis and standard heterosis of single crosses.

Characters	Yield			Oil content			Days to flower			Days to maturity		
	MP [‡]	HP	SH	MP	HP	SH	MP	HP	SH	MP	HP	SH
	%	%	%	%	%	%	%	%	%	%	%	%
Female 1× male 1	68.8 **	66.2 **	8.2	4.2 **	4.0 **	8.8 **	-1.2 **	-2.6 **	-1.3 **	-0.1	-0.4	-0.3
male 2	27.7 **	23.8 **	-21.9 **	0.9	2.7 *	7.5 **	1.6 **	0.6 **	1.0 **	0.9 **	0.5	1.5 **
male 3	42.6 **	30.4 **	-17.7 **	2.2	2.4	7.2 **	0.3	0.3	-1.3 **	0.3	0.1	0.7 *
male 4	43.5 **	27.2 **	-19.8 **	7.7 **	5.1 **	9.9 **	-0.7 **	-1.7 **	-1.3 **	-0.4	-1.0	-0.8
male 5	39.4 **	25.3 **	-0.9	0.9	1.0	5.7 **	-0.1	0.3	-2.1 **	0.5	0.0	1.0
male 6	16.5 *	10.8	-30.1 **	5.5 **	4.5 **	9.4 **	0.4 *	-0.4 *	-0.4 *	0.5	0.3	0.7
male 7	77.0 **	60.8 **	24.2 **	7.9 **	7.5 **	12.5 **	-1.2 **	-2.7 **	-1.2 **	-0.1	-0.4	0.3
male 8	35.2 **	20.9 **	-3.3	2.6 *	3.1 *	7.9 **	-1.3 **	-3.2 **	-1.0 **	-0.4	-1.0	0.3
male 9	88.3 **	81.1 **	14.3 **	6.5 **	5.6 **	10. **	0.3	-2.1 **	1.2 **	0.5	0.2	1.0 **
Female 2× male 1	68.6 **	55.4 **	20.0 **	2.3	-2.0	2.0	1.3 **	-0.3	1.0 **	0.3	0.0	0.3
male 2	-4.5	-15.6 **	-34.8 **	1.5	-4.6 **	3.4 **	2.3 **	1.1 **	1.6 **	0.8 *	0.5	1.5 **
male 3	63.8 **	37.4 **	6.1	5.2 **	0.3	5.4 **	1.8 **	1.6 **	0.0	0.2	0.1	0.7 *
male 4	53.4 **	25.2 **	-3.4	3.2 *	1.1	0.5	1.8 **	0.6 **	1.0 **	-0.1	-0.7	-0.4
male 5	53.7 **	51.9 **	20.1 **	-2.1	-6.5 **	-2.0	0.9 **	1.2 **	-1.3 **	-0.4	-0.7	0.3
male 6	27.0 **	10.3	-14.9 **	3.6 **	-0.1	2.6 *	2.9 **	1.9 **	1.9 **	0.4	0.3	0.7 *
male 7	37.4 **	37.4 **	6.1	4.5 **	0.2	4.1 **	0.4 **	-1.2 **	0.3	0.0	-0.2	0.5
male 8	43.6 **	41.1 **	12.8 **	1.7	-3.3 *	2.3	1.8 **	-0.3	2.0 **	-0.4	-0.9	0.4
male 9	32.4 **	16.2 **	-10.3 *	-1.1	-4.7 **	-2.0	1.1 **	-1.4 **	1.9 **	0.6	0.4	1.1
Female 3× male 1	23.8 **	10.5	-28.1 **	-3.8 **	-6.7 **	-2.9 *	-2.1 **	-3.9 **	-2.6 **	-0.7 *	-0.8	-1.2 **
male 2	42.6 **	32.7 **	-21.3 **	-2.0	-6.8 **	1.0	1.2 **	-0.2	0.3	0.6	-0.2	0.7 *
male 3	33.1 **	31.5 **	-31.2 **	-1.0	-4.5 **	0.4	-0.4 *	-0.7 **	-2.3 **	0.0	-0.6	0.0
male 4	31.2 **	28.2 **	-34.5 **	0.5	-0.3	-0.9	-1.1 **	-2.4 **	-2.0 **	0.1	0.0	-0.7 *
male 5	50.4 **	23.8 **	-2.1	-4.5 **	-7.8 **	-3.2 *	-2.8 **	-2.7 **	-5.1 **	0.2	-0.7	0.3
male 6	37.6 **	30.6 **	-25.7 **	-0.4	-2.7 *	-0.2	-0.4 *	-1.6 **	-1.6 **	0.6	0.1	0.5
male 7	26.6 **	5.2	-18.8 **	-0.5	-3.4 **	0.3	-0.9 **	-2.8 **	-1.3 **	-1.2 **	-1.9 **	-1.2 **
male 8	24.7 **	2.2	-18.3 **	-1.8	-5.5 **	-0.1	-2.1 **	-4.3 **	-2.1 **	-0.6 *	-1.6 **	-0.3
male 9	44.9 **	35.9 **	-20.8 **	-1.6	-4.0 **	-1.3	0.2	-2.5 **	0.7 **	-0.1	-0.8 *	-0.1
Female 4× male 1	64.8 **	59.7 **	10.8 *	4.2 **	-0.3	3.8 **	-0.2	-1.6 **	-0.3 **	-0.6	-1.2 **	-0.3
male 2	38.5 **	28.4 **	-10.9 *	3.4 *	-2.9 *	5.2 **	2.2 **	1.3 **	1.7 **	-0.2	-0.2	0.7 *
male 3	44.7 **	26.9 **	-11.9 **	-1.3	-5.9 **	-1.1	-1.8 **	-1.9 **	-3.3 **	-0.3	-0.4	0.5
male 4	50.5 **	28.1 **	-11.1 *	9.6 **	7.3 **	6.7 **	-0.5 **	-1.4 **	-1.0 **	-0.3	-1.2 **	-0.3
male 5	43.0 **	34.2 **	6.1	-1.7	-6.2 **	-1.6	-1.0 **	-0.5 **	-2.9 **	-0.4	-0.4	0.6
male 6	51.4 **	37.7 **	-4.4	-1.0	-4.6 **	-2.1	-0.6 **	-1.3 **	-1.3 **	-0.9 **	-1.1 **	-0.2
male 7	59.3 **	51.2 **	16.8 **	6.1 **	1.7	5.6 **	0.2	-1.2 **	0.3	-0.9 **	-1.0 **	-0.1
male 8	76.0 **	64.4 **	31.4 **	3.1 *	-2.1	3.6 **	0.3 *	-1.5 **	0.7 **	-0.9 **	-1.1 **	0.2
male 9	51.0 **	38.9 **	-3.6	6.7 **	2.8 *	5.7 **	0.9 **	-1.4 **	1.9 **	0.1	0.0	1.0 **
Female 5× male 1	20.4 **	6.3	-9.8 *	-0.9	-4.7 **	-0.8	-0.1	-0.3	1.4 **	0.1	-0.1	0.0
male 2	2.0	-13.4 **	-26.5 **	0.0	-5.7 **	2.2	2.1 **	1.4 **	3.2 **	1.1 **	0.7 *	1.7 **
male 3	20.6 **	-2.5	-17.3 **	0.9	-3.4 **	1.5	1.0 **	-0.7 **	1.0 **	0.0	-0.2	0.4
male 4	30.7 **	2.9	-12.7 **	5.2 **	3.4 *	2.8 *	0.1	-0.6 **	1.2 **	0.8 *	0.3	0.4
male 5	46.2 **	41.2 **	19.8 **	-0.4	-4.6 **	0.1	-0.4 *	-2.4 **	-0.7 **	0.7 *	0.3	1.3 **
male 6	21.8 **	1.7	-13.7 **	2.8 *	-0.5	2.1	1.8 **	1.0 **	2.7 **	1.0 **	0.8 *	1.2 **
male 7	22.8 **	17.3 **	-0.5	0.4	-3.4 **	0.3	0.4 *	0.3	2.0 **	0.5	0.2	1.0 **
male 8	61.5 **	56.9 **	33.1 **	1.3	-3.3 **	2.2	-0.7 **	-1.0 **	1.3 **	-0.4	-1.0 **	0.3
male 9	52.9 **	29 **	9.4 *	2.6	-0.8	2.0	-0.3 *	-1.1 **	2.2 **	0.6	0.3	1.0 **
Mean	41.9	29.2	-5.4	1.8	-1.3	2.8	0.2	-0.9	-0.1	0.0	-0.3	0.4

*, ** significant difference from mid-parent, high parent and hybrid check at 0.05 and 0.01 levels of probability, respectively.

‡ MP = heterosis over mid-parent; HP = heterobeltiosis, heterosis over high parent.
SH = standard heterosis, heterosis over hybrid check.

and heterobeltiosis for seed yield were observed for single crosses. Heterosis of single crosses for seed yield ranged from -4.5 to 88.3% with the mean of 41.9%. Only one out of 45 single crosses showed negative heterosis, and 43 out of 45 crosses showed significant and positive heterotic values. Heterobeltiosis of single crosses for seed yield ranged from -15.6 to 81.1% with the mean of 29.2%. Only three single crosses showed negative heterobeltiosis. Thirty six crosses out of 45 showed significant and positive heterobeltiotic values. Both the highest heterosis (88.3%) and heterobeltiosis (81.1%) were found in the same cross of female 1 $\times$ male 9 (QH303-4A $\times$ 1190). Standard heterosis of single crosses for seed yield ranged from -34.8 to 33.1% with the mean of -5.2%. Fifteen crosses out of 45 showed positive standard heterosis, and 11 crosses showed significant values. The highest standard heterosis (33.1%) of seed yield was found in the cross of female 5 $\times$ male 8 (Qianyou 8A $\times$ q034).

Improvement of oil content of rapeseed is one of the main objectives in rapeseed breeding programs. The positive heterosis is desirable for this trait. In this study, both positive and negative heterosis of single crosses were found for oil content. The range was from -4.5 to 9.6% with the mean of 1.8%. Twenty nine crosses out of 45 showed positive heterosis for oil content and eighteen crosses out of 29 were significant. The highest heterosis for oil content was found in the cross of female 4 $\times$ male 4 (Qianyou 6A $\times$ III176) with the value of 9.6%. Heterobeltiosis of oil content ranged from -7.8 to 7.5% with the mean of -1.3%. Sixteen crosses out of 45 gave positive heterobeltiosis for oil content and ten crosses out of 16 were significant. The highest heterobeltiosis was recorded for the cross of female 1 $\times$ male 7 (QH303-4A $\times$ III224) with the value of 7.5%. Standard heterosis ranged from -3.2 to 12.5%. Thirty four crosses out of 45 gave positive standard heterosis and twenty out of 34 were

significant. The highest standard heterosis was found in the cross of female 1 $\times$ male 7 (QH303-4A $\times$ III224) with the value of 12.5%.

The heterosis of days to flowering ranged from -2.8 to 2.9% with the mean of 0.2%. Twenty one crosses out of 45 showed negative heterosis for this trait, sixteen crosses out of 21 gave significant values, while the heterosis of 18 crosses out of 24 were positive and significant. The maximum significantly negative value (-2.8%) was found in the cross of female 3 $\times$ male 5 (Qianyou 3A $\times$ III188), while the highest positive value (2.9%) was found in the cross of female 2 $\times$ male 6 (24A $\times$ III199). The heterobeltiosis of days to flowering ranged from -4.3 to 1.9% with the mean of -0.9%. Thirty two crosses out of 45 gave negative heterobeltiosis, and twenty seven out of 32 crosses were significant. The maximum significantly negative value (-4.3%) was found in the cross of female 3 $\times$ male 8 (Qianyou 3A $\times$ q034), while the highest positive value (1.9%) was found in the cross of female 2 $\times$ male 6 (24A $\times$ III199). Standard heterosis ranged from -5.1 to 3.2% with the mean of -0.1%. Twenty one crosses out of 45 gave negative standard heterosis. The lowest significantly negative heterosis (-5.1%) was found in the cross of female 3 $\times$ male 5 (Qianyou 3A $\times$ III188). The highest positive standard heterosis value was found in the cross of female 5 $\times$ male 2 (Qianyou 8A $\times$ 2365).

Heterosis of days to maturity ranged from -1.2 to 1.1% with the mean of 0%. Out of 45 crosses, 21 crosses showed negative heterosis and 6 crosses exhibited significant and negative values, while 6 out of 24 crosses gave significant and positive values. The maximum negative value (-1.2%) was found in the cross of female 3 $\times$ male 7 (Qianyou 3A $\times$ III224). The highest positive heterosis (1.1%) was found in the cross of female 5 $\times$ male 2 (Qianyou 8A $\times$ 2365). Heterobeltiosis of days

to maturity ranged from -1.9 to 0.8% with the mean of -0.3%. Twenty eight crosses displayed negative heterobeltiosis and 10 crosses out of 28 were significant. The highest positive heterobeltiosis (0.8%) was found in the cross of female 5 $\times$ male 6 (Qianyou 8A $\times$ III199). Standard heterosis ranged from -1.2 to 1.7% with the mean of 0.4%. Negative standard heterosis was found in 12 crosses, while the other 33 crosses gave positive or no heterosis. Significant and positive standard heterosis was recorded in 16 crosses. The highest heterosis (1.7%) was observed in the cross of female 5 $\times$ male 2 (Qianyou 8A $\times$ 2365). The maximum negative value (-1.2%) was found in the crosses of female 3 $\times$ male 7 (Qianyou 3A $\times$ III224) and female 3 $\times$ male 1 (Qianyou 3A $\times$ 2313).

For hybrid breeding of rapeseed in China, the hybrid is acceptable only when it gives a better performance than standard varieties which are being grown widely. Therefore, standard heterosis was included in this study by using a commercial hybrid, Qianyou no. 20, as the standard check.

The heterosis and heterobeltiosis found for seed yield in this study with the ranges of -4.5 to 88.3% and -15.6 to 81.1%, respectively, were lower than that reported by some researchers (Brandle and McVetty, 1989; Teklewold and Becker, 2005; Singh, 2007). However, there were still some reports with lower rates of heterosis (Sernyk and Stefansson, 1983; Starmer et al., 1998; Shen et al., 2002).

The range of heterosis for oil content was bigger, but the mean heterosis was smaller than those found by some researchers (Shen et al., 2002; Teklewold and Becker, 2005; Hu and Liu, 1989). However, the range of heterosis was smaller than that found by Wang (1992) and Starmer et al. (1998).

For days to flowering and days to maturity, both positive and negative

heterosis were recorded. Similar rates of heterosis in *Brassica* were found for days to flowering by Teklewold and Becker (2005) and Ofori and Becker (2007). However, the degree of heterosis observed in this study for days to maturity was smaller than that found by Teklewold and Becker (2005) and Singh (2007). For these two characters, early flowering might provide ample period for seed formation process and early maturity might avoid the rising temperature and give plenty of time for next planting crop. Therefore, negative heterosis was also desirable for certain types of varieties. The values of heterosis for days to flowering and days to maturity were relatively small, this was due to the relatively small ranges for these characters. However, 8.8 days earlier for flowering in the cross of female 3 $\times$ male 5 (Qianyou 3A $\times$ III188) and 3 days earlier for maturity in the cross of female 3 $\times$ male 1 (Qianyou 3A $\times$ 2313) than standard check (Table 5.5) were very desirable in rapeseed production. Therefore, these two crosses should be considered as candidates for early hybrid breeding.

Comparisons of means of the parents and hybrids (Table 5.6) showed that the hybrids produced higher seed yield than parents. This was the manifestations of heterosis of this character. The percentages of heterosis and heterobeltiosis for seed yield of individual cross as shown in Table 5.10 were strikingly high, some even as high as 88.3% for heterosis and 81.1% for heterobeltiosis in the cross of female 1 $\times$ male 9 (QH303-4A $\times$ 1190), indicating the genetically diversity of this pair cross. The manifestations of heterosis are associated with SCA effects. These were responded by significant SCA effect of this cross, although not the highest one. However, this did not mean that the highest heterosis corresponded to the highest yielding hybrid as GCA effects are also taking part in the yield expression. The highest yielding hybrids

with considerable portions of both GCA and SCA effects should be the best choice for rapeseed breeders. In this study, the top eight crosses namely females $\times$ males 5×8 , 4×8 , 1×7 , 2×5 , 2×1 , 5×5 , 4×7 and 1×9 (Qianyou 8A $\times$ q034, Qianyou 6A $\times$ q034, QH303-4A $\times$ III224, 24A $\times$ III188, 24A $\times$ 2313, Qianyou 8A $\times$ III188, Qianyou 6A $\times$ III224 and QH303-4A $\times$ 1190) which yielded high for seed yield showed positive GCA effects for both parents and positive SCA effects, and at least one of these effects was significant. These crosses also showed significant and positive standard heterosis for seed yield. Therefore, these crosses should be taken as candidate hybrids in future rapeseed breeding program, especially crosses with high oil content.

5.5 Conclusion

A factorial cross was made in rapeseed using 5 RGMS lines as female and 9 inbred lines as male to produce 45 hybrids. The crosses, their parents and a check hybrid were tested in the evaluation trial at Guiyang and Zunyi, China during 2007 - 2008. Although growing conditions in which this experiment was conducted were not favorable to some extents, the data observed for all characters were not much affected and still reliable.

The results from the analysis of variance showed that rapeseed parents used in this study possessed some degrees of diversity for seed yield, oil content and days to flowering, but not for days to maturity. These could be observed in the manifestation of hybrids which were also significantly different for all characters. It also was found in this experiment that most of the GE effects were significant.

Many means for seed yield of individual hybrids tested at two locations were

higher than standard check indicating that these crosses were favorable. Eleven hybrids yielded high and significantly higher than standard check. This indicates that these crosses can be used for future breeding program, especially those with high oil content.

Results from the analysis of variance for combining ability demonstrated that both GCA and SCA effects were important for most characters. Relative importance of GCA and SCA effects for each trait as examining by the ratio of GCA sum of squares to hybrids sum of squares showed that, for all characters, GCA effects were more important than SCA effects. However, SCA effects were significant in the expression of seed yield, oil content and days to flowering, indicating that non-additive gene effects also contributed to the variation observed for these traits.

For individual parents, males 1, 5, 7 and 8 (2313, III188, III224 and q034), and females 2 and 4 (24AB and Qianyou 6AB) gave high GCA effects for seed yield. Male 7 (III224) and female 1 (QH303-4AB) gave high GCA effects for oil content. These lines should be useful in future breeding program for high yield and oil content. It may be suggested that males 8, 5 and 7 (q034, III188 and III224) should be used extensively in a breeding program aiming at developing breeding material to improve yield as they gave high GCA effects. Comparisons of means of the parents and hybrids (Table 5.6) showed that males 1 and 4 (2313 and III176) and their hybrids expressed early maturity. The early maturity was related to negative GCA effects of days to maturity. Both males 1 and 4 (2313 and III176) gave significantly negative GCA effects indicating these two lines should be useful in future breeding program for early maturity.

Our results of SCA effects indicate that high SCA cross could result from

crossing in any combinations between high or low GCA effect parents. High SCA effects of a cross indicated greater genetic diversity of the two parents. On the other hand, the high SCA cross of a character might not correspond with the mean performance of cross for the character as the GCA effects are also taking part in the character expression. Differences among hybrids were due to both GCA and SCA effects.

The percentages of heterosis and heterobeltiosis for seed yield of individual crosses were high, indicating the genetic diversity of crosses. The manifestations of heterosis are associated with SCA effects. However, this did not mean that the highest heterosis corresponded to the highest yielding hybrids. The highest yielding hybrids with considerable portion of both GCA and SCA effects should be the best choice for rapeseed breeders. The crosses of female 5 $\times$ male 8, female 4 $\times$ male 8 and female 1 $\times$ male 7 (Qianyou 8A $\times$ q034, Qianyou 6A $\times$ q034 and QH303-4A $\times$ III224) were promising for high yield.

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CHAPTER VI

SUMMARY

The inheritance of seed yield, oil content and other characters related to yield and oil content of rapeseed were studied in three experiments as follows:

Experiment I (generation mean analysis)

1. The distributions of F_2 populations of certain characters showed transgressive variations, indicating that dominant and recessive genes controlling these characters distributed in both parents. The accumulation of favorable genes in one parent should be made for the improvement of these characters.

2. Results from genetic analysis using six parameter model for oil, protein, erucic acid, oleic acid and glucosinolate contents, days to flowering and days to maturity showed that protein content in Cross II (III38 $\times$ III142) followed additive-dominance model with both additive and dominance effects were important. Other characters were controlled by both additive and non-additive gene effects. However, non-additive gene effects were not important for erucic acid and oleic acid contents, while additive gene effects played predominantly roles for these two characters.

3. High broad sense and narrow sense heritabilities were obtained for erucic acid in Cross I (III174 $\times$ Zi20). This indicates that additive gene effects controlled this character. High broad sense heritabilities and moderate narrow sense heritabilities for oleic acid and glucosinolate contents indicate that these characters were controlled mainly by genetic effects, and both additive and non-additive gene effects were

important.

4. Estimates for minimum number of genes showed that two major gene pairs controlled erucic acid and oleic acid contents in Cross I (III174 $\times$ Zi20), three major gene pairs and at least one major gene pair controlled glucosinolate content in Cross I (III174 $\times$ Zi20) and days to flowering in Cross II (III38 $\times$ III142), respectively. However, small number of gene pair was found for other characters studied.

Experiment II (diallel mating design)

1. Both GCA and SCA effects were important for seed yield, oil content, pods per plant, seeds per pod, 1,000 seed weight, branches per plant, plant height, days to flowering, and days to maturity. GCA effects were more important than SCA effects in all traits.

2. Certain lines gave significantly positive GCA effects for seed yield and oil content. These lines should be useful for improving these two characters.

3. Analysis of SCA effects revealed that a number of crosses showed significant SCA effects for each character. Certain crosses with significant SCA effects for seed yield also showed significant SCA effects for yield related traits. These indicate that there are some relationships between the magnitude of SCA effects for seed yield and that of yield related traits.

4. Both positive and negative heterosis and heterobeltiosis were found for all characters. The percentages of heterosis and heterobeltiosis for seed yield in some crosses were considerably high indicating the high degree genetic diversity among parents. It was found that percentages of heterosis and heterobeltiosis for seed yield were associated with those of yield related characters, especially pods per plant and seed size.

5. The results from correlation and path analyses showed that pods per plant, seeds per pod, 1,000-seed weight and plant height gave positive correlations with seed yield and contributed high direct contributions to this character. Other characters including branches per plant, days to flowering, days to maturity and oil content provided either negative or very low direct effects to seed yield.

Experiment III (NCII design)

1. The results from the analysis of variance showed that rapeseed parents used in this study possessed some degrees of diversity for seed yield, oil content and days to flowering, but not days to maturity. These could be observed in the manifestation of hybrids which were also significantly different for all characters.

2. Means for seed yield of many hybrids were higher than standard check indicating that these crosses were favorable. Eleven hybrids gave significantly higher seed yield than standard check. These crosses can be used for future breeding program, especially those with high oil content.

3. Both GCA and SCA effects were important for most characters. The ratios of GCA sum of squares to hybrids sum of squares indicate that, for all characters, GCA effects were more important than SCA effects.

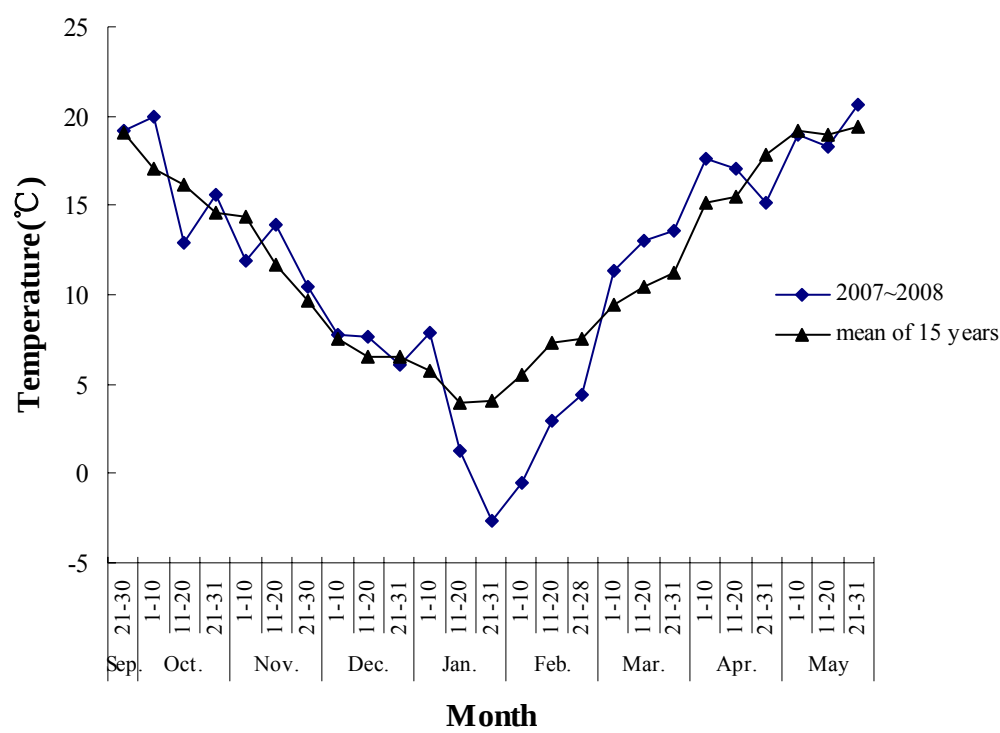
4. Certain male and female parents gave high GCA effects for seed yield and oil content. These lines should be useful in future breeding program for both characters.

5. The percentages of heterosis and heterobeltiosis for seed yield of individual crosses were high, indicating the genetic diversity of crosses. However, this did not mean that the highest heterosis corresponded to the highest yielding hybrids.

APPENDIX

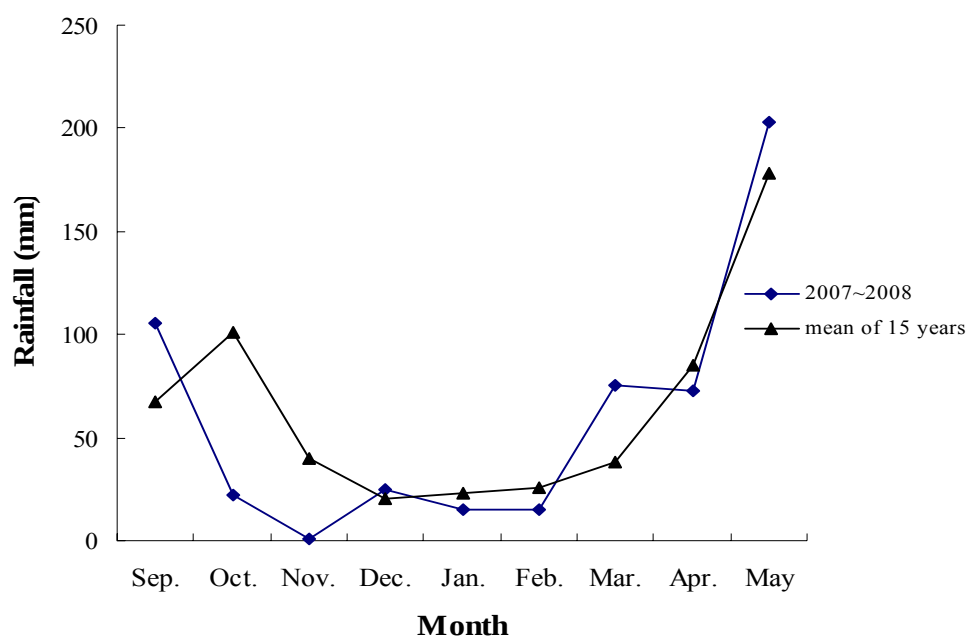
APPENDIX

Temperature



Attached figure 1 Average temperature at Guiyang during rapeseed growing season.

Rainfall



Attached figure 2 Rainfall at Guiyang during rapeseed growing season.

BIOGRAPHY

Zesu Huang was born on October 12, 1965 in Guizhou province, the People's Republic of China. She received her Bachelor's Degree in agronomy science from Southwest Agriculture University in 1986. She has engaged in the study of rapeseed breeding in Guizhou Academy of Agricultural Science since her graduation. In 1999, she continued her M.S. study at Guizhou University and obtained her Master's Degree in plant breeding in 2003. Then she got the opportunity to study for her Ph. D. in plant breeding under the supervision of Prof. Dr. Paisan Laosuwan in School of Crop Production Technology, Suranaree University of Technology, Thailand.