GENETIC VARIABILITY FOR YIELD AND QUALITY CHARACTERISTICS IN SOUTH AFRICAN PUMPKIN (*Cucurbita maxima* Duch.)

By

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Submitted in the fulfilment of the requirements for the degree

Magister Scientiae Agriculturae

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November 2002

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ACKNOWLEDGEMENTS

I would like to express my gratitude to the following people:

- My Heavenly Father for the ability to undertake this study;
- Dr. H. Maartens for her guidance during the course of the study;
- Prof. M. Labuschagne for the statistical analysis of the data;
- PANNAR Research Services for supplying the resources and making the study possible;
- Everybody who supported and encouraged me over the last year.

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CHAPTER 1

INTRODUCTION

The *Cucurbitaceae* consists of nearly a hundred genera and over 800 species. There is tremendous genetic diversity within the family and the range of adaptation for Cucurbit species include tropical and sub-tropical regions, arid deserts and temperate locations. A few species are adapted to production at elevations as high as 2000m (Ng, 1993).

Pumpkin (*Cucurbita maxima* Duch.) is an important vegetable consumed throughout Southern Africa, South America, India and Australia. *C. maxima* displays a variety of sizes and shapes with specific characteristics more important in certain areas than others. The latter resulted in specific varieties or types being produced in certain areas of the world, with the main common trait being an important source of β-carotene (Kubicki and Walczak, 1976). According to the FAO production yearbook (2001) 16 208 584Mt of pumpkins, squash and gourds were produced world-wide in 2001. During 2000 a total of R93.4 million *C. maxima* produce was sold on the South African fresh produce markets (South African National Department of Agriculture, 2000).

One of the most popular and effective methods of variety improvement, especially in the case of cross-pollinated species, is hybrid breeding. According to Korzeniewska and Niemirowicz-Szczytt (1993) the first heterosis in *C. maxima* has been detected almost a hundred years ago. Despite this, very little is known about heterosis of specific characteristics in pumpkin. According to Whitaker and Robinson (1986) one of the difficulties in breeding *Cucurbita* is that pollinations are made before it is possible to make selections for fruit type. Pumpkin cannot be judged for fruit type until mature, when it is too late to make additional pollinations. Breeders, therefore, often make more pollinations than required for the desired number of selections, and save seed only from the best fruit. Due to the monoecious nature of pumpkin, harvesting of seed from uncontrolled pollinations rarely have any advantage. Large space requirements and hand pollinations further resulted in very little effort

being made to exploit the great genetic variability available in pumpkin in breeding programmes.

Although much time and effort are currently given to virus resistance breeding (Robinson and Decker-Walters, 1997), many questions around agronomic and quality genetic expression are still unanswered. Although some work has been done on *C. moschata*, very little is known about the quantitative genetics of any characteristic in *C. maxima*.

Objectives of this study

The objectives of this study on the F1-derived diallel were:

- To study the genetic variability for agronomic and quality characteristics in pumpkin, *C. maxima*,
- To determine the amount of variation accounted for by additive and non-additive gene action in economic important characteristics,
- To study the heritability of pumpkin characteristics as well as to identify the expected response to direct and indirect selection,
- To identify which characteristics should be improved through hybrid breeding.

CHAPTER 2

LITERATURE REVIEW

2.1 Origin and early history

The *Cucurbitaceae* consists of two well defined subfamilies, eight tribes, and about 118 genera with a total of 825 species (Pitrat *et al*, 1999). Robinson and Decker-Walters (1997) found the family not to be closely related to any other plant family. According to Saade and Hernandez (1994) this family is the plant group with the most species used as human food, while the genus *Cucurbita* is one of the most important. Other important genera include watermelon, cucumber and melon and form part of the *Cucurbitoideae* subfamily (Keen *et al*, 1999).

Cucurbita represents a very interesting example of the domestication of different species with more or less the same usage in different areas: *Cucurbita pepo* is used in Mexico and the south of USA, *Cucurbita moschata* in central America and *Cucurbita maxima* in South America (Pitrat *et al*, 1999). In spite of the current marginalization of some of these species, from very remote times all have contributed essential food products to the diet of rural and some urban communities on the American continent and in many other parts of the world (Saade and Hernandez, 1994). According to Whitaker and Robinson (1986) and Nerson *et al* (2000), there are good evidence from archaeological sites in the south western United States, Mexico and South America (Argentina) that *C. pepo, C. moschata, C. mixta* and *C. maxima* were widely cultivated in pre-Colombian times (prior to 1492 A.D.).

In South Africa *C. maxima* is used as pumpkin. However, the term "pumpkin" applies to the edible fruit of any species of the *Cucurbita,* utilized when ripe as a table vegetable. For this reason pumpkin is not only restricted to *C. maxima*, but can also refer to *C. moschata* (e.g. butternut) and *C. pepo* L. (e.g. squashes and baby marrows) (Whitaker and Robinson, 1986). In the rest of the world "squash" is rather used than "pumpkin" with summer squash

referring to fruit used in the immature stage. Ng (1993) mentioned that squash is derived from Algonquin Indian "askoot asquash" which means "eaten green". However, *Cucurbita* fruit consumed in the mature stage is known as winter squash.

2.2 Cytology and mating system

There are about 25 to 27 *Cucurbita* species, all with 20 pairs of small, dotlike chromosomes (Bemis, 1973). According to Robinson and Decker-Walters (1997) *Cucurbita* is believed to be an ancient tertaploid genus derived from an ancestor with a base chromosome number of 10. Isozymic evidence has confirmed the polyploid nature of this genus. The polyploidy occurred long ago as indicated by all species of the genus having 20 pairs of chromosomes and disomic 3:1 gene ratios in segregating populations. Morphological differentiation of species appears to be based upon gene mutation, rather than differences in chromosome numbers or polyploidy. As far as known, chromosome translocations, deletions or inversions did not have a role in specie differentiation in *Cucurbita* (Francis and Bemis, 1970; Whitaker and Robinson, 1986).

According to Robinson and Decker-Walters (1997) the absence of chromosome mutations does not necessarily produce fertile interspecies hybrids. Both crosses between *C. pepo* and *C. maxima* with *C. moschata* produced partially fertile hybrids, but crosses between the first two species resulted in viable but sterile F1 plants. However, specific combinations of certain genotypes in different species will be more compatible than others. Superak *et al* (1993) mentioned that interspecific F1 hybrids between *C. maxima* and *C. moschata* are marketed commercially by Japanese seed companies.

Robinson and Decker-Walters (1997) reported most Cucurbits to be monoecious, that is, they have separate male and female flowers on the same plant. However, genes for different forms of sex expression are known for these crops, especially in watermelon, melon and cucumber. Monoecious

cultivars may also differ in the degree of female expression, some having a higher proportion of female to male flowers. The ratio between male and female flowers is also influenced by the environment as mentioned by Herbert (2002). Temperatures lower than 17°C and above 38°C promote the initiation of male flowers over female flowers, promoting pollination but lowering the yield in *C. pepo* summer squash.

Plants with monoecious flowers are normally cross-pollinated, but due to the absence of self-incompatibility in pumpkin, self-pollination may occur. In cross-pollinating species each plant will contain both homozygous and heterozygous loci, but it is the heterozygous loci that give the group of plants its characteristic genetic structure. In this structure of an almost limitless number of gene combinations, two plants with identical genotypes would almost never be found. Each generation brings a reshuffling and a regrouping of genes, a consequence of normal cross-pollination. Under natural influences, the population is relatively fluid, in which genes favouring adaptation and increased seed production tend to increase at the expense of genes unfavourable for adaptation or fitness. However, this genetic structure will be lost with successive self-pollination or inbreeding. For this reason a breeder should strive to maintain superior hybrid combinations in cross-pollinating crops like pumpkin (Poehlman, 1987).

Parthenocarpic fruit development has long been recognized as an important characteristic for greenhouse cucumbers (*Cucumis sativus*). European greenhouse varieties were selected in the 19th century for high yield, often without realizing that the basis for this productivity was their ability to set parthenocarpic fruit when bees and other pollinating insect were absent (Robinson and Reiners, 1999). According to Herbert (2002), the first commercial parthenocarpic *C. pepo* varieties are available. The latter will develop fruit in the absence of pollination, but no seed will be produced. According to Robinson and Decker-Walters (1997) parthenocarpy in cucumber and squash is promoted by low temperatures, short day lengths and old plant age.

2.3 Importance

Pitrat *et al* (1999) mentioned that *Cucurbita* species are mainly cultivated for their fruits (mature or immature) for human or animal consumption. However, seeds are also commonly used, including as a source of oil. Flowers, leaves and young stems are also eaten.

The Economic Research Service USDA (Lucier and Plummer, 2001b) forecasted the five leading producers of *Cucurbita* in the world (China, India, Ukraine, United States and Egypt) to produce 58.6% of the world production in 2001 as can be seen in Table 2.1. The figures however, include all squash and pumpkin species. According to the FAO production yearbook (2001) 16 208 584Mt of pumpkins, squash and gourds were produced world-wide in 2001 (Table 2.2). The Economic Research Service USDA (Lucier and Plummer, 2001a) reported that pumpkin acreage harvested in the United States have tripled since 1982 to 74 345 acres.

Table 2.1: Pumpkin/squash production in leading countries and the world, 1992-2001 (Mil cwt) (Lucier and Plummer, 2001b)

Country	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
China	32.5	43.3	49.7	54.4	65.5	67.8	71.2	73.9	79.3	83.7
India	65.0	68.3	68.3	69.4	70.5	72.8	73.9	75.0	75.0	75.0
Ukraine	8.1	22.1	17.4	23.9	20.0	24.5	22.2	17.3	16.9	20.9
USA									17.6	17.6
Egypt	7.5	7.8	8.3	9.7	11.0	12.5	13.6	14.3	14.3	14.3
Others	125.7	131.3	136.6	139.3	146.7	145.7	150.4	148.0	150.0	149.6
World	238.9	272.8	280.3	296.7	313.8	323.3	331.4	328.4	355.8	361.1

Table 2.2: Pumpkin, squash and gourd production, 2001 (Mt) (FAO Production Yearbook, 2001)

Area	Production (Mt) in 2001
World	16 208 584
Africa	1 804 604
Asia	10 560 335
Europe	2 170 286
North and Central America	624 589
South America	760 500
Australia	115 000
South Africa	338 000

According to the FAO, South Africa produced 338 000Mt of Cucurbits in 2001 (Table 2.2). The statistics released by the South African National Department of Agriculture for 2000 (Table 2.3) are much lower, but only includes vegetables sold on the 16 fresh produce markets. Table 2.4 is a summary of the average price of Cucurbits sold on the South African fresh produce markets, showing values of R872/t and R940/t for *C. maxima.* It is obvious that *C. maxima* is the most important specie in South Africa with an estimated value of R93.4 million for sold produce. However, baby marrows had the highest value per mass sold.

Table 2.3: Quantity of Cucurbits sold on the 16 South African fresh produce markets (1 000t) (South African National Department of Agriculture, 2000)

Product	Species	1992	1993	1994	1995	1996	1997	1998	1999	2000
Pumpkin	*C. maxima*	44.7	48.4	47.8	53.8	59.7	56.2	57.3	57.0	57.1
Gem squashes	*C. pepo*	30.8	32.1	26.6	26.7	28.8	26.9	25.5	26.4	25.9
Hubbard squashes	*C. maxima*	53.4	54.5	51.9	42.5	55.3	52.9	46.2	48.4	46.4
Baby marrows	*C. pepo*	0.8	0.5	0.4	0.4	0.4	0.4	0.4	0.6	2.4
Butternuts	*C. moschata*	28.1	33.8	33.2	34.7	40.5	45.5	46.6	48.2	46.1
Total		157.8	169.3	159.2	158.1	184.7	181.9	176.0	180.9	177.9

Table 2.4: Average price of Cucurbits sold on South African fresh produce markets (R/t) (South African National Department of Agriculture, 2000)

Product	Species	1992	1993	1994	1995	1996	1997	1998	1999	2000
Pumpkin	*C. maxima*	363	310	421	443	469	480	566	520	872
Gem Squashes	*C. pepo*	508	428	659	735	759	805	993	815	1153
Hubbard Squashes	*C. maxima*	471	439	557	717	678	664	839	783	940
Baby marrows	*C. pepo*	973	662	816	1369	1514	2013	1801	3028	4078
Butternuts	*C. moschata*	538	500	632	703	748	678	839	843	969

Robinson and Decker-Walters (1997) reported that *C. maxima* is mainly cultivated in South America, India and Africa, because it is generally more cold tolerant than *C. moschata* and *C. pepo*. It is possible to grow the latter at higher latitudes and elevations. Gwanama *et al* (2001) rated *C. moschata* to be one of the most important vegetable crops in Africa due to its contribution to nutrition through an abundant supply of minerals, vitamin C and especially β-carotene (pro-vitamin A). Kubicki and Walczak (1976) reported some inbred lines to have three times as much pro-vitamin A than the average respective amount in carrots, which are the main source of carotenes in Poland.

One of the most successful *C. maxima* breeding programmes is based in New Zealand. Prior to the 1980's, the grey storage pumpkin "Whangaparoa Crown" and hybrid cultivars "Early Dri-Crown" and "Crown Prince" of the same crown type were the most widely grown. Early breeding of pumpkin in New Zealand mainly involved the reselection of crown types and later the hybridization of these types by farmers and seedsmen. Later breeding efforts included the development of grey bush types. Since 1980, the major emphasis has been breeding buttercup hybrids (small dark green varieties) with extended storage life (Grant and Carter, 1991). According to Corrigan *et al* (2000) buttercup squash is an important export crop for New Zealand with annual exports valued at around $NZ60 million (90 000 ton/year), the third largest horticultural export crop after apples and kiwifruit (Ratnayake *et al*, 1999). The majority of the exported fruit goes to Japan where sweet buttercup squash is preferred. The latest trends are the improvement of flesh quality and thickness

as well as yield in the grey types. *C. moschata* is also starting to gain popularity in New Zealand, but predominantly in Australia due to a better flesh quality.

From the above it can be concluded that *Cucurbita* is an economic important crop in many parts of the world. However, there is also a negative side to it. *C. pepo* is a morphologically and ecologically diverse specie composed of genetically distinct groups of cultivars and free living populations. All of these diverse elements are completely interfertile resulting in self-sustaining populations. These wild populations occur as a significant weed problem in North America. These populations range from north eastern Mexico and Texas, east to Alabama and north through the Mississippi Valley to Illinois. They occupy a diversity of environments and ecological niches, including upland, seasonally dry thorn scrub habitats, to riverbanks and moist thickets, to a variety of riparian and lowland habitats. Different morphological and physiological adaptations have evolved in these areas including early fruit abscissions for river dispersal as well as quick seed germination in response to a short growing season (Keen *et al*, 1999).

2.4 Characteristics

Cucurbita is a tropical or semi-tropical plant group, although some species are found as far north as Indiana and Oregon (Whitaker and Robinson, 1986). Cucurbits are very frost susceptible, but are tolerant to high temperatures providing that the soil moisture is adequate. Ideally, they need four to five months of warm weather to grow and mature. Daily temperatures higher than 22°C are sufficient for growth, and a minimum soil temperature of 16°C is necessary for germination (Harper *et al*, 1998).

Root growth is characterized by the development of a taproot that may penetrate the soil to a depth of 1.8m or more and by a network of lateral roots that are positioned slightly below the surface (2.3 to 6.7cm). Mature plants have an extensive root system that may occupy as much as 28.3m^2. The tremendous absorbing power of such extensive root systems probably

accounts for the rapid, vigorous growth of squash, provided that an abundant supply of water and nutrients are available (Whitaker and Robinson, 1986).

The species that produce squashes and pumpkins are annual herbaceous vines with numerous runners, except for a number of cultivars of *C. pepo* and *C. maxima* with short internodes. They have mostly long, branched tendrils, and the leaves are large, alternate, shallow to deeply lobbed and palmate. The flowers are large, showy, with yellow or creamy corollas and are unisexual. They occur singly in the axils of leaves. The staminate (male) flowers are located near the centre of the plant and are born on long, slender pedicels. The pistillate (female) flowers are borne on short, ridged pedicels, distal to the staminate ones (Whitaker and Robinson, 1986). According to Gwanama *et al* (2001) male anthesis precedes female anthesis by a few days in *C. moshata*, although slightly earlier female anthesis has been reported.

Sex expression in *Cucurbita* is relatively stable. All species are monoecious, meaning pollen grains must be transported by some agent for fertilization to be accomplished. The heavy, sticky pollen grains, characteristic of *Cucurbita*, are usually transported by insects from the staminate flower to the receptive stigma of the pistillate (Robinson and Decker-Walters, 1997).

In all three pumpkin species, there is a great diversity in fruit size, shape and colour among cultivars. Some *C. maxima* cultivars produce the largest fruit of all squashes. Fruits of this species are orange, grey, green or white; smooth, ribbed or warted; round flat or oval and sometimes with a protuberance at the blossom end. Seeds are usually quite large and plump, white or brown, and rough or smooth (Whitaker and Robinson, 1986).

2.5 Resent achievements in *Cucurbit* breeding

One of the major breeding achievements in the resent past was the incorporation of the bush habit into commercial *C. maxima* hybrid cultivars. Taking the size of a pumpkin plant into account, the bush habit (induced through *Bu*) makes it possible to increase the amount of food produced in a

limited space by reducing the vine length. *Bu* is completely dominant during early growth and completely recessive during later stages of growth in *C. maxima* (Whitaker and Robinson, 1986). This allows the heterozygous hybrid to benefit from both the earliness of the bush growing habit as well as the competitive nature of the trailing habit for light reception. According to Carle *et al* (2000) genes that shorten internodes have been exploited in temperate types of *C. moschata* to produce short-vined varieties.

Gwanama *et al* (2000) mentioned that although pumpkin is adapted to a wide range of climatic and soil conditions, it is scientifically a neglected specie. The reason for the latter is given by Robinson and Decker-Walters (1997) who mentioned that large field space requirements for Cucurbits and the need for laborious hand pollinations for self-pollination and crosses have placed restrictions on Cucurbit breeding. Kubicki and Walczak (1976) also mentioned that Cucurbit breeding is very laborious, because all plants need to be self-pollinated before selection. Mohanty and Mishra (1999d) stated though a wide range of variability is encountered in this crop, very little effort has been made to exploit it in breeding programmes.

Although nuclear male sterility is known since 1944 in *C. pepo* (Shifriss, 1945) and *C. maxima* (Scott and Riner, 1946) hybrid seed production is still based on chemical or mechanical emasculation. Furthermore, three decades later most *C. moschata* genotypes in cultivation in Africa are still open-pollinated landraces, except for a couple of cultivars grown in South Africa (Gwanama *et al*, 2000).

In recent years, seedling expressed genes which reduce space and time requirements have expedited genetic research, especially in resistance breeding. Currently resistance breeding is the most active area of Cucurbit germplasm, breeding and genetic research worldwide. Most pumpkin breeding programmes use traditional genetic and plant breeding procedures, due to limited development made in the field of genetic (molecular) maps. However, molecular work especially on disease resistance receives a great deal of attention. Most pest resistance genes have been found in US or exotic

cultivars or in landraces, and cross-compatible relatives from centres of origin of diversity. *C. okeechobeensis* was successfully used in crosses with *C. maxima* and *C. pepo* to transfer powdery mildew resistance to these two species (Keen *et a*l, 1999).

Resistance genes for two potyviruses (Zucchini Yellow Mosaic Virus and Watermelon Mosaic Virus II) and one cucumovirus (Cucumber Mosaic Virus) were successfully transferred from *C. ecuadorensis* to *C. maxima* and *C. moschata* (Herrington, 1999; 2001). Related work has been done by Robinson and Moriarty at Cornell University as well as various seed companies in the world (Jahn, personal communication, 2001).

2.6 Heterosis

The improvement of characteristics with the reduction in homozygosis is known as heterosis or hybrid vigour. Therefore, heterosis can be described as a special form of expression of characteristics in the F1 generation, resulting in the superiority of the hybrid performance over some measure of parental performance. Falconer and Mackay (1996) describe heterosis as the difference between the hybrid and the mean of the two parents and this is expressed as a percentage of the mid-parent value. Wricke and Weber (1986) describe high parent heterosis as the difference between the hybrid and the better parent also expressed as a percentage. It is however mentioned that the latter makes no sense in connection with the quantitative genetics theory, since both parents contribute to the phenomenon of heterosis. According to Falconer and Mackay (1996), loci without dominance cause neither inbreeding depression nor heterosis.

Inbreeding is often defined as any system of mating that leads to an increase in homozygosity in cross-pollinating species (Poehlman, 1987). Inbreeding occurs by mating individuals that are related by ancestry or through self-pollination. The decline in vigour and size with inbreeding is known as inbreeding depression. However, according to Bushnell (1922), Robinson *et al*

(1970) and Whitaker and Robinson (1986) little, if any, depression of vigour upon inbreeding is reported in Cucurbits.

Heterosis in *Cucurbita* has already been reported by Curtis (1939), and Hutchins and Croston (1941). Korzeniewska and Niemirowicz-Szczytt (1993) mentioned that Bushell reported the first hybrids in winter squash in 1922. In the same paper it was mentioned that 20% of summer squash seed produced in the USA in 1968 was F1 hybrid seed.

Korzeniewska and Niemirowicz-Szczytt (1993) estimated heterosis in relation to the better parent for yield to be 28 to 122% and 16 to 127% in two different seasons in *C. maxima*. For fruit weight, heterosis varied between 30 to 57% and 10 to 100% and for dry matter content only two hybrids showed rather low heterosis (18 to 41%).

Heterosis over the better parent was observed for vine length (17.8%), number of primary branches per plant (18.1%), number of female flowers per plant (70.0%), number of fruits per plant (150.0%), average fruit weight (68.7%), flesh thickness (48.4%) and yield per plant (181.5%). Crosses between high and low performing parents exhibited greater hybrid vigour. Heterosis for yield was generally accompanied by heterosis for yield components (Mohanty and Mishra, 1999a).

Mohanty and Mishra (1999c) calculated heterosis values of 37.7, 28.6, 76.9, 142.9, 96.3, 48.9 and 188.7% over the better parent and 52.1, 36.9, 89.6, 161.5, 109.9, 68.9 and 197.1% over the mid-parent for vine length, number of primary branches, female flowers, fruit per plant, average fruit weight, flesh thickness and yield per plant, respectively. It was concluded that heterosis for yield was the cumulated effect of heterosis for most yield attributes. However, vine length and number of branches did not contribute much towards yield. A summary of estimates of heterosis by different authors is presented in Table 2.5.

Table 2.5: Heterosis estimates for *Cucurbita* (As adapted from different authers)

Author	Korzeniewska and Niemirowicz-Szczytt (1993)	Mohanty and Mishra (1999a)	Mohanty and Mishra (1999c)	Mohanty and Mishra (1999c)
Species	***C. maxima***	***C. moschata***	***C. moschata***	***C. moschata***
Method	**Better parent**	**Better parent**	**Better parent**	**Mid-parent**
Yield	28-122% 16-127%	181.5%	188.7%	197.1%
Fruit weight	30-57% 10-100%	68.7%	96.3%	109.%
Dry matter content	18-41%			
Vine Length		17.8%	37.7%	52.1%
Number of primary branches per plant		18.1%	28.6%	36.9%
Number of female flowers per plant		70.0%	76.9%	89.6%
Number of fruit per plant		150.0%	142.9%	161.5%
Flesh thickness		48.4%	48.9%	68.9%

Observations on flowering characteristics (days to anthesis of first male and female flowers, node where the first male and female flowers appear and number of male and female flowers per plant) were recorded by Mohanty and Mishra (1999b). Heterosis was calculated as percentage deviation of F1 mean over the mid-parent and better parent in each cross for all the traits. Observations on the crosses with the highest heterosis revealed that none of the crosses had the highest heterosis for all traits simultaneously, but five hybrids showed significant positive heterosis for all the characteristics studied.

Yield (kg) per plant and five yield components were studied in *C. pepo* lines and their F1 hybrids. No differences were observed among genotypes for numbers of staminate and pistillate flowers per plant. Intergenotypic differences were found for fruit yield and fruit number per plant. A wide

variation for percentage fruit set was also recorded. Means of F1 hybrids were higher than parental means for the traits examined, but no reciprocal differences were observed for any trait, except fruit yield. Heterosis over the mid-parent as well as the better parent were found for the yield traits but were negative for flowering traits as well as number of fruit (Kasrawi, 1994).

C. moschata was assessed to develop high yielding varieties and F1 hybrids with desirable fruit characteristics. Important quantitative characteristics including yield showed appreciable heterosis. Overdominance was calculated for vine length, fruit per plant, fruit size index and fruit flesh thickness, and dominance gene action for fruit weight and yield per plant (Sirohi, 1993).

Johannsson and Stephenson (1998) documented that the pollen from F1 plants were more vigorous *in vitro* than pollen of either inbred parents or F2 plants. This might have been due to the greater ability of the F1 hybrid sporophyte to provide nutrients during pollen development. However, the larger proportion of variance in pollen performance found within F1 plants than within the parents, indicated that hybrid vigour extends to the microgametophytic generation, and that the microgametophyte's own genotype influences at least to some extent the germination and initial growth of pollen tubes.

2.7 Combining ability

Griffing reported in 1956 that the importance of combining ability was becoming increasingly important in plant and animal breeding since it allows the breeder to study and compare the performances of lines in hybrid combinations. Sprague and Tatum (1942) defined general combining ability (GCA) as the average performance of a line in hybrid combination. Specific combining ability (SCA) is used in those cases where the performance of certain crosses deviated from what is expected based on the average performance of the lines involved. GCA effects provide an indication of the importance of genes which have largely additive effects, while SCA effects indicate the importance of non-additive effects (Kupper and Staub, 1988).

Mohanty (2000b) revealed the involvement of both additive and non-additive gene action, regulating the inheritance of yield and its components except fruit weight, number of branches and female flowers per plant. Additive genetic variance alone controlled the number of branches per plant, whereas non-additive gene action exclusively governed fruit weight and number of female flowers per plant. Non-additive gene effects were predominant with pronounced epistasis and over-dominance for all the traits except number of branches per plant. This corroborated by a low estimate of heritability in the narrow sense for these characteristics. Reciprocal recurrent selection, bi-parental mating and/or diallel selective mating are suggested for genetic improvement of yield and its attributing traits in pumpkin.

Observations on six flowering characteristics (days to anthesis of first male and female flower, node on which the first male and female flowers appear and number of male and female flowers per plant) were evaluated by Mohanty (1999). General and specific combining ability values were significant for all the characteristics except number of female flowers per plant. High values of the general predictability ratio for days to anthesis of first male and female flowers indicated that the performance in these characteristics could be predicted with greater reliability based on the GCA (additive) component alone, but low values of the general predictability ratio for the other characteristics indicated that prediction based on SCA (non-additive) component alone would be effective. The average degree of dominance was less than unity for days to anthesis of male and female flowers indicating partial dominance, but was more than unity for the rest of the flowering attributes indicating the prevalence of overdominance.

Mohanty and Mohanty (1999) observed both additive and non-additive gene action for days to anthesis of first male and female flowers in *C. moschata*. Non-additive gene action was exclusively responsible for the expression of the node on which the first male and female flowers appeared and number of male and female flowers per plant. Low heritability in the narrow sense was recorded for all the characteristics except the first male flowering node.

Overdominance was prevalent for all the six characteristics studied. Heterosis breeding was suggested for the improvement of all the flowering traits.

Fruit weight and flesh thickness were governed by both additive and non-additive gene effects, whereas numbers of male and female flowers, fruit number and yield per plant were controlled by dominance and epistatic gene action. Non-allelic interaction was prevalent for all characteristics except flesh thickness. Unequal distribution of positive and negative effects among parents was observed for fruit weight and yield. Most dominant genes exerted positive effects. Complete dominance was recorded for fruit weight (Mohanty and Mishra, 1998)

Mohanty (2000a) reported the contribution of both additive and non-additive gene action controlling the expression of yield and its components, except average fruit weight, which was exclusively regulated by non-additive gene effects. Epistasis was pronounced for all the characteristics. A close correspondence was observed between *per se* performance and combining ability effects for the attributes studied. Higher yield was mainly associated with increased number of fruits per plant, average fruit weight and flesh thickness.

Korzeniewska and Niemirowicz-Szczytt (1993) estimated combining abilities for fruit weight, fruit number and dry matter content. In all three cases GCA were much higher than SCA indicating additive gene action although non-additive effects prove to be significant. Reciprocal effects also appeared to be significant indicating a considerable influence of cytoplasmic factors on the inheritance of these traits.

According to Balliu and Hallidri (2000), significant differences between GCA for most yield components and at the same time the irrelevance of SCA clearly suggest that the average fruit weight is mainly controlled by additive gene effects in cucumber. On the other hand the significance of GCA and SCA suggests that the significant differences in sex-expression appeared to be under both additive and non-additive control. Large ratios between the

variances of GCA and SCA confirmed the importance of additive effects in determining hybrid growth rate although the significance of SCA indicated that dominance and/or epistatic effects were also involved. A summary of the reported additive and non-additive gene action is given in Table 2.6.

Both the phenotypic coefficient of variance (σ^2_P) and the genotypic coefficient of variance (σ^2_G) were high for yield per plant (49.3 and 34.2% respectively) and number of fruit per plant (42.2 and 20.8% respectively), but low for vine length (13.28 and 9.76% respectively) and number of primary branches per plant (13.1 and 3.26% respectively). Heritabilities for yield, number of fruit, vine length and number of primary branches were calculated to be 0.69, 0.49, 0.73 and 0.25 using the above mentioned genotypic and phenotypic variance coefficients. A much higher σ^2_P than σ^2_G is mainly due to the interaction of the genotypes with the environment. Traits susceptible to environmental fluctuations included fruit per plant, average fruit weight, yield per plant, number of female and male flowers per plant, and the node on which first male and female flower appears (Mohanty and Mishra, 1999d). Narrower differences between σ^2_P and σ^2_G suggested stability in environmental fluctuations. It also suggested that genetic factors were predominantly responsible for the expression of these attributes and selection could be made effectively on the basis of phenotypic performance (Falconer and Mackay,1996).

Table 2.6: The type of gene action for various characteristics in *Cucurbita*

Author	**Gwanama *et al* (2001)**	**Mohanty (2000b)**	**Mohanty (1999)**	**Mohanty and Mohanty (1999)**	**Mohanty and Mishra (1998)**	**Mohanty (2000a)**	**Korzeniewska and Niemirowicz-Szczytt (1993)**	**Balliu and Hallidri (2000)**
Species	***C. moschata***	***C. moschata***	***C. moschata***	***C. moschata***	***C. moschata***	***C. moschata***	***C. maxima***	***Cucumis sativus***
Days to female anthesis	A & N		A	A & N				
Days to first mature fruit	A & N		A	A & N				
Weight of first mature fruit	A & N							
Mean fruit weight	A & N	N			A & N	N	A & N	A & N
Soluble solids	A & N							
Yield		A & N			N	A & N		
Dry matter content							A & N	
Number of primary branches per plant		A						
Number of female flowers per plant		N	N	N	N			
Flesh thickness					A & N			
Node producing first male flower			N	N				
Node producing first female flower			N	N				

A = Additive gene action

N = Non-additive gene action

2.8 Heritability

Heritability (h^2) is used to specify the proportion of total variability that is due to genetic causes. Broad sense heritability (h^2_b) is the ratio of the total genotypic variance over the phenotypic variance. In contrast, narrow sense heritability (h^2_n) is the ratio of the additive genetic variance over the phenotypic variance. The latter is a more useful concept to the breeder because it measures the relative importance of the additive genetic variance, which is the genetic variance that can be transmitted to the next generation through selection. This concept is also used to predict gain from selection for the trait under consideration (Fehr, 1991). If the genetic variation is large in relation to the environmental variation, then the heritability will be high. If the genetic variation is small in relation to the environmental variation, the heritability will be low. Selection will be more effective in the former situation. It can also be said that the larger the difference between the genotypic and phenotypic variation, the larger the environmental influence on the expression of the characteristic.

According to Falconer and Mackay (1996) the change produced by selection, that mainly interests a breeder is the change in the population mean. This is the response to selection and is the difference of mean phenotypic value between the offspring of the selected parents and the whole of the parental generation before selection. Selection can be achieved either by direct selection or indirect selection. In the former case the selection will take place for the trait that needs to be improved. The change in characteristic Y due to selection of characteristic X is known as indirect selection response.

A plant breeder is usually evaluating mixed populations of breeding material to identify the superior individual plants or breeding lines. In practice, the lower the heritability, the greater the number of plants that should be selected to ensure that some of the plants selected are superior genetically and not just due to environmental effects. Also, if the proportion of plants selected is low, there is a danger of genetic erosion, or the lack of genetic diversity, for

traits other than the one under selection which would have a deleterious effect on future selection (Fehr, 1991).

Panse (1957) stated that if the heritability is mainly due to additive effects, it would be associated with high genetic advance and if it is due to non-additive effects the genetic advance would be low. Characteristics showing high heritability along with high genetic gain possess high selective value. These characteristics can be improved by simple methods like mass selection, following hybridization and selection in early generations. Characteristics with moderate to high estimates of heritabilities with low genetic gain are conditioned by non-additive gene action and the presence of high genotype and environment interaction. If the heritability is being exhibited due to the favourable influence of the environment rather than genotype, then simple selection will not be rewarding. These characteristics can be improved by the development of hybrid varieties or the utilization of transgressive segregates in heterosis breeding programmes. This implies that the breeder can go for selection over several successive generations following hybridization of desirable transgressive segregates. Further, low heritability along with low genetic gain indicate marked influence of the environment for expression of these traits and that selection would be ineffective. These traits should be tested under diverse environments for their effective selection.

Mohanty and Mishra (1999d) assessed the relative amount of heritable portion of variation with the help of heritability estimates and genetic advance expressed as a percentage of the mean (genetic gain). The heritability expresses the proportion of the total variance that is attributable to the average effect of the genes and determines the degree of the resemblance between relatives. High estimates of broad-sense heritability were observed for days to anthesis of first male (64.0%) and female flowers (55.2%), flesh thickness (58.3%) and vine length (54.0%), whereas moderate values were recorded for yield per plant (48.8%), number of male flowers per plant (34.2%) and node on which the first female flower appears (34.1%). Low values for this parameter indicate that these traits are prone to environmental variations and phenotypic selection may not be rewarding. In a hybridization programme

the highly heritable characteristics may be selected early in the programme, and selection of characteristics with low heritability may be postponed untill they are closer to homozygosity. Selection is effective for improvement of highly heritable characteristics, probably due to more additive factors. However, the most important role of heritability lies in its predictive role which implies whether a population will respond to selection pressure or in other words, whether selection will be operative. Heritability itself provides no indication of the amount of genetic progress that could result from selection of the best individual. This happens because the broad sense heritability is based on total genetic variation, which includes both additive and non-additive components.

Johnson *et al* (1955) found that heritability estimates in conjunction with genetic gains are more effective and reliable in predicting the improvement through selection. Rapid progress in selection can be achieved when high heritability is accompanied with high genetic gain. Since a magnitude of genetic advance is influenced by the units of measurement, it was further expressed as a percentage of the population mean and it was considered as an important selection parameter.

Heritability coefficients calculated per genetic unit of the population for the content of β-carotene and soluble solids were as high as 92.6% and 84.3% respectively. High values of h^2 obtained for these groups of varieties and inbred lines are caused by high genetic variability of the material and indicate a strong genetic determination of variation of these characteristics and possibilities to select new valuable forms (Kubicki and Walczak, 1976).

Gwanama *et al* (2001) indicated the presence of both additive and non-additive gene action in flowering and fruit characteristics and concluded that only low to moderate heritabilities could be expected. This was in agreement with other findings in *Cucurbitaceae.* According to Smith *et al* (1978) and Strefeler and Wehner (1986) heritabilities of fruit yield traits in *Cucumis sativus* (cucumber) have been found to be between 0.02 and 0.25.

Mohanty *et al* (1999) observed a preponderance of dominance and non-additive gene action for all the characteristics supported by low heritability in the narrow sense. Pronounced epistasis for number of female flowers and fruits, average fruit weight and yield per plant was observed. Dominant genes for vine length and flesh thickness were indicated. Overdominance was prevalent for all the traits. Polygenic inheritance of yield and yield contributing characteristics were concluded and heterosis breeding was suggested for the improvement of yield and yield components in *C. moschata*.

High heritabilities were estimated for root traits and vine length in melon, using parent-offspring analysis. Some of these values in excess of 1.0 are likely due to the dramatic heterotic effect on certain traits for several crosses, but was not surprising given the amount of diversity and heterozygosity present. According to Crosby (2000) these results support the assertion that additive genetic variation is important in the development of these traits.

High phenotypic (σ^2_P) and genotypic coefficients of variation (σ^2_G) were observed for yield and number of fruits per plant. A moderate heritability (43.1%) along with moderately high genetic gain (43.96%) were recorded for yield per plant, indicating that this trait could be improved by rigid selection in early generations. Days to first anthesis, first female flowering node, flesh thickness, vine length and number of male flowers per plant showed moderate to high heritabilities accompanied by low genetic gain (Mohanty and Mishra, 1999d). The latter can only be possible if incorrect selections are being made or when selection intensity is not strong enough, since genetic gain are only influenced by heritability, phenotypic variance and selection intensity. If phenotypic variance is limited, high genetic gain should not be expected.

CHAPTER 3

MATERIAL AND METHODS

3.1 Experimental material

Pumpkin (*Cucurbita maxima*) genotypes, taken from the germplasm collection of PANNAR Research Services at Greytown, South Africa, were used as parental lines in this study. Progenies were derived through crossing the parental genotypes selected from the germplasm.

3.1.1 Parental genotypes

Six parental genotypes were used in this study. Selection for these genotypes was considered on the basis of variability among characteristics contributing to yield and flesh quality of pumpkin fruit. The genotypes included varieties or cultivars that have been developed and released for commercial production and elite breeding lines in advanced stages of testing. All genotypes went through at least eight generations of selfing before this study commenced. Levels of homozygosity for the characteristics studied were assumed sufficient. The six parental genotypes are briefly discussed below.

GENOTYPE: A

A is a commercial variety used in South America. The fruit is mainly eaten at an immature stage. The most prominent traits of this inbred line include small dark green fruit, produced on a bush habit with a very restricted vine. The shape of the fruit is transverse elliptic in a longitudinal cross section. A very thick, hard rind surrounding the mature fruit as well as very poor flesh quality makes this inbred line undesirable as a fresh market vegetable in South Africa.

GENOTYPE: B

This inbred line was developed from the buttercup type hybrid pumpkins commercially available in Japan. Small, smooth, dark green pumpkins are produced on a veining growing habit. The flesh quality (dryness) is exceptionally good, but very thin flesh makes it unacceptable to the South African market. Fruit shape is transverse elliptic.

GENOTYPE: C

Genotype C is one of the parents of the most successful white semi-bush hybrid available in South Africa. The white transverse elliptic fruit is produced on a bush growing habit. A relatively low flesh quality, with high occurrence of green pigments in the flesh is representative of all white varieties know in South Africa.

GENOTYPE: D

D is one of the first grey bush lines developed by PANNAR Research Services. The fruit has relatively poor flesh quality with a transverse elliptic fruit shape.

GENOTYPE: E

E is a commercial variety, which has been in cultivation for quite some time. Dark green fruit is produced on a vigorously growing vine habit. The typical hubbard fruit shape with large fruit size is characteristic of this variety. Very good flesh quality makes it a popular eating pumpkin.

GENOTYPE: F

Genotype F produces globular grey fruit on a branching bush growing habit. The fruit produced by this commercial variety is known to have thick flesh

resulting in a small seed cavity. The flesh seems to be of good quality, but tends to be stringy which makes it unacceptable as a table vegetable in South Africa.

3.1.2 Progenies

The progenies used in this study were generated through crossing the six selected parental genotypes. Twenty plants of each of the genotypes were grown according to standard cultivation practices on the PANNAR Research Services production farm in Komatipoort during the winter of 2001. The cultivation practices are discussed in detail under the methods used.

Anthesis of female flowers started seven to 10 days earlier on parental genotypes with bush growing habits than on the veining types. The latter in combination with only one female flower per plant, approximately every third day, hampered pollinations. Due to practical reasons only limited time was available for pollinations which resulted in the reciprocal crosses of the original crosses planned. Table 3.1 gives an indication of the seed harvested and used as progenies. Fifteen crosses were harvested from the six parents (n) according to the formula given by Griffing (1956):

$$\text{Number of crosses} = \frac{n(n-1)}{2}$$

The total entries were therefore 21 (parents and crosses) calculated according to the following formula:

$$\mathcal{N} = \frac{n(n-1)}{2} + n$$

$$= \frac{n(n+1)}{2}$$

where: $\mathcal{N}$ is the number of entries in the trial and

n is the number of parents

Table 3.1: Mating design and the crosses generated for the study

		Male parent genotypes					
		A	**B**	**C**	**D**	**E**	**F**
Female parent genotypes	**A**	S	X	X	X	X	
	B		S				
	C		X	S		X	X
	D		X	X	S	X	X
	E		X			S	
	F	X	X			X	S

S = Selfed parent

X = Cross

Crosses were made using a hand pollination technique. A limited number of plants as well as a limited number of female flowers resulted in the making of reciprocal crosses of some of the half diallel combinations. This would not have influenced the analysis since personal experience showed maternal effects to be absent. Due to the unisexual nature of the flowers, emasculation was unnecessary. However, both male and female flowers were closed the evening before the morning they would normally open to prevent pollen contamination through insects after anthesis. The following morning, pollen from the closed male flowers from the paternal parent was transferred to the stigma of the closed female flowers of the maternal parent. The female flowers were then closed again to prevent pollen contamination. All pollinations were completed between 8:00 and 10:00.

The crosses and selfings, from the plants planted in March 2001, were harvested in August 2001. Seed from well-ripened fruit were removed and fermented for a period of 36 to 48 hours. The fermentation process made it possible to separate all viable and non-viable seed through a flotation technique in water. It also helped to remove pathogenic organisms from the seed surface. After the seed was dried they were stored at 10°C to be used as seed during the trials planted the following summer season.

3.2 Methods

3.2.1 Entries and experimental design

Twenty one entries, namely six parental genotypes and the fifteen progenies developed by incomplete diallel mating among the six genotypes were included in this study. The trial was planted in a randomised complete block design with six replications, with each plot containing 10 plants. Three of the replications were used for destructive measurements during the growing period and the other three were used to determine other measurements on matured fruit. Two border rows were planted surrounding the trial. The entries which appeared in the trial are listed below with the female mentioned first:

1.	A X A	8.	A X C	15.	F X B
2.	B X B	9.	A X D	16.	D X C
3.	C X C	10.	A X E	17.	C X E
4.	D X D	11.	F X A	18.	C X F
5.	E X E	12.	C X B	19.	D X E
6.	F X F	13.	D X B	20.	D X F
7.	A X B	14.	E X B	21.	F X E

3.2.2 Land preparation

The trial was planted 15km south of Greytown in Kwa-Zulu Natal. The land was ripped, followed by ploughing and disking before 400kg/ha 2:3:4 were broadcast spread over the area. This was followed by disking and Kongskilde cultivation to result in a fine seed bed. A planter was then used to draw lines 90cm apart to ease the planting process and to apply another 250kg/ha 2:3:4 within the row.

3.2.3 Planting

The 126 plots were marked out to result in a plant spacing of 1.8m between the rows and 0.9m between plants within the rows. The relatively high plant density was selected due to the bush and semi-bush growing habit of most of the genotypes in the trial. Direct sowing was used with three seeds per station planted 2cm beneath the surface directly in the seedbed. This was followed by the first irrigation. The planting date was 25 September 2001. After germination seedlings were thinned to one plant per station.

3.2.4 Management of trials

All weeding was done by hand for the full growing season of the crop. After emergence of the first true leaf all seedlings were sprayed twice (14 days apart) with Molly to compensate for the molybdenum deficiency in the soil. Three LAN topdressings of 100kg/ha were applied, of which the first were done at the fourth leaf stage. The second and third topdressing were applied 14 and 28 days respectively after the first.

During the early stages of seedling development overhead sprinkler irrigation was applied every seven to ten days. However, after the fourth week of planting, rainfall figures were high enough to withdraw all irrigation to the end of the growing season. In total the trial received 337.1mm rain during the period from plant to harvest excluding additional irrigation during the first month.

Lebaycid (fenthion) was applied twice during the flowering and fruit set period as a preventative measure for any insect damage. Powdery mildew (*Sphaerotheca fuliginea* and *Erysiphe cichoracearum*) was controlled with Calixin (tridemorph) according to the recommended dosage starting three weeks after the first fruit set.

3.3 Characteristics measured

Destructive measurements were taken on three of the replications and included only measurements on the ovaries of open flowers. Non-destructive measurements taken during the same period included measurements on the leaves and petioles. The rest of the measurements included yield and yield components and fruit quality characteristics. The latter was taken during January 2002 after all the fruit reached maturity.

3.3.1 Ovary morphology

During the peak flowering season, flowers were harvested on three consecutive Saturdays for evaluation. Only limited numbers of female flowers are produced on a pumpkin plant and flowers wilt within a few hours after they opened depending on the temperature. Flowers that opened on the Thursday were already noticeably larger and the corolla was completely dried out on the Saturday. The differences in sizes of flowers produced on primary and secondary branches were eliminated by excluding the latter.

The ovaries were longitudinally cut through their centres. A slice, approximately 1mm thick, of each ovary was stained with an Iodine solution to intensify the contrasts between different tissues. The stained ovary segments were placed onto a grid before digital photographs were taken. The grid consisted of squares with a side length of 1mm. The photographs were taken of the different ovaries for accurate evaluation at a later stage. The grid made it possible to determine exact measurements of the different ovaries.

The Iodine solution was made up as follows (Liebenberg, personal communication, 1994):

0.5g	potassium-iodide (KI)
0.5g	Iodine
5ml	H_2O
45ml	Absolute Alcohol

From the literature available, no information could be found where ovary morphology was successfully used in pumpkin breeding. However, from personal experience it was evident that a large amount of variation existed in ovary morphology. The resemblances between ovary and mature fruit shape of hubbard as well as in very flat pumpkin varieties, indicated that possible correlations between ovary morphology and fruit morphology may exist. The idea was strengthened by the correlation between ovary blossom end scar sizes during anthesis and the scar size on mature fruit. However, the latter was not evaluated in this study, since it was not accurately measurable from the photographs. The ovary characteristics measured were therefore traits that could possibly be used by the breeder, should they have any significant phenotypic correlations with other traits evaluated at a later stage in a plant's life cycle.

Ovary width: length ratio (OW:L)

Due to possible differences in size of ovaries between flowers that opened the same day and the previous day, ratios were determined from the printed photographs to eliminate all units. The OW:L ratio is therefore an indication of the shape of the ovary rather than the exact dimensions. The values were presented as percentages. The ratio was calculated to determine the correlation with mainly the fruit width:length ratio.

Ovary top flesh thickness (OTT)

OTT was calculated as a percentage between the top flesh thickness, the distance from the stem attachment to the locule (ovule cavity), and the total length of the ovary. It is possible that it might have a correlation with fruit shoulder thickness.

Ovary shoulder thickness (OST)

These measurements were taken at a 45 degree angle of the OTT measurement on both sides of the ovary. The average was taken on these

two values and presented as a ratio with the total length of the ovary, expressed as a percentage. OST might also be correlated with fruit shoulder thickness.

Ovary blossom end scar size (OBES)

The attachment where the corolla and calyx join the ovary will develop into a blossom end scar which is noticeable on the mature fruit. The distance between these two attachments, on a longitudinal cross section through an ovary, in relation to the total width of the ovary was presented as an OBES percentage.

3.3.2 Leaf morphology

Since large leave varieties usually have large fruit with poor quality, it could be possible to find correlations between some of these characteristics. In case pumpkin leaves and fruit consist out of a fixed amount of cells, it could be possible that genes influencing cell size will also influence leave and fruit dimensions as well as flesh quality.

Morphological leaf characteristics were measured during the third week of anthesis. At this stage the different growing habits were well established and plants were in their optimum growing period. Leaf blades and petioles produced during this stage were the maximum size that was produced during the growing season.

Leaf blade length (LBL)

The ovate to cordate (heart shaped) leaves are palmately veined, meaning all the nerves attach to the petiole (leaf stem) at one point. LBL was measured from the petiole to the end of the middle nerve which is the longest. Only the leaf highest from the soil surface was measured. Since very limited variation exists in *C. maxima* leaf shape, only one measurement was taken per leaf. Measurements were taken in cm.

Leaf petiole length (LPL)

The importance of LBL is that it correlates with the radius of the canopy size, especially on bush growing habits. Plants with longer LPL's have larger canopies with a reduced shading effect. This will influence light absorption and may have an effect on photosynthesis.

The petiole of the same leaf that was used for LBL was measured from the stem attachment to the leaf blade attachment in cm.

3.3.3 Yield data

The trial was harvested the 3rd of January 2002 after all plants died. In both cases of yield and fruit number, the plot was taken as a unit with no data recorded for single plants.

Harvesting was done according to commercial practices. Fruit was harvested only once, after at least 90% of the fruit reached maturity. Only marketable fruit was weighed to determine the yield and the number of fruit was used to calculate the average mass of individual fruit.

3.3.4 Fruit morphology

Fruit measurements were handled the same way the ovary measurements with photographs being taken of all fruit evaluated. In the latter case, a scale was used to convert measurements to the exact original sizes of the fruit in mm.

Since fruit hollowness and flesh density influence fruit mass, more information is needed to get a more accurate description of pumpkin fruit dimensions. Width (W) was measured at the widest transverse position of a fruit, with total length (TL) being the distance between the stem attachment and the blossom end scar. Maximum length (ML) was taken at the longest position parallel to the total length. As previously mentioned, a great deal of variation exists in

fruit shape. Although fruit shape was not described, the W:ML ratio presented as a percentage was used as an indication of fruit shape. A W:ML ratio of one represents a round fruit shape. Ratios larger than one indicate flatter fruit shapes.

3.3.5 Flesh thickness

To compare flesh thickness of different fruit sizes, all thicknesses are expressed as a percentage of either W, ML or TL.

Side thickness was taken at the widest transverse position of the fruit on both sides. The average of these two values expressed as a percentage of W was used as side thickness (ST). Top flesh thickness (TT) was measured as the distance between the stem attachment and the seed cavity and is expressed as a percentage of TL. The distance between the seed cavity and the blossom end scar presented as a percentage of TL is the middle bottom flesh thickness (MBT).

The thickness of the shoulder was also measured at a 45 degree angle to the TL on both sides of the fruit. Again the average of these two values expressed as a percentage to ML was used as shoulder thickness (SHT). Next to the blossom end scar, parallel to the TL, the average of another two measurements of flesh thickness was taken as bottom flesh thickness (BT) presented as a ML percentage.

3.3.6 Flesh quality or density

Flesh quality is usually measured as the percentage dry matter content. The higher the value, the better or drier the flesh. The latter is not only laborious and time consuming, it is also impractical when large quantities need to be evaluated. In this trial flesh quality was evaluated by means of a penetrometer also known as a fruit pressure tester. It measures the pressure necessary to force a plunger of specified size into the flesh of the fruit as described by Harvey *et al* (1997). In this trial a plunger with a width of 3mm was forced

25mm into the flesh in the shoulder area of the fruit. Two measurements were taken with the average being used as the density value.

3.4 Statistical analysis

The raw fruit data for each characteristic consisted of nine values obtained from nine different fruit, harvested from the same plot for each replication. Flower data and leaf data consisted of six and four values respectively per plot. Yield data was measured as a value per plot and later converted to yield per plant. Due to limited calculation ability of Agrobase (2000) based on Griffing (1956), the data was simplified in order to be processed. This included the calculation of averages per plot for all characteristics measured.

The computer programme, Agrobase 2000, was used for analysis of variance and calculation of phenotypic correlations and genotypic correlations. All other analysis was done with Microsoft Office, Excel.

3.4.1 Analysis of variance (ANOVA)

An ANOVA was performed for a randomised complete block design for all characteristics measured. These analyses included all genotypes (parents and crosses) and provided means, mean squares, F-values, probability levels of significance, least significant differences (LSD) and coefficients of variation (CV).

3.4.2 Performance of genotypes

Averages for all genotypes were calculated for each characteristic measured. These averages were used to rank the genotypes according to their performances. Histograms were drawn, using these averages, in Excel. CV values were also calculated for each genotype.

3.4.3. Combining ability

Griffing (1956) described two main models and four different methods for the analysis of diallel data. For the purpose of this study Model, 1 Method 2 was used. The model implies that the material used, is a chosen or fixed set of genotypes on which certain genetic information is required. The method stipulates that only the parents and one set of F1's are included but not the reciprocal F1's.

The mathematical model for the combining ability analysis is assumed to be:

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{bc}\sum_{k}\sum_{l} e_{ijkl} \qquad \begin{cases} i,j = 1,.....,p \\ k = 1,.....,b \\ l = 1,.....,c \end{cases}$$

where:

	xij	=	mean of the x_{ij}th genotype over k and l
	u	=	population mean
	g_i	=	the GCA effect of the ith parent
	g_j	=	the GCA effect of the jth parent
	s_{ij}	=	the SCA effect assuming that $s_{ij} = s_{ji}$
	e_{ijkl}	=	the effect peculiar to the $ijkl$th observation
	i, j	=	parent number where i and j = 1 to p
	p	=	number of parents
	k	=	block number, with b blocks
	l	=	individual number, with c individuals per plot
	b	=	number of blocks (repetitions)
	c	=	number individuals/plants.

The analysis of variance for combining ability, with expected mean squares, is presented in Table 3.2.

Table 3.2: Analysis of variance for Model1, Method 2 (Griffing, 1956).

Source	D.F.	Sum of Squares	Mean Squares	Expectation of Mean Squares
GCA	p-1	S_g	M_g	$\sigma^2 + (p+2)\left(\frac{1}{p-1}\right)\sum g_i^2$
SCA	$p(p-1)/2$	S_s	M_s	$\sigma^2 + \frac{2}{p(p-1)}\sum_i \sum s_{ij}^2$
Error	m	S_e	M_e	σ^2

Where: $$S_g = \frac{1}{p+2}\left\{\sum_i \left(X_{i.} + x_{ii}\right)^2 - \frac{4}{p} X_{..}^2\right\}$$

$$S_s = \sum_{i \le j} \sum x_{ij}^2 - \frac{1}{p+2}\sum_i \left(X_{i.} + x_{ii}\right)^2 + \frac{2}{(p+1)(p+2)} X_{..}^2$$

The effects may be estimated as follow:

$$\hat{u} = \frac{2}{p(p+1)} X_{..}$$

$$\hat{g} = \frac{1}{p+2}\left[X_{i.} + x_{ii} - \frac{2}{p} X_{..}\right]$$

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

Variances of effects and of differences between effects may be estimated as follow:

$$var(\hat{u}) = \frac{2}{p(p+1)}\hat{\sigma}^2$$

$$var(\hat{g}_i) = \frac{p-1}{p(p+2)}\hat{\sigma}^2$$

$$var(\hat{s}_{ii}) = \frac{p(p-1)}{(p+1)(p+2)}\hat{\sigma}^2$$

$$var(\hat{s}_{ij}) = \frac{p^2+p+2}{(p+1)(p+2)}\hat{\sigma}^2 \qquad (i \neq j)$$

$$var(\hat{g}_i - \hat{g}_j) = \frac{2}{p+2}\hat{\sigma}^2 \qquad (i \neq j)$$

$$var(\hat{s}_{ii} - \hat{s}_{jj}) = \frac{2(p-2)}{p+2}\hat{\sigma}^2 \qquad (i \neq j)$$

$$var(\hat{s}_{ii} - \hat{s}_{ik}) = \frac{2(p+1)}{p+2}\hat{\sigma}^2 \qquad (i \neq j,k; j \neq k)$$

$$var(\hat{s}_{ij} - \hat{s}_{kl}) = \frac{2p}{p+2}\hat{\sigma}^2 \qquad (i \neq j,k,l; j \neq k,l; k \neq l)$$

Since least significant differences for GCA and SCA were not computed by Agrobase, it was calculated using the following formulas (Labuschagne, personal communication, 2002):

$$LSD_{GCA} = \sqrt{var(g_i - g_j)} \times tp \qquad (t = 0.05)$$

$$LSD_{SCA} = \sqrt{var(s_{ij})} \times tp \qquad (t = 0.05)$$

GCA:SCA ratio

The ratio was calculated to study the predominance of the effects and to assess the relative importance of additive or non-additive effects. The ratio will indicate whether the characteristic is controlled by additive or non-additive

(dominant) gene action. The mean squares for the GCA and SCA were used for calculating these ratios (M_g:M_s).

According to Baker (1978), the closer the ratio

$$2\sigma^2_{GCA} / \left(2\sigma^2_{GCA} + \sigma^2_{SCA}\right)$$

is to unity, the greater is the predictability based on general combining ability alone. The calculation of σ^2_{GCA} and σ^2_{SCA} are discussed under paragraph 3.4.4.

3.4.4 Heritability

Heritability can be defined as the portion of the total phenotypic variance among individuals that is attributable to genetic differences between them. Falconer and Mackay (1996) distinguished between broad sense and narrow sense heritability. Heritability in the broad sense expresses the extent to which individuals' phenotypes are determined by the genotypes. Therefore broad sense heritability (h^2_b) is estimated from the ratio of the total genetic variance to the phenotypic variance. It can be estimated with:

$$h^2_b = \frac{\sigma^2_G}{\sigma^2_P}$$

where: σ^2_G = total genotypic variance

σ^2_P = total phenotypic variance

Narrow sense heritabilities (h^2_n) are estimated from the ratio of the additive portion of the genetic variance to the phenotypic variance. The latter determines the degree of the resemblance between relatives and is therefore of the greatest importance in breeding programmes. Narrow sense heritability can be calculated from:

$$h^2_n = \frac{\sigma^2_A}{\sigma^2_P}$$

where: $\sigma^2_A = 2\sigma^2_{GCA}$

$$\sigma^2_{GCA} = \frac{M_g - M_s}{p-2}$$

where:

σ^2_A	=	additive variance
σ^2_{GCA}	=	general combining ability variance
M_g	=	general combining ability mean squares
M_s	=	specific combining ability mean squares
p	=	number of parents

The variance components were calculated according to the computational formulas of Griffing (1956):

$$\sigma^2_G = 2\sigma^2_{GCA} + \sigma^2_{SCA}$$

$$\sigma^2_P = 2\sigma^2_G + 2\sigma^2_E$$

where: $\sigma^2_{SCA} = M_s - M_e$

where:

σ^2_{SCA}	=	specific combining ability variance
σ^2_E	=	environmental variance
M_e	=	combining ability error mean squares

3.4.5 Correlations

The phenotypic and genotypic correlations were calculated using Agrobase (2000).

3.4.5.1 Phenotypic correlations

The association between two characteristics that can be directly observed is the correlation of the phenotypic values. A phenotypic correlation is the ratio of the appropriate covariance to the product of the two standard deviations.

Phenotypic correlations have been calculated using the formula (Falconer and Mackay, 1996):

$$r_P = \frac{cov_P}{\sigma_{PX}\sigma_{PY}}$$

where: r_P = phenotypic correlation between X and Y

cov_P = phenotypic covariance between X and Y

σ_{PX} and σ_{PY} = phenotypic standard deviation of characteristics X and Y.

3.4.5.2 Genetic correlations

Genetic correlations have been calculated using the formula:

$$r_A = \frac{cov_{XY}}{\sqrt{var_X var_Y}}$$

where: r_A = genetic correlation between X and Y

cov_{XY} = genetic covariance of the characteristics X and Y

var_X and var_Y = genetic variance of the characteristic and Y respectively

Genetic covariance and genetic variance refer to the difference in covariance and variance of a genetically variable and genetically uniform population (Falconer and Mackay, 1996). However, the genetic correlations in this study were estimated by calculating the correlations between the GCAs.

3.4.6 Response to selection

Selection response is the difference of the mean phenotypic value between the offspring of the selected parents and the whole of the parental generation before selection.

The response of a characteristic when directly selected was estimated with the following formulae:

$$R_X = ih_X\sigma_{AX}$$

and

$$R_X = ih_X^2\sigma_{PX}$$

where:

R_X	=	response in characteristic X
i	=	intensity of selection, obtained from Appendix Table A in Falconer and Mackay (1996). For this study i was taken as 2. 63, with 5% of the population being selected.
h_X	=	square root of narrow sense heritability of characteristic X
h_X^2	=	narrow sense heritability of characteristic X
σ_{AX}	=	standard deviation of breeding values of characteristic X
σ_{PX}	=	phenotypic standard deviation of characteristic X

The correlated response of characteristic Y (CR_Y) as the result of the selection of characteristic X was calculated according to the following equation:

$$CR_Y = ih_Xh_Yr_A\sigma_{PY}$$

According to the latter it might be possible to achieve more progress under selection for a correlated response than from selection for the desired characteristic itself. If Y needs to be improved, indirect selection by means of X, will only have benefit if h_Xh_Y is larger than h_Y^2 and the genetic correlation (r_A)

between X and Y, also known as the correlation between breeding values, is relatively high.

3.4.7 Heterosis

Two types of heterosis were calculated based on the mean values of the genotypes.

3.4.7.1 Mid-parent heterosis (Average heterosis)

Mid-parent heterosis (MPH) as the deviation of the off-spring from the mid-parent value, is often expressed as a percentage of the mid-parent value. According to Falconer and Mackay (1996) MPH can be calculated from the formula:

$$H_{F_1} = \frac{M_{F_1} - M_{\bar{P}}}{M_{\bar{P}}} \times 100$$

where: H_{F_1} = percentage heterosis in the F1

M_{F_1} = mean performance of the F1 cross

$M_{\bar{P}}$ = mid-parent value, mean of two parents obtained from the mean values of the two parents

3.4.7.2 High parent heterosis (Better parent heterosis)

High parent heterosis (HPH) was calculated from the following equation:

$$H_{F_1} = \frac{M_{F_1} - M_{HP}}{M_{HP}} \times 100$$

where: M_{HP} = mean value of the better parent.

CHAPTER 4

RESULTS AND DISCUSSION

4.1 Analysis of variance (ANOVA)

An ANOVA was done on all the data obtained from the F1 hybrids and parents for 19 different characteristics. The mean squares for various sources of variance are listed in Table 4.1. The differences between genotypes were significant ($p<0.01$) for all the characteristics measured. The analysis included the parents and the F1 progenies. No significant differences were recorded for the replications except for LPL.

Table 4.1: Mean squares of various agronomic and quality characteristics (Parents and F1s)

Source of variation	D.F.	OW:L	OTT	OST	OBES	LPL
Replications	2	0.0010	1.2280	0.9410	6.4240	88.4650 **
Genotypes	20	0.0176 **	53.3800 **	54.9260 **	171.9880 **	171.5500 **
Residual	40	0.001	1.545	1.366	19.458	12.1880

Source of variation	D.F.	LBL	Yield	Fruit mass	Fruit number	W
Replications	2	0.0040	0.9790	0.0430	0.1000	74.2630
Genotypes	20	46.7230 **	10.7710 **	12.5130 **	8.3630 **	7477.4570 **
Residual	40	2.2560	0.7400	0.0830	0.0770	70.0290

Source of variation	D.F.	ML	TL	W:ML	ST	TT
Replications	2	1.7040	17.2600	0.0030	1.2000	0.6140
Genotypes	20	6070.5670 **	5893.3700 **	0.2680 **	33.6880 **	30.8350 **
Residual	40	38.6360	33.1300	0.0010	2.3010	1.4770

Source of variation	D.F.	MBT	SHT	BT	Density
Replications	2	1.6400	0.6370	1.8110	4.7160
Genotypes	20	27.6620 **	55.6090 **	60.0480 **	620.0390 **
Residual	40	1.9840	1.2990	1.1440	11.0130

** = $p < 0.01$ and * = $p < 0.05$

From the results it can be concluded that the parents and crosses were phenotypically different from one another. The environmental differences between blocks had a significant effect on LPL only and can, for all practical purposes, be ignored for all other characteristics.

4.2 Performance of genotypes

The LSD-value ($p<0.05$) of the different characteristics was used to identify significant differences among the averages of the different genotypes. All averages of genotypes for the different characteristics are listed in Table 4.2. and are illustrated in Figure 4.1 to Figure 4.19 in the Appendix.

4.2.1 Ovary morphology

Ovary width: length ratio (OW:L)

From Figure 4.1 it can be seen that the highest ranking parent was C (1.36), followed by D (1.15), A (0.96) and B (0.95). Parent C differed significantly from all other parents. The worst performing parent which differed significantly from all other parents was E (0.50) with F (0.63) in the second lowest ranking. The best performing hybrids were DxC (1.31) and AxC (1.29), which differed significantly from all other crosses but not from one another. The hybrid with the lowest ranking was FxE (0.61), which differed significantly from all the other hybrids. C (1.36) was the only parent to be significantly better than the highest ranking hybrids.

Ovary top flesh thickness (OTT)

The OTT of the parental lines and their F1 hybrids are illustrated in Figure 4.2. The parent with the highest ranking was E (32.56) followed by F (27.90) and B (27.32). Parent E differed significantly from the other five parents. The parents with the lowest and second lowest ranking were D (19.84) and C (21.22) respectively, which did not differ significantly from one another, but did differ from the other four parents. FxE (33.10) and ExB (32.79) were the best performing hybrids and did not differ significantly from one other, but did differ from the remaining 13 crosses. FxE and ExB were the only crosses to have a higher OTT ranking than E, but they were not significantly better. The worst performing hybrid was AxD (19.37), which differed significantly from all the other crosses, except AxC (19.49).

Ovary side flesh thickness (OST)

In Figure 4.3 the OST averages for the parents and the F1 hybrids are illustrated. The parent with the highest OST was C (23.49), which differed significantly from the other five parents. C was followed by A (21.45) and B (21.33). Parent E (11.35) was the lowest ranking parent and differed significantly from all the other parents, except F (12.01). The best performing hybrid was calculated to be CxB (26.44), which differed significantly from the other 14 hybrids. The crosses that followed CxB were AxB (24.74), CxE (23.95) and AxC (22.97). The lowest ranking F1 hybrid was FxE (12.07), which differed significantly from all other crosses. FxE was followed by ExB (13.90), which also differed significantly from all the other crosses.

Ovary blossom end scar size (OBES)

OBES for the parents and the F1 hybrids are showed in Figure 4.4. The highest ranking parent was B (66.40) and it was followed by F (64.54) and A (60.46). However, these three parents did not differ significantly from one another. However, B differed significantly from the remaining three parents. The parent with the smallest OBES value was D (51.21), which did not differ significantly from C (54.52), but it differed from the other four parents. FxB (74.85) was the only cross to have a significantly higher OBES value, than not only B, but also the other 14 F1 hybrids. FxB was followed by ExB (62.14), DxB (61.91) and FxE (61.49). The lowest value was calculated for CxE (44.09), but it did not differ significantly from AxC (46.89), DxE (47.03) and AxD (47.75).

4.2.2 Leaf morphology

Leaf petiole length (LPL)

The LPL values for all the parents and F1 hybrids are illustrated in Figure 4.5. C (57.67) was the parent with the longest petiole, followed by D (57.17). C and D did not differ significantly from one another, but they did however differed from the remaining parents. The lowest ranking parent was B (36.83), which was followed by E (37.67), A (41.25) and F (42.92). B, E and A did not differ significantly from one

another. FxA (63.25) was the highest ranking hybrid and it was followed by AxD (62.42), CxF (57.17) and DxC (56.58). FxA differed significantly from all the other crosses, except AxD. FxA was also the only F1 hybrid to be significantly better than C. The worst performing hybrid was ExB (43.50), which did not differ significantly from FxB (47.17), but it did however differed from all the other crosses. FxB also did not differ significantly from FxE (48.33). All parents except C and D had lower rankings than all the F1 hybrids.

Leaf blade length (LBL)

The different LBL averages for the parents and F1 hybrids are presented in Figure 4.6. The parent with the largest LBL was C (33.00), which differed significantly from all other parents, except D (31.00). The same four most inferior parents for LPL (A (22.83), B (22.08), F (24.00) and E (23.25)) had the shortest LBL and did not differ significantly from one another. The best performing F1 hybrid was DxC (33.50), which differed significantly from all other hybrids except CxF (33.17), AxD (32.50), FxA (32.08) and AxC (31.75). The latter four hybrids also did not differ significantly from C. DxC (33.50) and ExB (23.17) were the worst performing hybrids. DxC differed significantly from all other hybrids, except ExB.

4.2.3 Yield data

Yield per plant

Figure 4.7 illustrates yield per plant for the different parental lines and F1 hybrids. D (6.53) was the parent with the highest yield and differed significantly from all the other parents. D was followed by C (4.97) and E (4.87), which did not differ significantly from one another. The lowest ranking parent for yield per plant was B (2.87), which did not differ significantly from F (2.93) and A (3.63). DxE (10.70) was the cross with the highest yield and it differed significantly from all the other crosses. DxE was followed by CxE (9.43), which also differed significantly from the other F1 hybrids. FxB (3.77) had the lowest yield per plant, but did not differ significantly from ExB (4.63). D was the only parental genotype in the trial to show above average yield per plant.

Fruit mass

The fruit mass averages for the different genotypes are illustrated in Figure 4.8. The fruit mass for parents C (4.50), D (4.27) and E (4.27) did not differ significantly from one another, with C having the highest rank. The parent with the lowest ranking was F (1.10), followed by B (1.47) and A (2.07). F differed significantly from the other parents, except B. CxE (7.87) ranked the highest among the crosses for fruit mass and differed significantly from the other hybrids, except DxE (7.83). DxE was followed by DxC (5.23) and CxB (4.00), but it had a significantly higher yield. Only CxE, DxE and DxC were significantly better than C.

Fruit number

The parents and their F1 hybrids are illustrated in Figure 4.9 according to the number of fruit produced per plant. The parent which produced the most fruit per plant was F (2.73), and it was followed by B (1.93) and A (1.73). F differed significantly from the other parents. The lowest ranking parent was C (1.10), which did not differ significantly from the second lowest ranking parent, namely E (1.13). Five of the 15 hybrids produced more fruit per plant than F and included AxB (6.77), FxA (5.43), AxD (5.43), AxE (4.47) and AxC (3.97). The worst performing hybrid was CxE (1.17), followed by DxC (1.27), DxE (1.37) and CxB (1.40). The latter four hybrids did not differ significantly from one another.

4.2.4 Fruit morphology

Width (W)

The widths of the different genotypes are presented in Figure 4.10. Parent C (248.82) with the widest fruit differed significantly from all the other parents in the trial and was followed by D (234.11) and E (200.89). The worst performing parent F (139.19), differed significantly from all the other parents. DxE (305.08), CxE (298.30) and DxC (268.48) were significantly wider than C. DxE and CxE had the highest and second highest rankings of the F1 hybrids. Although they did not differ significantly from one

another, they were significantly wider than all the other crosses. The lowest ranking hybrid was AxB (141.30) and it did not differ significantly from FxA (145.41).

Maximum length (ML)

From Figure 4.11 it can be seen that parent E (275.22) was the highest ranking parent for ML and it differed significantly from all the other parents. The second highest ranking parent was C (138.03) followed by A (135.61) and D (135.12). The latter three did not differ significantly from one another. C differed significantly from the remaining two parents. B (103.21) had the shortest ML and differed significantly from all the other parents. None of the hybrids had a longer ML than E. The highest ranking F1 hybrid was DxE (219.70), followed by FxE (196.71), CxE (186.63) and ExB (170.80), which all differed significantly from one another as well as from the remaining hybrids. AxB (128.38) was the cross with the lowest rank, but it did not differ significantly from AxC (95.61) and AxD (97.41).

Total length (TL)

The average TL of the parents and their F1 hybrids are illustrated in Figure 4.12. Parent E (267.28) had the highest ranking and differed significantly from all other parental genotypes. E was followed by F (125.61), C (114.77) and A (114.12). The worst performing parent was B (99.13), followed by D (107.59). E had a significantly higher TL than any of the hybrids. The best performing hybrid was DxE (197.79), which did not differ significantly from FxE (191.24). These two hybrids differed significantly from the remaining 13 hybrids, and they were followed by ExB (164.09), CxE (151.69) and DxF (130.98). The hybrid with the lowest ranking was AxC (82.00), which did not differ significantly from AxD (86.17) and AxB (88.48).

Width: maximum length ratio (W:ML)

Fruit width in relation to ML is presented in Figure 4.13 for both the parental lines and their crosses. The most superior parent was C (1.81), which differed significantly from the other five parents. C was followed by D (1.74) and B (1.51). The parent with the lowest ranking was E (0.73) followed by F (1.09) and A (1.26). E differed

significantly from all the other parents. DxC (1.85) and AxC (1.84) had the highest rankings, but did not differ significantly from one another or from the best parent C. However, DxC differed significantly from the remaining 13 F1 hybrids. The F1 hybrid with the lowest ranking was FxE (0.93) and it differed significantly from all the other hybrids. FxE was followed by ExB (1.17) and FxA (1.36).

4.2.5 Flesh thickness

Side thickness (ST)

Figure 4.14 is an illustration of the average ST values of the parents and their crosses. The parent with the thickest ST in the trial was C (35.04), which was significantly better than any of the other parents, except E (32.97). E did not differ significantly from F (32.47). The parent with the lowest ranking was D (25.91), followed by B (27.25). These two parents did not differ significantly from one another, but it did differ from the other four parents. C, E and F had higher ST values than the two superior hybrids, CxF (31.37) and CxB (31.36). Only C differed significantly from CxF and CxB. CxF differed significantly from all other crosses except CxB, DxC (30.21), FxE (29.99) and CxE (29.50). The hybrid with the lowest ranking was AxD (22.46), which did not differ significantly from FxA (24.22) and AxE (24.23).

Top flesh thickness (TT)

The TT of the parental genotypes and their F1 hybrids are presented in Figure 4.15. The highest ranking parent was D (25.15), which was followed by F (25.14) and B (24.57). All three these genotypes were not significantly different from one another. C (16.57) had the lowest parental ranking and differed significantly from the other parents. ExB (27.00) differed significantly from the other crosses, as well as all the parents, but it did not differ from FxE (26.47). The worst performing hybrid was AxC (17.16), but it did not differ significantly from DxE (17.59) and AxB (17.80).

Middle bottom flesh thickness (MBT)

In Figure 4.16 the MBT averages for the parents and the F1 hybrids are illustrated. D (22.97) was the highest ranking parent for MBT and differed significantly from the other parents. D was followed by E (17.76) and F (17.39). The lowest ranking parent was A (14.12), but it did not differ significantly from B (14.63). Only DxF (24.65) had a higher MBT than the best parent, D. However, DxF did not differ significantly from either CxF (22.93) or D (22.97), but it differed significantly from the remaining 13 hybrids. CxF was followed by FxA (21.96), CxE (2.29) and DxE (20.84). The F1 hybrid with the lowest ranking was FxE (14.89), which was followed by ExB (15.49), FxB (15.97), CxB (16.08) and DxB (16.68). The latter five crosses did not differ significantly from one another.

Shoulder flesh thickness (SHT)

The SHT averages for the parents and F1 hybrids are illustrated in Figure 4.17. The highest ranking parent was B (26.83), followed by C (26.14) and D (21.68). B differed significantly from all parents except C. The worst performing parent was E (12.36), which differed significantly from the other parents. The best performing hybrid was CxB (28.98), which differed significantly from the other crosses except CxE (28.11). CxE was followed by DxC (26.08), AxB (25.41) and AxC (25.22). The worst performing hybrid was FxE (15.45) and it differed significantly from the other crosses for SHT. The second lowest ranking hybrid was DxE (18.05), followed by ExB (18.09) and AxD (18.78).

Bottom flesh thickness (BT)

The BT of the parental genotypes and their F1 hybrids are presented in Figure 4.18. C (22.43) was the best performing parent, differing significantly from the other five parents. C was followed by D (19.88) and A (18.01). E (11.90) had the lowest ranking, followed by B (15.00) and F (15.97). E differed significantly from the other parents. Although C had a better ranking than any of the F1 hybrids, it did not differ significantly from the highest ranking hybrid CxF (21.64). CxF differed significantly from the other crosses except DxC (21.53), DxF (21.11) and CxE (20.79). FxE

(13.27) was the lowest ranking hybrid, but it did not differ significantly from ExB (13.83). ExB was followed by AxB (15.17) and AxD (15.70).

4.2.6 Density

Figure 4.19 illustrates the average densities for the parent lines and F1 hybrids. The highest average density was calculated for parent B (6.87). B differed significantly from the other parents, and was followed by E (4.34) and F (3.42). The lowest ranking parent was D (2.09), which did not differ significantly from C (2.17). ExB (6.42) was the only cross that did not differ significantly from C, but it differed significantly from the other F1 hybrids. ExB was followed by FxE (5.05) and FxB (4.61). The lowest ranking hybrid was AxC, which did not differ significantly from AxD (1.55).

Discussion

Significant differences were found between the parents and F1's for all characteristics measured, as well as within parents and crosses. It will thus be possible to improve these characteristics in pumpkin using this material by selecting within segregating populations. C was the superior parent in nine of the 19 characteristics measured, which included O:WL, OST, fruit mass, LPL, LBL, W, W:ML, ST and BT. However, for fruit number and TT, C had the lowest values. For yield, fruit number, LPL, LBL and MBT, parents in general had lower values than the crosses, indicating possible hybrid vigour for these characteristics. The opposite was noticed for ST where the parents had a higher ranking, indicating the possibility of limited positive hybrid vigour. Another phenomenon in some of the characteristics was that the best parent parented the best crosses as well as the most inferior parents parented the most inferior crosses. The latter was evident for OW:L, OTT, OST, yield, LBL, ML, W:ML, ST, SHT, BT and density indicating that both inferiority and superiority of parents can be transferred to their offspring.

Table 4.2: Genotype averages of various agronomic and quality characteristics (Parents and F1s)

Genotype	OW:L	OTT	OST	OBES	LPL	LBL	Yield	Fruit mass	Fruit number	W	ML	TL	W:ML	ST	TT	MBT	SHT	BT	Density
A	0.96	23.38	21.45	60.46	41.25	22.83	3.63	2.07	1.73	170.03	135.61	114.12	1.26	30.28	19.39	14.12	20.63	18.01	2.61
B	0.95	27.32	21.33	66.40	36.83	22.08	2.87	1.47	1.93	155.63	103.21	99.13	1.51	27.25	24.57	14.63	26.83	15.00	6.87
C	1.36	21.22	23.49	54.52	57.67	33.00	4.97	4.50	1.10	248.82	138.03	114.77	1.81	35.04	16.57	16.26	26.14	22.43	2.17
D	1.15	19.84	18.86	51.21	57.17	31.00	6.53	4.27	1.53	234.11	135.12	107.59	1.74	25.91	25.15	22.97	21.68	19.88	2.09
E	0.50	32.56	11.35	58.90	37.67	23.25	4.87	4.27	1.13	200.89	275.22	267.28	0.73	32.97	19.75	17.76	12.36	11.90	4.34
F	0.63	27.90	12.01	64.54	42.92	24.00	2.93	1.10	2.73	139.19	128.38	125.61	1.09	32.47	25.14	17.39	18.99	15.97	3.42
A X B	1.11	24.28	24.74	55.72	52.50	27.42	6.37	0.93	6.77	141.30	94.77	88.48	1.49	25.92	17.80	17.80	25.41	15.17	3.44
A X C	1.29	19.49	22.97	46.89	56.58	31.75	6.07	1.53	3.97	176.26	95.61	82.00	1.84	27.90	17.16	18.54	25.22	16.73	1.44
A X D	1.13	19.37	19.49	47.75	62.42	32.50	6.53	1.20	5.43	162.30	97.41	86.17	1.67	22.46	19.53	19.48	18.78	15.70	1.55
A X E	0.76	23.61	18.19	50.39	52.33	26.42	6.97	1.57	4.47	167.41	120.46	113.15	1.40	24.23	21.69	18.74	20.37	16.06	2.78
F X A	0.85	23.49	19.82	51.75	63.25	32.08	5.57	1.03	5.43	145.41	107.03	99.23	1.36	24.22	19.92	21.96	20.85	16.93	2.28
C X B	1.24	22.22	26.44	59.88	56.50	29.75	5.63	4.00	1.40	233.48	134.94	113.85	1.73	31.36	19.30	16.08	28.98	18.31	2.89
D X B	1.09	23.78	22.07	61.91	50.42	27.75	6.50	3.80	1.73	224.52	134.97	116.07	1.66	24.90	24.01	16.68	24.43	16.57	2.61
E X B	0.69	32.79	13.90	62.14	43.50	23.17	4.63	2.93	1.60	199.18	170.80	164.09	1.17	26.33	27.00	15.49	18.09	13.83	6.42
F X B	0.89	29.51	19.29	74.85	47.17	23.50	3.77	1.57	2.33	159.85	111.67	105.57	1.43	27.62	23.92	15.97	23.59	17.05	4.61
D X C	1.31	22.35	22.34	52.41	56.58	33.50	6.60	5.23	1.27	268.48	147.32	116.06	1.85	30.21	20.72	19.75	26.08	21.53	2.24
C X E	1.01	23.00	23.95	44.09	52.75	31.25	9.43	7.87	1.17	298.30	186.63	151.69	1.60	29.50	20.04	21.29	28.11	20.79	3.35
C X F	1.07	22.58	21.25	56.14	57.17	33.17	6.97	3.50	2.00	219.29	138.21	119.42	1.59	31.37	21.45	22.93	24.35	21.64	3.35
D X E	0.84	23.97	17.17	47.03	54.83	28.67	10.70	7.83	1.37	305.08	219.70	197.79	1.40	24.74	17.59	20.84	18.05	16.24	3.79
D X F	0.92	23.40	18.43	59.04	55.25	29.33	6.33	3.67	1.73	232.07	146.38	130.98	1.59	29.14	24.47	24.65	22.91	21.11	3.07
F X E	0.61	33.10	12.07	61.49	48.33	25.25	5.17	2.97	1.77	181.92	196.71	191.24	0.93	29.99	26.47	14.89	15.45	13.27	5.05
Mean	0.97	24.72	19.55	56.55	51.58	28.18	5.86	3.21	2.51	203.02	143.72	128.78	1.47	28.28	21.51	18.49	22.25	17.34	3.35
LSD (0.05)	0.04	1.71	1.61	6.06	4.80	2.07	1.18	0.40	0.38	11.51	8.55	7.91	0.05	2.09	1.67	1.94	1.57	1.11	0.46
C.V.%	3.32	5.03	5.98	7.80	6.77	5.33	14.68	9.01	11.10	4.12	4.32	4.47	2.55	5.36	5.65	7.62	5.12	4.66	9.90
b	0.99	0.95	0.95	0.82	0.88	0.91	0.88	0.99	0.98	0.98	0.99	0.99	0.99	0.88	0.91	0.88	0.96	0.95	0.97

4.3 Combining ability

4.3.1 Analysis of variance

The general combining ability effects (GCA) for all the characteristics evaluated were significant at the $p<0.05$ level of significance. All the characteristics also showed significant specific combining ability effects (SCA) at the same level of significance. GCA and SCA effects are presented in Table 4.3.

Table 4.3: Mean squares for combining ability for various pumpkin yield and quality characteristics (Parents and F1s)

Source	D.F.	OW:L		OTT		OST		OBES		LPL	
GCA	5	0.228	**	58.793	**	58.159	**	150.977	**	121.398	**
SCA	15	0.002	**	4.127	**	5.025	**	26.114	**	35.778	**
Residual	40	0.000		0.515		0.456		6.486		4.063	

Source	D.F.	LBL		Yield		Fruit mass		Fruit number		W	
GCA	5	45.522	**	6.249	**	11.581	**	5.218	**	7423.365	**
SCA	15	5.592	**	2.704	**	1.701	**	1.978	**	848.859	**
Residual	40	0.752		0.247		0.028		0.026		23.343	

Source	D.F.	ML		TL		W:ML		ST		TT	
GCA	5	6679.459	**	6696.437	**	0.312	**	25.732	**	25.104	**
SCA	15	471.543	**	387.130	**	0.015	**	6.395	**	5.336	**
Residual	40	12.879		11.043		0.000		0.767		0.492	

Source	D.F.	MBT		SHT		BT		Density	
GCA	5	17.889	**	57.158	**	25.784	**	668.198	**
SCA	15	6.331	**	5.663	**	2.954	**	52.840	**
Residual	40	0.661		0.433		0.218		3.671	

**** = p < 0.01 and * = p < 0.05**

Significant GCAs mean that true differences among these effects result in certain parents to have a greater ability than other parents to transfer their genetic superiority for a particular trait to their offspring. According to Baker (1978), if the specific combining ability mean square is not significant, one could accept that the performance of a single-cross can be adequately predicted on the basis of general combining ability alone. Under these circumstances the best performing progeny will be produced by crossing the two parents having the highest GCA effects. However, in this specific trial all characteristics showed significant SCA effects, meaning that phenotypic observations differed from GCA predicted values. According to Yadav

and Singh (1988) both kinds of gene effects, additive and non-additive, appeared to be important in controlling the inheritance of the characteristics, when both GCA and SCA are significant.

4.3.2 Combining ability effects

Combining ability effects can be interpreted by the higher the value, the greater the relative ability of a line to transfer its genetic superiority to the next generation. A small combining ability effect means that relative to the other parents in the population the particular parent has a low ability to transfer its genetic superiority to its offspring (Huxley and Van Houten, 1997). In general it can be assumed that the smaller the SCA is the more accurate the phenotypic value of a hybrid can be predicted with the GCAs of the parents.

Effects are referred to as large and small when they are large positive or negative effects respectively. Tenkouano *et al* (1998) referred to the largest positive values as the largest effects and the largest negative values as smallest effects. This can be explained by the closer the value is to zero, positive or negative, the smaller the effect will be and the further removed the value is from zero, positive or negative, the larger the effect. The GCA and SCA effects are listed in Table 4.4 and Table 4.5 respectively.

The GCA:SCA ratio was calculated for each trait from the mean squares of the GCA and SCA from the combining ability tables. Ratios can be grouped into low, medium, high or very high. Low values are considered below one; medium between one and two; high between two and 10 and very high above 10. In this study the ratio values were grouped in two classes, namely high and very high. These ratios are presented in Table 4.6. as well as the percentage variation due to the GCA effects or additive variance.

4.3.2.1 Ovary morphology

Ovary width: length ratio (OW:L)

C (0.23) and E (-0.23) respectively ranked the highest and lowest for GCA of OW:L. Both these values were significantly different from all the other values. C was followed by D (0.10) also differing significantly from all other genotypes. A (0.03) and B (0.02) were the only GCAs that did not differ significantly from one another and they were also the values closest to zero.

The highest SCA effect was calculated for AxB (0.085), which did not differ significantly from FxB (0.055) or AxC (0.052). For OW:L only four crosses had negative SCA effects. The largest different significant negative effect was calculated for ExB (-0.061). Only the four mentioned crosses differed significantly from zero.

In general it could be said that crosses performed better than what was expected or predicted from the GCAs. In order to increase OW:L, C would be the best parent available, while E has the best ability to lower the ratio. A and B will have the smallest influence on the next generation. With reference to Table 4.2, all crosses parented by C performed better than average, confirming the high GCA of C.

The GCA effects accounted for 98.3% of the genetic variation. However, the non-additive effects were still significant enough to influence the offspring. Eleven of the 15 values were accurately predicted by the GCAs. The GCA:SCA ratio was extremely high (114.00) confirming that OW:L is mainly controlled by additive genes.

Ovary top flesh thickness (OTT)

E (3.57) differed significantly from all the other genotypes with the highest estimated GCA for OTT. E was followed by F (1.85) which did not differ significantly from B (1.77). The largest negative GCA effect was calculated for C (-2.62), but it was not significantly different from D (-2.56) and A (-2.01).

For OTT only four SCA effects were positive. The top three did not differ significantly from one another, with FxE (2.96) having the highest estimated effect, followed by DxC (2.81) and ExB (2.73). The largest negative SCA was calculated as -2.67 (AxE and CxE). The latter did not differ significantly from DxE (-1.76), CxB (-1.65), CxF (-1.37) and FxA (-1.08). AxE, CxE, DxE, ExB, DxC and FxE differed significantly from zero.

Due to the high percentage (88.3%) variance caused by GCA effects, it can be concluded that most of the variation is influenced by additive effects although non-additive effects still play a significant role. A GCA:SCA ratio of 14.25 confirmed the important role of additive effects. Under these circumstances E had the greatest ability to transfer its superiority to its offspring in order to improve OTT. The performances of nine crosses were accurately predicted by GCA effects.

Ovary side thickness (OST)

From the observations it was calculated that the GCA of OST for C (3.38) differed significantly from all other values. This was the greatest computed effect. C was followed by B (1.53) which did not differ significantly from A (1.41). The largest negative effect was calculated for E (-3.61), differing significantly from all the other values. The smallest effect was computed for D (0.04), which was small enough not to differ significantly from zero. The genotype performance results summarised in Table 4.2 showed that all crosses having C as the one parent performed better than average, confirming the high GCA of C for OST.

Ten of the 15 crosses had positive SCA effects which mean that the crosses performed better than what could be predicted with the GCAs. The highest effect was calculated for CxE (4.62) which differed significantly from all other crosses. ExB (-3.57) had the largest negative effect, which differed significantly from all other values. The only crosses significantly different for zero were ExB (-3.57), DxF (1.58), FxA (1.61), CxB (1.98), AxB (2.25) and CxE (-4.62).

The additive component explained 94.7% of the variation. The GCA:SCA ratio for OST was calculated to be 11.57. The best parent included in this trial to improve

OST was C. Six values were significantly different when predicted by the GCA effects, which included five positive effects. D will have a minimal effect on its progeny, while E has the ability to transfer it inferior performance to its offspring. The highest (C) and lowest (E) general combiners resulted in the highest ranking hybrids (CxE), which is corresponding with the results obtained by Mohanty (2000a) for flesh thickness.

Ovary blossom end scar size (OBES)

B (6.43) and F (4.28) ranked first and second respectively and did not differ significantly from one another. The remaining parents E (-1.61), A (-2.80), D (-3.16) and C (-3.42) did not differ significantly from one another, with C having the smallest value.

For OBES the largest positive deviation from the expected values calculated from the GCA effects was estimated for FxB (7.31). FxB differed significantly from all crosses except from DxC (2.45), DxB (2.09) and FxE (1.99). Eight negative effects were calculated for OBES and CxE (-7.43) had the smallest value. However, CxF (-1.55) was the only negative effect, which differed significantly from CxE. CxE, FxA (-6.56) and FxB were the only effects significantly different from zero.

Additive effects explained 76.1% of the variation. This was confirmed by a high GCA:SCA ratio of 5.78. It is obvious that non-additive or dominance effects are also influencing the genetic expression of OBES. B and F would be the best parents to use to improve OBES. The remaining parents may not have a significant effect. The non-additive genetic portion will make an improvement under selection with inbreeding and crossing, more likely than selection without inbreeding.

4.3.2.2. Leaf morphology

Leaf petiole length (LPL)

Parents C (4.24), D (4.10) and A (1.07) ranked first, second and third respectively for LPL according to GCA effects. They did not differ significantly from one another, but

they did differ from the other parents. The largest negative GCAs were calculated for E (-4.24) and B (-4.66), which did not differ significantly from one another. F (-0.50) will have the smallest effect on the next generation.

FxA (11.11) had the highest positive SCA effect which differed significantly from all the other crosses. AxD (5.67) and CxB (5.35) as well as FxA were the only effects differing significantly from zero. Only AxC (-0.30), DxB (-0.60) and DxC (-3.33) of the 15 crosses had negative SCA effects and they did not differ significantly from one another.

The significant different SCA effects caused differences between the expected and observed values for LPL. The GCA effects accounted for 57.4% of the genotypic variation. The remaining 42.6% was due to SCA effects. This was confirmed by a GCA:SCA ratio of 3.39. The parent with the smallest effects on the offspring was F. The lines B and E seem to have the highest ability to reduce LPL.

Leaf blade length (LBL)

In this experiment, C (3.52) and D (2.07) had the largest positive GCA effects for LBL. These values did not differ significantly from one another, but they were significantly higher than all the other values. B (-2.68) ranked lowest, but it did not differ significantly from E (-2.00). In Table 4.2 none of the crosses parented by either C or D were significantly lower than the average for LBL. This is in agreement with the high positive GCA effects calculated for C and D.

FxA (4.82) ranked the highest according to SCA for LBL. FxA differed significantly from all the other crosses. There were only five crosses that had negative SCA effects. The largest negative effects did not differ significantly from zero. The effects that differed significantly from zero included FxA (4.82), AxD (2.43), CxF (2.20) and AxB (2.10).

The GCA effects accounted for 80.5% of the genetic variation in LBL. A high GCA:SCA ratio of 8.14 confirmed the importance of additive gene action. Significant differences between expected values and real values of crosses accounted for the

remaining 19.5% of genotypic variation. The best parent to be used to increase LBL will be C and D, while B and E will have the opposite effect.

4.3.2.3 Yield components

Yield per plant

D (1.09), E (0.70) and C (0.45) ranked first, second and third respectively for GCA of yield and they did not differ significantly from one another. A (-0.28), F (-0.92) and B (-1.05) differed significantly from the previously mentioned, but not from one another. A, C and E did not differ significantly from zero. All crosses parented by D performed above average (Table 4.2). This confirms the high GCA effect of D for yield.

DxE (3.05) and CxE (2.42) had the largest SCA effects and they did not differ significantly from one another. DxE differed significantly from the other genotypes. The lowest SCA value was calculated for ExB (-0.88), but it did not differ significantly from zero. The only values that differed significantly from zero were DxE (3.05), CxE (2.42), AxB (1.84) and CxF (1.57).

The best parents to be used under these circumstances to improve yield per plant will be D, E and C. All SCA effects significantly different from zero were positive. This indicates that the crosses performed better than what was predicted by the GCA effects. The highest SCA effects were calculated for the crosses parented by the lines with the highest GCAs. GCA and SCA effects were both significant, but only 41.9% of the genotypic variation was accounted for by additive effects. The computed GCA:SCA ratio was 2.31. The remaining 58.1% was due to non-additive effects which may be an indication of significant heterosis.

Fruit mass

For fruit mass E (1.16) had the highest GCA effect, but it did not differ significantly from C (1.09) and D (0.98). All effects differed significantly from zero. The lowest negative GCA effect was calculated for A (-1.50) which differed significantly from all the other values. It is prominent that the best performing crosses in Table 4.2 for fruit

mass were made up from the best parents. This indicates that the superiority of the best parents was transferred to their offspring.

Considering fruit mass, nine of the 15 crosses had positive SCA effects. DxE (2.49) had the largest effect, followed by CxE (2.42). The two were not significantly different from each other and both were significantly different from the other 13 crosses. AxD (-1.48) had the smallest negative value and did not differ significantly from AxE (-1.29) and AxC (-1.26). The only values that did not differ significantly from zero were DxC (-0.04), AxB (0.02), FxB (0.08), CxF (0.15) and FxA (0.27).

Significant differences in both the GCA and SCA effects suggest that certain lines have a better ability to transfer their genetic superiority to the crosses they parented. However, the expected and observed performances will deviate significantly in some of the cases. SCA effects (non-additive) were not only significant, but contributed 25.3% of the genotypic variance compared to the 74.7% due to additive variance. The computed GCA:SCA ratio was 6.81. E, C and D have the largest ability to increase fruit mass in combination with other lines, while A will have the opposite effect.

Fruit number

The highest GCA for fruit number was calculated for parent A (1.50) which differed significantly from all the other parents. Parent E (-0.61) and C (-0.69) did not differ significantly, with C having the lowest value. B (0.02) and F (0.15) did not differ significantly from zero. From the genotype performances in Table 4.2 it can be seen that all crosses producing more fruit than average were parented by A. This is in agreement with the high GCA calculated for A.

AxB (2.74) differed significantly from all the other crosses for fruit number with the highest positive SCA effect. Other significant positive effects were calculated for AxD (1.80), FxA (1.28), AxE (1.07) and AxC (0.65). The five crosses with the highest SCA effects were all parented by A. The negative effects differing significantly from zero, included DxF (-0.55), CxB (-0.43) and DxB (-0.43), but they did not differ significantly from one another.

A GCA:SCA ratio of 2.64 indicated the importance of both additive and non-additive gene action. The non-additive effects accounted for 54.6% of the genotypic variation. The remaining 45.4% were due to additive effects. E and C have the greatest ability to reduce fruit number under these conditions, while A will increase the fruit number.

4.3.2.4 Fruit morphology

Width (W)

From the data collected C (34.03) had the highest GCA followed by D (29.94), but they were not significantly different. C and D differed significantly from the other parents. A (-36.05) had the smallest negative value and differed significantly from all the other lines. All the genotypes differed significantly from zero.

The highest SCA effect was calculated for DxE (55.55), but it did not differ significantly from CxE (44.68). Both DxE and CxE differed significantly from all the other crosses. Effects significantly different from zero were calculated for DxE (55.55), CxE (44.68), DxF (24.64) and CxB (15.37) as well as for FxE (-12.13), AxE (-16.12), AxC (-24.75) and AxD (-34.61) that had negative values. Four of the five crosses with the smallest SCA values were parented by A and included AxB (-6.72), AxE (-16.12), AxC (-24.75) and AxD (-34.61). The fifth cross was FxE (-12.13).

C and D are the lines with the best ability to improve W. According to the data 79.9% of the genetic variance was due to GCA and although SCA effects were significant it only contributed to 12.9% of the variation. This was confirmed by a GCA:SCA ratio of 8.75. A will result in the largest reduction in width, probably due to a reduction in size.

Maximum length (ML)

E (54.84) ranked the highest for GCA in ML in the trail and differed significantly from all the other parents. A (-27.45) had the largest negative GCA effect and differed

significantly from all other parental genotypes. The smallest effects were calculated for D (1.25) and C (-3.41) which did not differ significantly from zero.

From the data the SCA for ML for DxE (19.90) was calculated as the significant largest positive effect. CxB (13.69) did not differ significantly from DxE. The only other positive effect significantly larger than zero was computed for DxB (9.06). Four of the five largest computed values were crosses parented by D. Seven SCA effects of the 15 crosses did not differ significantly from zero. The largest negative effect was -50.65 (AxE) and it differed significantly from all the other values. Other negative values, significantly different from zero, included AxD (-20.12), AxC (-17.26), ExB (-8.69) and CxE (-8.52). The largest negative effects were much larger than the largest positive effects for ML.

A GCA:SCA ratio of 14.17 was calculated for ML. The GCA effects accounted for 87.1% of the genetic variation in ML. The rest was due to non-additive effects estimated according to SCA effects. Parent E will result in the largest fruit in terms of ML, while A will have the opposite effect.

Total length (TL)

The largest positive GCA effect for TL was calculated for E (56.39), which differed significantly from the other values. The smallest negative value was calculated for A (-25.52). The smallest effects were calculated for F (-0.47) and D (-4.90), which did not differ significantly from zero.

DxE (17.53) and CxB (10.57) ranked first and second respectively for SCA of TL. These were the only positive values differing significantly from zero. DxE differed significantly from all the crosses except CxB. The largest negative effect was computed for AxE (-46.49) and it differed significantly from all other values. Negative effects that differed significantly from zero were calculated for FxB (-8.34), AxC (-10.15), AxD (-12.19), CxE (-22.36) and AxE (-46.49).

GCA effects accounted for 89.4% of the variation in TL, which is equal to a GCA:SCA ratio of 17.3. The latter is an indication of the importance of mainly additive gene action for TL. E has the greatest ability to increase TL, while A will reduce TL.

Width: maximum length ratio (W:ML)

The GCA effect for W:ML for C (0.24) was significantly higher than all the other parents. This was followed by D (0.17) which was also significantly different from the other parents. The GCA value for E (-0.29) was significantly smaller than the other parents. The smallest effects were calculated for A (0.00) and B (0.03).

Five of the crosses had a significant positive SCA effect with AxE (0.22) having the highest rank. AxE did not differ significantly from CxE (0.18) but it did however differed from all the other crosses.

From the significant different GCAs it is clear that C would be the ideal parent to use to improve the flatness of fruit. GCA effects accounted for 90.8% of the variation in W:ML. This was confirmed by a computed GCA:SCA ratio of 20.80. E has the greatest ability to increase fruit depth. A and B seem to have minimum effects on W:ML, while C will decrease fruit depth.

4.3.2.5 Flesh thickness

Side thickness (ST)

Parent C (2.81) ranked significantly higher in the GCA for ST. The smallest value was calculated for D (-1.83). The smallest effects, not differing significantly from zero, were calculated for parents B (-0.92), E (0.35) and F (1.17). This is in agreement with the data in Table 4.2 where all progeny parented by B performed below average, except CxB and all crosses parented by C were average or above.

The estimated SCA effects for ST included DxF (1.53) with the highest ranking. The latter did not differ significantly from CxB (1.19), DxC (0.96), FxE (0.20) and AxB (0.14). No calculated positive effects were significantly different from zero. The only

effects that differed significantly from zero were FxA (-3.64), AxE (-2.82), AxD (-2.40) and DxE (-2.05).

According to the ST data, C had the highest ability to increase ST. Additive effects resulted in 63.2% of the variation. The remaining 36.8% was due to non-additive variation. A GCA:SCA ratio of 4.02 confirmed the latter.

Top flesh thickness (TT)

F (2.00) had the highest GCA for TT, but did not differ significantly from B (1.33). C (-2.34) ranked the lowest, but it did not differ significantly from A (-1.96).

ExB (3.94) had the highest SCA effect, but it did not differ significantly from FxE (2.75). The largest negative effects, significantly different from zero, were calculated for DxE (-4.89), AxB (-3.07) and FxA (-1.63). DxE differed significantly from all the other crosses.

A computed GCA:SCA ratio of 4.71 was calculated for TT. The significant differences in the SCAs were responsible for 32.9% of the genotypic variance. Additive effects accounted for 67.1% of the variation in TT. F and B have the highest ability to improve TT.

Middle bottom flesh thickness (MBT)

The estimated GCA for MBT of D (2.24) was significantly higher than the GCAs of the other genotypes. This is in agreement with the performances mentioned in Table 4.2, where four of the five crosses parented by D were above average. This indicates that D's superiority was transferred to its progeny. The largest negative effect was calculated for B (-2.27), which differed significantly from all the other values. A (-0.58), E (-0.33) and C (0.21) had the smallest GCA effects and they did not differ significantly from zero.

The SCA for the top five crosses did not differ significantly from one another, which included CxF (3.51), FxA (3.33), DxF (3.20), CxE (2.92) and AxB (2.16). CxF was

found to have the highest SCA. The smallest negative value was calculated for FxE (-3.99). FxE differed significantly from all the other crosses. Nine of the SCA effects of the crosses did not differ significantly from zero.

SCA effects accounted for 49.5% of the variation, while 50.5% was due to GCA effects. This was confirmed by the GCA:SCA ratio of 2.83. From this trial it seems that D would be the best choice to improve MBT under these circumstances.

Shoulder thickness (SHT)

C (3.66) and B (2.30) ranked first and second respectively for calculated GCA effects of SHT. These values differed significantly from one another as well as from the other parents. E (-3.87) had the smallest GCA value for SHT which differed significantly from all the other genotypes. The smallest effects were calculated for D (-0.27), A (-0.48) and F (-1.33) which did not differ significantly from zero.

SHT had nine positive SCA effects. The largest effect was calculated for CxE (6.07) which differed significantly from all the other crosses. Other crosses differing significantly from zero were AxE (2.47), DxF (2.26), FxE (-1.60), ExB (-2.59) and AxD (-2.72). The largest positive effect was much greater than the largest negative effect.

The deviations between the expected and observed values accounted for 16.1% of the genetic variance. The remaining 83.1% was due to additive effects. The latter was affirmed by the computed GCA:SCA ratio of 10.1 for SHT. B and C, but especially C would be useful for the improvement of SHT under these conditions.

Bottom flesh thickness (BT)

In this experiment C (2.81) had a significant larger GCA for BT than the rest of the parents. E (-2.17) had the smallest calculated GCA value, which was significantly different from the other parents. A (-0.59) and F (0.07) were not significantly different from zero.

SCA effects for CxE (2.81) and DxF (2.51) did not differ significantly from one another. CxE differed significantly from all the other crosses. The largest negative effects were calculated for AxC (-2.83), AxD (-2.23) and FxE (-1.97). The latter three did not differ significantly from one another. AxC (-2.83), AxD (-2.23) and FxE (-1.97) as well as CxE (2.81), DxF (2.51), AxE (1.49) and CxF (1.42) were the only effects significantly different from zero.

Additive genetic effects accounted for 80.7% of the variation in BT. A GCA:SCA ratio of 8.73 also showed that non-additive gene effects were less important. C would be the best parent to improve BT under these circumstances.

4.3.2.6 Density

GCAs calculated from this trial resulted in B (1.28) with a significant higher effect than the other parents. E (0.83) ranked second and also differed significantly from the other parents. The lowest value was estimated for A (-0.84), but it did not differ significantly from C (-0.73) or D (-0.75). E (0.22) was the only parent not significantly different from zero.

ExB (0.96) ranked the highest for density according to SCA, but it did not differ significantly from FxE (0.66). ExB differed significantly from all the other crosses. ExB (0.96), FxE (0.66), CxF (0.52), FxA (-0.45), AxE (-0.55), CxB (-1.01) and DxB (-1.27) were significantly different from zero. DxB and CxB had the largest negative effects and they did not differ significantly from one another.

The GCA effects accounted for 86.2% of the genetic variation. The latter was confirmed by the GCA:SCA ratio of 12.65 indicating the additive gene effects to be more important in the expression of density. The genotype with the greatest ability to improve fruit quality was B followed by E.

Discussion

The pooled analysis of variance for combining ability reflected that both the general combining ability (GCA) and specific combining ability (SCA) mean squares were

significant. Thus both additive and non-additive gene effects appeared to be important in controlling the inheritance of all the characteristics (Yadav and Singh, 1988). However, additive and non-additive effects were not equally important in all the characteristics evaluated.

In OW:L, OTT, OST, OBES, LBL, W, TL, ML, W:ML, SHT, BT and density additive gene effects contributed to more than 75% of the genetic variation, but the non-additive gene effects were still significant enough to allow the phenotypic observations to deviate from the GCA expected performances. The expression of LPL, fruit mass, ST, TT and MBT were between 50 and 75% controlled by additive gene action, with non-additive genes playing at least a 25% role in the expression of these traits. It was only in yield and fruit number that non-additive gene action played a larger role in the expression of these traits.

Korzeniewska and Niemirowicz-Szczytt (1993), Mohanty and Mishra (1998), Balliu and Hallidri (2000) and Gwanama *et al* (2001) all found that both additive and non-additive gene action were involved in mean fruit weight expression. Mohanty (2000a; 2000b) also mentioned the involvement of additive and non-additive gene action in the expression of yield. Mohanty and Mishra (1998) also found additive and non-additive gene action to be involved in the expression of flesh thickness. Unfortunately exact figures are not available to be compared with the results found in this study, but it does not seem to be contradictive.

According to Falconer and Mackay (1996) inbreeding and crossing (hybrid breeding) are likely to be a better means of improvement than selection without inbreeding when much of the genetic variance of a characteristic is non-additive as in the case of yield and fruit number. A line's inbred performance is correlated with its performance in crosses to some extent depending on how much of the variance is due to additive genes. The improvement made by the preliminary selection of the lines for their general combining ability comes from the additive variance in the base population. Any further improvement, making use of the non-additive genetic variance must come from selection for specific combining ability.

Since some of the parents had not significant different GCA, it can be assumed that in some cases more than one parent can be used to improve a specific characteristic. From the data the following could be concluded. For ease of discussion only the largest GCA effects and effects not significantly different from them will be discussed. In order to improve LPL, and fruit number, A will be the best option to use in a hybrid combination, however OTT, OBES, yield, fruit mass, W, ML, TL and density can be expected to be reduced. B will have a positive effect on OBES and density, but LPL, LBL and yield can be expected to be poorer. The parent that can be expected to influence the most characteristics in a positive way, was C. C had high positive GCAs for OW:L, OST, LPL, LBL, yield, fruit mass, W, W:ML, ST, SHT and BT. The high negative GCAs of C will result in hybrids that perform poorer for OTT, OBES and fruit number. Yield, LPL, LBL, fruit mass, W and MBT can be expected to be positively influenced when D is used as a parent in a hybrid combination, but OTT, OBES, ST and density might be influenced negatively. E was the parent to influence the most characteristics in a negative way in a hybrid combination which included OW:L, OST, OBES, LPL, LBL, fruit number, W:ML, MBT, SHT and BT. However, E had high positive GCAs for OTT, yield, fruit mass, ML and TL. F seemed to have the least influence and only had high GCA for OBES and yield. OBES will be influenced positively, while yield will be reduced when F is used in a hybrid combination.

Parent E had in general the lowest GCA for the most characteristics, however, it was the line that parented the most crosses with the largest positive SCA effects, indicating that crosses parented by E performed in general better than what was predicted with the GCAs.

The characteristics where the superior and inferior parents (according to phenotypic performance) corresponded with the parents with the highest and lowest GCA effects, included OW:L, OTT, OST, LPL, LBL, yield, W:ML and BT. For these characteristics both the best parents' superiority and the worst performing parents' inferiority were transferred to their offspring. For OBES, W, TL, ML, ST, MBT and density only the best parents' superiority was transferred to the offspring and not necessarily the inferiority of the weakest parent. Fruit number, TT and SHT showed

the opposite where only the inferiority of the weakest parent was transferred to the next generation.

For LPL, A had the highest GCA, but it was one of the worst phenotypic performers. For this reason it could be expected that the variation accounted for by the GCA will be less than accounted for by SCA. However, this was the only characteristic that showed significant differences between replications.

It should also be accentuated that these GCA and SCA effects were calculated for this specific population and that the same parents may show deviations from their recorded performances in another trial when compared to different parents or under different environmental conditions, especially since only one location was used for this trial and the trial was completed over one season.

Table 4.4: GCA effects for various agronomic and quality characteristics in pumpkin

Parents	OW:L	OTT	OST	OBES	LPL	LBL	Yield	Fruit mass	Fruit number	W	ML	TL	W:ML	ST	TT	MBT	SHT	BT	Density
A	0.03	-2.01	1.41	-2.80	1.07	-0.17	-0.28	-1.50	1.50	-36.05	-27.45	-25.52	0.00	-1.58	-1.96	-0.58	-0.48	-0.59	-0.84
B	0.02	1.77	1.53	6.43	-4.66	-2.68	-1.05	-0.78	0.02	-18.95	-19.06	-14.39	0.03	-0.92	1.33	-2.27	2.30	-1.31	1.28
C	0.23	-2.62	3.38	-3.42	4.24	3.52	0.45	1.09	-0.69	34.03	-3.41	-11.11	0.24	2.81	-2.34	0.21	3.66	2.81	-0.73
D	0.10	-2.56	0.04	-3.16	4.10	2.07	1.09	0.98	-0.37	29.94	1.25	-4.90	0.17	-1.83	0.76	2.24	-0.27	1.19	-0.75
E	-0.23	3.57	-3.61	-1.61	-4.24	-2.00	0.70	1.16	-0.61	16.56	54.84	56.39	-0.29	0.35	0.22	-0.33	-3.87	-2.17	0.83
F	-0.15	1.85	-2.75	4.56	-0.50	-0.74	-0.92	-0.94	0.15	-25.53	-6.16	-0.47	-0.15	1.17	2.00	0.72	-1.33	0.07	0.22
LSD (0.01)	0.03	1.21	1.14	4.28	3.39	1.46	0.84	0.28	0.27	8.13	6.04	5.59	0.03	1.47	1.18	1.37	1.11	0.79	0.32

Table 4.5: SCA effects for various agronomic and quality characteristics in pumpkin

Genotypes	OW:L	OTT	OST	OBES	LPL	LBL	Yield	Fruit mass	Fruit number	W	ML	TL	W:ML	ST	TT	MBT	SHT	BT	Density
AxB	0.085	-0.21	2.25	-4.46	4.52	2.10	1.84	0.02	2.74	-6.72	-2.45	-0.39	0.00	0.14	-3.07	2.16	1.34	-0.27	-0.35
AxC	0.052	-0.60	-1.37	-3.43	-0.30	0.23	0.04	-1.26	0.65	-24.75	-17.26	-10.15	0.13	-1.61	-0.05	0.43	-0.20	-2.83	-0.33
AxD	0.023	-0.79	-1.51	-2.84	5.67	2.43	-0.14	-1.48	1.80	-34.61	-20.12	-12.19	0.03	-2.40	-0.78	-0.67	-2.72	-2.23	-0.21
AxE	-0.012	-2.67	0.85	-1.74	3.93	0.41	0.69	-1.29	1.07	-16.12	-50.65	-46.49	0.22	-2.82	1.93	1.17	2.47	1.49	-0.55
FxA	-0.004	-1.08	1.61	-6.56	11.11	4.82	0.91	0.27	1.28	3.97	-3.08	-3.56	0.04	-3.64	-1.63	3.33	0.41	0.12	-0.45
CxB	0.024	-1.65	1.98	0.32	5.35	0.74	0.37	0.49	-0.43	15.37	13.69	10.57	-0.01	1.19	-1.20	-0.36	0.78	-0.53	-1.01
DxB	0.005	-0.15	0.95	2.09	-0.60	0.19	0.60	0.40	-0.43	10.50	9.06	6.58	0.00	-0.63	0.42	-1.78	0.15	-0.65	-1.27
ExB	-0.061	2.73	-3.57	0.77	0.83	-0.33	-0.88	-0.65	-0.31	-1.45	-8.69	-6.69	-0.03	-1.38	3.94	-0.40	-2.59	-0.03	0.96
FxB	0.055	1.16	0.96	7.31	0.75	-1.25	-0.13	0.08	-0.34	1.31	-6.83	-8.34	0.09	-0.91	-0.91	-0.98	0.37	0.94	-0.24
DxC	0.008	2.81	-0.64	2.45	-3.33	-0.27	-0.80	-0.04	-0.18	1.49	5.77	3.29	-0.03	0.96	0.79	-1.19	0.44	0.18	0.37
CxE	0.040	-2.67	4.62	-7.43	1.18	1.55	2.42	2.42	-0.03	44.68	-8.52	-22.36	0.18	-1.94	0.66	2.92	6.07	2.81	-0.10
CxF	0.015	-1.37	1.07	-1.55	1.86	2.20	1.57	0.15	0.04	7.77	4.06	2.22	0.03	-0.89	0.29	3.51	-0.23	1.42	0.52
DxE	0.004	-1.76	1.19	-4.75	3.40	0.42	3.05	2.49	-0.16	55.55	19.90	17.53	0.05	-2.05	-4.89	0.44	-0.06	-0.12	0.37
DxF	-0.004	-0.61	1.58	1.09	0.08	-0.17	0.30	0.42	-0.55	24.64	7.57	7.57	0.10	1.53	0.21	3.20	2.26	2.51	0.25
FxE	0.027	2.96	-1.13	1.99	1.50	-0.19	-0.48	-0.46	-0.28	-12.13	4.31	6.55	-0.10	0.20	2.75	-3.99	-1.60	-1.97	0.66
LSD (0.01)	0.045	1.66	1.56	5.87	4.65	2.00	1.15	0.38	0.37	11.14	8.28	7.66	0.05	2.02	1.62	1.88	1.52	1.08	0.44

Table 4.6: GCA: SCA mean square ratio for various agronomic and quality characteristics in pumpkin

	OW:L	OTT	OST	OBES	LPL	LBL	Yield	Fruit mass	Fruit number	W	ML	TL	W:ML	ST	TT	MBT	SHT	BT	Density
GCA:SCA	114.00	14.25	11.57	5.78	3.39	8.14	2.31	6.81	2.64	8.75	14.17	17.30	20.80	4.02	4.71	2.83	10.09	8.73	12.65
% variation due to GCA	98.26	88.33	94.71	76.08	57.44	80.49	41.91	74.70	45.35	79.93	87.13	89.35	90.83	63.21	67.11	50.48	83.12	80.67	86.22

4.4 Heritability

Broad sense (h^2_b) and narrow sense (h^2_n) heritabilities were calculated for each characteristic. These computed heritabilities are presented in Table 4.7. For the purposes of discussion, the values are divided into four groups: low (0 to 0.25), moderate (0.26 to 0.50), high (0.51 to 0.75) and very high (0.76 and above).

All estimates of broad sense heritability were found to be very high, with the highest value being 0.99 for W:ML. The lowest value was calculated for OBES (0.81). Very high narrow sense heritabilities were calculated for OW:L (0.97), OST (0.91), W:ML (0.90), TL (0.89), ML (0.86), density (0.84), OTT (0.84), SHT (0.80), W (0.79) and BT (0.77). Heritabilities for fruit mass (0.74), LBL (0.74), OBES (0.62), TT (0.61) and ST (0.55) were found to be high. The remaining characteristics had moderate narrow sense heritabilities which include LPL (0.49), fruit number (0.44), MBT (0.43) and yield (0.36). No narrow sense heritabilities were low.

Discussion

In this trial high broad sense heritabilities indicated that the phenotypic variation due to environmental variation was very limited. Most of the variation found was thus due to the differences in genotypes. A possible explanation is that individual plant values were not used since Agrobase 2000 could not accommodate it. The individual values were used to determine a plot average, which was used to determine the heritabilities. In the calculation of these averages most of the variation between individuals within the same genotype was removed. Since all individuals in a specific plot are genotypically identical (F1 hybrids), the variation that was removed was environmental variation. For this reason calculated broad sense heritabilities in this trial are overestimated values. This may also be the reason why the broad sense heritabilities found by Mohanty and Mishra (1999d) were much lower for yield per plant (0.48), fruit mass (0.22), number of fruit (0.24) and flesh thickness (0.58). However, the results from this study can be used in this breeding programme since selection will be done under the same environmental conditions in future.

Characteristics with very high broad sense heritabilities will have high genetic variance, including additive and non-additive variance, in comparison to the environmental variance. This was the case for all characteristics studied in this trial. Mohanty and Mishra (1999d) mentioned that the highly heritable characteristics should be selected at very early stages in the programme while populations are still very heterozygous.

Characteristics with very high broad sense heritabilities and very high narrow sense heritabilities will have high additive genetic variance with low non-additive variance. The characteristics included OW:L, OTT, OST, W, TL, ML, W:ML, SHT, BT and density. According to the percentage variation due to GCAs, OBES should also have been in this group. However, due to a relatively high environmental variance value it fell into the next group with slightly higher non-additive variance.

The characteristics with very high broad sense heritabilities and high moderate narrow sense heritabilities included OBES, LBL, fruit mass, ST, TT and BT. These traits will have low environmental variation in comparison to the total genetic variation, but they will have a larger percentage non-additive variance than the characteristics in the previous paragraph.

LPL, yield, fruit number and MBT had the highest amount of non-additive variance, although the additive variance still played an important role. These characteristics had the lowest narrow sense heritabilities. According to Mohanty and Mishra (1999d) characteristics with low heritabilities should be selected under diverse environments for maximum response to selection. However, this is only possible in the case of family selection or selection of pure lines and is not an option in early segregating generations where all individuals have different genotypes. Alternatively these characteristics can be improved by developing hybrid varieties. The same authors calculated broad sense heritability for yield to be 0.43, compared to the 0.85 found in this study.

Table 4.7 Estimates of heritabilities for various agronomic and quality characteristics in pumpkin (Parents and F1s)

	OW:L	OTT	OST	OBES	LPL	LBL	Yield	Fruit mass	Fruit number	W	ML	TL	W:ML	ST	TT	MBT	SHT	BT	Density
σ^2A	0.11	27.33	28.07	62.43	42.81	19.97	1.77	4.94	1.62	3287.25	3103.96	3154.65	0.15	9.67	9.88	5.78	25.75	11.42	307.68
σ^2G	0.12	30.95	29.64	82.06	74.53	24.81	4.23	6.61	3.57	4112.77	3562.62	3530.74	0.16	15.30	14.73	11.45	30.98	14.15	356.85
σ^2E	0.00	1.55	1.37	19.46	12.19	2.26	0.74	0.08	0.08	70.03	38.64	33.13	0.00	2.30	1.48	1.98	1.30	0.65	11.01
σ^2P	0.12	32.49	31.00	101.52	86.71	27.06	4.97	6.70	3.65	4182.80	3601.26	3563.87	0.16	17.60	16.21	13.43	32.28	14.81	367.86
h^2b	0.99	0.95	0.96	0.81	0.86	0.92	0.85	0.99	0.98	0.98	0.99	0.99	0.99	0.87	0.91	0.85	0.96	0.96	0.97
h^2n	0.97	0.84	0.91	0.61	0.49	0.74	0.36	0.74	0.44	0.79	0.86	0.89	0.90	0.55	0.61	0.43	0.80	0.77	0.84

4.5 Correlations

Both phenotypic and genotypic correlations were determined. Estimates close to 1.00 and -1.00 indicate a strong correlation. The closer the value is to zero the weaker the correlation. The level of significance will however determine its relevance.

4.5.1 Phenotypic correlations

The plot means of all characteristics measured were subjected to linear-correlation analysis. The results are presented in a correlation matrix in Table 4.8. Only correlations at a significance level of 0.05 and smaller will be discussed. Significance at 0.05 and 0.01 will be indicated with * and ** respectively.

4.5.1.1 Ovary morphology

Ovary width: length ratio (OW:L)

OW:L was significant positively correlated with W:ML (0.92**), OST (0.84**), SHT (0.76**) and BT (0.72**), LBL (0.66**), PLP (0.54**) and W (0.31*). It had negative significant correlations with OTT (-0.79**), TL (-0.65**), density (-0.56**), ML (-0.51**), TT (-0.46**) and OBES (-0.30*).

Ovary top flesh thickness (OTT)

Significant positive correlations for OTT, were found with density (0.78**), TL (0.61**), OBES (0.60**), TT (0.51**) and ML (0.48**). Negative significant correlations estimated with OTT included W:ML (-0.81**), OW:L (-0.79**), LBL (-0.73**), BT (-0.67**), OST (-0.66**), LPL (-0.65**), SHT (-0.53**), MBT (-0.45**), yield (-0.36**) and W (-0.26*).

Ovary side flesh thickness (OST)

OST expressed positive significant correlations with SHT (0.86**), OW:L (0.84**), W:ML (0.80**), BT (0.59**), LBL (0.47**) and LPL (0.42**). Other significant

correlations calculated were negative and included OTT (-0.66**), TL (-0.65**), ML (-0.53**), TT (-0.50**) and density (-0.40**).

Ovary blossom end scar size (OBES)

Significant positive correlations with OBES were calculated for OTT (0.60**), density (0.53**) and TT (0.51**). OBES had negative significant correlations with yield (-0.63**), LBL (-0.62**), LPL (-0.53**), MBT (-0.49**), W (-0.39**), fruit mass (-0.36**), W:ML (-0.34**), BT (-0.32*) and OW:L (-0.30*).

4.5.1.2 Leaf morphology

Leaf petiole length (LPL)

LPL had positive significant phenotypic correlations with LBL (0.82**), W:ML (0.60**), OW:L (0.54**), MBT (0.52**), yield (0.49**), BT (0.49**), OST (0.42**), fruit number (0.30*), SHT (0.28*) and W (0.26*). Significant negative correlations with LPL included OTT (-0.65**), density (-0.65**), OBES (-0.53**), TL (-0.39**), TT (-0.35**) and ML (-0.31*).

Leaf blade length (LBL)

Positive significant phenotypic correlations with LBL included LPL (0.82**), W:ML (0.68**), BT (0.67**), OW:L (0.66**), MBT (0.59**), fruit mass (0.51**), OST (0.47**), W (0.43**), SHT (0.39**) and fruit number (0.30*). OTT (-0.73**), density (-0.68**), OBES (-0.62**), TT (-0.45**) and TL (-0.33**) had significant negative phenotypic correlations with LBL.

4.5.1.3 Yield components

Yield

Yield had significant positive phenotypic correlations with fruit mass (0.67**), W (0.66**), LPL (0.49**), W:ML (0.31*), BT (0.31*) and ML (0.27*). OBES (-0.63**),

MBT (-0.52**), OTT (-0.36**), TT (-0.32*), density (-0.31*) and ST (-0.27*) had negative significant correlations with yield.

Fruit mass

W (0.96**), yield (0.67**), ML (0.66**), TL (0.51**), LBL (0.51**) BT (0.45**) and MBT (0.30*) had significant positive correlations with fruit mass. Significant negative phenotypic correlations with fruit mass were calculated for fruit number (-0.66**) and OBES (-0.36**).

Fruit number

LPL (0.30*) and LBL (0.30*) were the only characteristics that had significant positive phenotypic correlations with fruit number. Significant negative correlations with fruit number were estimated for fruit mass (-0.66**), W (-0.64**), ML (-0.59**), ST (-0.53**), TL (-0.50**), BT (-0.31*), LBL (-0.30*), density (-0.28*) and TT (-0.26*).

4.5.1.4 Fruit morphology

Width (W)

Fruit mass (0.96**), yield (0.66**), BT (0.59**), ML (0.52**), LBL (0.43**), MBT (0.36**), TL (0.35**), W:ML (0.35**), OW:L (0.31*) and LPL (0.26*) had significant positive correlations with W. Fruit number (-0.64**), OBES (-0.39**) and OTT (-0.26*) were the only characteristics that had significant negative phenotypic correlations with W.

Maximum length (ML)

ML had significant positive correlations with TL (0.98**), fruit mass (0.66**), W (0.52**), OTT (0.48**), ST (0.33**), density (0.31*) and yield (0.27*). Significant negative correlations with ML were calculated for fruit number (-0.59**), W:ML (-0.58**), SHT (-0.53**), OST (-0.53**), OW:L (-0.51**) and LPL (-0.31*).

Total length (TL)

ML (0.98**), OTT (0.61**), fruit mass (0.51**), W (0.35**), ST (0.29*) and density (0.41**) had positive phenotypic correlations with TL. Negative significant correlations for TL were calculated for W:ML (-0.71**), OST (-0.65**), OW:L (-0.65**), SHT (-0.64**), fruit number (-0.50**), LPL (-0.39**), BT (-0.37**) and LBL (-0.33**).

Width:Maximum length ratio (W:ML)

Significant positive phenotypic correlations calculated for W:ML with other characteristics included OW:L (0.92**), OST (0.80**), SHT (0.79**), BT (0.74**), LBL (0.68**), LPL (0.60**), W (0.35**), MBT (0.31*) and yield (0.31*). OTT (-0.81**), TL (-0.71**), ML (-0.58**), density (-0.54**), OBES (-0.34**) and TT (-0.32*) had negative significant phenotypic correlations with W:ML.

4.5.1.5 Flesh thickness

Side flesh thickness (ST)

ML (0.33**), TL (0.29*) and BT (0.29*) were the only characteristics to have significant positive correlations with ST. Other significant negative correlations were calculated for fruit number (-0.53**) and yield (-0.27*).

Top flesh thickness (TT)

OTT (0.51**), density (0.51**) and OBES (0.51**) were the only characteristics with significant positive correlations with TT. OST (-0.50**), OW:L (-0.46**), LBL (-0.45**), LPL (-0.35**), yield (-0.32*), W:ML (-0.32*), fruit number (-0.26*) and BT (-0.26*) had negative significant correlations with TT.

Middle bottom flesh thickness (MBT)

The highest significant positive correlation with MBT was calculated for LBL (0.59**) and was followed by yield (0.52**), LPL (0.52**), BT (0.44**), W (0.36**), W:ML

(0.31*) and fruit mass (0.30*). OBES (-0.49**), OTT (-0.45**) and density (-0.40**) were the only significant negative correlations found with MBT.

Shoulder thickness (SHT)

Significant positive correlations for SHT were calculated for OST (0.86**), W:ML (0.79**), OW:L (0.76**), BT (0.62**), LBL (0.39**) and LPL (0.28*). TL (-0.64**), OTT (-0.53**) and ML (-0.53**) had significant negative correlations with SH.

Bottom thickness (BT)

BT had a significant positive correlation with W:ML (0.74**), followed by OW:L (0.72**), LBL (0.67**), SHT (0.63**), OST (0.59**), W (0.59**), LPL (0.49**), fruit mass (0.45**), MBT (0.44**), yield (0.31*) and ST (0.29*). Significant negative correlations with BT were calculated for OTT (-0.67**), density (-0.53**), TL (-0.37**), OBES (-0.32*), fruit number (-0.31*) and TT (-0.26*).

4.5.1.6 Density

OTT (0.78**), OBES (0.53**), TT (0.51**), TL (0.41**) and ML (0.31*) had significant positive correlations with density. LBL (-0.68**), LPL (-0.65**), OW:L (-0.56**), W:ML (-0.54**), BT (-0.53**), MBT (-0.40**), OST (-0.40**), yield (-0.31*) and fruit number (-0.28**) had significant negative correlations with density.

Discussion

A phenotypic correlation between two characteristics is influenced by the phenotypic covariance in the two characteristics as well as by the individual phenotypic variances of the two characteristics, which are influenced by the genotype and the environment. It has already been mentioned that in this trial some of the environmental variation has been removed by making use of plot averages. However, it will still contain some of the environmental variation, the additive component and the non-additive component.

Phenotypic correlations are probably easier to calculate, since randomly chosen individuals from any variable population can be used to determine them. However, under certain conditions it may be more reliable to calculate genotypic correlations rather than phenotypic correlations, since the latter will only include the additive variance. These conditions include cases where the phenotype is easily influenced by environmental variation or where non-additive gene action plays a large role in the expression of a characteristic. In the previous sections it was shown that yield, fruit number, LPL and MBT fall into the latter category, with low narrow sense heritabilities. It was also shown that yield and fruit number had more non-additive variance than additive variance. Selection for these traits may not be rewarding due to the favourable influence of the environment rather than the genotype. With the remaining characteristics where the environment and non-additive gene action had a smaller influence, phenotypic correlations may be more useful.

As previously mentioned all pumpkins need to be hand-pollinated before selection takes place. Part of this study was to develop means of selection, which can be completed before pollination. This will reduce the amount of unnecessary hand-pollinations that will only be eliminated during harvesting. The characteristics that can be evaluated prior to pollination include OW:L, OTT, OST, OBES, LPL and LBL. It was therefore important to identify from these characteristics, those that have high correlations with characteristics that can only be evaluated at a mature fruit stage. Another problem is that flowers that have been pollinated through insects in a breeding population are removed to stimulate continuous female flower production. This has an influence on the number of fruit set per plant, yield and to a lesser extend fruit mass. Due to the latter, it was important to identify yield, fruit mass and fruit number correlations with other characteristics.

It is important to note that phenotypic correlations should not be used to predict how a characteristic will respond in the next generation as a result to the selection of another characteristic. It can however be used to predict the performance of a characteristic in an individual if the same individual can be evaluated for another characteristic.

The following are the strongest significant phenotypic correlations calculated for the different traits. W:ML had strong correlations with OW:L (0.92), OTT (-0.81) and OST (0.80). It is obvious that a strong correlation exist between the shape of the ovary and the mature fruit. It can therefore be assumed that a plant will produce fruit with a high W:ML ratio if it had a high OW:L ratio, a thin OTT or a thick OST in the flowering stage.

Other strong correlations were calculated for SHT and OW:L (0.76), OST (0.86) and W:ML (0.79), indicating that a strong relationship exist not only between the SHT and ovary shape, but also with fruit shape. Thicker shoulder flesh in the fruit can be expected when the ovary had a thicker shoulder. It can also be expected that the flatter the ovary shape and the fruit shape are, the thicker the shoulder will be.

OTT had a strong positive correlation with density (0.78) as well as a strong negative correlation with OW:L (-0.79). Therefore, the thicker the OTT, the higher the density will be and the flatter the fruit shape.

As expected TL and ML (0.98) were also highly correlated as well as the correlation between fruit mass and W was calculated to be high (0.96). LPL and LBL had a correlation of 0.82, but due to the low narrow sense heritability of LPL this correlation may be less accurate than a genotypic correlation.

Mohanty (2000a) reported that high yield was mainly associated with increased number of fruits per plant, average fruit weight and flesh thickness. However, the only positive significant phenotypic correlation found in this study to correspond with the latter was the correlation between yield and average fruit weight. Since yield is the product of fruit mass and fruit number it is expected that these two characteristics will be negatively correlated with one another, as shown in this study. If it is assumed that a plant can only produce a certain amount of fruit, and fruit mass increases then fruit number have to decrease. The opposite is also true. It was shown in this study that fruit number and yield are not significantly correlated. Selections for high yield can therefore not be based on the amount of fruit produced by a plant. It is unknown where and how Mohanty (2000a) measured flesh thickness and it might be the reason why a different result was obtained from this study. However, if thickness was

not expressed as a ratio to the width or length of the fruit, it was more an indication of the fruit size than the relative flesh thickness. It will then be possible for flesh thickness to be positively correlated with yield.

Table 4.8: Phenotypic correlation coefficients for various agronomic and quality characteristics in pumpkin

	OW:L	OTT	OST	OBES	LPL	LBL	Yield	Fruit mass	Fruit number	W	ML	TL	W:ML	ST	TT	MBT	SHT	BT	Density
OW:L	1.00																		
OTT	-0.79 **	1.00																	
OST	0.84 **	-0.66 **	1.00																
OBES	-0.30 *	0.60 **	-0.20	1.00															
LPL	0.54 **	-0.65 **	0.42 **	-0.53 **	1.00														
LBL	0.66 **	-0.73 **	0.47 **	-0.62 **	0.82 **	1.00													
Yield	0.20	-0.36 **	0.21	-0.63 **	0.49 **	0.13	1.00												
Fruit mass	0.13	-0.10	0.09	-0.36 **	0.13	0.51 **	0.67 **	1.00											
Fruit number	0.05	-0.23	0.15	-0.20	0.30 *	0.30 *	0.03	-0.66 **	1.00										
W	0.31 *	-0.26 *	0.21	-0.39 **	0.26 *	0.43 **	0.66 **	0.96 **	-0.64 **	1.00									
ML	-0.51 **	0.48 **	-0.53 **	-0.06	-0.31 *	-0.20	0.27 *	0.66 **	-0.59 **	0.52 **	1.00								
TL	-0.65 **	0.61 **	-0.65 **	0.04	-0.39 **	-0.33 **	0.16	0.51 **	-0.50 **	0.35 **	0.98 **	1.00							
W:ML	0.92 **	-0.81 **	0.80 **	-0.34 **	0.60 **	0.68 **	0.31 *	0.15	0.06	0.35 **	-0.58 **	-0.71 **	1.00						
ST	0.03	0.17	-0.05	0.23	-0.23	-0.04	-0.27 *	0.22	-0.53 **	0.20	0.33 **	0.29 *	-0.14	1.00					
TT	-0.46 **	0.51 **	-0.50 **	0.51 **	-0.35 **	-0.45 **	-0.32 *	-0.17	-0.26 *	-0.19	0.04	0.11	-0.32 *	-0.07	1.00				
MBT	0.14	-0.45 **	0.05	-0.49 **	0.52 **	0.59 **	0.52 **	0.30 *	0.09	0.36 **	0.03	-0.05	0.31 *	-0.15	-0.09	1.00			
SHT	0.76 **	-0.53 **	0.86 **	-0.05	0.28 *	0.39 **	0.11	0.11	-0.02	0.24	-0.53 **	-0.64 **	0.79 **	0.15	-0.22	0.07	1.00		
BT	0.72 **	-0.67 **	0.59 **	-0.32 *	0.49 **	0.67 **	0.31 *	0.45 **	-0.31 *	0.59 **	-0.19	-0.37 **	0.74 **	0.29 *	-0.26 *	0.44 **	0.63 **	1.00	
Density	-0.56 **	0.78 **	-0.40 **	0.53 **	-0.65 **	-0.68 **	-0.31 *	-0.03	-0.28 *	-0.14	0.31 *	0.41 **	-0.54 **	0.05	0.51 **	-0.40 **	-0.21	-0.53 **	1.00

** = $p < 0.01$ and * = $p < 0.05$

4.5.2 Genotypic correlations

The GCAs of the different parents, of all characteristics measured, were subjected to a linear-correlation analysis. The results are presented in a correlation matrix in Table 4.9. Genotypic correlations for most of the characteristics studied were not significant. Only one GCA value per parent was used with a total of only six parents. This limited amount of data makes it difficult to prove the significance of the genotypic correlations. Therefore only genotypic correlations with relatively high values will be discussed.

4.5.2.1 Ovary morphology

Ovary width: length ratio (OW:L)

OW:L had high positive correlations with W:ML (0.99), OST (0.93), SHT (0.87), BT (0.81), LBL (0.77) and LPL (0.73). OTT (-0.88), TL (-0.71) and density (-0.62) were negatively correlated with OW:L.

Ovary top flesh thickness (OTT)

Density (0.90), TL (0.68), OBES (0.62) and TT (0.62) had strong positive correlations with OTT. Negative genotypic correlations with OTT were calculated for LPL (-0.91), OW:L (-0.88), W:ML (-0.87), LBL (-0.85), BT (-0.79) and OST (-0.74).

Ovary side flesh thickness (OST)

OST had positive genotypic correlations with OW:L (0.93), SHT (0.91) and W:ML (0.88). Negative correlations were calculated for TL (-0.76), OTT (-0.74), ML (-0.67) and TT (-0.62).

Ovary blossom end scar size (OBES)

Only a few characteristics had relatively high genotypic correlations with OBES. The positive correlations included density (0.76), TT (0.74) and OTT (0.62). Negative correlations were found for yield (-0.85), LBL (-0.69) and LPL (-0.66).

4.5.2.2 Leaf morphology

Leaf petiole length (LPL)

The highest positive genotypic correlations with LPL were LBL (0.96) followed by BT (0.90), W:ML (0.75), OW:L (0.73) and MBT (0.72). The strongest negative genotypic correlations with LPL were found for density (-0.94), OTT (-0.91) and OBES (-0.66).

Leaf blade length (LBL)

LPL (0.96), BT (0.94), OW:L (0.77), W:ML (0.77), MBT (0.66), W (0.62) had positive genotypic correlations with LBL. Negative correlations included OTT (-0.85), density (-0.85) and OBES (-0.69).

4.5.2.3 Yield components

Yield per plant

Fruit mass (0.84), W (0.84) and MBT (0.63) had positive genotypic correlations with yield. The only relatively strong negative genotypic correlation with yield was calculated for OBES (-0.85).

Fruit mass

W (0.97), yield (0.84) and ML (0.71) had positive correlations with fruit mass. Fruit number (-0.87) had a strong negative correlation with fruit mass.

Fruit number

Fruit mass (-0.87), W (-0.84) and ML (-0.64) had negative genotypic correlations with fruit number. No characteristics showed strong positive correlations with fruit number.

4.5.2.4 Fruit morphology

Width (W)

W had the highest positive genotypic correlation with fruit mass (0.97) followed by yield (0.84) and LBL (0.62). Fruit number (-0.84) had a negative correlation with W.

Maximum length (ML)

The calculations showed ML to have strong positive correlations with TL (0.98) and fruit mass (0.71). Negative genotypic correlations were calculated for OST (-0.67), fruit number (-0.64) and SHT (-0.64).

Total length (TL)

The only positive genotypic correlations found with TL were for ML (0.98) and OTT (0.68). OST (-0.76), SHT (-0.72), OW:L (-0.71) and W:ML (-0.71) had negative correlations with TL.

Width: maximum length ratio (W:ML)

The W:ML ratio had the highest genotypic correlation with OW:L (0.99), which was followed by OST (0.88), SHT (0.85), BT (0.83), LBL (0.77) and LPL (0.75). OTT (-0.87), TL (-0.71) and density (-0.60) were the only relatively high negative correlations with W:ML.

4.5.2.5 Flesh thickness

Side flesh thickness (ST)

The strongest genotypic correlation found for ST was with fruit number (-0.51), which was negative. This was followed by a positive correlation with BT (0.45).

Top flesh thickness (TT)

TT had positive correlations with OBES (0.74), density (0.63) and OTT (0.62). OST (-0.62) had the strongest negative genotypic correlation with TT.

Middle bottom flesh thickness (MBT)

A genotypic correlation of 0.72 was calculated between MBT and LPL. Other positive correlations with MBT were calculated for LBL (0.66) and yield (0.63). Density (-0.63) had the strongest negative correlation with MBT.

Shoulder flesh thickness (SHT)

OST (0.91), OW:L (0.87), W:ML (0.85) and BT (0.65) had positive correlations with SHT. TL (-0.72) and ML (-0.64) were the only characteristics to have relatively strong negative correlations with SHT.

Bottom flesh thickness (BT)

The characteristics with the strongest genotypic correlations calculated for BT included LBL (0.95), LPL (0.90), W:ML (0.83), OW:L (0.81), SHT (0.65), OTT (-0.79) and density (-0.72). The latter two were negative correlations.

4.5.2.6 Density

OTT (0.90), OBES (0.76) and TT (0.63) had positive genotypic correlations with density. Negative correlations with density were calculated for LPL (-0.94), LBL (-0.85), BT (-0.72), MBT (-0.64), OW:L (-0.62) and W:ML (-0.60).

Discussion

In general the genotypic correlations were much stronger than the phenotypic correlations. The reason may be that the non-additive variance and as well as the environmental variation were removed from the computed genotypic correlations. For characteristics that have large proportions non-additive gene expression, like yield and fruit number, genotypic correlations should rather be used than phenotypic correlations.

W:ML were highly correlated with OW:L (0.99), OTT (-0.87), OST (0.88), LPL (0.75) and LBL (0.77). From this information it can be concluded that plants showing high OW:L ratios will tend to have high W:ML ratios. Flatter fruit can be expected when the OTT is thinner or with a thicker OST. Flat fruit can also be expected when LPL and LBL values are high.

Density had high genotypic correlations with OTT (0.90), OBES (0.76), LPL (-0.94) and LBL (-0.85). The latter indicates that high density can be expected when the OTT is thick or when the ovary blossom end scar is large in relation to the ovary width. Density will be low when plants have long petioles and large leaves. The density seems to be positively correlated with that of ovary morphology, but negatively correlated with leaf morphology.

BT had high genotypic correlations with OW:L (0.81), OTT (-0.79), LPL (0.90), LBL (0.95) as well as W:ML (0.83). Fruit with thick BT can be expected when flowers have high OW:L ratios, a thin ovary top flesh thickness, a long petiole, large leaves and flat mature fruit.

The additive inheritance of SHT were correlated with OW:L (0.87), OST (0.91) and W:ML (0.85), which indicated that thick shoulder flesh can be expected when fruit and ovary shapes are flat and ovary side thickness are thick.

TL was negatively correlated with OST (-0.76) meaning that plants producing thick ovary side thicknesses are more prone to produce longer fruit. Positive genotypic correlations were also calculated for yield and fruit mass (0.84), with a negative correlation between fruit number and fruit mass (-0.87). From this it is obvious that large fruit are produced on high yielding plants or on plants with a limited number of fruit. This is in agreement with the following where W had high genotypic correlations with yield (0.84), fruit mass (0.97) and fruit number (-0.84).

Yield was negatively correlated with OBES (-0.85), meaning the larger the OBES, the lower yield could be expected.

OTT had negative correlations with LPL (-0.91) and LBL (-0.85), while LBL had positive correlations with OW:L (0.77) and LPL (0.96). OW:L also had high correlations with OTT (-0.88) and OST (0.93). None of these correlations involved fruit morphology and will therefore have limited applications in pumpkin breeding.

Table 4.9 Genotypic correlation coefficients for various agronomic and quality characteristics in pumpkin (Parents and F1s)

	OW:L	OTT	OST	OBES	LPL	LBL	Yield	Fruit mass	Fruit number	W	ML	TL	W:ML	ST	TT	MBT	SHT	BT	Density
OW:L	1.00 **	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
OTT	-0.88	1.00																	
OST	0.93	-0.74	1.00																
OBES	-0.38	0.62	-0.21	1.00															
LPL	0.73	-0.91	0.49	-0.66	1.00														
LBL	0.77	-0.85	0.53	-0.69	0.96 *	1.00													
Yield	0.21	-0.37	-0.04	-0.85	0.49	0.57	1.00												
Fruit mass	0.15	-0.08	-0.07	-0.53	0.27	0.46	0.84	1.00											
Fruit number	-0.04	-0.19	0.15	0.06	-0.03	-0.25	-0.48	-0.87	1.00										
W	0.36	-0.28	0.11	-0.57	0.44	0.62	0.84	0.97 *	-0.84	1.00									
ML	-0.57	0.54	-0.67	-0.25	-0.32	-0.17	0.56	0.71	-0.64	0.53	1.00								
TL	-0.71	0.68	-0.76	-0.10	-0.47	-0.34	0.41	0.57	-0.55	0.37	0.98 *	1.00							
W:ML	0.99 *	-0.87	0.88	-0.33	0.75	0.77	0.23	0.18	-0.09	0.39	-0.57	-0.71	1.00						
ST	0.09	0.09	0.06	-0.01	0.14	0.34	-0.02	0.34	-0.51	0.33	0.23	0.19	0.04	1.00					
TT	-0.57	0.62	-0.62	0.74	-0.49	-0.56	-0.35	-0.14	-0.20	-0.22	0.14	0.25	-0.44	-0.23	1.00				
MBT	0.14	-0.44	-0.21	-0.52	0.72	0.66	0.63	0.45	-0.26	0.50	0.18	0.07	0.24	0.02	0.05	1.00			
SHT	0.87	-0.56	0.91	0.08	0.39	0.47	-0.20	-0.04	-0.09	0.15	-0.64	-0.72	0.85	0.27	-0.35	-0.22	1.00		
BT	0.81	-0.79	0.59	-0.42	0.90	0.95	0.32	0.33	-0.27	0.51	-0.33	-0.48	0.83	0.45	-0.41	0.55	0.65	1.00	
Density	-0.62	0.90	-0.43	0.76	-0.94	-0.85	-0.46	-0.09	-0.25	-0.24	0.33	0.46	-0.60	0.00	0.63	-0.64	-0.21	-0.72	1.00

*** = p < 0.05**

4.6 Response to selection

The most important use of heritability lies in its predictive role which implies whether a population will respond to selection pressure or in other words, whether selection will be operative. However, heritability and correlation (both phenotypic and genotypic) values provide no indication of the amount of genetic progress that would result from selection of the best individuals. A correlation on its own is only a relationship between characteristics and gives no indication of how the population will respond to selection. Selection response is influenced by the intensity of the selection, the variance of the characteristics (or the correlation between the characteristics in the case of indirect selection) and the heritability of the characteristics. In the case of direct selection the variance and the heritability of a specific characteristic are the only variables influencing the response to selection of the specific characteristic. With indirect selection responses (correlated responses) the variables of both the characteristic being selected as well as the responding characteristic will play a role.

Direct and indirect selection responses are presented in Table 4.10. All responses were calculated using a five percent selection intensity. The responses were presented both as a response in the units in what the characteristics were measured as well as percentages (in bold) of the population means.

4.6.1 Ovary morphology

Ovary width: length ratio (OW:L)

Direct selection for OW:L will result in a 70.56% improvement on the population mean. Selection for W:ML will result in a 0.65 selection response which is 66.92% improvement on the population mean of OW:L. The second best characteristic that can be used to improve OW:L is OST that will result in a 0.61 calculated response equal to 63.36% expected improvement in the population mean in the next generation. SHT and BT will result in 55.26% and 55.13% improvement in OW:L population mean respectively. Characteristics that will result in a large negative

correlated response in OW:L include OTT (-57.65%), TL (-47.70%), density (-40.30%), ML (-37.69%), TT (-31.95%) and OBES (-21.25%).

Ovary top flesh thickness (OTT)

Selection for OTT will cause a direct response of 9.89 or a 40.02% improvement in the mean. Indirect selection for OTT using density, TL and OBES will cause responses of 35.90%, 28.02% and 21.37% respectively in the OTT population mean. Selection of characteristics to influence OTT negatively includes OW:L (-37.85%), W:ML (-36.12%), BT (-33.10%), LBL (-31.77%), OST (-30.73%) and LPL (-27.90%).

Ovary side flesh thickness (OST)

OST will improve with 53.18% of the population mean as a response to direct selection. Indirect selection using OW:L, W:ML, and SHT will result in improvements of 51.38%, 46.51% and 45.48% on the population mean in the next generation. Deterioration in OST will be caused when one selects for TL (-40.17%), OTT (-37.96%), ML (-34.66%) or TT (-27.21%).

Ovary blossom end scar size (OBES)

An improvement of 22.61% can be expected as a direct selection response in OBES. In terms of indirect selection density (20.10%), TT (16.62%) and OTT (16.51%) will also result in positive responses. Large negative responses in OBES will be a result of selection for LBL (-16.97%), yield (-14.59%), W (-14.49%), BT (-13.83%) and LPL (-13.38%).

4.6.2 Leaf morphology

Leaf petiole length (LPL)

Direct selection for LPL will result in an improvement of 18.39% on the population mean of LPL. A similar, but slightly better, response can be expected for LPL as a result to selection for BT (21.73%), LBL (21.56%), W:ML (18.74%) or OW:L

(18.95%). The opposite can be expected when parents for the next generation is selected according to density (-22.40%) or OTT (-21.85%).

Leaf blade length (LBL)

LBL can be improved according to the calculated response with 28.10% through direct selection which is equal to 7.92cm. LBL had relatively large correlated responses with BT (28.81%), OW:L (24.81%), W:ML (24.03%), LPL (22.05%) and TW (17.93%). Negative correlated responses were calculated for LBL with OTT (-25.44%) and density (-25.33%) expressed as a percentage of the population mean.

4.6.3 Yield components

Yield per plant

A 28.00% improvement in yield can be expected as a response to direct selection. Selection response as a result due to selection for W and fruit mass was calculated to be 34.91% and 33.90% as a percentage of the population mean. Other positive selection responses calculated for yield included ML (24.43%), LBL (22.84%), MBT (19.46%) and BT (18.53%). OBES (-31.15%) and density (-19.89%) were calculated to have large negative correlated responses with yield.

Fruit mass

Direct selection response for fruit mass was calculated to be 3.94 which is a 122.88% improvement on the population mean. The indirect selection response between W and fruit mass was calculated to be 123.56%. Other characteristics that had a positive response in fruit mass included LBL (56.49%), yield (71.94%), ML (94.00%), TL (76.20%) and BT (53.13%). The largest negative correlated response calculated to cause a decline in fruit mass was -83.08% for fruit number, followed by OBES (-59.18%).

Fruit number

An improvement of 69.84% can be expected as a response to selection if the best 5% of the population is selected for fruit number. The only other characteristics that will result in a positive response in fruit number are OST (14.5%) and OBES (5.29%). The largest negative responses in fruit number were calculated for fruit mass (-78.46%), W (-77.79%), ML (-61.86%) and TL (-53.78%).

4.6.4 Fruit morphology

Width (W)

Selection for W with a 5% selection intensity was calculated to respond with a 51.65% improvement, equal to 104.86mm. Selection for fruit mass had a correlated response of 48.75% improvement in the population mean for W. This was followed by BT (31.16%), LBL (30.94%), yield (29.23%) and ML (28.73%). Fruit number (-32.49%) and OBES (-25.90%) had the largest negative correlated responses with W.

Maximum length (ML)

Direct selection for ML was found to result in a 74.24% improvement in the population mean after one generation. Other positive selection responses calculated for ML included TL (73.82%), fruit mass (48.61%), OTT (39.57%) and width (37.65%). According to the calculated values OST (-50.83%), SHT (-45.76%), OW:L (-44.82%) and W:ML (-42.99%) will result in a decline in ML after selection.

Total length (TL)

A 84.66% improvement on TL can be expected as a result to direct selection. ML (81.97%) and OTT (56.34%) resulted in positive relatively large correlated selection responses in TL. Large negative responses in TL will be a result of selection for OST (-65.39%), OW:L (-62.97%), W:ML (-60.52%) and SHT (-57.71%).

Width: maximum length ratio (W:ML)

According to the calculated direct selection response, a 51.38% improvement in the population mean can be expected in the next generation. The highest increase in W:ML can be expected after selection for OW:L (52.58%) as a result to correlated response to selection. Other positive correlated responses calculated were OST (45.06%), BT (42.33%) and SHT (40.83%). The largest negative response in W:ML was calculated for OTT (-43.22%) followed by TL (-36.02%), density (-29.67%) and ML (-28.41%).

4.6.5 Flesh thickness

Side flesh thickness (ST)

The best response option to improve side thickness is through direct selection that will result in a response of 16.82% improvement. The highest improvement in ST through indirect selection is selection for BT (7.63%) followed by W (6.70%), LBL (6.65%) and fruit mass (6.62%). ST had large negative selection responses for fruit number (-7.72%) and TT (-4.11%).

Top flesh thickness (TT)

TT had a positive direct selection response of 23.55%. Large indirect selection responses in TT were calculated for OBES (17.46%), density (17.41%), OTT (17.22%), OST (-17.88%) and OW:L (-17.03%) of which the latter two were negative.

Middle bottom flesh thickness (MBT)

Direct selection resulted in a calculated response of 17.60% in the MBT population mean. The largest positive calculated correlated response for MBT was calculated for LBL (15.11%), which was followed by LPL (13.64%) and BT (13.34%). The largest negative correlated responses included density (-15.67%), OBES (-10.97%) and OTT (-10.91%).

Shoulder flesh thickness (SHT)

A calculated 42.01% improvement on SHT can be expected as a result of direct selection. Improvement in SHT through correlated response was calculated using OST (40.78%), OW:L (40.18%), W:ML (37.78%) and BT (27.18%). The following negative responses in SHT can be expected as a result of selection for TL (-31.78%), ML (-27.98%) and OTT (-23.97%).

Bottom flesh thickness (BT)

A 50.72% improvement in the population mean can be expected upon direct selection for BT. OW:L, LBL, W:ML and LPL will result in positive correlated response of 47.27%, 46.97%, 46.20% and 36.23% in BT. Negative responses in BT can be expected due to selection for OTT (-43.22%) and density (-38.72%).

4.6.6 Density

Density can be improved with 3.31 units which is equal a 98.74% improvement on the population mean through direct selection. Selection for OTT had a calculated response of 89.10% in density. Other positive correlated responses include OBES (64.56%), TT (53.22%) and TL (47.13%). Negative correlated responses in density was calculated when selection for LBL (-78.50%), BT (-73.60%) LPL (-70.98%) and OW:L (-65.67%) were done.

Discussion

Different characteristics will respond differently to selection, depending on the heritability and variability of the characteristic as well as the intensity of selection. Under normal circumstances direct selection would be applied in order to improve a characteristic. However, in cases where a characteristic could not be evaluated for some reason, it may be useful to apply selection to another trait that shows a high genotypic correlation with the characteristic that needs to be improved. It may also happen that the computed correlated response may be larger than the direct

selection response, meaning that more progress will be made through indirect selection than with direct selection.

The characteristics that showed maximum progress upon direct selection included OW:L, OTT, OST, OBES, fruit number, W, ML, TL, ST, TT and MBT. Improvement in LPL can be equally successful through direct selection as through selection for LBL, OW:L, W:ML and BT. For LBL similar results can also be expected when one selects directly for LBL or indirectly using BT.

Direct selection for increased yield will result in a 28.00% gain in population mean, but selection for larger fruit mass and W, that can be more accurately measured than yield in a breeding population, will result in increased yields of 33.9% and 34.91% respectively. Although optimal improvement cannot be gained through indirect selection prior to flowering, selection for longer leaf petioles and larger leaves will result in higher population means for yield in the next generation.

W:ML, as an indication of fruit shape at a mature fruit stage, can also be equally successful selected for at flowering stage using OW:L. Again selection for LPL and LBL will not result in the same improvement, but it will improve the population mean in the next generation.

An improvement of 42.01% in the population mean can be obtained with direct selection for SHT, but selection for OW:L and OST in the flower stage would have increased SHT with 40.18% and 40.78% respectively. Only the selected individuals will have to be pollinated and therefore much larger populations can be handled to result in a larger percentage improvement per generation. This is not only the case for SHT, but the same tendency was noticed for BT. Indirect selection for OW:L and LBL at a flower stage will result in 47.27% and 46.97% gain per generation, in relation to the 50.71% gain in population mean due to direct selection.

Direct selection for flesh density at a mature stage can cause a 98.74% improvement in one generation. However, selection for OTT at the flowering stage can improve the population mean with 89.10% per generation.

Of all the characteristics evaluated prior to pollination, OBES seems to have the lowest relevance. It only resulted in a relatively large positive correlated response for density, probably only because parent B with the largest OBES also had the highest density.

From all characteristics evaluated, yield, SHT, ST and density are the most important. A reduction in the other characteristics may not necessarily result in the elimination of the genotype. Selection for OW:L , LPL and LBL will mainly result in the improvement in the four characteristics, except density. Selection for OTT will result in the improvement in density and OST mainly in SHT.

Mohanty and Mishra (1999d) mentioned that characteristics with high heritabilities that show a high response to selection should be improved through intense selection in early generations. According to this study it included OW:L, OST, W, TL, ML, W:ML, BT and density.

Table 4.16: Correlated response among various quality and agronomic characteristics in pumpkin

		Characteristic to be selected																		
Responding characteristic		Charac-teristic mean	0W:L	OTT	OST	OBES	LPL	LBL	Yield	Fruit mass	Fruit number	W	ML	TL	W:ML	ST	TT	MBT	SHT	BT	Density
	OW:L	0.97	0.68 70.56%	-0.56 -57.65%	0.61 63.36%	-0.21 -21.25%	0.36 36.86%	0.46 47.17%	0.09 9.08%	0.09 9.38%	-0.02 -1.82%	0.22 22.91%	-0.37 -37.69%	-0.46 -47.70%	0.65 66.92%	0.05 4.93%	-0.31 -31.95%	0.07 6.79%	0.54 55.26%	0.53 55.13%	-0.39 -40.30%
	OTT	24.72	-9.36 -37.85%	9.89 40.02%	-7.60 -30.73%	5.28 21.37%	-6.90 -27.90%	-7.86 -31.77%	-2.40 -9.71%	-0.76 -3.06%	-1.40 -5.65%	-2.67 -10.80%	5.40 21.85%	6.93 28.02%	-8.93 -36.12%	0.75 3.05%	5.24 21.21%	-3.14 -12.69%	-5.35 -21.65%	-8.18 -33.10%	8.88 35.90%
	OST	19.55	10.05 51.38%	-7.42 -37.96%	10.40 53.18%	-1.84 -9.39%	3.74 19.13%	4.93 25.23%	-0.24 -1.21%	-0.69 -3.53%	1.06 5.42%	1.11 5.69%	-6.78 -34.66%	-7.85 -40.17%	9.09 46.51%	0.45 2.29%	-5.32 -27.21%	-1.52 -7.75%	8.89 45.48%	6.28 32.11%	-4.31 -22.06%
	OBES	56.55	-6.10 -10.78%	9.34 16.51%	-3.32 -5.87%	12.78 22.61%	-7.56 -13.38%	-9.59 -16.97%	-8.25 -14.59%	-7.39 -13.06%	0.70 1.23%	-8.19 -14.49%	-3.72 -6.59%	-1.48 -2.61%	-5.06 -8.94%	-0.16 -0.28%	9.40 16.62%	-5.58 -9.86%	1.16 2.06%	-7.82 -13.83%	11.37 20.10%
	LPL	51.58	9.78 18.95%	-11.27 -21.85%	6.26 12.13%	-6.99 -13.56%	9.48 18.39%	11.12 21.56%	3.96 7.67%	3.08 5.97%	-0.23 -0.45%	5.23 10.14%	-4.00 -7.75%	-6.00 -11.64%	9.67 18.74%	1.40 2.72%	-5.20 -10.08%	6.41 12.42%	4.69 9.10%	11.21 21.73%	-11.55 -22.40%
	LBL	28.18	6.99 24.81%	-7.17 -25.44%	4.61 16.36%	-4.95 -17.58%	6.21 22.05%	7.92 28.10%	3.12 11.08%	3.64 12.92%	-1.53 -5.43%	5.05 17.93%	-1.45 -5.15%	-2.98 -10.56%	6.77 24.03%	2.33 8.27%	-4.03 -14.29%	3.96 14.07%	3.86 13.71%	8.12 28.81%	-7.14 -25.33%
	Yield	5.86	0.58 9.84%	-0.94 -16.02%	-0.09 -1.61%	-1.83 -31.15%	0.95 16.17%	1.34 22.84%	1.64 28.00%	1.99 33.90%	-0.88 -15.09%	2.05 34.91%	1.43 24.43%	1.05 17.91%	0.59 10.12%	-0.04 -0.66%	-0.75 -12.88%	1.14 19.46%	-0.50 -8.53%	1.09 18.53%	-1.17 -19.89%
	Fruit mass	3.21	0.69 21.56%	-0.34 -10.71%	-0.32 -10.02%	-1.90 -59.18%	0.86 26.68%	1.81 56.49%	2.31 71.94%	3.94 122.88%	-2.66 -83.08%	3.96 123.56%	3.01 94.00%	2.44 76.20%	0.78 24.25%	1.15 36.02%	-0.51 -15.91%	1.34 41.91%	-0.15 -4.73%	1.70 53.13%	-0.39 -12.23%
	Fruit number	2.51	-0.10 -3.95%	-0.47 -18.70%	0.36 14.50%	0.13 5.29%	-0.05 -1.89%	-0.56 -22.43%	-0.76 -30.24%	-1.97 -78.46%	1.75 69.84%	-1.95 -77.79%	-1.55 -61.86%	-1.35 -53.78%	-0.23 -9.29%	-0.99 -39.70%	-0.40 -16.05%	-0.45 -17.96%	-0.20 -8.15%	-0.68 -27.20%	-0.60 -24.14%
	W	203.02	42.19 20.78%	-30.29 -14.92%	12.93 6.37%	-52.59 -25.90%	36.32 17.89%	62.82 30.94%	59.34 29.23%	98.97 48.75%	-65.97 -32.49%	104.86 51.65%	58.32 28.73%	40.75 20.07%	44.14 21.74%	29.23 14.40%	-20.17 -9.93%	38.95 19.19%	15.62 7.70%	63.26 31.16%	-25.76 -12.69%
	ML	143.72	-64.42 -44.82%	56.87 39.57%	-73.05 -50.83%	-22.18 -15.43%	-25.75 -17.91%	-16.74 -11.65%	38.53 26.81%	69.87 48.61%	-48.68 -33.87%	54.11 37.65%	106.71 74.24%	106.10 73.82%	-61.79 -42.99%	20.01 13.92%	12.97 9.02%	13.51 9.40%	-65.77 -45.76%	-29.46 -20.50%	35.20 24.49%
	TL	128.78	-81.09 -62.97%	72.55 56.34%	-84.21 -65.39%	-8.76 -6.80%	-38.48 -29.89%	-34.16 -26.52%	28.10 21.82%	56.34 43.75%	-42.10 -32.69%	37.62 29.21%	105.55 81.97%	109.02 84.66%	-77.93 -60.52%	16.67 12.95%	22.77 17.68%	5.34 4.14%	-74.32 -57.71%	-47.26 -36.70%	49.17 38.18%
	W:ML	1.47	0.77 52.58%	-0.64 -43.22%	0.66 45.06%	-0.20 -13.85%	0.42 28.64%	0.53 35.91%	0.11 7.33%	0.12 8.29%	-0.05 -3.36%	0.28 18.83%	-0.42 -28.41%	-0.53 -36.02%	0.76 51.38%	0.02 1.67%	-0.27 -18.50%	0.13 8.52%	0.60 40.83%	0.62 42.33%	-0.44 -29.67%
	ST	28.28	0.59 2.08%	0.55 1.96%	0.34 1.19%	-0.07 -0.24%	0.63 2.24%	1.88 6.65%	-0.07 -0.26%	1.87 6.62%	-2.18 -7.72%	1.90 6.70%	1.40 4.95%	1.17 4.14%	0.25 0.90%	4.75 16.82%	-1.16 -4.11%	0.07 0.24%	1.56 5.52%	2.16 7.63%	0.02 0.06%
	TT	21.51	-3.66 -17.03%	3.70 17.22%	-3.85 -17.88%	3.76 17.46%	-2.25 -10.45%	-3.12 -14.48%	-1.36 -6.33%	-0.79 -3.69%	-0.85 -3.94%	-1.26 -5.84%	0.87 4.05%	1.54 7.14%	-2.70 -12.55%	-1.12 -5.19%	5.07 23.55%	0.23 1.05%	-2.02 -9.40%	-2.89 -13.45%	3.74 17.41%
	MBT	18.49	0.71 3.84%	-2.02 -10.91%	-1.00 -5.40%	-2.03 -10.97%	2.52 13.64%	2.79 15.11%	1.87 10.14%	1.90 10.29%	-0.86 -4.67%	2.21 11.94%	0.83 4.46%	0.33 1.77%	1.13 6.12%	0.06 0.31%	0.20 1.11%	3.25 17.60%	-0.98 -5.33%	2.47 13.34%	-2.90 -15.67%
	SHT	22.25	8.94 40.18%	-5.33 -23.97%	9.07 40.78%	0.66 2.95%	2.86 12.86%	4.22 18.95%	-1.27 -5.73%	-0.33 -1.49%	-0.61 -2.73%	1.37 6.17%	-6.23 -27.98%	-7.07 -31.78%	8.41 37.78%	2.11 9.49%	-2.85 -12.82%	-1.53 -6.86%	9.35 42.01%	6.05 27.18%	-2.05 -9.19%
	BT	19.68	9.30 47.27%	-8.51 -43.22%	6.68 33.95%	-4.60 -23.37%	7.13 36.23%	9.25 46.97%	2.89 14.66%	3.90 19.81%	-2.11 -10.74%	5.80 29.45%	-2.91 -14.78%	-4.69 -23.84%	9.09 46.20%	3.05 15.48%	-4.26 -21.64%	3.99 20.25%	6.31 32.05%	9.98 50.72%	-7.62 -38.72%
	Density	3.35	-2.20 -65.67%	2.99 89.10%	-1.49 -44.33%	2.16 64.56%	-2.38 -70.98%	-2.63 -78.50%	-1.00 -29.92%	-0.29 -8.67%	-0.61 -18.11%	-0.76 -22.79%	1.13 33.57%	1.58 47.13%	-2.06 -61.53%	0.01 0.22%	1.78 53.22%	-1.52 -45.24%	-0.69 -20.61%	-2.47 -73.60%	3.31 98.74%

4.7 Heterosis

Mid-parent and high parent heterosis were calculated for all the agronomic and quality characteristics measured. The estimated values are presented in Table 4.11.

4.7.1 Ovary morphology

Ovary width: length ratio (OW:L)

Fourteen of the 15 hybrids expressed mid-parent heterosis for OW:L. The largest amount of positive heterosis was found for AxB (29.82%), which was followed by FxA (22.30%), AxC (21.70%), AxE (20.63%) and FxB (20.27%). However, only four crosses showed positive high parent heterosis, which included AxB (16.84%), FxA (11.84%), DxC (5.65%) and FxB (4.71%). FxE (-7.58%) was the only cross that expressed negative mid-parent heterosis. The highest negative high parent heterosis was found in DxE (-22.94%) followed by ExB (-18.82%) and CxE (-18.55%). OW:L seems to express mainly positive mid-parent heterosis.

Ovary top flesh thickness (OTT)

Positive mid-parent heterosis for OTT was calculated for only five crosses of which ExB (17.00%) showed the highest value. ExB was followed by FxB (14.85%), DxB (9.76%), FxE (9.08%) and DxC (6.28%). All other crosses expressed negative heterosis with the highest value calculated for CxE (-16.03%). The same crosses that showed positive mid-parent heterosis also showed positive high parent heterosis, with only a different ranking. The limited amount of heterosis calculated is in agreement with the performances of the genotypes (Table 4.2), where three of the best six genotypes were pure breeding parents.

Ovary shoulder thickness (OST)

Only three crosses expressed negative mid-parent heterosis with ExB (-10.81%) showing the largest amount of negative heterosis. The same cross had a high parent heterosis value of -29.87%. The highest positive mid-parent heterosis was calculated

for FxA (31.26%) followed by CxE (26.75%), AxB (25.20%) and AxE (23.16%). Only five parents showed positive high parent heterosis which included AxB (15.99%), CxB (12.56%) and DxB (11.35%) which were all parented by B. In general more positive heterosis was expressed with the highest positive mid-parent value further separated from zero than the smallest negative value.

Ovary blossom end scar size (OBES)

Four of the 15 crosses had positive mid-parent heterosis. These four crosses included FxB (28.73%), DxB (20.26%), CxB (12.69%) and ExB (12.32%). The same four crosses also had positive high parent heterosis, but with a different ranking. The highest mid-parent positive heterosis was greater than the highest negative heterosis, which was calculated for CxE (-25.76%). The highest positive high parent heterosis was calculated for DxB (19.63%).

4.7.2 Leaf morphology

Leaf petiole length (LPL)

All except five crosses had positive mid-parent heterosis for LPL. FxA (32.81%) was the highest, followed by DxE (24.49%), DxF (18.38%) and AxB (17.77%). Seven crosses had positive high parent heterosis. The highest value was also FxA (20.87%) and it was followed by FxE (11.10%). The highest negative high parent heterosis was computed for ExB (-31.23%). This relatively high heterosis values are in agreement with the results in Table 4.2, where the four lowest ranking genotypes were parental lines.

Leaf blade length (LBL)

Positive mid-parent heterosis for LBL was calculated for all except four crosses. The highest value was calculated for FxA (27.25%), followed by CxF (23.42%), CxE (17.92%) and DxF (13.35%). FxA (21.42%) had the highest high parent heterosis followed by CxF (11.50%) and DxC (8.06%). Five crosses expressed negative high parent heterosis with ExB (-27.77) and FxB (-26.75%) having the highest negative

values. Similarly to LPL the four lowest ranking genotypes in Table 4.2 were parents, indicating the presence of hybrid vigour in LBL.

4.7.3 Yield components

Yield per plant

Three and eight crosses respectively had negative mid-parent and high parent heterosis for yield. Very high heterosis was calculated for yield with DxE (88.21%) in the highest rank of mid-parent heterosis. DxE was followed by CxE (79.62%) and CxF (62.85%). The highest negative mid-parent heterosis was calculated for ExB (-11.30%) followed by FxB (-11.29%). CxE (67.50%) had the highest high parent heterosis followed by DxE (64.62%). The lowest high parent heterosis was calculated for FxB (-32.32%), followed by FxA (-20.09%). Positive heterosis was far greater than the negative heterosis for yield. These results are in agreement with the data in Table 4.2, where five of the seven genotypes with the lowest ranking for yield were parents.

Fruit mass

Eleven of the 15 crosses expressed positive mid-parent heterosis. The highest value for fruit mass was calculated for DxE (94.05%), followed by CxE (90.33%). These two crosses also had the highest high parent heterosis with 84.31% and 83.37% computed for CxE and DxE respectively. The lowest mid-parent heterosis percentages were calculated for AxD (-58.90), AxC (-49.59%), AxE (-46.23%), AxB (-38.82%) and FxA (-22.85%). The lowest values for high parent heterosis were calculated for the same crosses in the same ranking with the following values, -71.90%, -66.00%, -63.23%, -40.76% and -34.39%. Although very high positive heterosis values were calculated, some crosses expressed very high negative heterosis for fruit mass as well.

Fruit number

For fruit number, the five crosses with the highest mid-parent heterosis were all parented by A and included AxB (111.56%), AxD (81.00%), AxE (59.64%), FxA

(50.83%) and AxC (42.55%). In contrast the four crosses with the lowest mid-parent heterosis values were all parented by B and included CxB (-57.12%), ExB (-51.22%), DxB (-50.29%) and FxB (-42.89%). The highest high parent heterosis was calculated for AxB (51.45%) followed by AxD (21.48%) and FxA (21.48%). All other high parent heterosis values were negative with the smallest value being -74.22% calculated for CxB. This was followed by ExB (-70.53%), DxB (-68.14%) and FxB (-57.09%).

4.7.4 Fruit morphology

Width (W)

Ten of the 15 crosses expressed positive mid-parent heterosis. DxE had a calculated value of 43.43% which was followed by CxE (37.35%). The lowest mid-parent heterosis was computed for AxD (-19.16%) which had a high parent heterosis of -30.67%. The largest high parent heterosis was calculated for DxE (35.88%) followed by CxE (27.76%).

Maximum length (ML)

Of the seven crosses expressing positive mid-parent heterosis FxE (31.50%) had the highest value. DxB (11.48%) and DxF (11.17%) were respectively second and third. The lowest value was computed for AxE (-39.11%) which had a high parent heterosis value of -56.23%. Only four crosses expressed positive high parent heterosis and included FxE (15.17%), DxC (9.03%), DxF (8.45%) and CxF (2.42%).

Total length (TL)

Only six crosses showed positive mid-parent heterosis of which FxE (32.03%) had the highest value. FxE was followed by DxB (12.24%). The largest negative mid-parent heterosis value was computed for AxE (-40.51%). According to the high parent heterosis for TL, FxE (16.55%) had the highest rank, followed by DxB (7.88%), DxF (4.28%) and DxC (1.94%). The largest negative high parent heterosis value was calculated for AxE (-57.67%).

Width: maximum length ratio (W:ML)

FxE (-17.70%) was the only cross to express negative mid-parent heterosis for W:ML. The highest heterosis was calculated for AxE (31.46%) followed by CxE (30.08%) and DxE (17.15%). Crosses that expressed positive high parent heterosis included DxC (6.32%), FxB (5.15%) and AxC (1.66%). All other crosses expressed negative high parent heterosis for W:ML. Much more positive mid-parent heterosis was expressed for W:ML than negative heterosis.

4.7.5 Flesh thickness

Side flesh thickness (ST)

Only five crosses showed positive mid-parent heterosis, with CxB (5.84%) in the highest rank. CxB was followed by DxC (5.50%), FxE (2.01%), DxF (1.59%) and AxB (0.70%). All other crosses had negative values for ST. All high parent heterosis values for ST were negative, with CxF (-3.39) showing the least negative heterosis. The highest negative high parent heterosis was expressed by AxE (-26.51%). This limited amount of heterosis is in agreement with the performances of the genotypes in Table 4.2 where the top three genotypes were pure breeding parents indicating that heterosis effects do not play a large role in ST.

Top flesh thickness (TT)

Seven of the 15 crosses showed positive mid-parent heterosis for TT. ExB (36.12%) showed the highest heterosis. DxB (6.55%) (second in ranking) was much lower and was followed by FxB (6.17%) and CxB (5.78%). ExB (35.54%) also had the highest high parent heterosis and was followed by CxE (1.47%) and AxE (0.00%). All other crosses expressed negative high parent heterosis.

Middle bottom flesh thickness (MBT)

Nine of the 15 crosses had positive mid-parent heterosis values. The highest value was calculated for DxF (44.70%) which was followed by CxF (37.02%), CxE

(25.83%), FxA (21.56%) and DxE (21.02%). The cross with the highest negative mid-parent heterosis was DxB (-25.75%). DxF (41.75%) showed the highest high parent heterosis, followed by CxF (31.86%) and CxE (19.88). The lowest high parent heterosis for MBT was found for ExB (-29.46%).

Shoulder flesh thickness (SHT)

Only three mid-parent heterosis values for SHT were negative. The highest mid-parent heterosis value was calculated for CxB (35.99%) and it was followed by AxE (24.47%) and FxA (23.35%). The lowest mid-parent value was calculated for FxE (-16.67%). DxF (13.14%) expressed the largest positive high parent heterosis and was followed by ExB (12.68%). The most negative high parent heterosis was expressed by DxC (-26.12%). In general more positive heterosis was expressed with the highest positive mid-parent value further separated from zero than the smallest negative value.

Bottom flesh thickness (BT)

Seven crosses showed negative mid-parent heterosis for BT. The cross with the highest rank for mid-parent heterosis was CxE (50.35%). CxE was followed by DxF (33.01%) and CxF (31.97%). The highest negative value for mid-parent heterosis was expressed by AxD (-15.64%) that was not as far removed from zero as the largest positive value. The best high parent heterosis was computed for DxF (22.73%) and it was followed by CxE (17.66%), CxF (15.40%) and DxC (8.45%). The highest negative high parent heterosis computed for BT was for AxD (-28.91%).

4.7.6 Density

Very high percentages were calculated for mid-parent heterosis for density. The highest value was computed for ExB (93.81%), followed by FxB (61.52%), CxB (30.02%) and DxB (19.40%). AxC (-41.64%), AxD (-36.26%), AxB (-28.66%), FxA (-26.43%) and AxE (-21.86%) were included in the lowest mid-parent heterosis values computed for density. These five crosses also had the lowest high parent heterosis values with AxC (-48.09) being the smallest. The cross with the most

positive high parent heterosis value was ExB (47.89%), followed by FxB (34.61), CxB (26.72%) and DxB (14.45%).

Discussion

All characteristics showed positive and negative mid-parent heterosis and high parent heterosis except ST which showed only negative high parent heterosis. Mid-parent heterosis for yield (-11.30 to 88.21%), fruit mass (-58.90 to 94.05%), fruit number (-57.12 to 11.56%) and density (-41.64 to 93.81%) were the highest in this trial, with differences between the highest and lowest values within the characteristics being, 99.52%, 152.96%, 168.68% and 135.45% respectively. The highest high parent heterosis calculated in the trial for these characteristics were for yield (-32.32 to 67.50%), fruit mass (-71.90 to 84.31%), fruit number (-74.22 to 51.45%) and density (-49.88% to 47.89%). For the four characteristics showing the highest heterosis in this trial, fruit mass and density also had high heritabilities, meaning that it can show great improvement through selection in early generations, but certain hybrid combinations will result in further improvement due to hybrid vigour. Even higher heterosis values were calculated for yield and fruit weight by Korzeniewska and Niemirowicz-Szczytt (1993), Mohanty and Mishra (1999a) and Mohanty and Mishra (1999c), probably due to higher variation between their parental lines. Mohanty and Mishra (1999a; 1999c) did not mention where flesh thickness in the fruit was measured, but their calculated heterosis values were again slightly higher than those calculated from this trial.

The very high heterosis for yield can be confirmed by only significant positive SCA effects calculated and in addition to the latter, five of the seven worst performers in the trial were parental genotypes.

Very high fruit number mid-parent heterosis was calculated only for the crosses parented by A. All other crosses showed negative mid-parent heterosis. This may be the reason why A had a significantly larger GCA effect than any of the other parents. The best performing parent was F, who had a GCA not significantly different from zero, meaning that it does not have the ability to transfer its superiority to its offspring.

ML, TL and ST were the only characteristics that showed higher negative mid-parent heterosis than positive mid-parent heterosis percentages. All other traits tend to express more positive mid-parent heterosis percentages. More specifically in the case of ST, all high-parent heterosis were negative with only five crosses showing positive mid-parent heterosis. This may be explained by no positive SCA effects significantly different from zero as well as three of the parents that did not have significant GCAs.

The fact that only six crosses showed positive mid-parent heterosis for fruit number can be explained by three parental genotypes included in the best six phenotypic performances. These were also the only genotypes with higher averages than the trial average.

Although W:ML did not show very high heterosis, 14 of the 15 crosses expressed positive heterosis. This may indicate that in this population all parents tend to compliment one another rather than to express negative heterosis. It may be a case where dominance gene action is more important than overdominance or additive gene action.

Mean heterosis values were calculated to get a general idea on the average effect heterosis will have in the different characteristics. Characteristics that showed high mean mid-parent heterosis included yield (24.04), fruit mass (18.33), OW:L (13.45), OST (12.11), W:ML (11.57) and W (10.09). These characteristics will in general be more likely to show hybrid vigour than any of the other. Characteristics with big differences between the mean heterosis values and mean of the absolute values of the heterosis values, are characteristics that will show only positive or negative hybrid vigour in certain parent combinations. Fruit number and density showed this phenomenon which could be explained by SCA effects.

	OW:L		OTT		OST		OBES		LPL		LBL		Yield		Fruit mass		Fruit number		W	
	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH
AXB	29.82	16.84	-4.65	-11.13	25.20	15.99	-4.58	-16.08	17.77	0.32	13.07	3.79	29.47	-8.61	-38.82	-40.76	111.56	51.45	-12.52	-15.60
AXC	21.70	-5.15	-13.05	-17.45	10.22	-2.21	-10.61	-13.99	2.87	-1.89	6.87	-3.79	1.68	-12.91	-49.59	-66.00	42.55	-11.19	-15.31	-29.16
AXD	18.32	-1.74	-10.84	-17.96	5.21	3.34	-6.00	-6.76	14.01	9.18	13.20	4.84	-3.26	-6.31	-58.90	-71.90	81.00	21.48	-19.16	-30.67
AXE	20.63	0.00	-15.93	-27.49	23.16	0.00	-7.79	-14.45	16.29	0.00	6.38	0.00	17.74	0.00	-46.23	-63.23	59.64	0.00	-9.09	-16.67
FXA	22.30	11.84	-8.79	-15.81	31.26	8.96	-9.95	-19.82	32.81	20.87	27.25	21.42	12.53	-20.09	-22.85	-34.39	50.83	21.48	-5.15	-13.14
CXB	12.22	-8.82	-0.60	-5.41	22.10	12.56	12.69	9.83	-6.55	-10.67	-8.57	-9.85	6.83	1.08	44.67	-11.11	-57.12	-74.22	18.45	-6.17
DXB	9.00	-5.22	9.76	1.23	14.12	11.35	20.26	19.63	-16.26	-20.28	-12.02	-13.50	7.44	-0.46	43.40	-11.01	-50.29	-68.14	18.32	-4.10
EXB	2.22	-18.82	17.00	0.71	-10.81	-29.87	12.32	5.50	-13.79	-31.23	-16.25	-27.77	-11.30	-16.88	10.57	-31.38	-51.22	-70.53	15.03	-0.85
FXB	20.27	4.71	14.85	5.77	21.21	-2.67	28.73	15.97	-11.14	-25.42	-16.19	-26.75	-11.29	-32.32	47.42	42.73	-42.89	-57.09	12.33	9.93
DXC	9.62	5.65	6.28	0.59	-1.37	-15.51	-5.64	-12.47	-0.45	-1.03	10.29	8.06	8.55	1.07	26.48	22.48	-13.31	-16.99	14.84	14.68
CXE	16.09	-18.55	-16.03	-29.36	26.75	-9.42	-25.76	-26.37	12.03	-6.64	17.92	5.04	79.62	67.50	90.33	84.31	-7.51	-16.43	37.35	27.76
CXF	14.44	-13.71	-9.90	-19.07	10.53	-19.63	-9.76	-13.02	15.01	1.19	23.42	11.50	62.85	23.80	37.25	-12.50	-3.15	-26.74	17.69	-6.08
DXE	5.66	-22.94	-14.91	-26.38	2.75	-22.20	-22.14	-24.03	24.49	8.75	12.43	3.32	88.21	64.62	94.05	83.37	-4.20	-20.81	43.43	35.88
DXF	6.98	-15.60	-9.44	-16.13	8.16	-16.49	-6.62	-8.52	18.38	9.58	13.35	5.69	34.25	-2.62	49.80	-3.42	-22.42	-36.63	27.61	3.36
FXE	-7.58	-11.59	9.08	0.95	-6.83	-13.17	-2.92	-4.73	11.85	11.10	7.06	5.21	36.77	11.66	47.39	1.37	-18.24	-35.16	7.53	-8.67
Mean	13.45	-5.54	-3.15	-11.80	12.11	-5.26	-2.52	-7.29	-7.82	-2.41	6.55	-0.85	24.01	4.64	18.33	-7.43	5.02	-22.64	10.09	-2.63
ABS Mean	14.46	10.74	10.74	13.03	14.64	12.22	12.38	14.08	14.25	10.54	13.62	10.03	27.45	17.99	47.18	38.66	41.06	35.22	18.25	14.85

MPH = Mid-parent heterosis; HPH = High parent heterosis; ABS = Absolute value

	ML		TL		W:ML		ST		TT		MBT		SHT		BT		Density	
	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH
AXB	-15.26	-21.33	-16.64	-21.80	2.41	-1.32	0.70	-4.88	-23.04	-27.55	6.68	-5.02	7.67	-5.29	-0.67	-4.97	-28.66	-49.88
AXC	-26.02	-30.73	-28.04	-28.55	14.64	1.66	-5.85	-20.38	-10.30	-20.89	5.94	-1.07	8.45	-3.52	-11.31	-27.57	-41.64	-48.09
AXD	-23.77	-27.91	-21.93	-23.84	6.37	-4.02	-10.41	-13.32	-16.61	-22.35	-6.59	-15.19	-10.68	-13.38	-15.64	-28.91	-36.26	-44.14
AXE	-39.11	-56.23	-40.51	-57.67	31.46	0.00	-15.28	-26.51	4.68	0.00	2.68	0.00	24.47	0.00	16.39	0.00	-21.86	-35.88
FXA	-13.98	-16.63	-16.88	-21.00	9.24	-2.86	-14.57	-25.41	-14.93	-20.76	21.56	17.18	23.35	10.86	9.46	6.84	-26.43	-33.32
CXB	10.13	-2.24	6.40	-0.80	9.15	-4.42	5.84	-10.50	5.78	-3.11	-15.86	-26.78	35.99	-3.00	-3.97	-19.50	30.02	26.72
DXB	11.48	-0.11	12.24	7.88	7.10	-4.60	-0.66	-3.90	6.55	-4.53	-25.75	-27.38	1.52	-15.98	-10.89	-22.83	19.40	14.45
EXB	-10.63	-37.94	-10.46	-38.61	11.96	-13.97	-7.92	-20.14	36.12	35.54	-22.00	-29.46	14.88	12.68	-5.59	-21.06	93.81	47.89
FXB	-5.13	-13.02	-6.09	-15.95	16.73	5.15	-2.56	-14.94	6.17	-4.85	-18.83	-27.28	2.96	-10.01	4.72	-0.98	61.52	34.61
DXC	9.10	9.03	4.82	1.94	6.63	6.32	5.50	-3.67	-6.77	-17.61	1.15	-14.02	-1.88	-26.12	15.92	8.45	-10.13	-22.54
CXE	-9.00	-32.19	-20.40	-43.25	30.08	-7.51	-8.29	-10.52	2.64	1.47	25.83	19.88	5.53	-6.22	50.35	17.66	-7.47	-22.89
CXF	4.97	2.42	-0.26	-4.93	12.77	-8.09	-1.71	-3.39	-3.47	-14.68	37.02	31.86	8.94	-13.24	31.97	15.40	6.19	-2.04
DXE	7.12	-20.17	3.19	-26.00	17.15	-15.66	-14.50	-24.96	-19.61	-26.74	21.02	17.34	5.95	2.36	14.13	-6.54	9.15	-12.56
DXF	11.17	8.45	8.39	4.28	15.64	-4.22	1.59	-10.26	-0.43	-2.67	44.70	41.75	18.42	13.14	33.01	22.73	1.57	-10.46
FXE	31.50	15.17	32.03	16.55	-17.70	-20.51	2.01	-7.64	1.53	-1.96	-9.43	-14.38	-16.67	-18.64	-11.13	-16.21	2.67	-21.27
Mean	-3.83	-14.89	-6.28	-16.78	11.57	-4.94	-4.41	-13.36	-2.11	-8.71	4.54	-2.17	8.59	-5.09	7.78	-5.17	3.46	-11.96
ABS Mean	15.22	19.57	15.22	20.87	13.93	6.69	6.49	13.36	10.57	13.65	17.67	19.24	12.49	10.30	15.68	14.64	26.45	28.45

MPH = Mid-parent heterosis; HPH = High parent heterosis; ABS = Absolute value

CHAPTER 5

SUMMARY

1. The objective of this study was to study the inheritance of agronomic and quality characteristics in South African pumpkin germplasm and to identify characteristics that could be improved through hybrid breeding.

2. Six parental lines were crossed. The parents with the 15 F1-crosses were planted in Greytown as a randomized block design with six replications. Three of the replications were used for destructive measurements at the flowering stage, while the other three were used to evaluate yield and quality characteristics at a mature harvesting stage.

3. Significant phenotypic differences were found among the parental lines and their F1-offsprings for all the characteristics evaluated. C was the superior parent in nine of the 19 characteristics measured. For yield, fruit number, LPL, LBL and MBT parents in general tend to have a lower ranking than the crosses. The opposite was noticed for ST where the pure breeding parents performed better.

4. Specific combining abilities were calculated to be significant for all the characteristics, indicating that general combining ability predicted performances deviated from the observed performances for some of the crosses.

5. The calculated percentage variation due to GCA indicated that for most of the characteristics mostly additive variance influenced the expression of the characteristic. For LPL, yield, fruit mass, fruit number, ST, TT and MBT a large percentage (>25%) of the variation were influenced by non-additive gene action.

6. Very high broad sense heritabilities were calculated for all the traits. The lowest value was calculated for OBES (0.81). Very high narrow sense heritabilities were calculated for W, ML, TL, W:ML, SHT, BT, density, OW:L, OTT and OST. Heritabilities for fruit mass, LBL, ST, TT and OBES were calculated to be high. Moderate heritabilities were calculated for yield, fruit number, LPL and MBT.

7. Ovary and leaf morphology showed strong phenotypic and genotypic correlations with fruit characteristics expressed at a mature stage. OW:L and OST had respectively genetic correlations of 0.87 and 0.91 with SHT. OTT had a genetic correlation of 0.90 with density. Density had negative correlations with LPL (-0.94) and LBL (-0.85).

8. The highest direct response to selection was calculated for fruit mass, which showed a 122.88% improvement on the population mean. Direct selection response for density was calculated to be 98.74%. For most characteristics it was concluded that gain through indirect selection could be as successful as with direct selection.

9. Positive mid-parent heterosis and high parent heterosis were calculated for all characteristics except ST that showed only negative HPH. Yield (-11.30 to 88.21%), fruit mass (-58.90 to 94.05%), fruit number (-57.12 to 11.56%) and density (-41.64 to 93.81%) were identified to express the highest heterosis in the trial.

HOOFSTUK 5

OPSOMMING

1. Die doel van die studie was om die oorerwing van agronomiese en kwaliteitseieskappe in Suid-Afrikaanse pampoenkiemplasma te bestudeer.

2. Ses ouerlyne is in 'n dialleelontwerp gekruis. Die ses ouers asook die 15 F1-kruisings is in Greytown geplant. Die proef is geplant as 'n gerandomiseerde blokontwerp met ses herhalings. Drie herhalings is vir destruktiewe waarnemings tydens blomstadium gebruik. Die oorblywende drie herhalings is gebruik vir die evaluering van opbrengs- en kwaliteitseienskappe na oes, nadat die vrugte volwassenheid bereik het.

3. Vir beide die ouerlyne en F1-kruisings is betekenisvolle verskille bereken vir gemideldes van alle eieskappe. C was die beste ouer vir nege van die 19 eienskappe wat geëvalueer is. Vir opbrengs, vrugaantal, LPL, LBL en MBT het die ouers oor die algemeen swakker presteer as die kruisings. Die teenoorgestelde is waargeneem vir ST waar die suiwertelende ouers beter presteer het.

4. Die berekende spesifieke kombineervermoë was betekenisvol vir alle eienskappe. Dit wil sê die voorspelde voorkomste het afgewyk van die waargeneemde voorkomste.

5. Die berekende persentasie variasie as gevolg van algemene kombineervermoë het aangedui dat die meeste van die eienskappe se uitdrukking hoofsaaklik deur additiewe variansie beïnvloed word. Vir LPL, opbrengs, vrugmassa, vrugaantal, ST, TT en MBT is 'n groot persentasie (>25%) van die variasie veroorsaak deur nie-additiewe geenwerking.

6. Baie hoë waardes vir erflikheid in die breë sin is vir alle eienskappe bereken. Die laagste waarde is vir OBES (0.81) bereken. Baie hoë waardes vir erflikheid in die nou sin is vir W, ML, TL, W:ML, SHT, BT digtheid, OW:L, OTT en OST bereken. Hoë erfbaarhede vir vrugmassa, LBL, ST, TT en OBES is ook bereken. Erfbaarhede vir opbrengs, vrugaantal, LPL en MBT is bereken as matig.

7. Vrugbeginsel- en blaarmorfologie het sterk fenotipiese en genotipiese korrelasies getoon met vrugeienskappe wat op 'n volwasse stadium uitgedruk word. OW:L en OST het afsonderlik genetiese korrelasies van 0.87 en 0.91 met SHT getoon. OTT het 'n genetiese korrelasie van 0.90 met digtheid gehad. Digtheid was negatief gekorreleerd met LPL (-0.94) en LBL (-0.85).

8. Die hoogste direkte seleksie respons is bereken vir vrugmassa, wat 'n 122.88% verbetering op die populasie gemiddeld tot gevolg gehad het. Direkte seleksie respons vir digtheid was 98.74%. Vir meeste eienskappe kon afgelei word dat verbetering deur indirekte seleksie net so suksesvol kan wees as met direkte seleksie.

9. Positiewe mid-ouer en beter-ouer heterose is bereken vir alle eienskappe behalwe vir ST wat net negatiewe beter-ouer heterose getoon het. Opbrengs (-11.30-88.21%), vrugmassa (-58.90-94.05%), vrugaantal (57.12-11.56%) en digtheid (-41.64-93.81%) het die meeste heterose in die proef getoon.

CHAPTER 6

CONCLUSION AND RECOMMENDATION

From the results it could be concluded that a great amount of genetic variation existed in the material for all the characteristics evaluated. For this reason it is possible to improve yield and quality characteristics in pumpkin using this material and by selecting within segregating populations. However, all traits will not respond to the same degree to selection and for maximum improvement in the shortest time different approaches will be necessary.

The lines in this trial were selected to obtain maximum variation, which did not necessarily make them the best lines available. However, based on their GCA effects, they can definitely be used to improve certain characteristics in pumpkin. The result of the correlated response of some characteristics showed the possibility of indirect selection for some characteristics. However, the negative correlated response of some characteristics must also be taken into account.

Yield, fruit mass, fruit number and density were identified to express the highest heterosis. For maximum progress these characteristics should be improved through selection while being inbred. The hybrid vigour should then be exploited by selection of the best crosses from a trial made up of all possible hybrid combinations. Fruit mass and density also showed high heritabilities that could be used for the improvement of the characteristics.

OW:L, OST, W, TL, ML, W:ML, BT, LBL, fruit mass and density had high heritabilities that show high responses to selection and should be improved through intense selection in early generations. OTT and SHT had high heritabilities but poor to moderate response to selection and will need to be selected over several successive generations. Selection in early generations for characteristics with low heritability will be ineffective and they should be selected under diverse environments for maximum improvement. These characteristics included OBES, LPL, ST, TT and MBT.

The results of positive phenotypic and genotypic correlations showed the possibility of indirect selection to enhance improvement of characteristics expressed at a mature stage. The most applicable positive correlations were calculated between ovary morphology and SHT as well as between OTT and density. Useful negative correlations were calculated between leaf morphology and density.

Response to selection and correlated response were computed to give an indication of the amount of gain that can be obtained with direct and indirect selection. For most characteristics it was concluded that gain through indirect selection could be as successful as with direct selection.

ABBREVIATION LIST

A	Additive
ANOVA	Analysis of variance
b	Repeatability
BT	Bottom flesh thickness
Bu	Bush gene
CR_Y	Correlated response of characteristic Y
CV	Coefficient of variance
DF	Degrees of freedom
F1	Filial generation one
FAO	Food and Agricultural Organization Yearbook
GCA	General combining ability
h^2_b	Broad sense heritability
h^2_n	Narrow sense heritability
HPH	High parent heterosis
LBL	Leaf blade length
LPL	Leaf petiole length
LSD	Least significant difference
MBT	Middle bottom flesh thickness
M_e	Combining ability error mean squares
M_g	General combining ability mean squares
ML	Maximum length
MPH	Mid-parent heterosis
M_s	Specific combining ability mean squares
N	Non-additive
OBES	Ovary blossom end scar size
OST	Ovary side thickness
OTT	Ovary top flesh thickness
OW:L	Ovary width: length ratio
r	correlation
SCA	Specific combining ability
SHT	Shoulder flesh thickness

ST	Side flesh thickness
TL	Total length
TT	Top flesh thickness
USDA	United States Department of Agriculture
W	Width
W:ML	Width: maximum length ratio
σ^2_A	Additive variance
σ^2_E	Environmental variance
σ^2_G	Total genotypic variance
σ^2_g	General combining ability variance
σ^2_P	Total phenotypic variance
σ^2_s	Specific combining ability variance

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APPENDIX

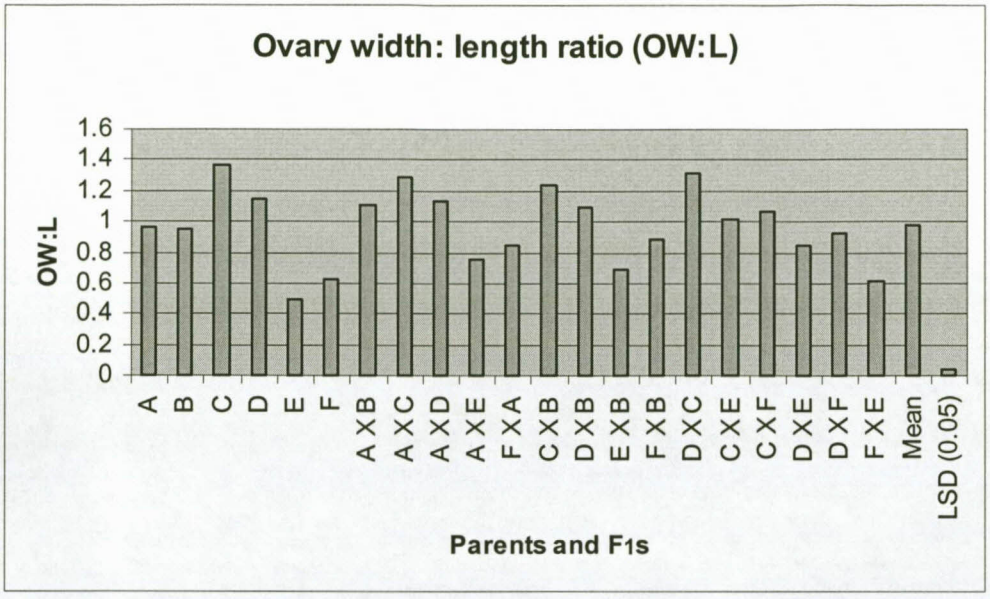

Fig. 4.1: Ovary width: length ratio

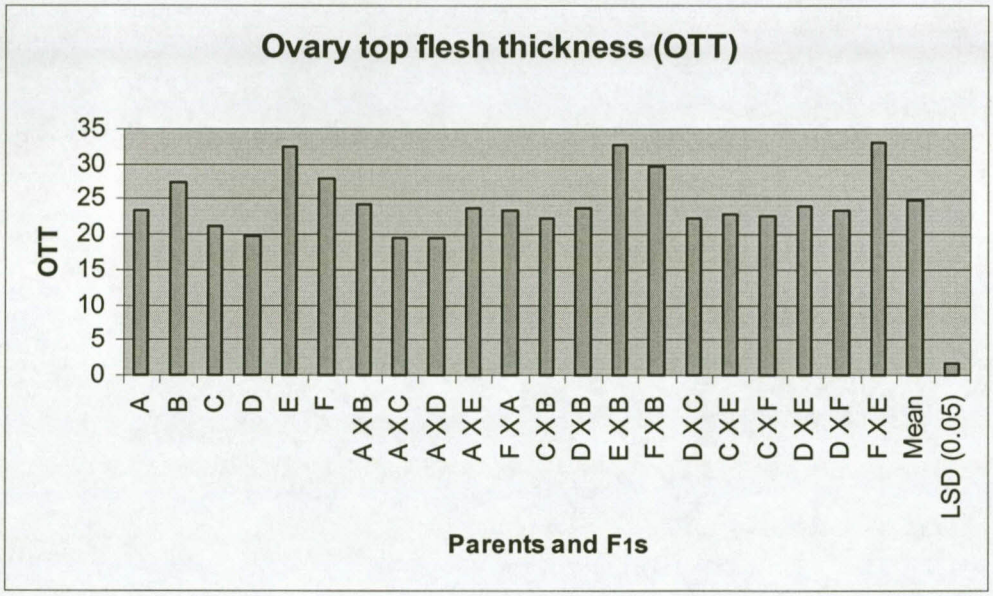

Fig. 4.2: Ovary top flesh thickness

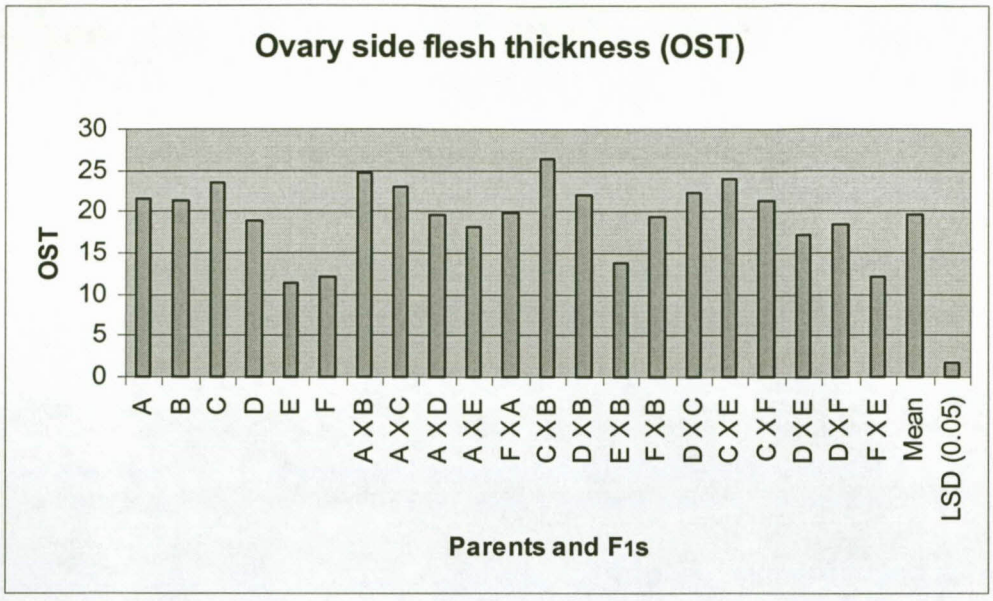

Fig. 4.3: Ovary side flesh thickness

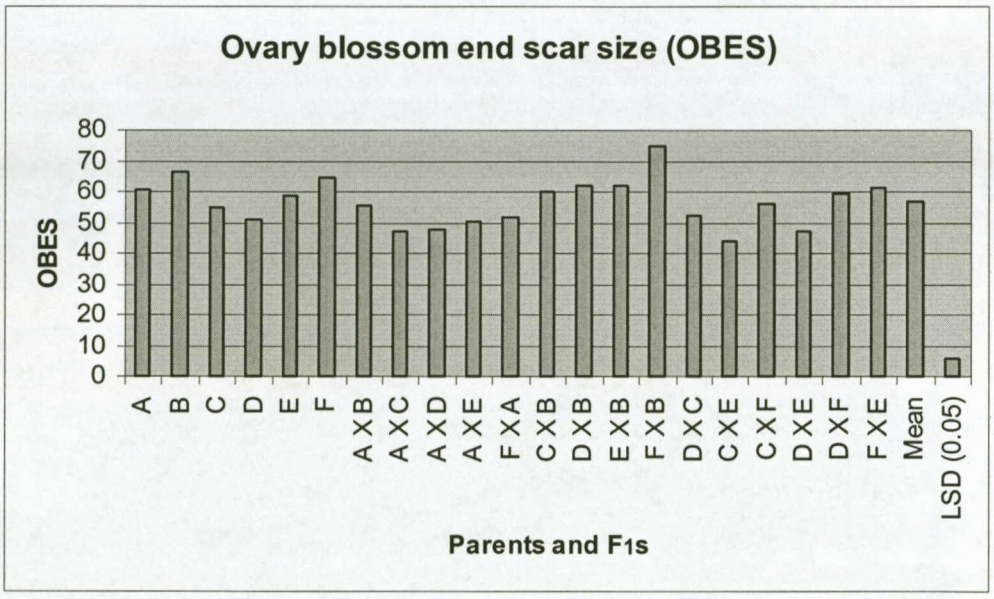

Fig. 4.4: Ovary blossom end scar size

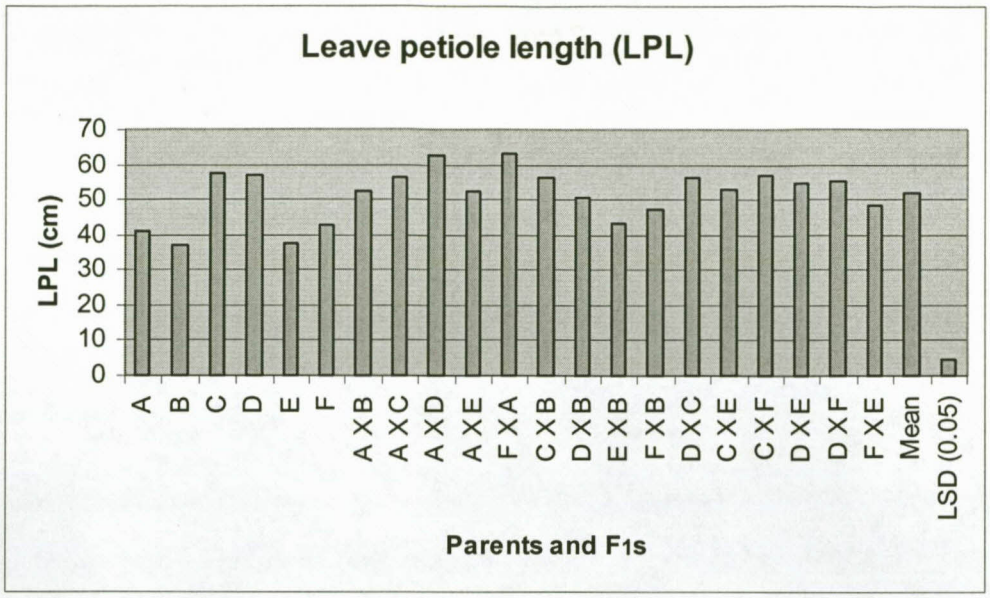

Fig. 4.5: Leave petiole length

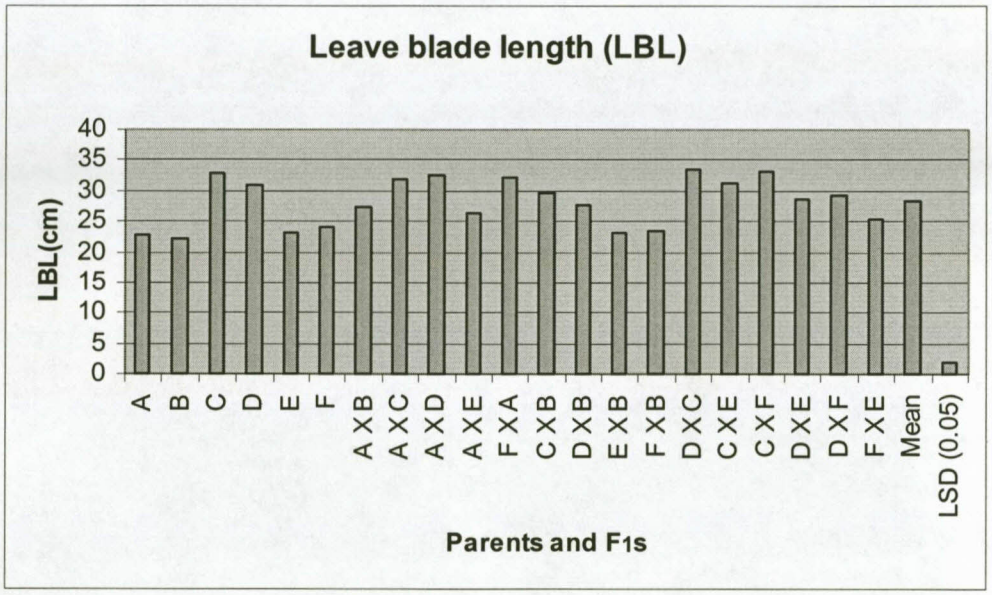

Fig. 4.6: Leave blade length

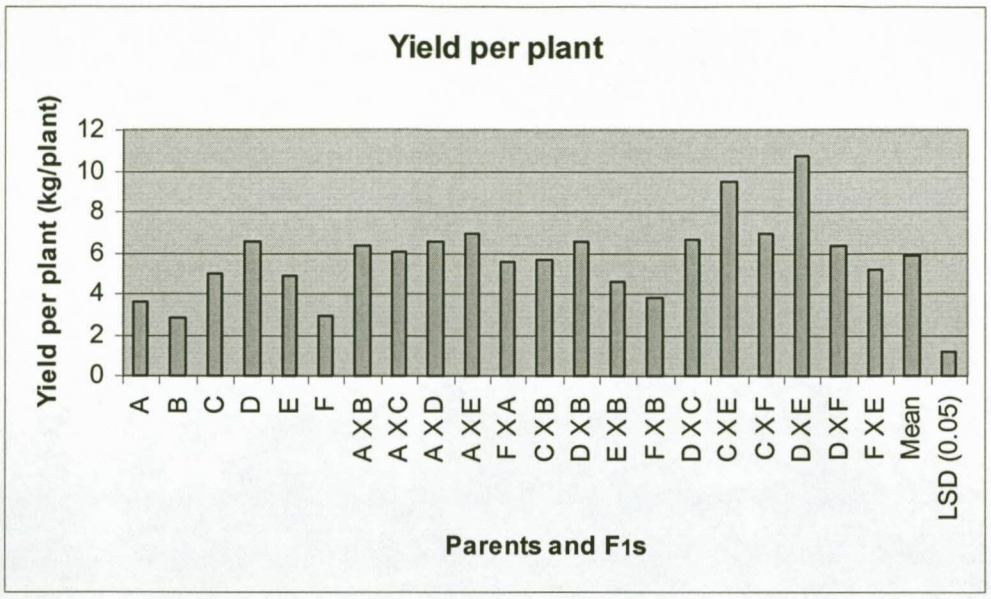

Fig. 4.7: Yield per plant

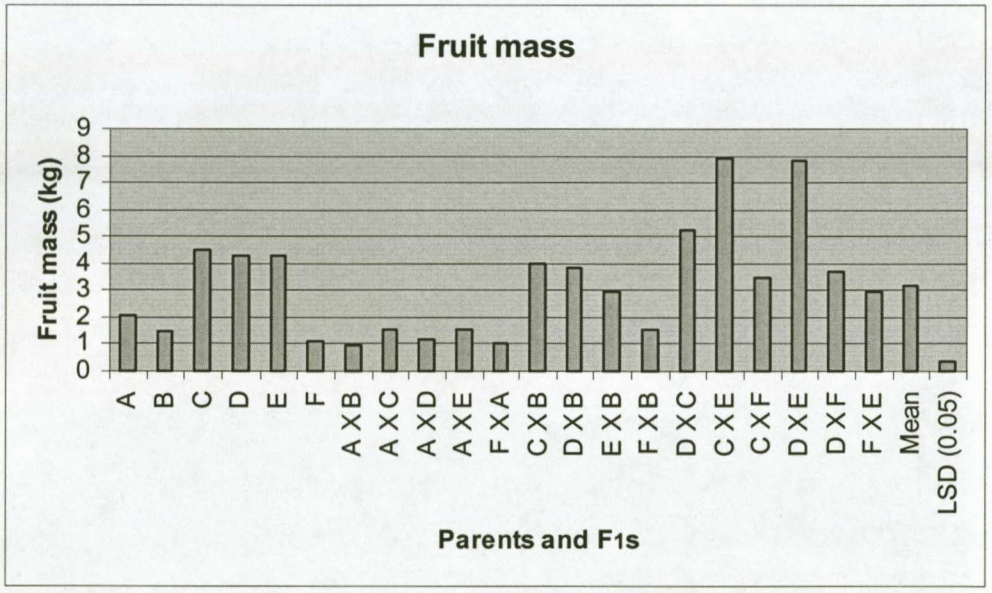

Fig. 4.8: Fruit mass

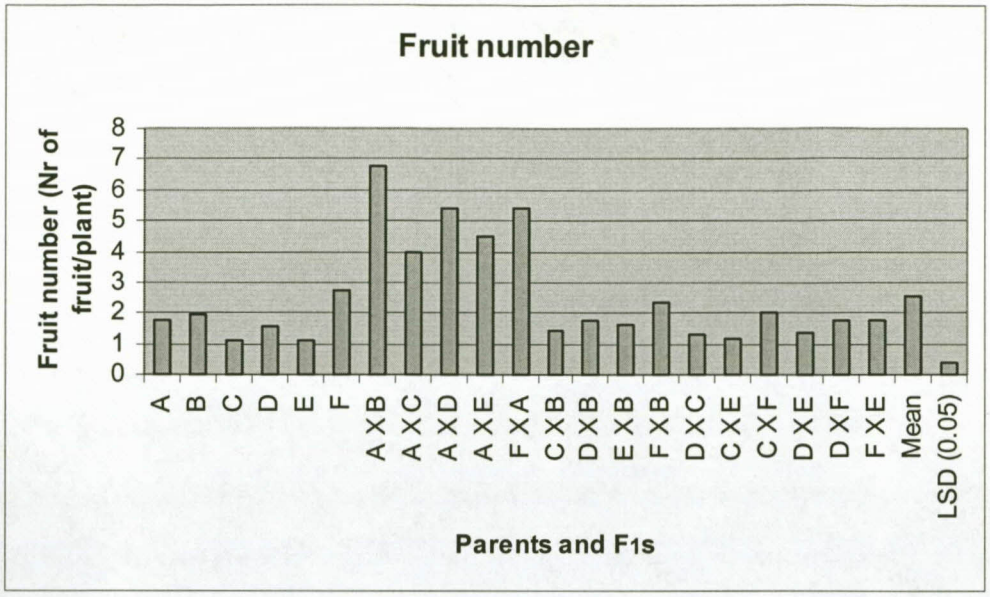

Fig. 4.9: Fruit number

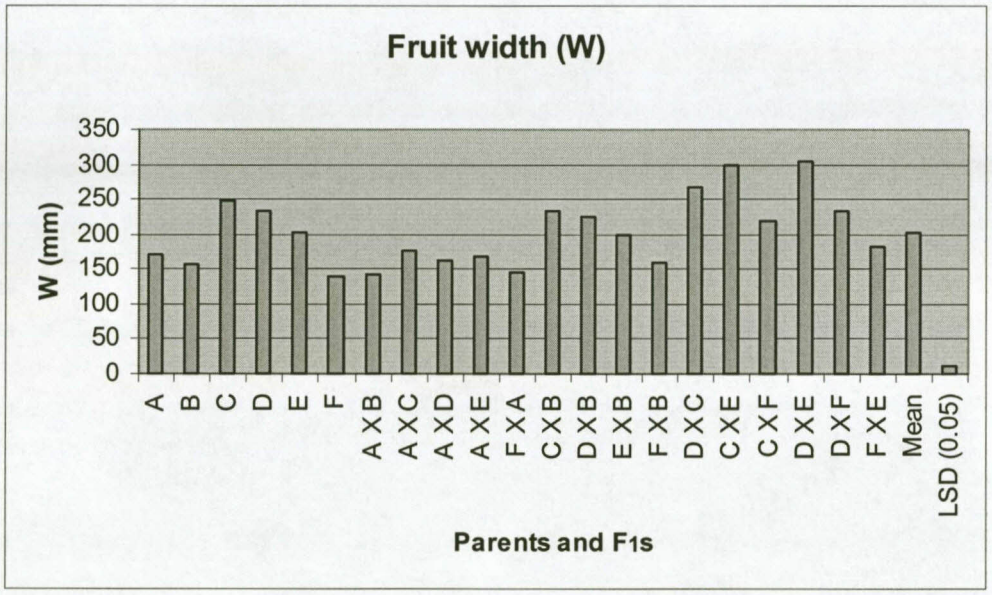

Fig. 4.10: Fruit width

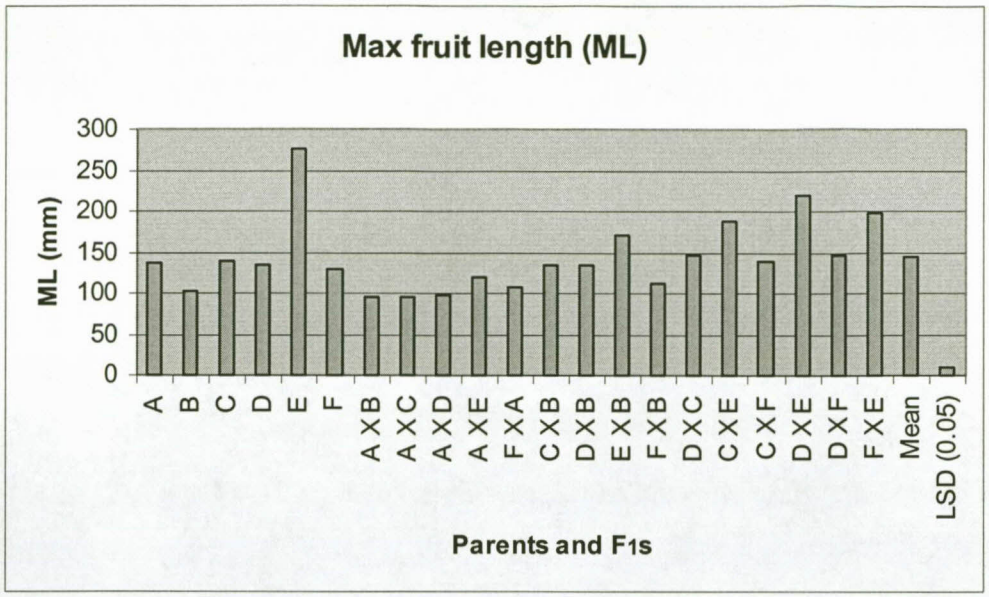

Fig. 4.11: Maximum fruit length

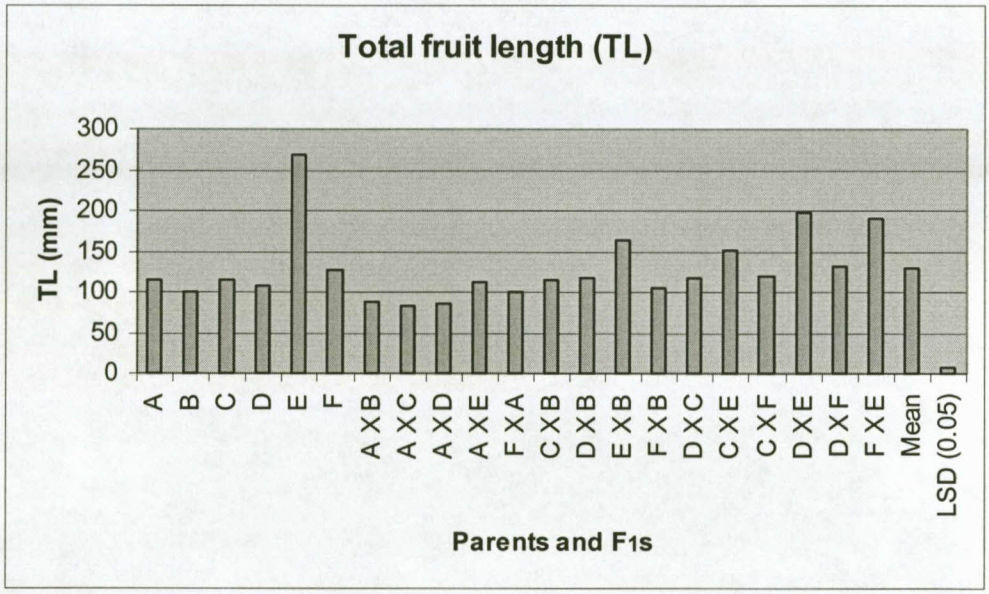

Fig. 4.12: Total fruit length

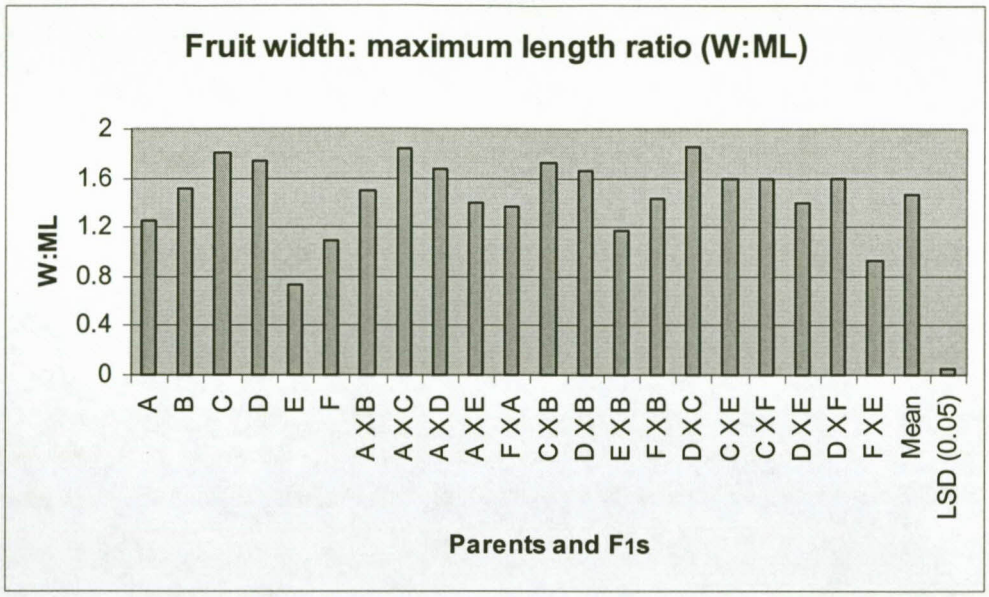

Fig. 4.13: Fruit width: maximum length ratio

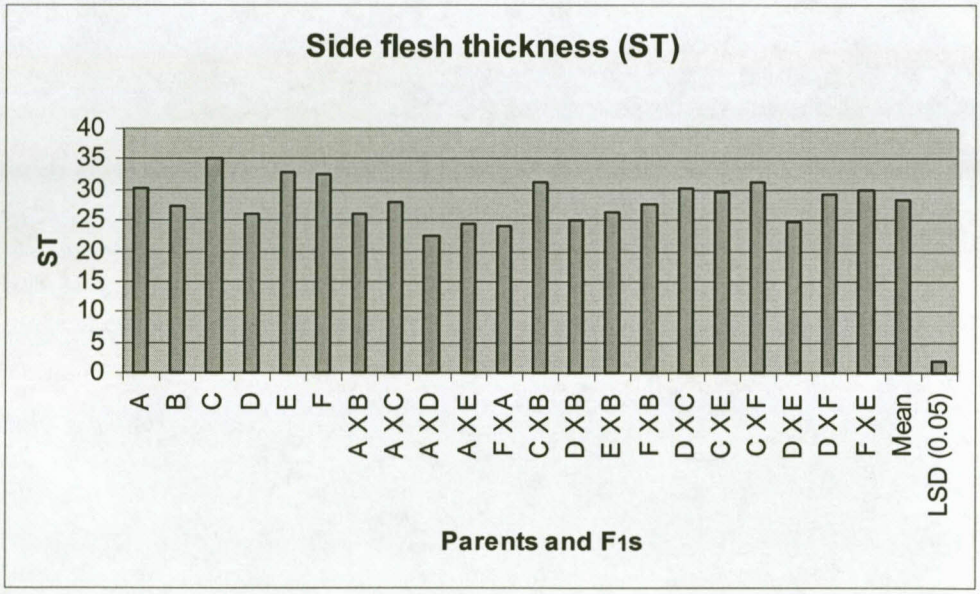

Fig. 4.14: Side flesh thickness

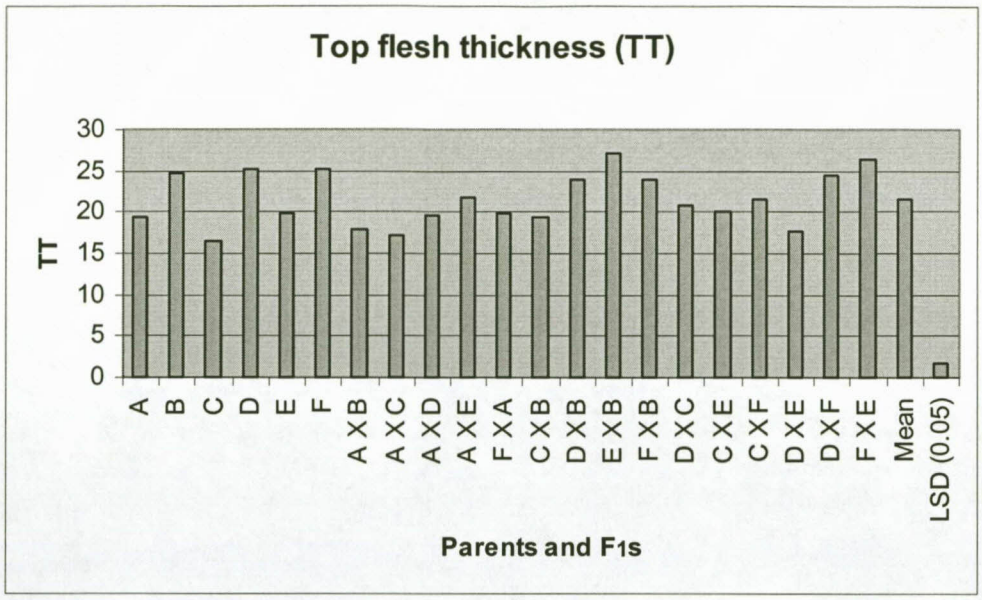

Fig. 4.15: Top flesh thickness

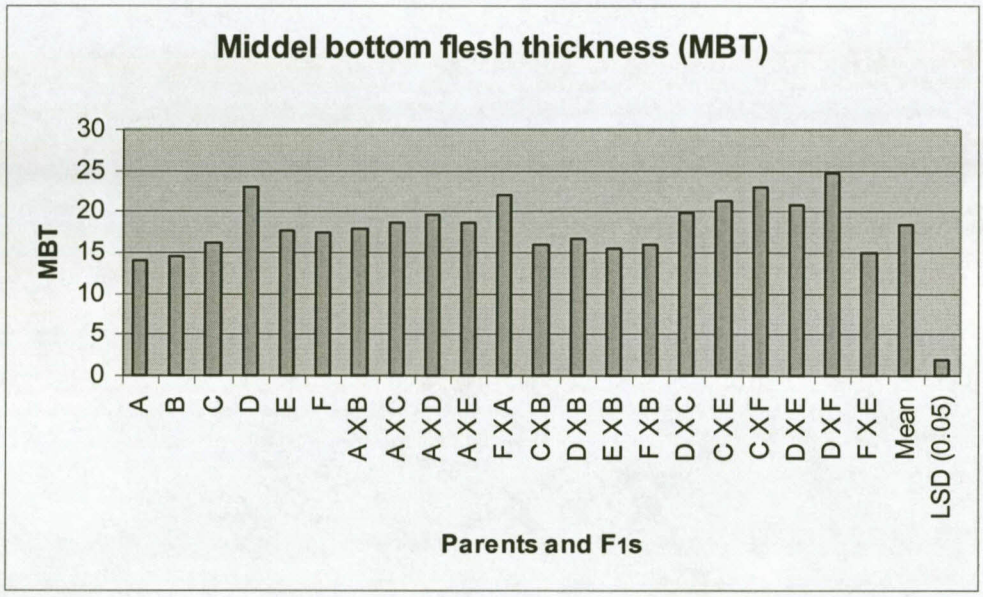

Fig. 4.16: Middle bottom flesh thickness

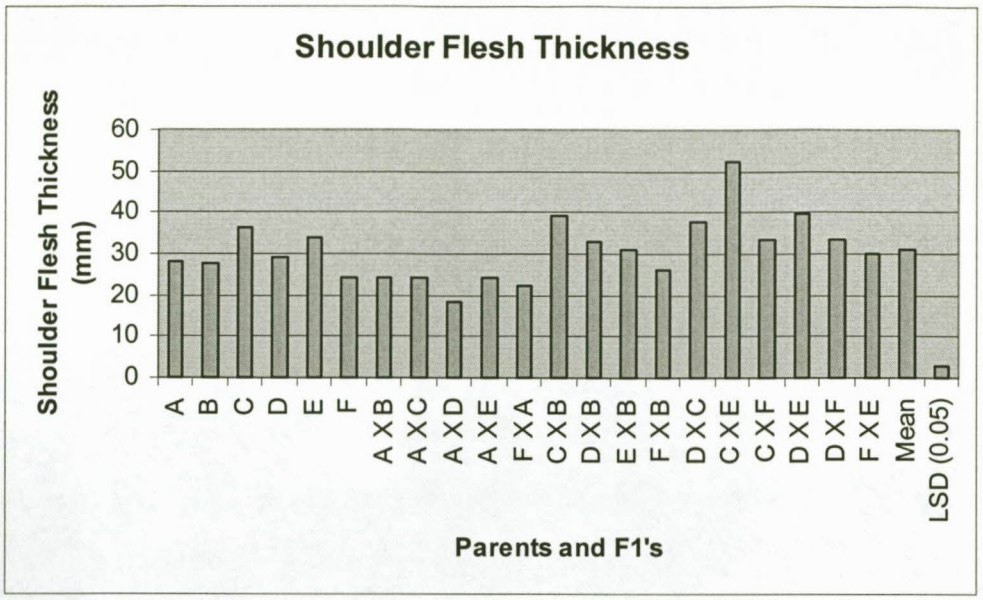

Fig. 4.17: Shoulder flesh thickness

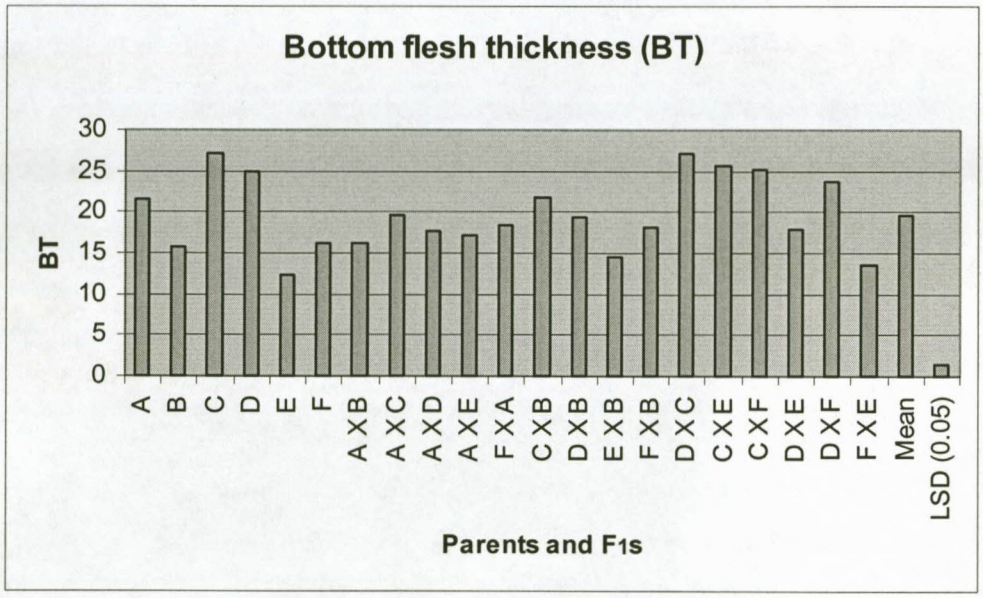

Fig. 4.18: Bottom flesh thickness

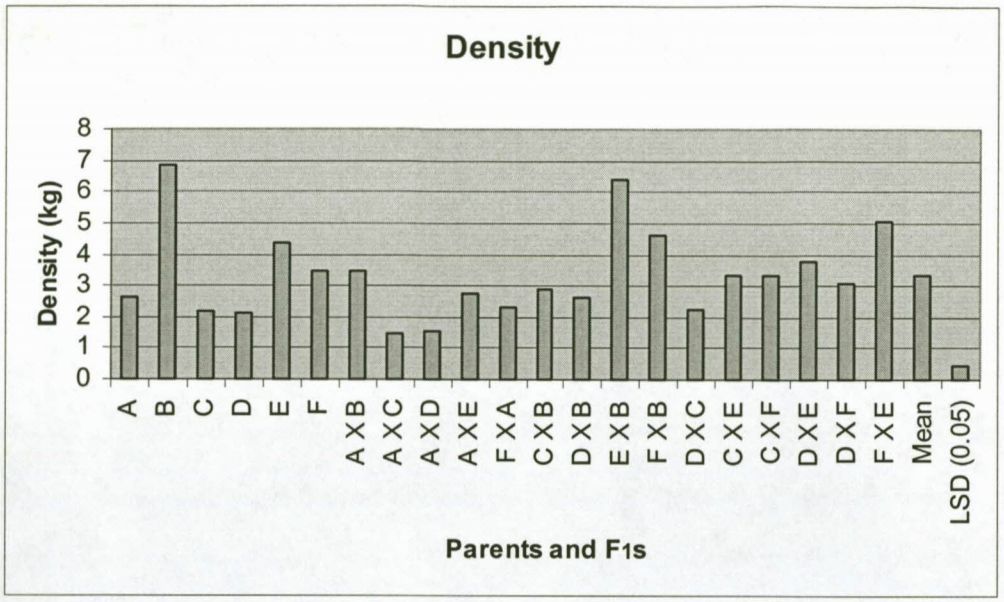

Fig. 4.19: Density