ABSTRACT

LOU, LINGLI. Inheritance of Fruit Characteristics in Watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai]. (Under the direction of Todd C. Wehner, M.S.)

Watermelon fruit characters may affect customer acceptance of the watermelon fruit. The qualitative fruit traits, such as flesh color, seed size, seed coat color, rind pattern, fruit shape, exhibit wide ranges of phenotypes. The flesh color can be red, orange, yellow, or white. The seed length of watermelon also varies from 4.4mm to 16.5mm. The seeds can have various coat colors or other decorations. The rind of watermelon fruits can be striped or solid colored, which are further characterized by different stripe widths, stripe colors, backgrounds colors, and additional modifications. The fruit shape can be elongate, oblong, and round. Other fruit traits include shape of fruit blossom end, fruit surface characters, and hollow-hearted flesh. By crossing watermelon cultivars with different phenotypes, we studied the inheritance of the various phenotypes and identified and verified genes responsible for the flesh color, seed size, rind pattern, and fruit shape. In addition, we studied the quantitative traits of the fruit weight and total soluble solids content. The calculated broad-sense and narrow-sense heritability for fruit weight is low to medium, indicating large environmental effect on fruit weight. Medium to high heritability is found for the total soluble solid content, suggesting possible gains from selection.

Inheritance of Fruit Characteristics in Watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai]

by
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BIOGRAPHY

I was born in Pujiang Zhejiang, China. The small village where I was born and grown up is a quiet and beautiful place with a small creek running in the front of it and small hills lying behind it. I spent a lot of time playing in the creek or wondering on the small hill when I was a kid and I become a naturalist and love the nature a lot as I grown up. I feel everything in the nature is fascinating even just by looking at it. I choose to learn biology when I go to college. After my graduation, I worked in an environmental monitoring station as a lab assistant for the environmental and drinking water quality monitoring for 2 years before I came to U.S. with my husband. I decided to continue my experience and education in NC State in 2006 and enjoy working as a horticulturist.

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CHAPTER ONE

GENETIC CONTROL OF SEED CHARACTERS IN WATERMELON – A REVIEW

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Introduction

Watermelon [*Citrullus lanatus* (Thunb.) Matsumura & Nakai] is a vining, annual vegetable crop. Native to southern and tropical Africa and probably Asia, and naturalized in the Americas, it is now cultivated in warm regions worldwide. Watermelon counts for 6.8% of vegetable production area around the world (FAO, 2002; Guner and Wehner, 2004). The ripe fruit is directly edible and is normally served cool as a dessert. The immature fruit can be cooked as vegetable. The fruit can also be used in confectionary. Small white-fleshed cultivars are used for preserves. Baked watermelon seeds from large-seeded cultivars have traditionally been popular snacks. Watermelon seeds are also used in soups and for producing seed oil.

Breeding for improving production, quality and disease resistance in watermelon cultivars is of considerable commercial interest. Other breeding goals include diversification of the fruit and plant types, and adaptation to specific areas. Since the late 1800s, hundreds of watermelon cultivars have been developed in the United States. Some examples of popular cultivars include 'Charleston Gray', 'Allsweet', and 'Sugar Baby'.

Watermelon is a diploid with 22 chromosomes and a relatively small genome size of $4.2x10^8$ bp (Arumuganathan and Earle, 1991). Extensive genetic studies and breeding experiments since the 1930s have identified more than one hundred genes. These genes are related to phenotypes in seed and seedling, vine, flower, fruit, and resistance (Robinson et al., 1976; Cucurbit Gene List Committee, 1979, 1982, 1987; Henderson, 1991, 1992; Rhodes and

Zhang et al., 1995; Rhodes and Dane, 1999; Wehner, 2008). A comprehensive list of these genes can be found in recent reviews (Guner and Wehner, 2004; Wehner, 2008).

Seed traits are important for the watermelon market. Seed characters, such as seed size and seed color, may to a certain extent affect customer acceptance of the watermelon fruit. In breeding seedless watermelon, the size of the undeveloped seeds in the triploid determines the acceptability of the watermelon as "seedless". Therefore it is advantageous to breed high-quality watermelon cultivars having small seed as parents for the seedless triploids. In terms of seed coat color, black and brown seeded cultivars are often preferred in the market, since light-colored or white seed coat colors may mislead consumers to think that the fruit is not ripe. In the market when edible seeds are of interest, seed coat colors other than black and brown are also pursued. For example, there is considerable interest to develop watermelon cultivars having high yield of red-coated edible seeds (Zhang, 1996b).

Watermelon seed is also known for its rich nutrient content. Although not common in the United States, in some countries, watermelon seed is considered an important dietary item (Oyolu, 1977; Zhang, 1996b). It has been determined that watermelon seed contains high amounts of minerals such as Ca, P, Mg, K, Zn and Fe, and other nutrients (Oyolu, 1977; Oyenuga and Fetuga, 1975). In China, baked watermelon seed from large-seeded cultivars has traditionally been a popular snack and is therefore of commercial interest. Another example comes from egusi seed, where the fruit is not edible but the seed has been used in the diet in some African countries (Oyolu, 1977).

Because of the importance of seed traits, there has been a lot of research on the underlying genetic mechanisms that controls these traits (Kanda, 1931; Poole et al., 1941;

Porter, 1937; Suzuki et al., 1971; El-Hafez et al., 1981; Sharma and Choudhury, 1982; Tanaka et al., 1995; Zhang, 1996b; Zhen and Jin, 1995; Kang et al., 2000). Following is a review of research on watermelon seed traits of size, coat color, and coat pattern.

Seed Size

Watermelon seed length can vary from as long as 16.5 mm to as short as 4.4 mm (Poole et al., 1941; Zhang, 1995a; Tanaka et al., 1995). Watermelon seed length has been used as a measure of seed size by researchers, since length is highly correlated with width (Poole et al., 1941; Zhang et al., 1995; Hawkins and Dane, 2001). The size of seeds can be classified according to their length: long seeds with length of 11.5-16.5 mm (or 13 mm in average), medium seeds with length of 7.5-11.5 mm (or 10 mm in average), and short seeds with length of 4.5-7.5 mm (or 6 mm in average). This classification may not be very strict. A study crossing a line having seed length of 12.7 mm to one with 7.4 mm by Konsler and Barham (1958) suggested that 7.4 mm might belong to the medium size. In addition, an even smaller seed size ("tomato seed"), with an average length less than 4.5 mm, was also proposed (Zhang et al., 1995; Zhang, 1996a).

Early researchers (Weetman, 1937) investigated the inheritance of seed weight and demonstrated the segregation ratio did not fit well to the monogenic segregation ratio 3:1 but was close enough to suggest that light weight phenotype was monogenic dominant over heavy weight. However, correlation of seed weight and size was not significant in Weetman's experiment (Weetman, 1937). Poole et al. suggested that the light and heavy

seeds corresponded to medium and large seed sizes (Poole et al., 1941; Konsler and Barham, 1958), since seed size is usually correlated with seed length (Poole et al., 1941; Zhang, 1995a; Hawkins and Dane, 2001). Poole et al. (1941) also demonstrated good correlation (r = 0.913) between seed length and width when crossing 'Sun Moon and Stars' × 'Winter Queen'. This correlation was also confirmed by other researchers (Zhang et al., 1995; Zhang, 1996a; Hawkins and Dane, 2001).

Poole et al. (1941) investigated crosses between short and long, short and medium, and medium and long seeds. The result showed the seed size is controlled digenically as medium sized seeds were dominant to both short and long, while two recessive genes, *l* and *s*, determine the long and short phenotypes of the seeds, respectively. Poole et al. also found that *s* is epistatic to *l*. Therefore the following designations were given to the genotypes corresponding to different seed sizes: *LL SS* for medium, *ll SS* for long, and *LL ss* or *ll ss* for short seeds. Konsler and Barham crossed a large seeded cultivar with seed length 12.7 mm ('Charleston Gray') to a medium seeded breeding line with seed length 7.4 mm (N.C.9-2), and the results showed the medium seed was single gene dominant to the long seed, which is consistent with Poole's study (Konsler and Barham, 1958). Shimotsuma also confirmed the monohybrid inheritance of medium over long in the cross between a large-seeded line, V.No.3 and a medium-seeded line, V.No.1 (Shimotsuma, 1963).

Tanaka et al. (1995), however, reported that the *l* and *s* genes proposed by Poole could not explain their results from the cross of 'Sweet Princess' (average seed length 6.5 mm) and 'Fujihikari' (average seed length 8.5 mm). They found that the short seed type was due to a single gene dominant over medium, contradicting previous findings. They proposed an

additional dominant *Ti* (tiny controlling the short seed type in 'Sweet Princess' (Tanaka et al., 1995).

Zhang et al. studied the inheritance of a small seed type called “tomato seed” (average length of 4.4 mm) (Zhang et al., 1995). It is smaller than the short seed described earlier By crossing a large edible seed cultivar with a “tomato seed” cultivar, an additional gene was proposed by the authors to explain the observed segregation ratio in the progenies. Zhang (1996b) confirmed this gene in the cross 'Sugar Baby Tomato Seed' × 'Gn-1' (long seed, average 17.6 mm). The tomato seed type was incompletely dominant over long seed. The symbol *ts* was later given to the “tomato seed” type (Guner and Wehner, 2004).

Seed Coat Color

Watermelon seeds have various coat colors such as white, tan, black, brown, green, and red. Some seeds do not have uniform colors, for examples, some tan or white colored seeds have pink or black tips, or black rims (a peripheral band around the seed). Some other watermelon seeds have a main background color and a different foreground color which makes it is very hard to classify. Watermelon seed coat color is also difficult to classify due to the shades of different colors. It is reasonable that different researchers may classify the same phenotype as different or give same name to different phenotypes. Because of the discrepancy in describing the complicated seed coat color and pattern, it is sometimes difficult to find the correspondence of the coat colors in different published studies.

Studies of watermelon seed coat color began in the early 1930s. Kanda (1931) reported the first genetic study of watermelon seed characters including 13 crosses. He described 6 base colors (white, yellowish white, reddish brown, reddish orange, black, and yellowish green) and 5 patterns (black spot on the seed tip, black dots, black rim, yellow margin on the periphery of the both flat sides, and solid color) and proposed 7 pairs of genes controlling these characters. However, due to the ambiguity in naming the seed coat color, it is difficult to compare Kanda's classification with other studies. Therefore Kanda's classification and gene names are not widely adapted.

McKay (1936) studied the inheritance of tan, green and red seed coat colors in preserving and stock citron. The author demonstrated that both tan and green are monogenic dominant over red. The author also proposed that tan and green might be two independent factors dominant over red. The genotypes for tan and red were later assigned by Poole et al. (1941): *RR tt WW* for tan, and *rr tt WW* for red. *rr TT WW* was inferred to correspond to green (McKay, 1936; Poole, 1944).

Porter (1937) investigated crosses between black, tan and white and found the possibility of multiple factors controlling seed coat color. The results suggested that black is dominant over clump, tan, and white. The white seed color in 'Pride of Muscatine' referred in the paper is formally named as "white with tan tip" now (Wehner, 2008). This clearly demonstrates the ambiguity of classification of seed coat colors as mentioned above. It is difficult to confirm the results due to this ambiguity when some of the cultivars are no longer available. The white seeded cultivars used by Porter might include the real white and white with tan tip. Some other crosses were carried by Porter only in the F_1 generation, which

showed the dominance of black over white, red over white, black over green, and green over red. The green over red dominance is consistent with previous reports (McKay, 1936). Additionally, Porter (1937) also tested the linkage among main characteristics (rind toughness, flesh color, skin color) and no linkage was found.

Weetman (1937) crossed 'Long Iowa Belle' (described as light tan with peripheral black banded seeds) with 'Japan 4' (described as medium brown, black dotted seeds) and found the later has single gene dominance. These two coat colors were later referred as clump and black, respectively (Poole et al., 1941). The cross between 'Japan 6' (the seed color is described as reddish brown or tan as referred by Poole) and 'Long Iowa Belle' showed a 9:3:3:1 segregation ratio in F_2, indicating two-gene dominance (Weetman, 1937).

Poole et al. (1941) systematically examined the inheritance of several color types including black, tan, red, clump, white tan-tip, and white pink-tip and found that these phenotypes can be explained by a 3-gene model. The black seed-color is found to be dominant over other colors, consistent with previous reports. Poole et al. proposed three genes *r*, *t* and *w*, which interact to determine the seed color. From their crossing experiments, Poole et al. assigned the genotypes *RR TT WW* for black seeds, *RR tt WW* for tan, *RR TT ww* for clump, *RR tt ww* for white tan-tip, *rr tt WW* for red, and *rr tt ww* for white pink-tip. They did not have the genotypes *rr TT WW* and *rr TT ww* in the experiments. From earlier studies and the above genotypes, it can be inferred that *rr TT WW* should correspond to green seed color (McKay, 1936; Poole, 1944).

In addition, there is a fourth gene, *d*, suggested by Poole for the stippled surface with numerous black dots (usually with a visible tannish or reddish undercoat). The *d* gene is

considered as modifying factor to the black seed color and is only effective together with the *RR TT WW* genotype, so *RR TT WW DD* is black, and *RR TT WW dd* is dotted black (Poole et al., 1941).

Shimotsuma reported that brown seed color is dominant over white in the crosses of 3 wild watermelon lines (Shimotsuma, 1963). Shama and Choudhury (1982) showed fuscous black is one gene dominant over white seed coat color. However, it is not clear how the brown, fuscous black and white colors correspond to current accepted color classifications. Same confusion applies for several other inheritance studies of seed coat colors, which are not reviewed here.

Seed Coat Pattern

Other than size, and coat color, watermelon seed can have different seed coat textures and decorations such as dots, cracks or coverings. Some special seed types have particular characteristics, for instance the egusi seed has fleshy pericarp covering the seeds when it is inside a fruit, but it looks like the normal seed after washing and drying.

The inheritance of cracked seed coat was investigated by El-Hafez et al. (1981) by crossing cultivars with uniform seed, 'Kaho' and 'Congo', to a cracked seed cultivar, 'Leeby'. Crack seed coat was found to be controlled by a single recessive gene *cr*. Recently, Gusmini et al. (2004) reported a new gene, *eg*, related to the egusi seed type. This particular seed type is found in egusi watermelon, which has fleshy pericarp covering the seeds when the seeds are fresh. By crossing egusi-seed type breeding lines (PI 490383w and PI 560006) with

normal seed type cultivars ('Charleston Gray' and 'Calhoun Gray'), the authors found monohybrid inheritance of the *eg* gene.

The genes controlling seed size, color, and pattern can be used to develop new cultivars having interesting appearance, such as red seeds in red flesh, or green seeds in yellow flesh. They can also be used to provide cultivars that are nearly seedless, having tiny or tomato size seeds, or cultivars that have giant seeds and used in edible seed production. Small seed cultivars are also useful in developing triploid seedless watermelons.

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CHAPTER TWO

QUALITATIVE INHERITANCE OF FLESH COLOR AND SEED CHARACTERS IN WATERMELON

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Introduction

Watermelon [*Citrullus lanatus* (Thunb.) Matsumura & Nakai] is an important vegetable crop native to southern and tropical Africa and probably Asia, and now cultivated in warm regions worldwide. 93% of the watermelon fruit is water, and others are carbohydrates and small amounts of protein, fat, minerals, and vitamins. Lycopene, one of the major nutritional components of watermelon fruit (4,100 μg/100g, range 2,300–7,200), is an anticarcinogenic compound found in red flesh cultivars (Wehner, 2008b). Lycopene is a red-colored pigment that may help reduce the risk of certain cancers, such as prostate, pancreas, and stomach (Wehner, 2008b). Dark red watermelon cultivars have higher lycopene content than light red cultivars. Watermelon seed is also known for its rich nutrient content. It has been determined that watermelon seed contains high amounts of minerals such as Ca, P, Mg, K, Zn and Fe, and other nutrients (Oyolu, 1977; Oyenuga and Fetuga, 1975).

Breeding for improving production, quality and disease resistance in watermelon cultivars is of considerable commercial interest. Since the late 1800s, hundreds of watermelon cultivars have been developed in the United States. Extensive genetic studies and breeding experiments since the 1930s have identified more than one hundred genes in watermelon (Guner and Wehner, 2004; Wehner, 2008a).

Flesh Color

Watermelon fruit exhibits a wide range of flesh color, including red, orange, yellow, green and white. The red, orange and yellow colors in watermelon flesh are due to the accumulation in the chromoplasts of different levels of carotenoids and tetraterpenoid

pigments, a family of organic pigments beneficial to human health (Tadmor et al., 2004a). Red-fleshed watermelons have high levels of lycopene (a major red-pigmented carotenoid in watermelon) and/or small amount of β-carotene. Orange-fleshed watermelons accumulate high levels of pro-lycopene or β-carotene. Salmon yellow watermelons contain small amounts of pro-lycopene and canary yellow watermelons contain trace amount of lutein and β-carotene. White-fleshed watermelons have no carotenoid content (Di Mascio et al., 1989; Tomes et al., 1963; Tadmor et al., 2004b; Perkin-Veazie et al., 2001). The inheritance of watermelon flesh color has been investigated extensively and several genes have been identified. These include genes for scarlet red, coral red, orange, salmon yellow, canary yellow and white colors (Henderson et al., 1998; Guner and Wehner, 2003, 2004; Gusmini and Wehner, 2006a, 2006b). Understanding the genetics of the inheritance of flesh color is of great importance. For example, the fruit flesh color in watermelon is correlated to the content of carotenoids and tetraterpenoid pigments (lycopene is the major red pigment), which are beneficial to human health. Therefore, understanding the genetics of the flesh color helps to breed cultivars producing higher level of lycopene, which are favored on the market.

The genetics of watermelon flesh color has been investigated since 1930s. A series of three alleles at the *y* locus is responsible for producing coral red (*Y*), orange (y^o), and salmon yellow (*y*) flesh colors. *Y* was dominant to y^o and *y*, and y^o was dominant to *y* (Porter, 1937; Poole, 1944; Henderson et al., 1989, 1998). *Scr* was designated as the gene controlling scarlet red, a dark red color in cultivars 'Dixielee' and 'Red-N-Sweet', which is darker than the coral red color (*Y*) of many common cultivars including 'Charleston Gray', 'Allsweet', and 'Angeleno Black Seeded'. Scarlet red is dominant to coral red, so Gusmini and Wehner

proposed that the genotype of scarlet red cultivar 'Dixielee' and 'Red-N-Sweet' was *ScrScr YY* and that of coral red cultivar 'Angeleno Black Seeded' was *scrscr YY* (Gusmini and Wehner, 2006a). But the possibility that *Scr* is another allele of the *Y* locus was not eliminated and further investigation was necessary.

Another gene, *C* (*C* was from 'Honey Cream' and NC-517, *c* was from 'Dove'), was found to control the canary yellow flesh color (*CC YY I-CI-C*) and it was epistatic to coral red (*cc YY i-Ci-C*) in the absence of *i-C* (Poole, 1944; Henderson et al., 1998). A related gene *i-C* was reported as an inhibitor of canary yellow (Henderson et al., 1998; Rhodes and Dane, 1999). Genotype *CC YY I-CI-C* is canary yellow for 'Yellow Baby' or 'Yellow Doll' due to the inhibition of *YY* (coral red) by *CC* (Canary yellow*)* in the presence of *I-CI-C*; genotype *cc* $y^o y^o$ *I-CI-C* is orange for 'Tendersweet Orange Flesh'; *cc yy I-CI-C* is salmon yellow for 'Golden Honey'; *cc YY i-Ci-C* is coral red for 'Sweet Princess'.

Shimotsuma conducted a cross between a red-fleshed breeding line V.No.1 and white-fleshed breeding line V.No.3 and found that this trait is controlled by two factors: *Wf* (originally named as *W* by Shimotsuma and renamed by Henderson as *Wf*) and *B* (originally named as *Y* by Shimotsuma and renamed by Henderson as *B*). *Wf* is epistatic to *B* and genotypes *WfWf BB* or *WfWf bb* are white-fleshed. Genotype *wfwf BB* is yellow fleshed and *wfwf bb* is red fleshed. *Wf* and *B* are from breeding line V.No.3, and *wf* and *b* are from V.No.1 (Shimotsuma, 1963; Robinson et al., 1976; Henderson, 1992).

Seed Coat Color and Pattern

Watermelon seeds have various coat colors such as white, tan, black, green, and red (Kanda, 1931). Some seeds may have a peripheral band around the seed (or called rim), or other decorations such as dots, colored tips, or cracked seed coat. Seed coat color and pattern also affect the customer acceptance of watermelon fruit. Black and brown seeded cultivars are often preferred in the market, since light-colored or white seed coat colors may mislead consumers to think that the fruit is not ripe. Other seed type, such as red seed, are also interested by breeders when edible seeds are of interest (Zhang, 1996b).

Poole et al. (1941) proposed a 3-gene model for the inheritance of seed coat color. The black seed color was dominant, with three recessive genes *r*, *w* and *t* that interact to determine other colors (Poole et al., 1941). The following genotypes were assigned: *RR TT WW* for black seeds, *RR tt WW* for tan, *RR TT ww* for clump, *RR tt ww* for white tan-tip, *rr tt WW* for red, and *rr tt ww* for white pink-tip (McKay, 1936; Poole, 1944). The genotypes *rr TT WW* and *rr TT ww* were not used in the experiments, but it can be inferred that *rr TT WW* corresponds to green seed color (McKay, 1936; Poole, 1944). In addition, there is a *d* gene, which is effective only with the *RR TT WW* genotype, where *RR TT WW DD* is black, *RR TT WW dd* is dotted black (Poole et al., 1941).

The cracked seed coat trait was found to be controlled by a single recessive gene *cr*. It is recessive to the normal uniform seed coat (*Cr*) (El-Hafez et al., 1981). Gusmini et al. (2004) reported a new gene, *eg*, related the egusi seed trait. This trait is found in egusi watermelon, which has fleshy pericarp covering the seeds and looks like the normal type watermelon seed after washing and drying. The *eg* gene found in two plant introduction accessions (PI

490383w and PI 560006) was recessive to the normal seeded cultivars 'Charleston Gray' and 'Calhoun Gray' (*Eg*).

Seed Size

Watermelon seed size is usually measured using seed length, since there is a strong correlation (r = 0.913) between the length and width of the seed (Poole et al., 1941). The seed sizes are classified in 3 types: long seeds with length of 11.5-16.5 mm (or 13 mm in average), medium 7.5-11.5 mm (or 10 mm in average), short 4.5-7.5 mm (or 6 mm in average) (Poole et al., 1941). Besides, smaller seed sizes are also found in watermelon, such as tomato seed (*ts*) with an average length of 4.4 mm.

The early results from Poole et al. (1941) showed that seed size is controlled digenically: medium sized seed is dominant over both short and long, and two recessive genes, *l* and *s*, determine the long and short phenotypes of the seeds, respectively, with *s* epistatic to *l*. The following designations were given to the genotypes corresponding to different seed sizes: *LL SS* (from 'Klondike') for medium length seed, *ll SS* (from 'Peerless') for long seed, and *LL ss* ('Baby Delight'), and *ll ss* (no type line) for short seed (Poole et al., 1941). The *l* gene was confirmed in later experiments (Konsler and Barham, 1958; Shimotsuma, 1936).

Another short size seed was called tiny seed and the gene controlling this phenotype was found non-allelic to *l, s* (Tanaka et al., 1995). *Ti* is from ‘Sweet Princess’ (average seed length 6.5 mm), dominant over medium length seed (*ti*) from 'Fujihikari' (average seed length 8.5 mm) (Tanaka et al., 1995).

In addition, an even smaller seed size (tomato seed), with an average length of 4.4 mm, was reported. The gene *ts*, as from 'Sugar Baby tomato seed mutant', is recessive to long seed (*Ts*) from 'Gn-1' (Zhang et al., 1994; Zhang, 1996a).

Although there have been extensive studies on flesh color and seed traits of watermelon, there is still a lot of research needed to describe the inheritance of fruit quality traits. Therefore, we conducted this experiment with the following objectives: 1) investigate the inheritance of rose flesh color; 2) study the interaction of scarlet red (*Scr*) and coral red (*Y*) flesh color genes; 3) investigate the inheritance of hollow hearted endocarp; 4) investigate the inheritance of tan with black rimed seed coat; 5) confirm the inheritance of some published genes, such as seed size (*l*).

Materials and Methods

Traits and Families

We used six families to investigate the inheritance of watermelon fruit flesh color. Two families were used to study hollow heart resistance, three families for seed coat color, and four families for seed size (Table 2-1). A total of 10 watermelon inbred lines were used in the experiment. We developed seven generations for each family: parent A (P_a), parent B (P_b), F_1, F_1' (F_1 reciprocal), F_2, backcross to Parent A (BC_1P_a) and backcross to parent B (BC_1P_b). Crosses were made in the greenhouses at North Carolina State University in Raleigh, North Carolina. Seeds of the inbred lines used in these experiments were obtained from the

gene mutant collection of the Cucurbit Genetics Cooperative (Curators: T.C. Wehner and S.R. King).

Listed below are the phenotype descriptions of the 10 watermelon cultivars used as parents for the relevant crosses:

'PDS 808' has rose flesh color (Fig. 1). 'Red-N-Sweet' has scarlet flesh color, long seed length and brown with black dotted seed coat (Fig. 2). 'Crimson Sweet' has coral red flesh and medium size seed (Fig. 3). 'Allsweet' has coral red flesh (Fig. 4). 'Black Diamond' has coral red flesh (Fig. 5). 'Tendersweet Orange Flesh' has orange flesh color as indicated in the name, tan with black rimed seed (Fig. 6). 'Charleston Gray' has coral red flesh color, long length seed, and hollow hearted endocarp (Fig. 7). 'King&Queen' has coral red flesh color and medium seed length (Fig. 8). 'Peacock Shipper' has coral red flesh, medium size black seed (Fig. 9). 'Cream of Saskatchewan' has white flesh color and medium size black seed (Fig. 10).

Cultural Practices

Seeds of the seven generations for each family were sown in 72-cell polyethylene flats in the greenhouses at North Carolina State University. An artificial soilless growing medium was used (composed of Canadian sphagnum peat moss, perlite, vermiculite, and processed pine bark). The flats were moistened to capacity after seeding, and held in the greenhouse at 25-30 °C until full emergence (Fig. 11). The transplants were moved to cold frames for acclimation one week before transplanting. The seedlings were transplanted by

hand at the two-true-leaf stage. Missing or damaged transplants were replaced a week after the initial transplanting.

The fields had raised and shaped beds (rows) on 3.1-m centers with single hills 1.2 m apart. The beds were made up with drip irrigation tubes and covered with black polyethylene mulch. The experiment was conducted using horticultural practices recommended by the North Carolina Extension Service (Sanders, 2004). In order to keep families, generations, and plants separate for data collection, each plant was manually trained each week into a spiral shape by turning all the vines in a clockwise circle around the crown until about 70% of the plants in the field had set fruit (Fig. 12). The vine training allowed easy tracing of the fruit to the plant that produced it, giving high accuracy for the system.

One fully-mature fruit was harvested from each plant. Fruit was determined to be ripe by looking for a dried tendril nearest the fruit, a light-colored ground spot, and a dull sound of the fruit when thumped (Maynard, 2001).

Experiment Design

Field experiments were performed in the summer of 2008 at two North Carolina locations: Cunningham Research Station in Kinston, and Horticultural Crops Research Station in Clinton. We used two sets (two locations) as a precautionary measure in case adverse weather, stressful environmental conditions or disease epidemics might damage the plants in a particular set. All seven generations (P_aS_1, P_bS_1, F_1, F_1', F_2, BC_1P_a, BC_1P_b) of each family were planted at each location. For each location, there were 10 plants of P_aS_1, 10 of

P_bS_1, 10 of F_1, 10 of F_1', 30 of BC_1P_a, 30 of BC_1P_b, 100 of F_2. At Kinston each field was 0.4 ha with six rows 85 m long. Each family occupied three rows. At Clinton, each field was 0.4 ha with eight rows 60 m long, and each family occupied four rows.

The data were analyzed by location and then pooled over locations for each tested trait. Segregation analysis and goodness-of-fit tests were performed based on χ^2 testing of the expected segregation ratios for a single gene, using the SAS-STAT statistical package (SAS Institute, Cary, North Carolina) and the SASGene 1.2 statement (Liu et al., 1997). For the families involving a heterozygote with a third phenotype (incompletely dominance) other than the two parents, or 2 loci of genes involved, the calculation was done manually. All χ^2 tests were performed with a 95% confidence level. For the F_1 and F_1', when both had the same phenotype, the F_1 and F_1' were combined as one generation. When different phenotypes were present, they were treated as separate generations.

Gene nomenclature rules for the Cucurbitaceae (Cucurbit Gene List Committee, 1982) were used for naming the new genes discovered.

Results and Discussion

Flesh Color

A family made up of crossing 'PDS 808' (rose flesh) and 'Red-N-Sweet' (scarlet red flesh) was carried out to study the inheritance of rose flesh color (Table 2-1). However, the rose color was very similar to other red flesh colors, and it was difficult to differentiate them. Difficulty in distinguishing may also arise from differences in fruit maturity. Similar

situations were found in the three other families involving coral red flesh color ('Crimson Sweet', 'Allsweet', and 'Charleston Gray') with scarlet red 'Red-N-Sweet'. No useful data was collected for these families. To avoid the difficulties of determine the subtle color differences, the future experiments can be performed by measuring the pigment contents quantitatively. In addition, the fruit should be harvested at the same ripe level to improve the accuracy.

In the family of 'Cream of Saskatchewan' (white fleshed) and 'Red-N-Sweet' (scarlet red), the inheritance of white flesh and scarlet red flesh was studied. In both locations, all F_1 and BC_1P_a had an unexpected flesh color that was not present in either of the parents (red center with yellow margin. Fig. 13), while all F_1', F_2 and BC_1P_b had the same scarlet red flesh as 'Red-N-Sweet'. A Mendelian segregation pattern was not found in the progenies for white and scarlet flesh in this family.

In the family of 'Tendersweet Orange Flesh' (orange flesh) and 'Red-N-Sweet' (scarlet red), the progenies in generations F_1, BC_1P_a, BC_1P_b and F_2 had different flesh colors, but there were still very obviously two classes of color, yellow (or orange) and scarle red (or red), disregarding the different shades. All F_1 fruit were red indicating dominance over orange. The F_2 progenies segregated in 3 scarlet : 1 orange. The goodness-of-fit tests for the F_2, BC_1P_a, and BC_1P_b data were significant (χ^2=0.00, 2.46, 0.00, P-value=0.95, 0.11, 1.00, respectively at Kinston; χ^2=1.00, 1.29, 0.00, P-value=0.31, 0.25, 1.00, respectively at Clinton; χ^2=0.53, 3.63, 0.00, P-value=0.46, 0.056, 1.00, respectively for pooled data) (Table 2-2). The segregation ratios showed that scarlet red flesh color was the major allele dominant over orange flesh color, but the different shades in the progenies indicates there may be modifying genes as well as environmental effects.

Earlier research showed that there was a single locus controlling yellow flesh color with three alleles, *Y* (coral red), y^O (orange), *y* (salmon yellow), with *Y* dominant to y^O and *y*, and y^O dominant to *y* (Porter, 1937; Poole, 1944; Henderson et al., 1989, 1998). Also, scarlet red was found to be a single gene dominant over coral red and was proposed as a different locus, with genotype *ScrScr YY* for scarlet red and *scrscr YY* for coral red was proposed (Gusmini and Wehner, 2006a). But the possibility that *Scr* is another allele of the *Y* locus has not been eliminated. If the two-locus hypothesis proposed by Gusmini and Wehner were correct, the segregation pattern in F_2 progenies of the family 'Tendersweet Orange Flesh' (*ss* y^Oy^O) × 'Red-N-Sweet' (*ScrScr YY*) would be 9 (*Scr_ Y_*): 3 (*Scr_* y^Oy^O): 3 (*scrscr Y_*): 1 (*scrscr* y^Oy^O), which would give 12 scarlet (*Scr_ Y_ and Scr_* y^Oy^O): 3 coral (*scrscr Y_*): 1 orange (*scrscr* y^Oy^O) in F_2 generation. This ratio is not consistent with the observation in our experiment (3 scarlet red: 1 orange). The alternative hypothesis that *Scr* is another allele at *Y* locus dominant over orange flesh would give a segregation ratio 3 scarlet red: 1 orange in F_2 progenies, which is consistent with our observations. So, the second hypothesis is supported by this experiment. And a corresponding modification of gene names is necessary as follows: *Scr* is renamed as Y^{Scr}, *Y* as y^{Crl}. Four alleles Y^{Scr} (scarlet red), y^{Crl} (coral red), y^O (orange), *y* (salmon yellow) are in the same locus controlling the flesh color.

Hollow Heart

Two families were investigated for the inheritance of the hollow hearted fruit. These two families include 'Tendersweet Orange Flesh' (hollow heart susceptible) × 'Red-N-Sweet' (hollow heart resistant) and 'Peacock Shipper' (hollow heart resistant) × 'Charleston Gray'

(hollow heart susceptible). No Mendelian inheritance was found for the trait in either family (Table 2-1).

Seed Coat Color

Three families were used to investigate seed coat color. These families include 'Red-N-Sweet' (brown with black dots seed coat) × 'King&Queen' (black seed coat), 'Cream of Saskatchewan' (black seed coat) × 'Red-N-Sweet', and 'Tendersweet Orange Flesh' (tan with black rim seed coat) × 'Red-N-Sweet' (brown with black dots seed coat) (Table 2-1).

In the family of 'Red-N-Sweet' (brown with black dots seed coat) × 'King&Queen' (black seed coat), all F_1 had black seed coat, which indicated that the black seed coat is dominant over the brown with black dots. F_2 segregated into 3 black : 1 brown with black dots. BC_1P_a had equal black seed and brown seed with dots. BC_1P_b had black seed. The goodness-of-fit tests for the F_2, BC_1P_a, and BC_1P_b data were significant (χ^2=0.82, 0.15, 0.00, P-value=0.36, 0.69, 1.00, respectively at Kinston; χ^2=0.09, 0.69, 0.00, P-value=0.75, 0.40, 1.00, respectively at Clinton; χ^2=0.74, 0.03, 0.00, P-value=0.38, 0.87, 1.00, respectively for pooled data) (Table 2-3). The segregation ratios in F_2, BC_1P_a and BC_1P_b suggest that the black seed coat is single gene dominant over brown with black dots seed coat. Based on literatures, we can conclude that the brown with black dots seed coat color in our experiment corresponds to the seed coat color described by Poole et al. (1941) as stippled surface with numerous black dots and visible tannish or reddish undercoat (also dotted black). Therefore, the gene acting in our experiment is the *d* gene. 'Red-N-Sweet' with brown with black dots seed coat has genotype *RR TT WW dd.* 'King&Queen' with black seed coat has genotype *RR*

TT WW DD (Table 2-7). However, in the family of 'Cream of Saskatchewan' (black seed coat) × 'Red-N-Sweet' (brown with black dots), the inheritance of brown with black dots seed coat did not fit this model. All F_1 and BC_1P_a in this family had black seed coat, all F_1', F_2 and BC_1P_b had brown with black dots seed coat. We were not able to explain this segregation pattern.

The third family of 'Tendersweet Orange Flesh' (tan with black rim seed coat) × 'Red-N-Sweet' (brown with black dots), showed that two loci were involved. All F_1 had black seed coat, and the F_2 segregated into four seed coat colors, black, tan with black rim, brown with black dots, and tan with black tip, with a ratio that fit 9:3:3:1. All BC_1P_a segregated into black seed coat and tan with rim seed coat, and all BC_1P_b segregated into black and brown with black dots. The goodness-of-fit tests for the F_2, BC_1P_a, and BC_1P_b data were significant (χ^2=2.05, 0.38, 0.33, P-value=0.56, 0.54, 0.57, respectively at Kinston; χ^2=1.85, 1.79, 0.86, P-value=0.60, 0.18, 0.35, respectively at Clinton; χ^2=4.01, 1.92, 1.14, P-value=0.26, 0.17, 0.29, respectively for pooled data) (Table 2-4.). The BC_1P_a, BC_1P_b, F_2 data showed that two genes are involved in this family. After comparing to the earlier studies, the following genotypes are proposed that can explain the segregation ratio in our experiment: *RR tt WW DD* for 'Tendersweet Orange Flesh' (tan with black rim seed coat), *RR TT WW dd for* 'Red-N-Sweet' (brown with black dots), *RR T_ WW D_* for the F_1 generation (black seed coat), *RR tt WW dd* for the tan with black tip seed coat in F_2 progenies (Table 2-7). The *t* and *d* genes are the two genes involved in this family. From this experiment, we can also conclude that the tan seed coat color (*RR tt WW*) described by the earlier researchers actually includes two classes: tan with black rim seed coat (*RR tt WW DD*) and tan with black tip (*RR tt WW dd*).

The *d* gene was considered as modifying factor to the black seed color and thought to be only effective together with the *RR TT WW* genotype (*RR TT WW DD* is black, and *RR TT WW dd* is dotted black) (Poole et al., 1941). The *d* gene acts more like a separate gene having equal role as *r t w* in controlling seed coat color.

Seed Size

Four families were investigated for the inheritance of seed size. These families include 'Peacock Shipper' (medium length seed) × 'Charleston Gray' (long seed), 'Red-N-Sweet' (long seed) × 'Crimson Sweet' (medium length seed), 'Cream of Saskatchewan' (medium length seed) × 'Red-N-Sweet' (long seed), and 'Red-N-Sweet' (long seed) × 'King&Queen' (medium length seed) (Table 2-1).

The first two families, 'Peacock Shipper' (medium length seed) × 'Charleston Gray' (long seed) and 'Red-N-Sweet' (long seed) × 'Crimson Sweet' (medium length seed), confirmed that medium length seed (*LL SS*)) is dominant over long seed (*ll SS*). All F_1 had medium length seed and the goodness-of-fit tests for the F_2, BC_1P_a, and BC_1P_b data were significant. For 'Peacock Shipper' and 'Charleston Gray', (for Kinston data, χ^2=0.35, 0.00, 0.89, P-value=0.55, 1.00, 0.34, respectively; for Clinton data, χ^2=0.95, 0.00, 1.00, P-value=0.32, 1.00, 0.31, respectively; and for pooled data χ^2=0.05, 0.00, 0.00, P-value=0.82, 1.00, 1.00, respectively) (Table 2-5). Significant χ^2 for F_2, BC_1P_a, and BC_1P_b data are also observed for 'Red-N-Sweet' × 'Crimson Sweet' (χ^2=2.05, 0.38, 0.00, P-value=0.56, 0.54, 1.00, respectively at Kinston; χ^2=0.87, 0.20, 0.00, P-value=0.28, 0.41, 1.00, respectively at Clinton; χ^2=2.00, 0.09, 0.00, P-value=0.15, 0.76, 1.00, respectively for pooled data) (Table 2-6).

However, in the other two families that also involved a long seeded cultivar and a medium length seeded cultivar, i.e., 'Cream of Saskatchewan' (medium length seed) × 'Red-N-Sweet' and 'Red-N-Sweet' × 'King&Queen' (medium length seed), we did not observe a Mendelian inheritance pattern.

Conclusions

For flesh color, an allelism test clarified the relationship of the genes *Scr* and *Y*. *Scr* was found to be an allele at the *y* locus. The complete series is now, Y^{Scr} (scarlet red from 'Red-N-Sweet'), y^{Crl} (coral red from 'Angeleno Black Seeded'), y^{O} (orange flesh from 'Tendersweet Orange Flesh'), and *y* (salmon yellow flesh from 'Golden Honey'). Y^{Scr} is dominant to y^{Crl}, y^{O} and *y*.

No Mendelian inheritance was observed in the families involving hollow heart. However, the *l* gene was confirmed in two families, 'Peacock Shipper' (medium length seed) × 'Charleston Gray' (long seed) and 'Red-N-Sweet' (long seed) × 'Crimson Sweet' (medium length seed), where medium length seed (*LL SS*) was dominant over long seed (*ll SS*).

The *d* gene is confirmed in the family of 'Red-N-Sweet' (brown with black dots seed coat) × 'King&Queen' (black seed coat); The *t* and *d* genes are confirmed in the family of 'Tendersweet Orange Flesh' (tan with black rim seed coat) × 'Red-N-Sweet' (brown with black dots). We also conclude that the tan seed coat color (*RR tt WW*) described by the earlier researchers includes two classes: tan with black rim seed coat (*RR tt WW DD*) and tan with black tip (*RR tt WW dd*). The *d* gene acts as a separate gene other than a modifying gene only

effective together with the *RR TT WW* genotype (*RR TT WW DD* is black, and *RR TT WW dd* is dotted black) and has equal role as *r t w* in controlling seed coat color. The genotype is *RR tt WW DD* for 'Tendersweet Orange Flesh' (tan with black rim seed coat), *RR TT WW dd* for 'Red-N-Sweet' (brown with black dots), *RR TT WW DD* for 'King&Queen' (black seed coat), and *RR tt WW dd* for the tan with black tip seed coat (no type line) (Table 2-7).

Understanding of the inheritance of fruit flesh color, seed coat color, seed size, and other fruit traits is an integral part of expanding the current knowledge of watermelon genes. Such knowledge is valuable for breeding watermelon cultivars with desired fruit traits. For example, genetic information of flesh colors, such as scarlet red, is helpful for breeding dark red fleshed cultivars with high level of beneficial pigments. Knowledge of the genes that control seed coat color and size is crucial for breeding different fruit types for different market, for example, middle size black and brown seeded cultivars are preferred in the market, small-seeded cultivars are used as parents for the production of triploid seedless cultivars, large-seeded cultivars with uncommon seed coat color are favored in the confectionary industry.

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Table 2-1. Families and traits analyzed for qualitative inheritance of flesh color in watermelon fruit during summer 2008 in Clinton and Kinston, North Carolina.

	Trait of interest	
Families	Phenotype	Gene
Study of new genes		
Flesh Color		
'PDS 808' × 'Red-N-Sweet'	Rose flesh color vs. scarlet red	–[a]
'Cream of Saskatchewan' × 'Red-N-Sweet'	White vs. scarlet red	–[a]
Hollow heart		
'Tendersweet OF' × 'Red-N-Sweet'	Hollow heart susceptible vs. resistant	–[a]
'Peacock Shipper' × 'Charleston Gray'	Hollow heart resistant vs. susceptible	–[a]
Verification of known genes		
Flesh color		
'Tendersweet OF' × 'Red-N-Sweet'	Scarlet red dominant over Orange	$Scr=Y^{Scr}$
'Red-N-Sweet' × 'Crimson Sweet'	Scarlet vs. coral	–[a]
'Red-N-Sweet' × 'Allsweet'	Scarlet vs. coral	–[a]
'Red-N-Sweet' × 'Charleston Gray'	Scarlet vs. coral	–[a]
Seed coat color		
'Red-N-Sweet' × 'King&Queen'	Dotted vs. black	*d*
'Cream of Saskatchewan' × 'Red-N-Sweet'	Black vs. brown with black dots	–[a]
'Tendersweet OF' × 'Red-N-Sweet'	Tan with black rim vs. brown with black dots	*t; d*
Seed size		
'Red-N-Sweet' × 'Crimson Sweet'	Long length seed vs. medium	*l*
'Peacock Shipper' × 'Charleston Gray'	Medium length seed vs. large	*l*
'Cream of Saskatchewan' × 'Red-N-Sweet'	Medium length seed vs. long	–[a]
'Red-N-Sweet' × 'King&Queen'	Long length seed vs. medium	–[a]

a No gene was found or verified.

Table 2-2. Single locus goodness-of-fit-test for flesh color in watermelon in family 'Tendersweet Orange Flesh' (orange flesh) × 'Red-N-Sweet' (scarlet red flesh).

Location/ Generation	Total no.	Scarlet red[b]	Orange flesh[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	10	0				
P_bS_1	10	5	0	5				
F_1	20	12	0	8				
F_2	100	64	21	15	3:1	0.00	1	0.95
BC_1P_a	30	17	9	4	1:1	2.46	1	0.11
BC_1P_b	30	27	0	3	1:0	0.00	1	1.00
Clinton[a]								
P_aS_1	10	0	10	0				
P_bS_1	10	8	0	2				
F_1	20	20	0	0				
F_2	100	60	15	25	3:1	1.00	1	0.31
BC_1P_a	30	17	11	2	1:1	1.29	1	0.25
BC_1P_b	30	29	0	1	1:0	0.00	1	1.00
Pooled[a]								
P_aS_1	20	0	20	0				
P_bS_1	20	13	0	7				
F_1	40	32	0	8				
F_2	200	124	36	40	3:1	0.53	1	0.46
BC_1P_a	60	34	20	6	1:1	3.63	1	0.056
BC_1P_b	60	56	0	4	1:0	0.00	1	1.00

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Scarlet red flesh color was dominant and P_b was the carrier.

c Orange flesh color was recessive and P_a was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity $\chi^2_{(0.05;\,1)}$

g P-value (Probability) >.05 was accepted as Single Locus.

Table 2-3. Single locus goodness-of-fit-test for stripe in watermelon in family 'Red-N-Sweet' (Brown with black dots; also black dotted) × 'King&Queen' (Black).

Location/ Generation	Total no.	Black[b]	Black dotted[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	10	0				
P_bS_1	10	10	0	0				
F_1	20	20	0	0				
F_2	100	72	19	9	3:1	0.82	1	0.36
BC_1P_a	30	14	12	4	1:1	0.15	1	0.69
BC_1P_b	30	29	0	1	1:0	0.00	1	1.00
Clinton[a]								
P_aS_1	10	0	6	4				
P_bS_1	10	5	0	5				
F_1	20	13	0	7				
F_2	100	68	21	11	3:1	0.09	1	0.75
BC_1P_a	30	5	8	17	1:1	0.69	1	0.40
BC_1P_b	30	27	0	3	1:0	0.00	1	1.00
Pooled[a]								
P_aS_1	20	0	16	4				
P_bS_1	20	15	0	5				
F_1	40	33	0	7				
F_2	200	140	40	20	3:1	0.74	1	0.38
BC_1P_a	60	19	20	21	1:1	0.03	1	0.87
BC_1P_b	60	56	0	4	1:0	0.00	1	1.00

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Black seed coat was dominant and P_b was the carrier.

c Black dotted seed coat was recessive and P_a was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 2-4. Two loci goodness-of-fit-test for seed coat color in watermelon in family 'Tendersweet Orange Flesh' (Tan with black rim) × 'Red-N-Sweet' (Brown with black dots; also black dotted).

Location/ Generation	Total no.	Black[b]	Tan with black rim[c]	Black dotted[d]	Tan with black tip[e]	Expected ratio[f]	Chi square[g]	df	Prob.[h]
Kinston[a]									
P_aS_1	10	0	10	0	0				
P_bS_1	10	0	0	5	0				
F_1	20	14	0	0	0				
F_2	100	47	14	20	2	9:3:3:1	2.05	3	0.56
BC_1P_a	30	14	11	0	1	1:1:0:0	0.38	1	0.54
BC_1P_b	30	12	0	15	0	1:0:1:0	0.33	1	0.57
Clinton[a]									
P_aS_1	10	0	10	0	0				
P_bS_1	10	0	0	8	0				
F_1	20	20	0	0	0				
F_2	100	36	14	19	5	9:3:3:1	1.85	3	0.60
BC_1P_a	30	17	10	0	1	1:1:0:0	1.79	1	0.18
BC_1P_b	30	12	0	17	0	1:0:1:0	0.86	1	0.35
Pooled[a]									
P_aS_1	20	0	20	0	0				
P_bS_1	20	0	0	13	0				
F_1	40	14	0	0	0				
F_2	200	83	28	39	7	9:3:3:1	4.01	3	0.26
BC_1P_a	60	31	21	0	2	1:1:0:0	1.92	1	0.17
BC_1P_b	60	24	0	32	0	1:0:1:0	1.14	1	0.29

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b The double dominant genotype *T_ D_* has black seed coat.
c Genotype *tt D_* has tan seed with black rim and Pa is the carrier.
d Genotype *T_ dd* has black dotted seed coat and Pb is the carrier.
e The double recessive genotype *tt dd* has tan seed with black tip.
f Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
g Heterogeneity χ^2 (0.05; 1)
h P-value (Probability) >.05 was accepted as Single Locus.

Table 2-5. Single locus goodness-of-fit-test for seed size in watermelon in family 'Peacock Shipper' (Medium) × 'Charleston Gray' (Large).

Location/ Generation	Total no.	Medium[b]	Large[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	7	0	3				
P_bS_1	10	0	10	0				
F_1	20	20	0	0				
F_2	100	68	26	6	3:1	0.35	1	0.55
BC_1P_a	30	30	0	0	1:0	0.00	1	1.00
BC_1P_b	30	7	11	12	1:1	0.89	1	0.34
Clinton[a]								
P_aS_1	10	7	0	3				
P_bS_1	10	0	7	3				
F_1	20	17	0	3				
F_2	100	63	16	21	3:1	0.95	1	0.32
BC_1P_a	30	23	0	7	1:0	0.00	1	1.00
BC_1P_b	30	10	6	14	1:1	1.00	1	0.31
Pooled[a]								
P_aS_1	20	14	0	6				
P_bS_1	20	0	17	3				
F_1	40	37	0	3				
F_2	200	131	42	27	3:1	0.05	1	0.82
BC_1P_a	60	53	0	7	1:0	0.00	1	1.00
BC_1P_b	60	17	17	26	1:1	0.00	1	1.00

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b Medium seed size was dominant and P_a was the carrier.
c Large seed size was recessive and P_b was the carrier.
d Some plants were missing or damaged.
e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
f Heterogeneity χ^2 (0.05; 1)
g P-value (Probability) >.05 was accepted as Single Locus.

Table 2-6. Single locus goodness-of-fit-test for seed size in watermelon in family 'Red-N-Sweet' (Large) × 'Crimson Sweet' (Medium).

Location/ Generation	Total no.	Medium[b]	Large[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	9	1				
P_bS_1	10	7	0	3				
F_1	20	17	0	3				
F_2	100	52	13	35	3:1	0.87	1	0.35
BC_1P_a	30	11	9	10	1:1	0.20	1	0.65
BC_1P_b	30	23	0	7	1:0	0.00	1	1.00
Clinton[a]								
P_aS_1	10	0	10	0				
P_bS_1	10	8	0	2				
F_1	20	17	0	3				
F_2	100	68	17	15	3:1	1.13	1	0.28
BC_1P_a	30	10	14	6	1:1	0.67	1	0.41
BC_1P_b	30	21	0	9	1:0	0.00	1	1.00
Pooled[a]								
P_aS_1	20	0	19	1				
P_bS_1	20	15	0	5				
F_1	40	34	0	6				
F_2	200	120	30	50	3:1	2.00	1	0.15
BC_1P_a	60	21	23	16	1:1	0.09	1	0.76
BC_1P_b	60	44	0	16	1:0	0.00	1	1.00

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b Medium seed size was dominant and P_b was the carrier.
c Large seed size was recessive and P_a was the carrier.
d Some plants were missing or damaged.
e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
f Heterogeneity χ^2 (0.05; 1)
g P-value (Probability) >.05 was accepted as Single Locus.

Table 2-7. Suggested genotypes and corresponding phenotypes for the genes controlling seed coat color in watermelon.

Genotype suggested	Phenotype	Type line
RR TT WW dd	Black dotted with a brown undercoat	Red-N-Sweet
RR TT WW DD	Black	King&Queen
RR tt WW DD	Tan with black rim	Tendersweet Orange Flesh
RR tt WW dd	Tan with black tip	??[a]

a unknown type line based on available literature.

CHAPTER THREE

QUALITATIVE INHERITANCE OF EXTERIOR FRUIT CHARACTERS IN WATERMELON

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Introduction

Watermelon [*Citrullus lanatus* (Thunb.) Matsumura & Nakai] is a major annual vegetable crop cultivated in warm regions worldwide. Watermelon fruit can be severed as a dessert, cooked as vegetable, and used in confectionary. Watermelon counts for 6.8% of vegetable production area around the world (FAO, 2002; Guner and Wehner, 2004). In the U.S., the Agricultural Marketing Resource Center recorded watermelon production at 4.29 billion pounds in 2007 and 4.3 billion pounds with a $492 million value for the fresh market in 2008. The top five states in U.S. watermelon production, accounting for more than 75% of the total production, were Georgia, Florida, Texas, California and Arizona (www.agmrc.org).

The genome size of watermelon is relatively small; the whole genome size of watermelon is $4.2x10^8$ bp which consists of 22 chromosomes for a diploid (Arumuganathan and Earle, 1991). Extensive genetic studies and breeding experiments since the 1930s have identified more than one hundred genes. Those genes are related to phenotypes in seed and seedling, vine, flower, fruit, and resistance (Wehner, 2008a). A comprehensive list of those genes can be found in recent reviews (Guner and Wehner, 2004; Wehner, 2008a).

The rind of watermelon fruit can be striped or solid colored. The solid rind patterns include solid dark green as in 'Black Diamond', solid medium green as in 'Peacock Shipper', solid light green as in 'King&Queen', gray (medium green reticulations on a light green background) as in 'Charleston Gray', or golden as in 'Royal Golden' (Guner and Wehner, 2003, 2004; Gusmini and Wehner, 2006a, 2006b).

The stripe patterns of watermelon can be characterized using different stripe widths (narrow, medium, wide), stripe colors, and background colors (dark green, medium green, light green). The phenotype of super narrow striped pattern on watermelon is also called lined or penciled. Since the stripe patterns are two sets of alternating light and dark colored stripes on the rind, there might be some ambiguity deciding which set are the "stripes". Here, we refer to the darker colored set as "stripes". This definition is consistent with the observation that the dark areas always cover the vascular boundaries underneath the watermelon rind (Korn, 2007). Although the developmental basis of the longitudinal stripe pattern in watermelon has not been studied in detail, a clonal mosaic model was proposed (Korn, 2007) based on observational evidence. The vascular bundles running beneath the dark green reticular stripes of 'Ruby Red' are in the same direction as stripes in a young (5-mm long) fruit. This phenomenon shows the association between the subsurface vascular bundles and the stripes. This association is also found on watermelon pedicels. Korn suggested that the vascular bundles are a pre-pattern determining the stripes on the fruit surface. The reticulations in the stripe composed by sets of polygons give the basis of the clonal mosaic model. This clonal mosaic model hypothesizes that an initial cell gives rise to a clone of various types of cells (the polygon) with dark green border, light green center, and medium green region between the dark green and light green. This model explains the formation of the multiple-celled polygons that compose the darker green stripes with reticulations on the fruit of 'Ruby Red'.

Besides being striped or solid colored, there are some additional modifications to watermelon rind pattern, such as the netted reticulations within stripes or on the whole fruit

surface, mottling (irregularly-shaped light color) on the otherwise solid dark colored background, different colored ground spots, furrowed fruit surface, and explosive rind. The reticulations are found on many cultivars, including some light green cultivars such as 'Charleston Gray' (the reticulations are more intensive near the surface of the vascular bundle and less intensive on the areas between vascular bundles). The reticulations are also found on the medium green stripes of some striped cultivars, such as 'Ruby Red' (described as the clonal mosaic model) (Korn, 2007), cultivar 'China 23' (which is the type line for the *p* gene) (Weetman, 1937), cultivar 'Crimson Sweet' (which is the medium wide striped cultivar in our experiment), and in the surrounding area of the ground spot of the otherwise solid dark green fruit such as 'Black Diamond'. It is possible that the dark green cultivar 'Black Diamond' is actually reticulated, but the reticulations are not visible due to the dark rind color.

The rind pattern of watermelon fruit is an important marketing factor since certain consumer groups may have particular preference of rind pattern. Striped rind pattern is usually preferred over some other rind patterns such as gray. Fruit rind pattern appears to be related to resistance to the pathogen and light rind colored cultivars are most susceptible and dark rind color cultivars are less susceptible. Striped rind cultivars appear to be intermediate in their resistance (Wehner, 2008b). Rind toughness is a big consideration for postharvest handling and shipping. Other external rind characters, such as furrowing and fruit shape, may also to a certain extent affect the customer acceptance of the fruit. Extensive research has explored over 100 genes in watermelon and the genes controlling watermelon external fruit traits are reviewed here.

Early studies by Porter (1937) and Weetman (1937) have identified a series of three alleles at the *g* locus that produce solid dark green (*G*), striped (g^s), or gray (*g*) rind pattern. Solid dark green (*G*) is dominant to striped (g^s) and gray (*g*). Striped rind pattern (g^s) is recessive to solid dark green (*G*) but dominant to gray (*g*). Here *G* is from 'California Klondike', *g* is from 'Thurmond Gray', and g^s is from 'Golden Honey'. However, there is no report of further investigations on the inheritance of the different stripe widths, stripe colors, and background colors. Therefore, it is interesting to conduct more inheritance research on such traits and provide more detailed genetic information.

The gene *ins* from 'Navajo Sweet' (*Ins* from 'Crimson Sweet') produces an interesting genotype having intermittent stripes, starting with narrow dark green stripes at the peduncle end of the fruit and becoming irregular in the middle and nearly absent at the blossom end of the fruit (Gusmini and Wehner, 2006).

Narrow (pencil-width) stripe on a light background on the rind of 'Japan 6' is called penciled (*p*) phenotype. It was found to be recessive to the netted (medium green colored network) (*P*) rind pattern of 'China 23' when disregarding the dark stripes on the light background (Weetman, 1937).

Another rind gene described by Weetman is the *m* gene from 'Long Iowa Belle' for the particular randomly-distributed and irregularly-shaped greenish-white mottling pattern. The mottling pattern differs from the rest of the fruit not only in color but also in the character in the epidermis. This special phenotype was called the 'Iowa Belle' (IB) phenotype by Weetman. It was recessive to the non-mottling trait of 'Japan 4' and 'China 23' when disregarding the stripes on 'China 23' (Weetman, 1937). Since many of the type lines used by

Weetman are not available, it is impossible to investigate the *p* and *m* genes (Weetman, 1937; Poole, 1944).

Cultivar 'Moon and Stars' has large yellow spots (moons) and small yellow spots (stars) over a dark green background, which occurs on the fruit rind as well as the foliage (cotyledons, true leaves). The trait is controlled by the gene (*Sp*) which is dominant to the uniform green color (*sp*) of 'Allsweet' (Poole, 1944; Rhodes, 1986).

The gene, *Yb*, produces the yellow belly trait on the fruit of 'Black Diamond Yellow Belly'. This cultivar has a dark yellow to orange colored ground spot on a solid dark green fruit and is dominant to the usual creamy white ground spot (*yb*) of 'Black Diamond' (Gusmini and Wehner, 2006a).

The golden gene, *go*, produces a golden yellow color of mature fruit as well as on the older leaves of 'Royal Golden'. This gene is recessive to the normal green leaves and fruit (*Go*) of 'NC 34-9-1' and 'NC 34-2-1' (Barham, 1956; Robinson et al., 1976).

The watermelon fruit with furrowed parallel indentations (*f*) was found to be recessive to the smooth surfaced fruit (*F*). Since type lines were not given in the original reference, 'Stone Mountain' or 'Black Diamond' was recommend as the type line for *f*, and 'Mickylee' for *F* (Poole, 1944; Wehner, 2008a).

The gene, *e*, from 'California Klondike' produces an explosive rind that is tender and bursting when cut. It is recessive to tough rind (*E*) from 'Thurmond Gray' and 'Golden Honey' (Poole, 1944). The explosive character was found to be not correlated with fruit rind thickness, but with rind cell wall thickness (Kenny and Porter, 1941).

With regard to fruit shape, watermelon fruit can be classified as round, oblong, and elongate, based on the length to width ratio. Weetman (1937) investigated the inheritance of fruit shape in the families of 'Long Iowa Belle' (elongate fruit) × 'Round Iowa Belle' and 'China 23' (both had round fruit), and 'Long Iowa Belle' × 'Japan 6' and 'Japan 4' (both had near-round shape). He found that elongate fruit shape (*OO*) was incompletely dominant to round fruit shape (*oo*) and the heterozygote (*Oo*) was intermediate oblong shaped (semi long shaped) (Weetman, 1937). Poole and Grimball (1945) confirmed this gene in the families of 'Peerless' × 'Baby Delight', and 'Northern Sweet' × 'Dove'.

The objectives of this experiment were to study the inheritance of exterior fruit traits of watermelon that have not been investigated, such as stripe width, solid colored rind, stripe color, rind reticulation, fruit shape, and blossom end shape (concave vs. convex). We were also interested in confirming some of the known genes, such as the *o* gene for fruit shape (elongate vs. round), and the *f* gene for fruit surface furrowing.

Materials and Methods

A total of 10 watermelon inbred cultivars or lines were used in the families. We developed seven generations for each family: parent A (P_a), parent B (P_b), F_1, F_1' (F_1 reciprocal), F_2, backcross to Parent A (BC_1P_a) and backcross to parent B (BC_1P_b). Seeds of the inbred lines used in these experiments were obtained from the gene mutant collection of the Cucurbit Genetics Cooperative (Curators: T.C. Wehner and S.R. King).

Listed below are the descriptions of the 10 watermelon inbred lines used as parents for the relevant families: breeding line 'PDS 808' has medium wide medium green stripes with unclear margins on a light green background (Fig. 1); 'Red-N-Sweet' has narrow dark green stripes with clear margins on a light green background, near-round fruit with concave blossom end (Fig. 2); 'Crimson Sweet' has medium wide medium green stripes with unclear margins on a light green background, near-round fruit with thick rind, smooth fruit surface (Fig. 3); 'Allsweet' has wide medium green stripes with unclear margins on a light green background, convex blossom end, elongate fruit, and smooth fruit surface (Fig. 4); 'Black Diamond' has solid dark rind, concave blossom end and furrowed fruit surface. (Fig. 5); 'Tendersweet Orange Flesh' has wide medium green stripes with unclear margins on a light green background, and oblong fruit. (Fig. 6); 'Charleston Gray' has gray rind (light green with reticulations), long seed, convex blossom end, elongate fruit shape, smooth fruit surface (Fig. 7); 'King&Queen' has light green rind with inconspicuous light green stripe (it is considered to be solid light green), round fruit (Fig. 8); 'Peacock Shipper' has solid medium dark green, concave blossom end, oblong fruit shape and furrowed fruit surface (Fig. 9); 'Cream of Saskatchewan' has narrow dark green stripes on a light green background (Fig. 10).

Cultural Practices

Seeds of the seven generations for each family were sown in 72-cell polyethylene flats in the greenhouses at North Carolina State University. An artificial soilless growing medium used for seed germination is composed of Canadian sphagnum peat moss, perlite, vermiculite, and processed pine bark. The flats were moistened to capacity after seeding and

held in the greenhouse at constant temperature (25-30 °C) until full emergence of seedlings (Fig. 11). The transplants were moved to open cold frames for acclimation one week before transplanting. The seedlings were transplanted by hand at the two-true-leaf stage. Missing or damaged transplants were replaced one week after the initial transplanting.

In the field, raised beds with drip irrigation tubes were covered with black polyethylene mulch. The experiment was conducted using horticultural practices recommended by the North Carolina Extension Service (Sanders, 2004). In order to keep plants separate for data collection, each was trained weekly into a spiral shape by turning all the vines in a clockwise circle around the crown until fruit set (Fig. 12). The vine training allowed easy tracing of the fruit to the plant that produced it.

One fully mature fruit was harvested from each plant. Fruit were determined to be ripe by looking for a dried tendril nearest the fruit, a light-colored ground spot, and a dull sound of the fruit when thumped (hit with a flat hand on the side of the fruit) (Maynard, 2001). Fruit traits were evaluated and recorded in the field.

Experiment Design and Data Analysis

Field experiments were performed in the summer of 2008 at two North Carolina locations: Cunningham Research Station in Kinston and Horticultural Crops Research Station in Clinton. We used two sets (two locations) as a precautionary measure in case of adverse weather, environmental stress, or disease epidemics that might destroy the crop. All six (or seven if F_1' were available) generations of each family were planted at each location. For each location, there were 10 plants of P_aS_1, 10 of P_bS_1, 10 of F_1, 10 of F_1', 30 of BC_1P_a, 30 of

BC_1P_b, 100 of F_2. At Kinston each field was 0.4 ha with six rows 85 m long and each family occupied three rows. At Clinton, each field was 0.4 ha with eight rows 60 m long, and each family occupied four rows. The fields had raised and shaped beds (rows) on 3.1-m centers with single hills 1.2 m apart.

The data were analyzed by location for each tested trait and then pooled over locations. Segregation analysis and goodness-of-fit tests were performed based on χ^2 testing of the expected segregation ratios for a single gene, using the SAS-STAT statistical package (SAS Institute, Cary, North Carolina) and the SASGene 1.2 statement (Liu et al., 1997). The calculations were done manually for the families involving a heterozygote with a third phenotype (incomplete dominance) other than the two parents, or when 2 gene loci were involved. All χ^2 tests were performed with a 95% confidence level. For the generations F_1 and F_1', when both had the same phenotype, F_1 and F_1' were combined as a single generation. When the F_1 differed from the reciprocal, they are treated as separate generations.

Gene nomenclature rules for the Cucurbitaceae family (Cucurbit Gene List Committee, 1982) were applied for naming the proposed new genes.

Results and Discussion

Fruit Stripe Width

Four families made up by crossing parents of different stripe widths were studied for the inheritance of stripe width, including 1) 'PDS 808' × 'Red-N-Sweet' (medium wide stripe versus narrow stripe); 2) 'Red-N-Sweet' × 'Crimson Sweet' (narrow stripe versus medium

wide stripe); 3) 'Red-N-Sweet' × 'Allsweet' (narrow stripe versus wide stripe); and 4) 'Tendersweet Orange Flesh' × 'Red-N-Sweet' (wide stripe versus narrow stripe). Seven families made up by crossing a striped parent and a solid parent were studied, including 1) 'Red-N-Sweet' × 'King&Queen' (narrow stripe versus solid light green); 2) 'Red-N-Sweet' × 'Charleston Gray' (narrow stripe versus gray); 3) 'Crimson Sweet' × 'Peacock Shipper' (medium wide stripe versus solid medium green); 4) 'Red-N-Sweet' × 'Black Diamond' (narrow stripe versus solid dark green); 5) 'Crimson Sweet' × 'King&Queen' (medium wide stripe versus solid light green); 6) 'Allsweet' × 'King&Queen' (wide stripe versus solid light green); and 7) 'Allsweet' × 'Black Diamond' (wide stripe versus solid dark green). Three families made up by crossing two solid green parents were studied, including 1) 'Peacock Shipper' × 'Charleston Gray' (solid medium green versus gray); 2) 'King&Queen' × 'Peacock Shipper' (solid light green versus solid medium green); and 3) 'Black Diamond' × 'Charleston Gray' (solid dark green versus gray) (Table 3-1).

In the family 'Red-N-Sweet' (narrow striped) × 'Crimson Sweet' (medium wide striped), all F_1 fruit had medium width stripes, which indicates the medium width stripe is dominant to narrow stripe. F_2 progenies segregated into medium width stripe and narrow stripe with a ratio 3:1. BC_1P_a segregated into medium width stripe and narrow stripe with a ratio 1:1. And all BC_1P_b were medium width stripe (table 3-2). The segregation ratio in the F_2 showed that the medium wide stripe was controlled by a single gene dominant over narrow stripe, and the BC_1P_a, and BC_1P_b data confirmed it.

However, in the family of 'PDS 808' (medium wide striped) × 'Red-N-Sweet' (narrow striped), no Mendelian pattern of inheritance was observed. All F_1, F_1', BC_1P_a, BC_1P_b, F_2 fruit had stripe width similar to 'Red-N-Sweet'.

In the family of 'Red-N-Sweet' (narrow striped) × 'Allsweet' (wide striped), all F_1 fruit were wide striped, indicating that wide stripe is dominant over narrow stripe. F_2 progenies in this family segregated into 3 wide stripe : 1 narrow stripe and BC_1P_a progenies had a 1:1 ratio of wide stripe vs. narrow stripe. All BC_1P_b were wide striped (Table 3-3). The 3:1 segregation ratio in the F_2 suggests that the wide stripe of 'Allsweet' is single gene dominant over the narrow stripe of 'Red-N-Sweet'. The BC_1P_a and BC_1P_b data further confirmed this hypothesis.

In another family also made up by crossing a wide striped parent with a narrow striped parent, 'Tendersweet Orange Flesh' (wide striped) × 'Red-N-Sweet' (narrow striped), the above hypothesis that wide is single gene dominant over narrow was confirmed again(Table 3-4). It is possible that the gene producing wide stripe in 'Allsweet' is the same gene as in 'Tendersweet Orange Flesh'. However, an allelism test would be necessary to confirm it.

The first two families involving a striped parent and a solid green parent are: 'Red-N-Sweet' × 'King&Queen' (light green rind with inconspicuous light narrow stripes, appearing solid light green) (Fig. 13) and 'Red-N-Sweet' × 'Charleston Gray' (narrow stripe versus gray). In the first family, all F_1 fruit had narrow stripes. That indicates narrow stripe was dominant over light green rind with inconspicuous light narrow stripes. (Table 3-5). The 3:1 (narrow : solid light green) segregation ratio in the F_2 suggests that the narrow stripe of 'Red-N-Sweet'

is a single gene, dominant over solid light green in 'King&Queen', and the BC_1P_a (all were narrow), and BC_1P_b (1 narrow : 1 solid light green) data confirmed it. Many would consider the rind pattern of 'King&Queen' to be solid light green, since the narrow light stripes on the fruit are inconspicuous and, on some individuals, are too faint to be seen. An allelism test would be necessary to determine whether the gene for solid medium green rind is an allele at the same locus of the gene producing wide, medium and narrow stripes.

In the other family of 'Red-N-Sweet' (narrow striped) × 'Charleston Gray' (light green with reticulations, also called gray), all F_1 fruit had narrow stripes, which indicates narrow stripe was dominant over gray. This is similar to the earlier family in which the narrow stripe of 'Red-N-Sweet' is dominant over the solid light green of 'King&Queen'. The segregation ratios in the F_2 (3 narrow : 1 light green) and BC_1P_b (1 narrow : 1 light green) further confirmed that the narrow stripe of 'Red-N-Sweet' is a single dominant gene (Table 3-6). An allelism test would be necessary to determine whether the gene producing gray is an allele at the same locus of the gene producing solid light green, and wide and narrow stripes.

In the family of 'Crimson Sweet' (medium wide striped) and 'Peacock Shipper' (solid medium green), all F_1 fruit had solid medium green rind and F_2 had 3 solid medium and 1 medium wide stripe. BC_1P_a had equal number of medium wide striped fruit and solid medium green fruit and all BC_1P_b were solid medium green (Table 3-7). These segregation ratios indicate that the solid medium green rind of 'Peacock Shipper' is a single gene dominant over medium width stripe of 'Crimson Sweet'. An allelism test would also be necessary to determine whether the gene producing solid medium green rind is an allele at the same locus of the gene producing wide, medium, and narrow stripes.

For the other four families involving a striped parent and a solid green parent, the data were more complicated. Intermediate phenotypes were often present in the F_1 and the green shades of F_2 progenies usually acted more like a quantitative trait and classification was impracticable.

In the family of 'Red-N-Sweet' (narrow striped) × 'Black Diamond' (solid dark green), all F_1 fruit had an intermediate phenotype. The green color shade of F_1 was lighter than 'Black Diamond' and darker than the light green background of 'Red-N-Sweet'. The fruit of the F_1 had inconspicuous stripes that were difficult to observe on some individuals (Fig. 14). F_2 progenies also segregated into three classes, the P_a phenotype, the P_b phenotype and the intermediate F_1 phenotype. But the green shade of the F_2 (disregarding the stripes) were difficult to classify and acted more like a quantitative trait. The goodness-of-fit tests for the F_2, BC_1P_a, and BC_1P_b data were not significant and this may be caused by the misclassification due to the difficulty of reading the inconspicuous stripes of the intermediate phenotype. The intermediate F_1 phenotype also indicated that the color shade and stripe are controlled by different loci. Porter (1937) investigated two similar families between solid dark green cultivars and striped cultivars, 'California Klondike' (solid dark green) × 'Golden Honey' (striped), and 'Golden Honey' (striped) × 'Angeleno Black Seeded' (solid dark green). In both of the F_1, fruit were intermediate with faint stripes different from both parents, and the F_2 had a 1:2:1 segregation ratio. But no backcross was conducted for the first family and no F_2 or backcross was provided for the second family to determine whether a single gene controlled the trait (Porter, 1937).

The family 'Crimson Sweet' (medium width stripe) × 'King&Queen' (solid light green) was conducted to investigate the inheritance of medium width stripe and solid light green rind. All F_1 fruit had medium width stripes that were narrower than the striped parent 'Crimson Sweet'. The F_2 and backcross had fruit with different widths. Disregarding the stripe width, there were two phenotypes in F_2, striped and solid, and the ratio was close to 3:1 (Table 3-8). All BC_1P_a fruit were striped. However, BC_1P_b fruit were also all striped, in which a 1:1 ratio of striped and light green fruit were expected for single gene dominance.

In the family of 'Allsweet' (wide striped) × 'King&Queen' (light green), all F_1 were medium striped. The F_2 progenies segregated into fruit with a mixture of different green shades and different stripe widths. The stripes blended with the background and are difficult to classify. All BC_1P_a were wide striped and BC_1P_b segregated into multiple phenotypes same as F_2 progenies. So, no Mendelian inheritance was found in this family.

In the last family, 'Allsweet' (wide striped) × 'Black Diamond' (solid dark green), all F_1 fruit also had intermediate solid medium green rind. The F_2 progenies segregated into striped and solid colored fruit with different shades of green. However, the goodness-of-fit tests were not significant (Table 3-9) when classifying the progenies into striped and solid classes.

As indicated earlier, 3 families were conducted between solid green parents. In the first family, 'Peacock Shipper' (solid medium green) × 'Charleston Gray' (light green; also called gray), all F_1 fruit had solid medium green rind, which indicated that the solid medium green rind is dominant over light green rind. Both parents have reticulations on the rind, but the reticulation was ignored for purposes of this trait. The F_2 progeny segregated into

medium green, light green, and a medium light green color between the light green of 'Charleston Gray' and the medium green of 'Peacock Shipper'. The segregation ratio was 3:1 when combining medium and medium light green fruit and comparing with light green color (Table 3-10). The segregation ratios in the F_2 and BC_1P_b suggest that the solid medium green rind of 'Peacock Shipper' is a single gene, dominant over the light green rind of 'Charleston Gray'. An allelism test would be necessary to determine whether the gene producing solid medium green rind is an allele at the same locus of the gene producing wide, medium, and narrow stripes.

Weetman (1937) conducted similar researches on watermelon rind by using two families. One of the families was 'Long Iowa Belle' (medium dark green with a distinctive greenish-white mottling) × 'Japan 6' (light green; called gray); and the other family was 'Long Iowa Belle' ×'Japan 4' (light green; called gray). Actually, 'Long Iowa Belle' has a medium dark green rind with a distinctive greenish-white mottling, similar to 'Peacock Shipper' when disregarding the modifying pattern, which is a greenish-white mottling and some reticulations. In Weetman's experiment, the F_1 was medium dark green and F_2 progeny segregated into medium dark, light and intermediate medium light green at a 3:1 ratio when combining light and intermediate medium light green fruit together to compare with the intermediate green. These families indicate that a single gene controlling dark green is completely dominant over light green. Weetman (1937) proposed that there were other genes determining the variations in shade from light to medium green. This study also demonstrated that the shade of fruit rind color and the modifying characters (such as the

greenish-white mottling on 'Long Iowa Belle', and the reticulation on 'Peacock Shipper' and 'Charleston Gray') are controlled by different loci.

In the second family, 'King&Queen' (light green) × 'Peacock Shipper' (solid medium green), the F_1 had medium green rind with inconspicuous dark narrow stripes. The F_2 progenies segregated into 4 phenotypes: 31 light green with inconspicuous stripes (same as 'King&Queen'), 46 solid medium green (same as 'Peacock Shipper'), 45 medium green rind with narrow medium green stripes, and 24 light green rind with narrow medium green stripes. All BC_1P_a were like 'King&Queen', while BC_1P_b segregated into 32 solid medium green and 18 light green with narrow medium green stripes. If all striped fruit are combined, the data suggest that the striped phenotype is a single gene dominant over the solid. The F_2 data (χ^2=2.19, P-value=0.14) approximately fit that hypothesis.

In the last family, 'Black Diamond' (solid dark green) × 'Charleston Gray' (light green with reticulations), all F_1 fruit had an intermediate rind color that was between the dark green of 'Black Diamond' and the light green of 'Charleston Gray'. In the F_2, many color shades between dark green and light green were observed, which indicated that solid color shade is controlled by several genes and behaves like a quantitative trait. In an earlier study, Porter (1937) investigated the inheritance of dark green and light green (or gray) in the family 'California Klondike' (similar to 'Black Diamond') and 'Thurmond Gray' (similar to 'Charleston Gray'), and found that F_1 were intermediate green lighter than 'California Klondike' but darker than 'Thurmond Gray'. Therefore, his results are similar to ours, which also showed an incomplete dominance of the dark green over light green. Another two families investigated by porter, both involving a solid dark green cultivar and a light color

cultivar, were 'California Klondike' (solid dark green) × 'Snow Ball' (yellowish-white), and 'Angeleno Black Seeded' (solid dark green, similar to cultivar 'Black Diamond') × 'Snow Ball' (Porter, 1937). But the crossing showed different results. These two families showed complete dominance of the dark green color over yellowish-white color in F_1. The 3:1 (dark green: yellowish-white) segregation ratio in F_2 also indicated a single gene dominance. Unfortunately, there were no backcrosses conducted to confirm the single gene for a complete dominance of the dark green over yellowish-white. As a result, no gene was identified from the study (Porter, 1937).

From the above results we conclude that (1) solid medium green is a single gene, dominant over medium wide stripes, (2) medium wide stripes is single gene, dominant over narrow stripes, and (3) narrow stripes is single gene, dominant over gray. Such relationships could be explained with a hypothetical multi-locus model: *AA BB CC* (solid medium green), *aa BB CC* (medium wide stripe), *aa bb CC* (narrow stripe) and *aa bb cc* (gray). However, crossing experiments between solid medium green and gray show simple 3:1 segregation in F_2 progenies, instead of the more complicated 27:9:9:9:3:3:1 patterns suggested by the hypothetical multi-locus model. Therefore, we suggest that solid medium green, medium width stripes, narrow stripes and gray are controlled by the same *g* locus described by by Porter (1937) and Weetman (1937): *G* is from 'California Klondike', g^s is from 'Golden Honey', and *g* is from 'Thurmond Gray'. A more complete series of alleles is proposed: *G* is from 'Peacock Shipper' as well as 'California Klondike', g^M is from 'Crimson Sweet', g^N is from 'Red-N-Sweet', and *g* is from 'Charleston Gray' as well as 'Golden Honey'.

In addition, we observed a single dominant gene for wide stripe ('Allsweet' and 'Tendersweet Orange Flesh') over narrow stripe ('Red-N-Sweet'), and narrow stripe over solid light green ('King&Queen'). A family between the wide striped parent and the solid light green parent is a good allelism test for investigating whether the wide stripe, narrow stripe, and solid light green is in the same locus. The family 'Allsweet' (wide) × 'King&Queen' (solid light green) did not show a clear 3:1 segregation in the F_2 and suggested that it is not a single gene difference between parent 'Allsweet' (wide) and 'King&Queen'. Although the data did not show an excellent 9:3:3:1 segregation pattern in the F_2, the observed complicated segregations in both F_2 and BC_1P_b were still good enough to suggest that more than one gene are responsible for producing the wide stripe, narrow stripe and solid light green phenotypes. Therefore we propose an additional recessive gene *ns* for the narrow stripe of 'Red-N-Sweet' controlling the phenotypes in these two families along with the *g* locus. However, the allele at the *g* locus of the wide striped parent and narrow striped parent cannot be determined based on this experiment. The following genotypes are proposed: *NsNs GG (or* g^Mg^M*, or* g^Ng^N*)* is for wide stripe from 'Allsweet' and 'Tendersweet Orange Flesh', *nsns* g^Ng^N for narrow stripe from 'Red-N-Sweet', and *nsns gg* for solid light green from 'King&Queen' (Table 3-22). Allelism tests between the wide striped 'Allsweet' and 'Tendersweet Orange Flesh' and the cultivars producing solid medium green (*GG*), medium wide stripe (g^Mg^M), and narrow stripe (g^Ng^N) would be necessary for further researches.

Fruit Stripe Pattern and Color

Besides stripe width, the stripe pattern can also have different characteristics. We observed two types of stripe margins in our experiments: one type has clear margin with well defined boundary that separates the stripe from the background; the other type has blurred margin and the stripe boundary is not well defined (Fig. 15). The stripe margin was measured in four families, 'PDS 808'(blurred) × 'Red-N-Sweet' (clear), 'Red-N-Sweet'(clear) × 'Crimson Sweet' (blurred), 'Red-N-Sweet'(clear) × 'Allsweet' (blurred), 'Tendersweet Orange Flesh' (blurred) × 'Red-N-Sweet'. Only one of the families, 'PDS 808' × 'Red-N-Sweet', didnot show the heterogeneity ratio (Table 3-11). In the other three families, we observed dominance of clear-margined stripes in F_1 and Mendelian segregation in F_2 and backcrosses, indicating that the clear margin type was recessive to the blurred margin type. The goodness-of-fit tests for the F_2, BC_1P_a, and BC_1P_b data of the other three families were significant (Tables 3-11, 3-12, 3-13). In addition, we found that the stripe width in these families correlated with the stripe margin types. Blurred margins are observed only in medium-width and wide striped fruit and the clear margins are only in the narrow-wide striped fruit.

Previous study has suggested a recessive *p* gene to describe the super narrow stripe (penciled stripe) in 'Japan 6', as opposed to medium stripe in 'China 23' (Weetman, 1937). Since penciled stripe type also has a clear margin, the previous study is consistent with our results. Based on our experiments, we could explain the stripe margins and width using two-linked-gene model. However, it is also possible to explain the data with one gene that determines the stripe width and the margin type. It may be that stripe width and margin type are produced by the same process during fruit development.

Stripe color was evaluated in four families (Table 3-1), 'Red-N-Sweet' (dark green stripe) × 'Crimson Sweet' (medium green stripe), 'Red-N-Sweet' × 'Allsweet' (medium green stripe), 'Crimson Sweet' × 'King&Queen' (solid light green stripe), and 'Allsweet' × 'King&Queen'. No Mendelian inheritance was observed.

Fruit Shape

Eight families were developed to evaluate the inheritance of oblong, round or near-round, and elongate fruit shapes. These families were: 1) 'Tendersweet Orange Flesh' (oblong) × 'Red-N-Sweet' (near-round), 2) 'Crimson Sweet' (near-round) × 'Peacock Shipper' (oblong), 3) 'Peacock Shipper' (oblong) × 'Charleston Gray' (elongate), 4) 'Black Diamond' (near-round) × 'Charleston Gray' (elongate), 5) 'Crimson Sweet' (near-round) × 'King&Queen' (round), 6) 'Red-N-Sweet' (near-round) × 'King&Queen' (round), 7) 'Allsweet' (elongate) × 'King&Queen' (round), 8) 'King&Queen' (round) × 'Peacock Shipper' (oblong). Three other families, which all involved an elongate parent and a near-round parent, were investigated to confirm the action of the *o* gene. With that gene, elongate (*OO*) was incompletely dominant over round (*oo*) or near-round shape and the heterozygote had oval (*Oo*) or oblong fruit shape. These three families are: 1) 'Red-N-Sweet' (near-round) × 'Allsweet' (elongate), 2) 'Red-N-Sweet' (near-round) × 'Charleston Gray' (elongate), 3) 'Allsweet' (elongate) × 'Black Diamond' (near-round) (Table 3-1).

Two families, 'Tendersweet Orange Flesh' (oblong) × 'Red-N-Sweet' (near-round), and 'Crimson Sweet' (near-round) × 'Peacock Shipper' (oblong) were conducted to evaluate the inheritance of oblong fruit shape. In both families, all F_1 fruit had near-round fruit shape

which indicated that near-round fruit shape was dominant over oblong fruit shape. F_2 progenies had 3 near-round and 1 oblong. Backcross to the oblong parent had equal near-round fruit and oblong fruit. All backcross to the near-round parent were near-round (Table 3-14, 3-15). The data in both families suggested that the near-round shape of 'Red-N-Sweet' and 'Crimson Sweet' was a single gene, dominant over the oblong fruit shape of 'Tendersweet Orange Flesh' and 'Peacock Shipper'. The known gene *O* cannot explain the observed data in this family and gene name *ob* is proposed here for the oblong fruit shape in 'Tendersweet Orange Flesh' and 'Peacock Shipper'. The *ob* genes are recessive to the near-round shape (*Ob*) of 'Red-N-Sweet' and 'Crimson Sweet'. An allelism test for further investigation is necessary to determine whether the genes in these two families are the same.

In the family 'Peacock Shipper' (oblong) × 'Charleston Gray' (elongate), all F_1 fruit had elongate fruit. Although the F_2 segregation ratio did not fit Mendelian inheritance in each location, it fit well when the data was pooled. In the pooled data, F_2 fruit segregated into 3 elongate vs. 1 oblong. BC_1P_a had 1 elongate vs. 1 oblong and BC_1P_b were elongate (Table 3-16). The results suggest that the elongate fruit of 'Charleston Gray' is single gene dominant over oblong fruit of 'Peacock Shipper'. Gene name *El* is proposed here for the elongate fruit of 'Charleston Gray' (*El*), dominant over the oblong fruit shape if 'Peacock Shipper' (*el*).

In the family 'Black Diamond' (near-round) × 'Charleston Gray' (elongate) all F_1 fruit had intermediate oblong fruit shape and F_2 progenies segregated into 3 classes, oblong, elongate, and near-round with a ratio close to 9:3:4. BC_1P_a segregated into nearly equal number of oblong shape fruit and near-round fruit and BC_1P_b segregated into nearly equal number of oblong shape fruit and elongate fruit. The goodness-of-fit tests for the F_2, BC_1P_a,

and BC_1P_b data was significant (Table 3-17). The data suggested that two loci controlled fruit shape in this family and genes *ob* and *O* are able to explain the segregation ratios in this family. Genotypes are proposed as follows: parent 'Black Diamond' has genotype *ObOb oo* and produces near-round fruit; parent 'Charleston Gray' has genotype *obob OO* and produces elongate fruit; F_1 progeny has genotype *Obob Oo* and produce oblong fruit. The genotype *oo* is epistatic and *Ob_ oo* and *obob oo* both produce near-round fruit (Table 3-23). In F_2, segregation ratio is 9 oblong (*Ob_ O_*) : 3 elongate (*obob O_*), and 4 near-round (*Ob_ oo* + *obob oo*).

Weetman (1937) investigated the inheritance of fruit shape in the families of 'Long Iowa Belle' (elongate fruit) × 'Round Iowa Belle' and 'China 23' (both had round fruit), 'Long Iowa Belle' × 'Japan 6' and 'Japan 4' (both had near-round shape). He found that elongate fruit shape (*OO*) was incompletely dominant to round fruit shape (*oo*) and the heterozygote (*Oo*) were oblong (intermediate) shaped. This earlier research showed that round fruit shape and near-round fruit shape may be controlled by the same gene. In our experiment, two families involving round fruit or near-round fruit were investigated to confirm the previous gene. The two families are 'Crimson Sweet' (near-round) × 'King&Queen' (round) and 'Red-N-Sweet' (near-round) × 'King&Queen'. No segregation was found in either of the families. The results suggest that the round and near-round fruit shape are controlled by the same gene.

The *o* gene was confirmed in three families, which are 'Red-N-Sweet' (near-round) × 'Allsweet' (elongate), 'Red-N-Sweet' (near-round) × 'Charleston Gray' (elongate), and 'Allsweet' (elongate) × 'Black Diamond' (near-round). All F_1 fruit had oblong fruit shape and the heterogeneity of all three families were significant. (Table 3-18, 3-19, 3-20).

Two other families involved 'King&Queen' (round fruit shape). However, they did not show the inheritance described above. In the family 'Allsweet' (elongate) × 'King&Queen' (round), F_1 fruit had oblong fruit shape and F_2 progenies segregated into three fruit shapes (elongate, oblong, and round). BC_1P_a had oblong and elongate fruit; BC_1P_b had oblong and round fruit. However, the goodness-of-fit tests for the F_2, BC_1P_a, were significant, but not significant for BC_1P_b (Table 3-21). In the family 'King&Queen' × 'Peacock Shipper', all F_1 fruit were near-round but different from the round shape of 'King&Queen'. There was segregation in F_2, BC_1P_b, but the goodness-of-fit tests for the F_2, BC_1P_a, BC_1P_b generations were not significant.

Fruit Blossom End and Furrowing

Three families were used to study the inheritance of fruit blossom end shape: 'Red-N-Sweet' (concave blossom end) × 'Allsweet'(convex blossom end), 'Allsweet' (convex blossom end) × 'Black Diamond' (concave blossom end), and 'Peacock Shipper' (concave blossom end) × 'Charleston Gray' (convex blossom end). No Mendelian inheritance was observed (Table 3-1).

Furrowed fruit surface (*f*) was found to be recessive to smooth surface (*F*) (Poole, 1944, Wehner, 2008a). However, the type lines were not given in the original reference. Three families were investigated to confirm this gene, 'Crimson Sweet' (smooth fruit surface) × 'Peacock Shipper' (furrowed fruit surface), 'Allsweet' (smooth fruit surface) × 'Black Diamond' (furrowed fruit surface), and 'Peacock Shipper' (furrowed fruit surface) ×

'Charleston Gray' (smooth fruit surface) (Table 3-1), and no Mendelian inheritance was observed.

Conclusions

From the crossing experiment, we have identified new genes or alleles that control external fruit characters. Such information can be used for breeding watermelons with desired appearance. The results for these fruit traits are summarized below:

Fruit Stripe

A more complete series of alleles at *g* locus is proposed to explain the inheritance of solid medium green, medium wide stripe, narrow stripe, gray fruit rind: *G* is from 'Peacock Shipper' as well as 'California Klondike', g^M is from 'Crimson Sweet', g^N is from 'Red-N-Sweet', and *g* is from 'Charleston Gray' as well as 'Golden Honey'. *G* is dominant to g^M, g^N and *g* (Table 3-22).

In addition a new gene *ns* for the narrow stripe of 'Red-N-Sweet' is proposed to control the inheritance of wide stripe, narrow stripe, solid light green along with the *g* locus. However, the allele at the *g* locus of the wide striped parent and narrow striped parent cannot be determined based on our experiment. The following genotypes are proposed: *NsNs GG (or* g^Mg^M*, or* g^Ng^N*)* is for wide stripe from 'Allsweet' and 'Tendersweet Orange Flesh', *nsns* g^Ng^N for narrow stripe from 'Red-N-Sweet', and *nsns gg* for solid light green from 'King&Queen' (Table 3-22). Allelism tests between the wide striped 'Allsweet' and 'Tendersweet Orange Flesh' and the cultivars producing solid medium green (*GG*), medium wide stripe (g^Mg^M), and

narrow stripe ($g^N g^N$) would be necessary for further researches. Future experiments might include the following: (1) 'Allsweet' (wide striped) × 'Peacock Shipper' (solid medium green), (2) 'Allsweet' × 'Crimson Sweet' (medium striped), and (3) 'King&Queen' (light green) × 'Charleston Gray' (gray).

The solid dark green rind in 'Black Diamond' was evaluated in three families, 'Red-N-Sweet' (narrow) ×'Black Diamond' (solid dark green), 'Allsweet' (wide) ×'Black Diamond', and 'Black Diamond' ×'Charleston Gray' (gray). The intermediate rind pattern in F_1 and the continuous green shades in F_2 indicate that the background color shade and stripe are controlled by different genes and solid color shade is controlled by multiple genes

Fruit Stripe Pattern and Color

The blurred stripe pattern is found to be controlled by a single gene that is dominant over clear stripe pattern. It is possibly the same as the *p* gene described by Weetman (1937) for producing the penciled stripe pattern. No inheritance pattern was found for the stripe color in this experiment.

Fruit Shape

The incompletely dominant gene *o* was confirmed in three families: 'Red-N-Sweet' (near-round) × 'Allsweet' (elongate), 'Red-N-Sweet' (near-round) × 'Charleston Gray' (elongate), and 'Allsweet' (elongate) × 'Black Diamond' (near-round). Gene *ob* was proposed for the oblong fruit shape in 'Tendersweet Orange Flesh' and 'Peacock Shipper'. The *ob* genes are recessive to the near-round shape of 'Red-N-Sweet' and 'Crimson Sweet' (*Ob*). Another

gene name *El* is proposed here for the elongate fruit of 'Charleston Gray' (*El*), dominant over the oblong fruit shape if 'Peacock Shipper' (*el*) (Table 3-23).

The results from the family 'Black Diamond' (near-round) × 'Charleston Gray' (elongate) showed that fruit shape is controlled by two genes. The genotypes are proposed as follows: 'Black Diamond' (near-round) is *ObOb oo*; 'Charleston Gray' (elongate) is *oo ObOb*; F_1 progeny (oblong) are *Obob Oo*. The locus *ob* is epistatic to *o*, so *obob O_* and *obob oo* both result in near-round fruit (Table 3-23).

Fruit Blossom End and Furrowing

The inheritance of the two different kinds of blossom end, concave and convex, was investigated in this experiment. However, a Mendelian inheritance pattern was not detected. Although furrowed fruit surface (*f*) was found to be recessive to smooth surface (*F*) as previously described for the gene *f* by Poole, this gene was not found in this experiment. Since type lines were not given in the original reference, 'Stone Mountain' or 'Black Diamond' was recommend as the type line for *f*, and 'Mickylee' for *F* (Poole, 1944; Wehner, 2008a).

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Table 3-1. Families and traits analyzed for qualitative inheritance of rind character in watermelon fruit during summer 2008 in Clinton and Kinston, North Carolina.

Families	Trait of interest	
	Phenotype	Gene
Study of new genes		
Stripe pattern		
'Red-N-Sweet' × 'Crimson Sweet'	Narrow stripe vs. medium wide	g^M,g^N
'PDS 808' × 'Red-N-Sweet'	Medium wide stripe vs. narrow	_a
'Red-N-Sweet' × 'Allsweet'	Narrow stripe vs. wide	*ns*
'Tendersweet OF' × 'Red-N-Sweet'	Wide stripe vs. narrow	*ns*
'Red-N-Sweet' × 'King&Queen'	Narrow stripe vs. solid light green	*ns*
'Red-N-Sweet' × 'Charleston Gray'	Narrow stripe vs. gray	g^N, *g*
'Crimson Sweet' × 'Peacock Shipper'	Medium stripe vs. solid medium green	*G*, g^M
'Red-N-Sweet' × 'Black Diamond'	Solid dark green vs. narrow stripe	_a
'Crimson Sweet' × 'King&Queen'	Solid light green vs. medium stripe	_a
'Allsweet' × 'King&Queen'	Wide stripe vs. solid light green	_a
'Allsweet' × 'Black Diamond'	Wide stripe vs. solid dark green	_a
'Peacock Shipper' × 'Charleston Gray'	Solid medium green vs. gray	*G*, *g*
'King&Queen' × 'Peacock Shipper'	Solid light green vs. solid medium green	_a
'Black Diamond' × 'Charleston Gray'	Solid dark green vs. Gray	_a
Stripe pattern (clear, mottled)		
'PDS 808' × 'Red-N-Sweet'	Blurred stripe pattern vs. clear	_[a]
'Red-N-Sweet' × 'Crimson Sweet'	Clear stripe pattern vs. blurred	*p*
'Red-N-Sweet' × 'Allsweet'	Clear stripe pattern vs. blurred	*p*
'Tendersweet OF' × 'Red-N-Sweet'	Blurred stripe pattern vs. clear	*p*
Stripe color		
'Red-N-Sweet' × 'Crimson Sweet'	Dark green stripe color vs. medium	_[a]
'Red-N-Sweet' × 'Allsweet'	Dark green stripe color vs. medium	_[a]
'Crimson Sweet' × 'King&Queen'	Medium green stripe color vs. light	_[a]
'Allsweet' × 'King&Queen'	Medium green stripe color vs. light	_[a]

a No gene was found or verified.

Table 3-1. Continued.

Families	Trait of interest	
	Phenotype	Gene
Study of new genes		
Fruit shape		
'Tendersweet OF' × 'Red-N-Sweet'	Oblong vs. near round	*ob*
'Crimson Sweet' × 'Peacock Shipper'	Near round vs. oblong	*ob*
'Peacock Shipper' × 'Charleston Gray'	Oblong fruit vs. elongate	*El*
'Black Diamond' × 'Charleston Gray'	Near round vs. elongate	*ob, O*
'Crimson Sweet' × 'King&Queen'	Near round vs. round	–[a]
'Red-N-Sweet' × 'King&Queen'	Near round vs. round	–[a]
'Allsweet' × 'King&Queen'	Elongate vs. round	–[a]
'King&Queen' × 'Peacock Shipper'	Round vs. oblong	–[a]
Blossom end		
'Red-N-Sweet' × 'Allsweet'	Concave blossom end vs. convex	–[a]
'Allsweet' × 'Black Diamond'	Convex blossom end vs. concave	–[a]
'Peacock Shipper' × 'Charleston Gray'	Concave blossom end vs. convex	–[a]
Verification of known genes		
Fruit shape		
'Red-N-Sweet' × 'Allsweet'	Near round vs. elongate	*O*
'Red-N-Sweet' × 'Charleston Gray'	Near round vs. elongate	*O*
'Allsweet' × 'Black Diamond'	Elongate vs. near round	*O*
Furrow		
'Crimson Sweet' × 'Peacock Shipper'	Smooth vs. furrowed	–[a]
'Allsweet' × 'Black Diamond'	Smooth vs. furrowed	–[a]
'Peacock Shipper' × 'Charleston Gray'	Furrowed vs. smooth	–[a]

a No gene was found or verified.

Table 3-2. Single locus goodness-of-fit-test for stripe width in watermelon in family 'Red-N-Sweet' (Narrow) × 'Crimson Sweet' (Medium).

Location/ Generation	Total no.	Medium stripe[b]	Narrow stripe[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	9	1				
P_bS_1	10	7	0	3				
F_1	20	17	0	3				
F_2	100	42	23	35	3:1	3.74	1	0.053
BC_1P_a	30	8	12	10	1:1	0.80	1	0.37
BC_1P_b	30	22	1	7	1:0	0.04	1	0.83
Clinton[a]								
P_aS_1	10	0	10	0				
P_bS_1	10	8	0	2				
F_1	20	17	0	3				
F_2	100	63	22	15	3:1	0.04	1	0.85
BC_1P_a	30	16	8	6	1:1	2.67	1	0.10
BC_1P_b	30	21	0	9	1:0	0.00	1	1.00
Pooled[a]								
P_aS_1	20	0	19	1				
P_bS_1	20	15	0	5				
F_1	40	34	0	6				
F_2	200	105	45	50	3:1	2.00	1	0.15
BC_1P_a	60	24	20	16	1:1	0.36	1	0.54
BC_1P_b	60	43	1	16	1:0	0.02	1	0.88

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Medium wide stripe was dominant and P_b was the carrier.

c Narrow stripe was recessive and P_a was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-3. Single locus goodness-of-fit-test for stripe width in watermelon in family 'Red-N-Sweet' (Narrow) × 'Allsweet' (Wide).

Location/ Generation	Total no.	Wide stripe[b]	Narrow stripe[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	8	2				
P_bS_1	10	4	0	6				
F_1	20	17	1	2				
F_2	100	49	22	29	3:1	1.36	1	0.24
BC_1P_a	30	5	7	18	1:1	0.33	1	0.56
BC_1P_b	30	23	1	6	1:0	0.04	1	0.83
Clinton[a]								
P_aS_1	10	0	2	8				
P_bS_1	10	4	0	6				
F_1	20	14	0	6				
F_2	100	49	17	34	3:1	0.02	1	0.88
BC_1P_a	30	10	8	12	1:1	0.22	1	0.63
BC_1P_b	30	19	2	9	1:0	0.19	1	0.66
Pooled[a]								
P_aS_1	20	0	10	10				
P_bS_1	20	8	0	12				
F_1	40	31	1	8				
F_2	200	98	39	63	3:1	0.88	1	0.34
BC_1P_a	60	15	15	30	1:1	0.00	1	1.00
BC_1P_b	60	42	3	15	1:0	0.20	1	0.65

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b Wide stripe was dominant and P_b was the carrier.
c Narrow stripe was recessive and P_a was the carrier.
d Some plants were missing or damaged.
e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
f Heterogeneity χ^2 (0.05; 1)
g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-4. Single locus goodness-of-fit-test for stripe width in watermelon in family 'Tendersweet Orange Flesh' (Wide) × 'Red-N-Sweet' (Narrow).

Location/ Generation	Total no.	Wide stripe[b]	Narrow stripe[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	10	0	0				
P_bS_1	10	0	5	5				
F_1	20	14	0	6				
F_2	100	65	19	16	3:1	0.25	1	0.61
BC_1P_a	30	26	0	4	1:0	0.00	1	1.00
BC_1P_b	30	14	13	3	1:1	0.04	1	0.84
Clinton[a]								
P_aS_1	10	10	0	0				
P_bS_1	10	0	8	2				
F_1	20	20	0	0				
F_2	100	60	15	25	3:1	1.00	1	0.31
BC_1P_a	30	28	0	2	1:0	0.00	1	1.00
BC_1P_b	30	13	16	1	1:1	0.31	1	0.57
Pooled[a]								
P_aS_1	20	20	0	0				
P_bS_1	20	0	13	7				
F_1	40	34	0	6				
F_2	200	125	34	41	3:1	1.11	1	0.29
BC_1P_a	60	54	0	6	1:0	0.00	1	1.00
BC_1P_b	60	27	29	4	1:1	0.07	1	0.78

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Wide stripe was dominant and P_a was the carrier.

c Narrow stripe was recessive and P_b was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-5. Single locus goodness-of-fit-test for stripe in watermelon in family 'Red-N-Sweet' (Narrow) × 'King&Queen' (Solid light green).

Location/ Generation	Total no.	Nrrow stripe[b]	Solid ligh green[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	10	0	0				
P_bS_1	10	0	10	0				
F_1	20	20	0	0				
F_2	100	70	25	5	3:1	0.09	1	0.76
BC_1P_a	30	29	0	1	1:0	0.00	1	1.00
BC_1P_b	30	19	11	0	1:1	2.13	1	0.14
Clinton[a]								
P_aS_1	10	7	0	3				
P_bS_1	10	0	5	5				
F_1	20	13	0	7				
F_2	100	73	16	11	3:1	2.34	1	0.12
BC_1P_a	30	13	1	16	1:0	0.07	1	0.78
BC_1P_b	30	17	12	1	1:1	0.86	1	0.35
Pooled[a]								
P_aS_1	20	17	0	3				
P_bS_1	20	0	15	5				
F_1	40	33	0	7				
F_2	200	143	41	16	3:1	0.72	1	0.39
BC_1P_a	60	42	1	17	1:0	0.02	1	0.87
BC_1P_b	60	36	23	1	1:1	2.86	1	0.09

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b Narrow stripe was dominant and P_a was the carrier.
c Solid light green was recessive and P_b was the carrier.
d Some plants were missing or damaged.
e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
f Heterogeneity χ^2 (0.05; 1)
g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-6. Single locus goodness-of-fit-test for stripe width in watermelon in family 'Red-N-Sweet' (Narrow) × 'Charleston Gray' (Gray).

Location/ Generation	Total no.	Narrow stripe[b]	Gray[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	10	0	0				
P_bS_1	10	0	2	8				
F_1	20	14	0	6				
F_2	100	70	19	11	3:1	0.63	1	0.42
BC_1P_a	30	28	0	2	1:0	0.00	1	1.00
BC_1P_b	30	12	15	3	1:1	0.33	1	0.56
Clinton[a]								
P_aS_1	10	9	0	1				
P_bS_1	10	0	6	4				
F_1	20	16	0	4				
F_2	100	58	20	22	3:1	0.02	1	0.89
BC_1P_a	30	26	0	4	1:0	0.00	1	1.00
BC_1P_b	30	14	15	1	1:1	0.03	1	0.85
Pooled[a]								
P_aS_1	20	19	0	1				
P_bS_1	20	0	8	12				
F_1	40	30	0	10				
F_2	200	128	39	33	3:1	0.24	1	0.62
BC_1P_a	60	54	0	6	1:0	0.00	1	1.00
BC_1P_b	60	26	30	4	1:1	0.29	1	0.59

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Narrow stripe was dominant and P_a was the carrier.

c Gray was recessive and P_b was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-7. Single locus goodness-of-fit-test for stripe width in watermelon in family 'Crimson Sweet' (Medium wide striped) × 'Peacock Shipper' (Solid light green).

Location/ Generation	Total no.	Solid medium green[b]	Medium stripe[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	8	2				
P_bS_1	10	10	0	0				
F_1	20	19	0	1				
F_2	100	65	17	18	3:1	0.80	1	0.37
BC_1P_a	30	13	15	2	1:1	0.14	1	0.70
BC_1P_b	30	27	0	3	1:0	0.00	1	1.00
Clinton[a]								
P_aS_1	10	0	10	0				
P_bS_1	10	10	0	0				
F_1	20	20	0	0				
F_2	100	73	19	8	3:1	0.93	1	0.33
BC_1P_a	30	14	14	2	1:1	0.00	1	1.00
BC_1P_b	30	29	0	1	1:0	0.00	1	1.00
Pooled[a]								
P_aS_1	20	0	18	2				
P_bS_1	20	20	0	0				
F_1	40	39	0	1				
F_2	200	138	36	26	3:1	1.72	1	0.18
BC_1P_a	60	27	29	4	1:1	0.07	1	0.78
BC_1P_b	60	56	0	4	1:0	0.00	1	1.00

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Solid medium green was dominant and P_b was the carrier.

c Medium wide stripe was recessive and Pa was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-8. Single locus goodness-of-fit-test for stripe width in watermelon in family 'Crimson Sweet' (Medium wide striped) × 'King&Queen' (Light green).

Location/ Generation	Total no.	Medium stripe[b]	Solid light green[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	8	0	2				
P_bS_1	10	0	7	3				
F_1	20	15	0	5				
F_2	100	52	23	25	3:1	1.28	1	0.25
BC_1P_a	30	27	0	3	1:0	0.00	1	1.00
BC_1P_b	30	27	0	3	1:1	27.00	1	0.000
Clinton[a]								
P_aS_1	10	9	0	1				
P_bS_1	10	0	9	1				
F_1	20	18	0	2				
F_2	100	60	19	21	3:1	0.04	1	0.84
BC_1P_a	30	27	0	3	1:0	0.00	1	1.00
BC_1P_b	30	28	0	2	1:1	28.00	1	0.000
Pooled[a]								
P_aS_1	20	17	0	3				
P_bS_1	20	0	16	4				
F_1	40	33	0	7				
F_2	200	112	42	46	3:1	0.42	1	0.51
BC_1P_a	60	54	0	6	1:0	0.00	1	1.00
BC_1P_b	60	55	0	5	1:1	55.00	1	0.000

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b Medium wide stripe was dominant and P_a was the carrier.
c Solid light green was recessive and P_b was the carrier.
d Some plants were missing or damaged.
e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
f Heterogeneity χ^2 (0.05; 1)
g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-9. Single locus goodness-of-fit-test for stripe width in watermelon in family 'Allsweet' (Wide striped) × 'Black Diamond' (Solid dark green).

Location/ Generation	Total no.	Solid dark green[b]	Wide stripe[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	9	1				
P_bS_1	10	10	0	0				
F_1	20	20	0	0				
F_2	100	75	21	4	3:1	0.50	1	0.47
BC_1P_a	30	18	12	0	1:1	1.20	1	0.27
BC_1P_b	30	22	3	5	1:0	0.36	1	0.54
Clinton[a]								
P_aS_1	10	0	8	2				
P_bS_1	10	10	0	0				
F_1	20	20	0	0				
F_2	100	81	15	4	3:1	4.50	1	0.033
BC_1P_a	30	17	12	1	1:1	0.86	1	0.35
BC_1P_b	30	27	1	2	1:0	0.04	1	0.85
Pooled[a]								
P_aS_1	20	0	17	3				
P_bS_1	20	20	0	0				
F_1	40	40	0	0				
F_2	200	156	36	8	3:1	4.00	1	0.045
BC_1P_a	60	35	24	1	1:1	2.05	1	0.15
BC_1P_b	60	49	4	7	1:0	0.30	1	0.58

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Solid dark green was dominant and P_b was the carrier.

c Wide striped was recessive and P_a was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-10. Single locus goodness-of-fit-test for fruit color in watermelon in family 'Peacock Shipper' (Solid medium green) × 'Charleston Gray' (Gray).

Location/ Generation	Total no.	Solid medium green[b]	Light green[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	7	0	3				
P_bS_1	10	0	10	0				
F_1	20	20	0	0				
F_2	100	71	23	6	3:1	0.01	1	0.90
BC_1P_a	30	30	0	0	1:0	0.00	1	1.00
BC_1P_b	30	9	9	12	1:1	0.00	1	1.00
Clinton[a]								
P_aS_1	10	7	0	3				
P_bS_1	10	0	7	3				
F_1	20	17	0	3				
F_2	100	61	18	21	3:1	0.21	1	0.64
BC_1P_a	30	23	0	7	1:0	0.00	1	1.00
BC_1P_b	30	8	8	14	1:1	0.00	1	1.00
Pooled[a]								
P_aS_1	20	14	0	6				
P_bS_1	20	0	17	3				
F_1	40	37	0	3				
F_2	200	132	41	27	3:1	0.16	1	0.69
BC_1P_a	60	53	0	7	1:0	0.00	1	1.00
BC_1P_b	60	17	17	26	1:1	0.00	1	1.00

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Solid medium green was dominant and P_a was the carrier.

c Light green was recessive and P_b was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-11. Single locus goodness-of-fit-test for stripe pattern in watermelon in family 'Red-N-Sweet' (Clear) × 'Crimson Sweet' (Blurred).

Location/ Generation	Total no.	Blurred[b]	Clear[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	9	1				
P_bS_1	10	7	0	3				
F_1	20	17	0	3				
F_2	100	41	24	35	3:1	4.93	1	0.026
BC_1P_a	30	7	13	10	1:1	1.80	1	0.17
BC_1P_b	30	22	1	7	1:0	0.04	1	0.83
Clinton[a]								
P_aS_1	10	0	10	0				
P_bS_1	10	8	0	2				
F_1	20	17	0	3				
F_2	100	65	20	15	3:1	0.10	1	0.75
BC_1P_a	30	16	9	5	1:1	1.96	1	0.16
BC_1P_b	30	21	0	9	1:0	0.00	1	1.00
Pooled[a]								
P_aS_1	20	0	19	1				
P_bS_1	20	15	0	5				
F_1	40	34	0	6				
F_2	200	106	44	50	3:1	1.50	1	0.22
BC_1P_a	60	23	22	15	1:1	0.02	1	0.88
BC_1P_b	60	43	1	16	1:0	0.02	1	0.88

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b Blurred stripe pattern was dominant and P_b was the carrier.
c Clear stripe was recessive and P_a was the carrier.
d Some plants were missing or damaged.
e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
f Heterogeneity χ^2 (0.05; 1)
g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-12. Single locus goodness-of-fit-test for stripe pattern in watermelon in family 'Red-N-Sweet (Clear) ' × 'Allsweet' (Blurred).

Location/ Generation	Total no.	Blurred[b]	Clear[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	8	2				
P_bS_1	10	4	0	6				
F_1	20	18	0	2				
F_2	100	52	18	30	3:1	0.02	1	0.89
BC_1P_a	30	5	7	18	1:1	0.33	1	0.56
BC_1P_b	30	24	0	6	1:0	0.00	1	1.00
Clinton[a]								
P_aS_1	10	0	2	8				
P_bS_1	10	4	0	6				
F_1	20	14	0	6				
F_2	100	49	17	34	3:1	0.02	1	0.88
BC_1P_a	30	10	8	12	1:1	0.22	1	0.63
BC_1P_b	30	21	0	9	1:0	0.00	1	1.00
Pooled[a]								
P_aS_1	20	0	10	10				
P_bS_1	20	8	0	12				
F_1	40	32	0	8				
F_2	200	101	35	64	3:1	0.04	1	0.84
BC_1P_a	60	15	15	30	1:1	0.00	1	1.00
BC_1P_b	60	45	0	15	1:0	0.00	1	1.00

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b Blurred stripe pattern was dominant and P_b was the carrier.
c Clear stripe was recessive and P_a was the carrier.
d Some plants were missing or damaged.
e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
f Heterogeneity χ^2 (0.05; 1)
g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-13. Single locus goodness-of-fit-test for stripe pattern in watermelon in family 'Tendersweet OF' (Blurred) × 'Red-N-Sweet' (Clear).

Location/ Generation	Total no.	Blurred[b]	Clear[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	10	0	0				
P_bS_1	10	0	5	5				
F_1	20	14	0	6				
F_2	100	64	20	16	3:1	0.06	1	0.80
BC_1P_a	30	26	0	4	1:0	0.00	1	1.00
BC_1P_b	30	14	13	3	1:1	0.04	1	0.84
Clinton[a]								
P_aS_1	10	10	0	0				
P_bS_1	10	0	8	2				
F_1	20	20	0	0				
F_2	100	56	19	25	3:1	0.00	1	0.94
BC_1P_a	30	28	0	2	1:0	0.00	1	1.00
BC_1P_b	30	17	12	1	1:1	0.86	1	0.35
Pooled[a]								
P_aS_1	20	20	0	0				
P_bS_1	20	0	13	7				
F_1	40	34	0	6				
F_2	200	120	39	41	3:1	0.02	1	0.89
BC_1P_a	60	54	0	6	1:0	0.00	1	1.00
BC_1P_b	60	31	25	4	1:1	0.64	1	0.42

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Blurred stripe pattern was dominant and P_a was the carrier.

c Clear stripe was recessive and P_b was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-14. Single locus goodness-of-fit-test for fruit shape in watermelon in family 'Tendersweet Orange Flesh' (Oblong) × 'Red-N-Sweet' (Near round).

Location/ Generation	Total no.	Near round[b]	Oblong[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	2	8	0				
P_bS_1	10	5	0	5				
F_1	20	14	0	6				
F_2	100	67	18	15	3:1	0.66	1	0.41
BC_1P_a	30	15	11	4	1:1	0.62	1	0.43
BC_1P_b	30	27	0	3	1:0	0.00	1	1.00
Clinton[a]								
P_aS_1	10	0	10	0				
P_bS_1	10	8	0	2				
F_1	20	20	0	0				
F_2	100	62	13	25	3:1	2.35	1	0.12
BC_1P_a	30	15	13	2	1:1	0.14	1	0.70
BC_1P_b	30	29	0	1	1:0	0.00	1	1.00
Pooled[a]								
P_aS_1	20	2	18	0				
P_bS_1	20	13	0	7				
F_1	40	34	0	6				
F_2	200	129	31	40	3:1	2.70	1	0.10
BC_1P_a	60	30	24	6	1:1	0.67	1	0.41
BC_1P_b	60	56	0	4	1:0	0.00	1	1.00

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Near round fruit shape was dominant and P_b was the carrier.

c Oblong fruit shape was recessive and P_a was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-15. Single locus goodness-of-fit-test for fruit shape in watermelon in family 'Crimson Sweet' (Near round) × 'Peacock Shipper' (Oblong).

Location/ Generation	Total no.	Near round[b]	Oblong[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	8	0	2				
P_bS_1	10	1	9	0				
F_1	20	16	3	1				
F_2	100	60	22	18	3:1	0.15	1	0.70
BC_1P_a	30	27	1	2	1:0	0.04	1	0.85
BC_1P_b	30	13	14	3	1:1	0.04	1	0.84
Clinton[a]								
P_aS_1	10	10	0	0				
P_bS_1	10	0	10	0				
F_1	20	19	1	0				
F_2	100	68	24	8	3:1	0.06	1	0.80
BC_1P_a	30	28	0	2	1:0	0.00	1	1.00
BC_1P_b	30	17	12	1	1:1	0.86	1	0.35
Pooled[a]								
P_aS_1	20	18	0	2				
P_bS_1	20	1	19	0				
F_1	40	35	4	1				
F_2	200	128	46	26	3:1	0.19	1	0.66
BC_1P_a	60	55	1	4	1:0	0.02	1	0.89
BC_1P_b	60	30	26	4	1:1	0.29	1	0.59

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Near round fruit shape was dominant and P_a was the carrier.

c Oblong was recessive and P_b was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-16. Single locus goodness-of-fit-test for fruit shape in watermelon in family 'Peacock Shipper' (Oblong) × 'Charleston Gray' (elongate).

Location/ Generation	Total no.	Elongate[b]	Oblong[c]	No. missing[d]	Expected ratio[e]	Chi square[f]	df	Prob.[g]
Kinston[a]								
P_aS_1	10	0	7	3				
P_bS_1	10	10	0	0				
F_1	20	20	0	0				
F_2	100	61	33	6	3:1	4.78	1	0.03
BC_1P_a	30	10	20	0	1:1	3.33	1	0.07
BC_1P_b	30	15	2	13	1:0	0.24	1	0.63
Clinton[a]								
P_aS_1	10	0	5	5				
P_bS_1	10	5	1	4				
F_1	20	17	0	3				
F_2	100	67	11	22	3:1	4.45	1	0.03
BC_1P_a	30	11	11	8	1:1	0.00	1	1.00
BC_1P_b	30	16	0	13	1:0	0.00	1	1.00
Pooled[a]								
P_aS_1	20	0	12	8				
P_bS_1	20	15	1	4				
F_1	40	37	0	3				
F_2	200	128	44	28	3:1	0.03	1	0.86
BC_1P_a	60	21	31	8	1:1	1.92	1	0.17
BC_1P_b	60	31	2	26	1:0	0.12	1	0.73

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.

b Elongate fruit shape was dominant and P_b was the carrier.

c Oblong fruit shape was recessive and P_a was the carrier.

d Some plants were missing or damaged.

e Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation

f Heterogeneity χ^2 (0.05; 1)

g P-value (Probability) >.05 was accepted as Single Locus.

Table 3-17. Two loci goodness-of-fit-test for fruit shape in watermelon in family 'Black Diamond' (Near round) × 'Charleston Gray' (Elongate).

Location/ Generation	Total no.	Oblong[b]	Near sround[c]	Elongate[d]	Missing[e]	Expected ratio[f]	Chi square[g]	df	Prob.[h]
Kinston[a]									
P_aS_1	10	0	9	0	1				
P_bS_1	10	1	0	7	2				
F_1	20	15	4	0	1				
F_2	100	52	27	13	8	9:4:3:0	1.64	2	0.44
BC_1P_a	30	15	15	0	0	1:1:0:0	0.00	1	1.00
BC_1P_b	30	17	0	13	0	1:0:1:0	0.53	1	0.47
Clinton[a]									
P_aS_1	10	0	9	0	1				
P_bS_1	10	0	1	7	2				
F_1	20	12	7	0	1				
F_2	100	41	29	13	17	9:4:3:0	4.08	2	0.13
BC_1P_a	30	12	17	0	1	1:1:0:0	0.53	1	0.47
BC_1P_b	30	13	2	12	3	1:0:1:0	0.15	1	0.70
Pooled[a]									
P_aS_1	20	0	18	0	2				
P_bS_1	20	1	1	14	4				
F_1	40	27	11	0	2				
F_2	200	93	56	26	25	9:4:3:0	4.49	2	0.11
BC_1P_a	60	27	32	0	1	1:1:0:0	0.27	1	0.60
BC_1P_b	60	30	2	25	3	1:0:1:0	0.17	1	0.68

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b The double dominant genotype *A_B_* has oblong fruit shape. *AB*: Oblong
c Genotype *A_bb* has near round fruit shape and Pa is the carrier.
d Genotype *aaB_* and *aabb* both have Elongate fruit shape.
e Some plants were missing or damaged.
f Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
g Heterogeneity χ^2 (0.05; 1)
h P-value (Probability) >.05 was accepted as Single Locus.

Table 3-18. Single locus goodness-of-fit-test for fruit shape in watermelon in family 'Red-N-Sweet' (Near round) × 'Allsweet' (Elongate).

Location/ Generation	Total no.	Near round[b]	Elongate[c]	Oblong[d]	No. missing[e]	Expected ratio[f]	Chi square[g]	df	Prob.[h]
Kinston[a]									
P_aS_1	10	8	0	0	2				
P_bS_1	10	0	4	0	6				
F_1	20	0	2	16	2				
F_2	100	17	16	32	35	1:1:2	0.09	2	0.96
BC_1P_a	30	7	1	4	18	1:0:1	0.83	1	0.36
BC_1P_b	30	0	11	13	6	0:1:1	0.17	1	0.68
Clinton[a]									
P_aS_1	10	2	0	0	8				
P_bS_1	10	0	4	0	6				
F_1	20	0	0	14	6				
F_2	100	17	14	35	34	1:1:2	0.56	2	0.76
BC_1P_a	30	9	0	9	12	1:0:1	0.00	1	1.00
BC_1P_b	30	0	10	11	9	0:1:1	0.00	1	1.00
Pooled[a]									
P_aS_1	20	10	0	0	10				
P_bS_1	20	0	8	0	12				
F_1	40	0	2	30	8				
F_2	200	34	30	67	69	1:1:2	0.36	2	0.84
BC_1P_a	60	16	1	13	30	1:0:1	0.33	1	0.57
BC_1P_b	60	0	21	24	15	0:1:1	0.09	1	0.76

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b P_a has near round fruit shape.
c P_b has elongate fruit shape.
d The heterozygote has intermediate oblong fruit shape.
e Some plants were missing or damaged.
f Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
g Heterogeneity χ^2 (0.05; 1)
h P-value (Probability) >.05 was accepted as Single Locus.

Table 3-19. Single locus goodness-of-fit-test for fruit shape in watermelon in family 'Red-N-Sweet' (Near round) × 'Charleston Gray' (Elongate).

Location/ Generation	Total no.	Near round[b]	Elongate[c]	Oblong[d]	No. missing[e]	Expected ratio[f]	Chi square[g]	df	Prob.[h]
Kinston[a]									
P_aS_1	10	10	0	0	0				
P_bS_1	10	0	2	0	8				
F_1	20	1	0	13	6				
F_2	100	25	18	46	11	1:1:2	1.16	2	0.56
BC_1P_a	30	13	0	15	2	1:0:1	0.14	1	0.71
BC_1P_b	30	0	14	13	3	0:1:1	0.00	1	1.00
Clinton[a]									
P_aS_1	10	9	0	0	1				
P_bS_1	10	0	6	0	4				
F_1	20	0	0	16	4				
F_2	100	19	18	40	23	1:1:2	0.08	2	0.96
BC_1P_a	30	12	0	14	4	1:0:1	0.15	1	0.70
BC_1P_b	30	0	11	18	1	0:1:1	1.42	1	0.23
Pooled[a]									
P_aS_1	20	19	0	0	1				
P_bS_1	20	0	8	0	12				
F_1	40	1	0	29	10				
F_2	200	44	36	86	34	1:1:2	0.58	2	0.75
BC_1P_a	60	25	0	29	6	1:0:1	0.30	1	0.58
BC_1P_b	60	0	25	31	4	0:1:1	0.64	1	0.42

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b P_a has near round fruit shape.
c P_b has elongate fruit shape.
d The heterozygote has intermediate oblong fruit shape.
e Some plants were missing or damaged.
f Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
g Heterogeneity χ^2 (0.05; 1)
h P-value (Probability) >.05 was accepted as Single Locus.

Table 3-20. Single locus goodness-of-fit-test for shape in watermelon in family 'Allsweet' (Elongate) × 'Black Diamond' (Near round).

Location/ Generation	Total no.	Elongate[b]	Near round[c]	Oblong[d]	No. missing[e]	Expected ratio[f]	Chi square[g]	df	Prob.[h]
Kinston[a]									
P_aS_1	10	9	0	0	1				
P_bS_1	10	0	10	0	0				
F_1	20	0	0	20	0				
F_2	100	18	24	54	4	1:1:2	2.25	2	0.32
BC_1P_a	30	15	1	14	0	1:0:1	0.07	1	0.79
BC_1P_b	30	2	11	12	5	0:1:1	0.17	1	0.68
Clinton[a]									
P_aS_1	10	8	0	0	2				
P_bS_1	10	0	10	0	0				
F_1	20	0	0	20	0				
F_2	100	19	30	46	5	1:1:2	2.25	2	0.32
BC_1P_a	30	13	0	16	1	1:0:1	0.14	1	0.71
BC_1P_b	30	0	11	17	2	0:1:1	1.29	1	0.26
Pooled[a]									
P_aS_1	20	17	0	0	3				
P_bS_1	20	0	20	0	0				
F_1	40	0	2	40	0				
F_2	200	37	54	100	9	1:1:2	3.00	2	0.22
BC_1P_a	60	28	1	30	1	1:0:1	0.07	1	0.79
BC_1P_b	60	2	22	29	7	0:1:1	0.74	1	0.39

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b P_a has elongate fruit shape.
c P_b has near round fruit shape.
d The heterozygote has intermediate oblong fruit shape.
e Some plants were missing or damaged.
f Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
g Heterogeneity χ^2 (0.05; 1)
h P-value (Probability) >.05 was accepted as Single Locus.

Table 3-21. Single locus goodness-of-fit-test for fruit shape in watermelon in family 'Allsweet' (Elongate) × 'King&Queen' (round).

Location/ Generation	Total no.	Elongate[b]	Near round[c]	Oblong[d]	No. missing[e]	Expected ratio[f]	Chi square[g]	df	Prob.[h]
Kinston[a]									
P_aS_1	10	10	0	0	0				
P_bS_1	10	0	10	0	0				
F_1	20	1	1	18	0				
F_2	100	27	27	42	4	1:1:2	1.5	2	0.47
BC_1P_a	30	15	1	12	2	1:0:1	0.36	1	0.55
BC_1P_b	30	0	6	24	0	0:1:1	10.8	1	0.00[h]
Clinton[a]									
P_aS_1	10	9	0	1	0				
P_bS_1	10	0	9	0	1				
F_1	20	0	0	16	4				
F_2	100	17	14	54	15	1:1:2	5.91	2	0.05
BC_1P_a	30	12	1	14	3	1:0:1	0.15	1	0.70
BC_1P_b	30	0	7	22	1	0:1:1	6.53	1	0.01[h]
Pooled[a]									
P_aS_1	20	19	0	1	0				
P_bS_1	20	0	19	0	1				
F_1	40	1	1	34	4				
F_2	200	44	41	96	19	1:1:2	0.65	2	0.72
BC_1P_a	60	27	2	26	5	1:0:1	0.01	1	0.92
BC_1P_b	60	0	13	46	1	0:1:1	17.4	1	0.00[h]

a Data are ratings from two locations: Kinston and Clinton; data are presented by location and pooled over locations.
b P_a has elongate fruit shape.
c P_b has round fruit shape.
d The heterozygote has intermediate oblong fruit shape.
e Some plants were missing or damaged.
f Expected was the hypothesized segregation ratio for single gene inheritance for each segregating generation
g Heterogeneity χ^2 (0.05; 1)
h P-value (Probability) >.05 was accepted as Single Locus.

Table 3-22. Suggested genotypes and corresponding phenotypes for the genes controlling stripe pattern in watermelon.

Genotype suggested		Phenotype	Type line
GG	??[a]	Solid medium green	California Klondike; Peacock Shipper
$g^M g^M$	??	Medium wide stripe	Crimson Sweet
$g^N g^N$	??	Narrow stripe	Red-N-Sweet
gg		Gray	Thurmond Gray; Charleston Gray
GG (or $g^M g^M$ *or* $g^N g^N$ *or ??*)	*NsNs*	Wide stripe	Allsweet; Tendersweet OF
$g^N g^N$	*nsns*	Narrow stripe	Red-N-Sweet
gg	n*sns*	Solid light green	King&Queen
gg	*NsNs*	??	??

a Unknown genotype or type line.

Table 3-23. Suggested genotypes and corresponding phenotypes for the genes controlling fruit shape in watermelon.

Genotype suggested			Phenotype	Type line
OO	*??*[a]	*??*	Elongate	Long Iowa Belle; Allsweet; Charleston Gray
oo	*??*	*??*	Round	Round Iowa Belle; China 23; Japan 4; Japan 6; Red-N-Sweet; Black Diamond
oo	*ObOb*	*elel*	Near-round	Black Diamond
OO	*obob*	*elel*	Elongate	Charleston Gray
??	*obob*	*ElEl*	Elongate	Peacock Shipper
OO	*obob*	*elel*	Oblong	Charleston Gray
oo	*ObOb*	*??*	Near-round	Red-N-Sweet; Crimson Sweet
??	*obob*	*ElEl*	Oblong	Tendersweet OF; Peacock Shipper
oo	*obob*	*??*	Near-round	??

a Unknown genotype or type line.

CHAPTER FOUR

QUANTITATIVE INHERITANCE OF FRUIT WEIGHT AND THE TOTAL SOLUBLE SOLIDS CONTENT IN WATERMELON

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Introduction

Watermelon [*Citrullus lanatus* (Thunb.) Matsumura & Nakai] is native to southern and tropical Africa and probably Asia. Watermelon is an important vegetable cultivated in warm regions world wide. The top five of watermelon production countries are China (accounts for 73% of the world watermelon production in 2004), Turkey, Iran, the United States, Egypt, and Mexico (www.fao.org). In the U. S., the Agricultural Marketing Resource Center recorded watermelon production at 4.29 billion pounds in 2007. In 2008, watermelon production totaled 4.3 billion pounds with a $492 million value for the fresh market. The top five states in U.S. watermelon production, accounting for more than 75 percent of the total production, were Georgia, Florida, Texas, California and Arizona (www.agmrc.org).

Extensive genetic studies and breeding experiments since the 1930s have identified more than one hundred genes are related to phenotypes in seed and seedling, vine, flower, frduit, and resistance (Wehner, 2008a). A comprehensive list of these genes can be found in recent reviews (Guner and Wehner, 2004; Wehner, 2008a).

Cultivated watermelon has a large variation in fruit weight, from less than 0.5 kg to more than 100 kg (Gusmini and Wehner, 2007). This variation in fruit weight has been used to satisfy different commercial interests. In the United States, the weight of commercial watermelon fruit can be classified into five categories: icebox (<5.5 kg), small or pee wee (5.5 to 8.0 kg), medium (8.1 to 11.0 kg), large (11.1 to 14.5 kg) and giant (> 14.5 kg) (Maynard, 2001). In 2003, a new fruit size category, mini watermelon, was introduced for

cultivars that produce round fruit, have a thin rind, and weighing between 1.5 to 4 kg (Schultheis et al., 2005).

Besides environmental factors, fruit weight also varies among cultivars. The cultivars 'Cobbs Gem', 'Carolina Cross #183', 'Florida Giant', and 'Weeks NC Giant' are popular cultivars that can produce giant fruit. For example, 'Carolina Cross #183' can produce fruit of about 100 kg (Gusmini and Wehner, 2007). One of the smallest fruited watermelon cultivar is 'New Hampshire Midget', released by the University of New Hampshire in 1951. This cultivar produces mini-sized fruit of about 1 kg weight (Wehner, 2002). Some wild watermelon accessions, such as *C. colocynthis*, have fruit weight of less than 0.5 kg (Gusmini and Wehner, 2007).

Over 100 genes have been reported that affect various qualitative traits in watermelon, but none controlling fruit weight (Gusmini and Wehner, 2007; Wehner, 2008a). Two studies on the inheritance of fruit weight have reported significant additive, dominance, and epistatic effects, with dominance and dominance-by-dominance being the largest gene effects (Brar and Nandpuri, 1974; Sharma and Choudhury, 1988). Gusmini and Wehner (2007) investigated the inheritance of six cultivars with very large and very small fruit and indicated that large-fruited parents had higher phenotypic variance than small-fruited parents, and narrow- and broad-sense heritability estimates were moderate (mean = 0.59 and 0.41, respectively) with a small number of effective factor (5.4) (the number of effective factor is an estimate of the number of genes controlling a trait). The authors suggested that, although watermelon fruit weight can be improved rapidly using a high selection intensity (5%), progeny testing was recommended (Gusmini and Wehner, 2007).

The total soluble solids content is another quantitative trait of great interest. The total soluble solids content is measured as degree of Brix using a refractometer and is translated into sugar content. The total soluble solids content is correlated to the sweetness of watermelon flesh. The flavor of watermelon was found to be acceptably correlated with total soluble solids content, but less correlated with sweetness (Pardo et al., 1997). The total soluble solids content can be classified as low (<6.50%), medium (6.50-9.99%) or high (>9.99%) (Sharma and Choudhury, 1988). High sugar content cultivars are selected by breeders. Some cultivars have Brix as high as 14% (Wehner, 2008b).

The total soluble solids content in unit amount of watermelon flesh is dependent on cultivar and environmental factors (Porter, 1940). Showalter (1961) reported a positive correlation between fruit weight and the total soluble solids content during fruit maturation. Total soluble solids content in watermelon increases as the fruit grows and matures. However, no correlation between fruit weight and the total soluble solids content was found for watermelons of the same ripeness. The total soluble solids content was found to be determined by three incompletely dominant genes in the cross 'Crimson Sweet' × 'New Hampshire Midget' (Suzuki and Hall, 1971). This conclusion was confirmed by a later study that found the total soluble solids content was controlled by 3 genes in the families 'Kaho' × 'Leeby' and 'Leeby' × 'Kaho' and 1 to 3 genes in the families 'Congo' × 'Leeby' (El-Hafez et al., 1985). The authors also found that watermelon with orange flesh color had a higher total soluble solids content than ones that were white. In another study, the high total soluble solids content was found to be partial dominant, and the narrow-sense heritability was 0.68 (Brar and Nandpuri, 1977). On the other hand, dominance gene effects and dominance by

dominance epistasis were found be to be important for total soluble solids content (Sharma and Choudhury, 1988).

The objective of this experiment was to measure the inheritance of single fruit weight and the total soluble solids content in watermelon. As part of the study, we measured the genetic, additive, and environmental variances, narrow-sense heritability, broad-sense heritability, and numbers of effective factors controlling these two traits.

Materials and Methods

Traits and Families

A total of 15 families were developed using 10 watermelon inbred cultivars or lines (Table 4-1). We developed six generations (P_aS_1, P_bS_1, F_1, F_2, BC_1P_a, BC_1P_b) for each family by making controlled crosses in the greenhouses at North Carolina State University in Raleigh, North Carolina. Seeds of the inbred lines used in these experiments were obtained from the gene mutant collection of the Cucurbit Genetics Cooperative (Curators: T.C. Wehner and S.R. King).

Ten watermelon cultivars were used as parents: 'PDS 808', 'Red-N-Sweet', 'Crimson Sweet', 'Allsweet', 'Black Diamond', 'Tendersweet Orange Flesh', 'Charleston Gray', 'King&Queen', 'Peacock Shipper', and 'Cream of Saskatchewan'. Fifteen families were developed using those parents for fruit weight traits (Table 4-1.), and 4 families were developed to study the total soluble solids content (Table 4-5).

Cultural Practices

Seeds of the six generations for each family were sown in 72-cell polyethylene flats in the greenhouses at North Carolina State University. An artificial soilless growing medium was used, consisting of Canadian sphagnum peat moss, perlite, vermiculite, and processed pine bark. The flats were moistened to capacity after seeding and kept in a greenhouse (25-30 °C) until full emergence (Fig. 11). The transplants were moved to cold frames for acclimation one week before transplanting. The seedlings were transplanted by hand at the two-true-leaf stage. Missing or damaged transplants were replaced a week after the initial transplanting.

In the field, raised beds were made up with drip irrigation tubes and covered with black polyethylene mulch. The experiment was conducted using horticultural practices recommended by the North Carolina Extension Service (Sanders, 2004). In order to keep plants separate for data collection, they were trained each week into a spiral shape until fruit began to set (Fig. 12). The vine training allowed easy tracing of the fruit to the plant that produced it.

One fully mature fruit was harvested from each plant. Fruit were determined to be ripe by looking for a dried tendril nearest the fruit, a light-colored ground spot, and a dull sound of the fruit when thumped (Maynard, 2001). Fruit weight was recorded, and fruit were cut in half to measure the total soluble solids content in degree of Brix using a portable digital refractometer. Distilled water was used to calibrate the refractometer. Samples were taken from the center of each fruit.

Experiment Design and Data Analysis.

Field experiments were performed in the summer of 2008 at two North Carolina locations: Cunningham Research Station in Kinston, and the Horticultural Crops Research Station in Clinton. All six generations of each family were planted at each location. For each location, there were 10 plants of P_aS_1, 10 of P_bS_1, 10 of F_1, 10 of F_1', 30 of BC_1P_a, 30 of BC_1P_b, and 100 of F_2. At Kinston families were planted in three rows 85 m long. At Clinton, each family was planted in 0.2 ha of field space with four rows 60 m long. The fields had raised and shaped beds (rows) on 3.1-m centers with single hills 1.2 m apart.

SASQuant 1.3 statement was used to analyze the data. The heritability and predicted selection response can be estimated by partitioning the total variance into genetic and environmental variances, and the genetic variance into additive and dominance components and inter-allelic interaction effects (Holland et al., 2003; Nyquist, 1991). The variance of the F_2 provides an estimate of phenotypic variance, while the mean variance of the non-segregating generations (P_a, P_b, and F_1) gives an estimate of environmental effects (Wright, 1968). The additive variance is derived by subtracting the variances of the backcrosses from twice the phenotypic (F_2) variance, as an extension of the single locus model under the hypothesis of absence of linkage and genotype by environment interactions (Warner, 1952). The broad- and narrow-sense heritability and the predicted gain from selection can then be calculated from the available estimates of genetic, additive, and phenotypic variances:

$$\sigma^2(P) = \sigma^2(F_2) \qquad \sigma^2(E) = \frac{\sigma^2(P_a) + \sigma^2(P_b) + \left[2 \times \sigma^2(F_1)\right]}{4}$$

$$\sigma^2(G) = \sigma^2(P) - \sigma^2(E) \qquad \sigma^2(A) = \left[2 \times \sigma^2(F_2)\right] - \left[\sigma^2(BC_1P_a) + \sigma^2(BC_1P_a)\right]$$

The number of effective factors is an estimate of genetic factors affecting a quantitative trait and is determined using 5 methods: (Lande, 1981; Mather and Jinks, 1982; Wright, 1968):

Lande's method I: $$\frac{\left[\mu(P_b)-\mu(P_a)\right]^2}{8\times\left\{\sigma^2(F_2)-\frac{\sigma^2(P_a)+\sigma^2(P_b)+\left[2\times\sigma^2(F_1)\right]}{4}\right\}}$$

Lande's method II: $$\frac{\left[\mu(P_b)-\mu(P_a)\right]^2}{8\times\left\{\left[2\times\sigma^2(F_2)\right]-\left[\sigma^2(BC_1P_a)+\sigma^2(BC_1P_a)\right]\right\}}$$

Lande's method III: $$\frac{\left[\mu(P_b)-\mu(P_a)\right]^2}{\left\{8\times\left[\sigma^2(BC_1P_a)+\sigma^2(BC_1P_a)-\sigma^2(F_1)\right]\right\}-\frac{\left[\sigma^2(P_a)+\sigma^2(P_b)\right]}{2}}$$

Mather's method: $$\frac{\frac{\left[\mu(P_b)-\mu(P_a)\right]^2}{2}}{\left[2\times\sigma^2(F_2)\right]-\left[\sigma^2(BC_1P_a)+\sigma^2(BC_1P_a)\right]}$$

Wright's method: $$\frac{\left[\mu(P_b)-\mu(P_a)\right]^2\times\left\{1.5-\left[2\times\frac{\mu(F_1)-\mu(P_a)}{\mu(P_b)-\mu(P_a)}\times\left(1-\frac{\mu(F_1)-\mu(P_a)}{\mu(P_b)-\mu(P_a)}\right)\right]\right\}}{8\times\left\{\sigma^2(F_2)-\frac{\sigma^2(P_a)+\sigma^2(P_b)+\left[2\times\sigma^2(F_1)\right]}{4}\right\}}$$

In the study by Gusmini and Wehner (2007), Wright's method and Lande's method I both provided good estimates for the genetic effective factors of watermelon fruit weight. The estimated gain from selection per cycle was calculated by the equation $k\times h_n^2\times\sqrt{\sigma^2(P)}$, where k is the selection differential in standard deviation units for selection intensities of 5%, 10%, or 20% (Hallauer and Miranda, 1988). The statistical analysis was performed using the SAS-STAT statistical package (SAS Institute, Cary, North Carolina).

Results and Discussion

Fifteen families were evaluated for the fruit weight (Table 4-1), and four families for the total soluble solids content: 1) 'Red-N-Sweet' × 'King&Queen', 2) 'Crimson Sweet' × 'King&Queen', 3) 'Allsweet' × 'King&Queen', 4) 'King&Queen' × 'Peacock Shipper' (Table 4-5).

Fruit Weight

Normal distributions for fruit weight were obtained for the F_2 generation in all 15 families. In this experiment, the parents in some families differed for fruit weight, and some did not (Table 4-1). Families are often developed in a plant breeding program where the parents do not differ for the weight per fruit, and we wanted to determine the differences in heritability for situations where there were large differences vs. no differences between the parents for that trait. We checked the consistency of the data by comparing the mean fruit weight for the same cultivars in different experiments. Several cultivars, including 'Red-N-Sweet', 'Crimson Sweet', 'Charleston Gray', and 'Black Diamond' were involved in multiple families, and the measured mean weights are consistent within the experiments (Table 4-1). Exceptions were found for the Clinton location of families 'Allsweet' × 'Black Diamond', 'Peacock Shipper' × 'Charleston Gray', 'Black Diamond' × 'Charleston Gray', and 'King&Queen' × 'Peacock Shipper'. The problem was that plants in these families were eliminated by disease that destroyed the vines so the harvested fruit were not fully developed. Therefore, data from these families were not analyzed.

For each family, we examined the deviation of mean weight in the F_1 generation from the average of their parent cultivars. Interestingly, the deviation depended on the difference

in the parent weight. For families where the mean weight difference between parents was large (>2 kg), the mean weight in the F_1 generation was close to the parent mean. Such families included 'Red-N-Sweet' × 'Black Diamond', 'Crimson sweet' × 'King&Queen', 'Crimson sweet' × 'Peacock Shipper', 'Cream of Saskatchewan' ×'Red-N-Sweet', 'Allsweet' × 'King&Queen', and 'Red-N-Sweet' × 'King&Queen'. However, for families where the mean weight difference in the parents was small (<2 kg), large deviations were found in F_1 mean weight from the parents' mean. This was the case for 'PDS 808' × 'Red-N-Sweet', 'Red-N-Sweet' × 'Crimson Sweet', 'Red-N-Sweet' × 'Allsweet', 'Tendersweet Orange Flesh' × 'Red-N-Sweet', 'Red-N-Sweet' × 'Charleston Gray', 'Allsweet' × 'Black Diamond', 'Allsweet' × 'Black Diamond', 'Peacock Shipper' × 'Charleston Gray', and 'Black Diamond' × 'Charleston Gray'. In other words, the additive effects were prominent only for the families that involved parents with large mean weight differences. In addition, we found that the mean weight in the F_1 generation was correlated with that in the F_2 generation. The R^2 values were 0.7179 at Kinston and 0.6658 at Clinton.

In two of the families (Red-N-Sweet × Crimson Sweet and Red-N-Sweet × Allsweet), the mean weight in the F_1 generations was significantly higher than the average of the mean weights of the parents. The enhancements were also observed in the F_2 and backcrossing generations, where the mean weights were higher than the parents' means, but lower than the F_1 mean. The above observations suggest that there are heterosis in these two families. The F_1 generation had the highest mean weight because the genotypes were all heterozygous, while the enhancements were slightly weaker in F_2 and backcross generations because only half of genotypes were heterozygous. Interestingly, for both families where the heterosis was

found, the mean weights of the two parents are similar. In contrast, we did not find heterosis in families where the mean weight differences are larger than 2 kg. One possible explanation is that the genotype differences might be smaller in the families where parents have similar mean weight so that the heterosis in very few loci will cause significant phenotypic difference. While in families where more loci are involved, the effect in one locus will be masked by the additive effects in other loci, and the phenotype are more similar.

As is the case for most traits, there was a correlation between the mean and variance for fruit weight for the parents (Table 4-2). However, the correlation was not high (R2= 0.3584 at Kinston). In fact, for parents with low means, the variances were the lowest. On the other hand, for parents with large weight means, the variances were not necessarily larger. For the F_1 generation, there was no correlation between the mean weight and the variance of the weight. Strong correlation between the mean and the variance for fruit weight was found in the F_2 generation (R^2= 0.8038 at Kinston). Environmental variance was larger than genetic variance for the majority of the families (Table 4-2). The heritability for fruit weight was low to medium. The broad-sense heritability was 0.42 at Kinston and 0.36 at Clinton. The narrow-sense heritability was 0.49 at Kinston and 0.46 at Clinton. The narrow-sense heritability was larger than the broad-sense heritability (theoretically impossible, but not uncommon with estimates), indicating that additive variance was important and dominance variance was not important in fruit weight.

The number of effective factors, an estimate of the number of genes controlling fruit weight, was estimated for each family and location. Most of the estimates for number of effective factors were zero, except in the family 'Red-N-Sweet' × ' King&Queen' at Kinston,

where the estimated number of effective factors was 15, and in 'Allsweet' × 'King&Queen' where the estimated number of effective factors was 2 (Table 4-4).

Total Soluble Solids Content

The total soluble solids content of the fruit was measured in four families in the two locations. Two families at Clinton did not develop properly because of disease, so the data were not analyzed. One of the cultivars ('King&Queen') was used as a parent in all families and the total soluble solids content measured for this cultivar in different experiments were consistent, indicating good repeatability over tests for the total soluble solids content.

For each of the families, the mean for the total soluble solids content in both the F_1 and F_2 were between the mean values of their parents (Table 4-5). This observation indicates that additive effects are large for the trait. As expected, the narrow-sense heritability was high (Table 4-7). The trend was also observed in the backcrosses.

The additive effect observed from the mean values is consistent with the variance analysis results (Table 4-7). The variance in the F_2 generation is larger than the parental variance in most of the families (Table 4-6). The total soluble solids content had a narrow-sense heritability of 0.48 at Kinston and 0.94 at Clinton. Broad-sense heritability is 0.53 at Kinston and 0.63 at Clinton (Table 4-7).

The number of effective factors was estimated for each family and location. The majority of the estimated numbers of effective factors was zero, except the family 'Red-N-Sweet' × ' King&Queen' in Kinston with the mean estimated number of effective factors of 5

(Table 4-8.). Due to the high narrow-sense heritability, the estimated gains from selection are also relatively high (Table 4-8).

Conclusion

The inheritance of the quantitative traits of the weight and total soluble solids content of watermelons fruits were studied. The results have implication in breeding watermelon cultivars with either heavy or light fruits, or fruits with higher total soluble solids content. For fruit weight, we found that the environmental variance was larger than the genetic variance and narrow-sense and broad-sense heritability were low to medium. This result indicates that the environmental effect is an important factor affecting the fruit weight and the low to medium heritability, which is consistent to the earlier research, indicates selection for fruit weight is only effective when a high selection intensity (5%) is used. For total soluble solids content, the variance in F_2 generation is larger than the parental variance and narrow-sense and broad-sense heritability were medium to high. The higher heritability indicates selection for total soluble solids content would be more effective using a same selection intensity.

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Table 4-1. Generation Means by Set Family for fruit weight (kg) for the watermelon families tested for fruit weight in 2008 at Clinton and Kinston, North Carolina[a].

Pedigree/ location	Mean					
	P_a	P_b	F_1	F_2	BC_1P_a	BC_1P_b
Kinston						
PDS 808 × Red-N-Sweet	11.6	10.7	7.8	9.6	7.7	11.5
Red-N-Sweet × Crimson Sweet	10.6	10.4	14.8	13.4	13.1	11.6
Red-N-Sweet × Allsweet	9.8	10.2	13.0	11.3	11.5	11.0
Red-N-Sweet × Black Diamond	10.7	15.1	12.4	9.6	8.6	11.2
Tendersweet OF × Red-N-Sweet	10.2	10.3	8.7	8.8	9.4	8.7
Red-N-Sweet × Charleston Gray	9.4	7.9	10.3	9.8	11.4	11.1
Crimson sweet × King&Queen	8.7	5.0	7.1	6.1	8.2	7.3
Crimson sweet × Peacock Shipper	11.2	7.0	9.7	8.4	9.8	7.0
Cream of Sask. × Red-N-Sweet	4.7	10.0	7.4	9.1	6.2	9.5
Allsweet × King&Queen	10.3	4.4	7.0	6.1	7.1	5.4
Allsweet × Black Diamond	10.0	9.5	8.9	9.7	8.2	10.0
Peacock Shipper × Charleston Gray	8.1	9.6	10.6	9.1	8.6	9.6
Black Diamond × Charleston Gray	9.9	9.5	10.7	10.8	10.0	10.4
King&Queen × Peacock shipper	5.7	7.8	7.2	6.7	5.6	7.7
Red-N-Sweet × King&Queen	11.5	5.4	8.4	8.3	9.9	7.7
Clinton						
PDS 808 × Red-N-Sweet	11.0	9.4	7.8	7.2	4.6	5.8
Red-N-Sweet × Crimson Sweet	9.8	10.0	11.6	8.8	7.6	8.0
Red-N-Sweet × Allsweet	10.9	10.4	13.1	9.8	6.7	10.5
Red-N-Sweet × Black Diamond	10.1	12.0	11.4	11.5	12.4	10.5
Tendersweet OF × Red-N-Sweet	12.1	11.0	11.3	11.8	12.1	12.5
Red-N-Sweet × Charleston Gray	7.0	8.6	10.4	10.0	9.5	10.5
Crimson sweet × King&Queen	10.2	5.2	8.1	7.2	8.6	9.0
Crimson sweet × Peacock Shipper	10.2	5.4	9.0	8.4	9.2	6.6
Cream of Sask. × Red-N-Sweet	5.7	7.9	7.5	8.5	7.7	8.5
Allsweet × King&Queen	6.1	4.1	5.6	5.3	5.8	5.3
Allsweet × Black Diamond	7.2	7.4	9.7	8.6	7.8	10.0
Peacock Shipper × Charleston Gray[b]	7.0	10.3	8.1	6.4	9.1	8.7
Black Diamond × Charleston Gray[b]	7.8	7.6	8.8	9.3	8.1	10.0
King&Queen × Peacock shipper[b]	4.9	7.2	5.8	3.9	4.4	5.3
Red-N-Sweet × King&Queen[b]	7.8	4.0	6.8	5.7	6.1	4.1

a Data are single-fruit weights (kg).

b Data in families Peacock Shipper × Charleston Gray, Black Diamond × Charleston Gray, King&Queen × Peacock shipper, and Red-N-Sweet × King&Queen at Clinton are not comparable due to disease that destroyed the vines.

Table 4-2. Phenotypic variances by generation for the watermelon families tested for fruit weight in 2008 at Clinton and Kinston, North Carolina[a].

Pedigree/ location	Variance					
	$\sigma^2(P_a)$	$\sigma^2(P_b)$	$\sigma^2(F_1)$	$\sigma^2(F_2)$	$\sigma^2(BC_1P_a)$	$\sigma^2(BC_1P_b)$
Kinston						
PDS 808 × Red-N-Sweet	6.12	4.13	5.58	8.22	4.62	7.75
Red-N-Sweet × Crimson Sweet	6.09	10.34	12.16	16.28	10.92	7.42
Red-N-Sweet × Allsweet	4.18	3.92	7.27	12.37	7.31	8.69
Red-N-Sweet × Black Diamond	2.58	23.88	17.58	10.38	4.47	8.85
Tendersweet OF × Red-N-Sweet	10.73	3.77	3.92	7.59	4.58	7.26
Red-N-Sweet × Charleston Gray	8.89	5.05	5.76	10.05	10.28	13.96
Crimson sweet × King&Queen	6.46	1.10	9.15	4.60	4.98	6.26
Crimson sweet × Peacock Shipper	13.47	2.62	11.04	6.97	12.86	1.28
Cream of Sask. × Red-N-Sweet	1.01	4.28	10.06	5.48	1.80	5.02
Allsweet × King&Queen	4.59	0.88	3.24	2.66	5.02	1.98
Allsweet × Black Diamond	3.01	19.70	11.44	8.01	3.66	30.81
Peacock Shipper × Charleston Gray	1.75	6.63	1.96	5.34	3.70	6.26
Black Diamond × Charleston Gray	18.78	3.65	7.82	7.38	10.02	4.91
King&Queen × Peacock shipper	2.35	1.39	1.10	3.84	1.45	5.26
Red-N-Sweet × King&Queen	5.41	2.24	2.40	5.46	8.18	2.39
Clinton						
PDS 808 × Red-N-Sweet	8.16	2.01	2.78	4.51	2.42	2.79
Red-N-Sweet × Crimson Sweet	7.48	6.27	5.28	5.62	8.33	5.59
Red-N-Sweet × Allsweet	14.84	11.95	3.55	7.34	3.35	7.25
Red-N-Sweet × Black Diamond	5.81	9.03	6.48	15.29	8.43	15.32
Tendersweet OF × Red-N-Sweet	9.38	5.46	4.81	12.94	10.15	9.83
Red-N-Sweet × Charleston Gray	5.52	3.96	5.25	6.86	5.28	6.67
Crimson sweet × King&Queen	11.34	0.47	3.04	3.34	4.32	3.65
Crimson sweet × Peacock Shipper	9.91	1.64	5.00	4.21	6.61	3.19
Cream of Sask. × Red-N-Sweet	0.79	2.52	2.75	4.45	3.35	3.63
Allsweet × King&Queen	3.08	1.13	2.50	2.71	1.65	3.10
Allsweet × Black Diamond	2.85	2.39	4.41	2.94	2.07	3.85
Peacock Shipper × Charleston Gray[b]	4.32	17.23	5.50	5.13	7.24	4.67
Black Diamond × Charleston Gray[b]	4.82	4.58	6.42	7.28	6.79	8.40
King&Queen × Peacock shipper[b]	2.68	1.61	2.48	14.22	1.79	2.66
Red-N-Sweet × King&Queen[b]	14.53	1.48	1.39	2.98	4.18	1.91

a Data are single-fruit weights (kg).

a Data in families Peacock Shipper × Charleston Gray, Black Diamond × Charleston Gray, King&Queen × Peacock shipper, and Red-N-Sweet × King&Queen at Clinton are not comparable due to disease that destroyed the vines.

Table 4-3. Variance and heritability estimates for the watermelon families tested for fruit weight in 2008 at Clinton and Kinston, North Carolina.

Pedigree/ location	Variance				Heritability	
	σ^2(P)[a]	σ^2(E)[b]	σ^2(G)[c]	σ^2(A)[d]	H[e]	h^2_n[f]
Kinston						
PDS 808 × Red-N-Sweet	8.22	5.35	2.86	4.05	0.35	0.49
Red-N-Sweet × Crimson Sweet	16.28	10.19	6.10	14.23	0.37	0.87
Red-N-Sweet × Allsweet	12.37	5.66	6.71	8.73	0.54	0.71
Red-N-Sweet × Black Diamond	10.38	15.41	-5.03	7.43	-0.48	0.72
Tendersweet OF × Red-N-Sweet	7.59	5.58	2.00	3.34	0.26	0.44
Red-N-Sweet × Charleston Gray	10.05	6.36	3.69	-4.13	0.37	-0.41
Crimson sweet × King&Queen	4.60	6.47	-1.86	-2.03	-0.40	-0.44
Crimson sweet × Peacock Shipper	6.97	9.54	-2.57	-0.21	-0.37	-0.03
Cream of Sask. × Red-N-Sweet	5.48	6.35	-0.87	4.15	-0.16	0.76
Allsweet × King&Queen	2.66	2.99	-0.33	-1.69	-0.13	-0.64
Allsweet × Black Diamond	8.01	11.40	-3.39	-18.46	-0.42	-2.31
Peacock Shipper × Charleston Gray	5.34	3.08	2.26	0.71	0.42	0.13
Black Diamond × Charleston Gray	7.38	9.52	-2.14	-0.17	-0.29	-0.02
King&Queen × Peacock shipper	3.84	1.48	2.36	0.97	0.61	0.25
Red-N-Sweet × King&Queen	5.46	3.11	2.35	0.35	0.43	0.06
Mean					**0.42**[g]	**0.49**[g]

a σ^2 (P) = phenotypic variance = $\sigma^2(F_2)$

b σ^2 (E) = environmental variance = $\frac{\sigma^2(P_a)+\sigma^2(P_b)+[2\times\sigma^2(F_1)]}{4}$

c σ^2 (G) = genetic variance = $\sigma^2(P)-\sigma^2(E)$

d σ^2 (A) = additive variance = $[2\times\sigma^2(F_2)]-[\sigma^2(BC_1P_a)+\sigma^2(BC_1P_a)]$

e H = broad-sense heritability

f h^2n = narrow-sense heritability

g The negative heritability was eliminated for calculation of the mean. Families Peacock Shipper × Charleston Gray, Black Diamond × Charleston Gray, King&Queen × Peacock shipper, and Red-N-Sweet × King&Queen are not included.

Table 4-3. Continued.

Pedigree/ location	Variance				Heritability	
	$\sigma^2(P)$[a]	$\sigma^2(E)$[b]	$\sigma^2(G)$[c]	$\sigma^2(A)$[d]	H[e]	h^2_n[f]
Clington						
PDS 808 × Red-N-Sweet	4.51	3.93	0.58	3.81	0.13	0.84
Red-N-Sweet × Crimson Sweet	5.62	6.08	-0.46	-2.67	-0.08	-0.48
Red-N-Sweet × Allsweet	7.34	8.47	-1.13	4.07	-0.15	0.55
Red-N-Sweet × Black Diamond	15.29	6.95	8.35	6.83	0.55	0.45
Tendersweet OF × Red-N-Sweet	12.94	6.12	6.83	5.90	0.53	0.46
Red-N-Sweet × Charleston Gray	6.86	4.99	1.87	1.77	0.27	0.26
Crimson sweet × King&Queen	3.34	4.47	-1.14	-1.31	-0.34	-0.39
Crimson sweet × Peacock Shipper	4.21	5.38	-1.17	-1.38	-0.28	-0.33
Cream of Sask. × Red-N-Sweet	4.45	2.20	2.24	1.90	0.50	0.43
Allsweet × King&Queen	2.71	2.30	0.41	0.67	0.15	0.25
Allsweet × Black Diamond	2.94	3.51	-0.57	-0.04	-0.19	-0.01
Peacock Shipper × Charleston Gray	5.13	8.14	-3.01	-1.65	-0.59	-0.32
Black Diamond × Charleston Gray	7.28	5.56	1.72	-0.63	0.24	-0.09
King&Queen × Peacock shipper	14.22	2.31	11.91	24.00	0.84	1.69
Red-N-Sweet × King&Queen	2.98	4.70	-1.72	-0.13	-0.58	-0.04
Mean					**0.36**[g]	**0.46**[g]

a σ^2 (P) = phenotypic variance = $\sigma^2(F_2)$

b σ^2 (E) = environmental variance = $\dfrac{\sigma^2(P_a)+\sigma^2(P_b)+\left[2\times\sigma^2(F_1)\right]}{4}$

c σ^2 (G) = genetic variance = $\sigma^2(P)-\sigma^2(E)$

d σ^2 (A) = additive variance = $\left[2\times\sigma^2(F_2)\right]-\left[\sigma^2(BC_1P_a)+\sigma^2(BC_1P_a)\right]$

e H = broad-sense heritability

f h^2n = narrow-sense heritability

g The negative heritability was eliminated for calculation of the mean. Families Peacock Shipper × Charleston Gray, Black Diamond × Charleston Gray, King&Queen × Peacock shipper, and Red-N-Sweet × King&Queen are not included.

Table 4-4. Estimates of number of effective factors and predicted gain from selection under different selection intensities for the watermelon families tested for fruit weight in 2008 at Clinton and Kinston, North Carolina.

Pedigree/ location	Effective number[a]						Gain from selection[b]		
	Lande I	Lande II	Lande III	Mather	Wight	Mean	5%	10%	20%
Kinston									
PDS 808 × Red-N-Sweet	1.0	0.1	0.0	0.0	0.1	0.2	2.9	2.5	2.0
Red-N-Sweet × Crimson Sweet	0.7	0.0	0.0	0.0	-0.0	0.1	7.3	6.2	4.9
Red-N-Sweet × Allsweet	0.3	0.0	0.0	0.0	0.0	0.1	5.1	4.4	3.5
Red-N-Sweet × Black Diamond	-0.5	1.3	-0.5	0.3	-0.1	0.1	4.8	4.1	3.2
Tendersweet OF × Red-N-Sweet	0.3	0.0	0.0	0.0	0.0	0.1	2.5	2.1	1.7
Red-N-Sweet × Charleston Gray	0.2	-0.3	0.1	-0.1	0.0	0.0	-2.7	-2.3	-1.8
Crimson sweet × King&Queen	-0.9	-3.4	-0.9	-0.9	-1.0	-1.4	-2.0	-1.7	-1.3
Crimson sweet × Peacock Shipper	-0.9	-42.9	-0.9	-10.7	-0.5	-11.2	-0.2	-0.1	-0.1
Cream of Sask. × Red-N-Sweet	-4.1	3.5	-4.1	0.9	-0.6	-0.9	3.6	3.1	2.5
Allsweet × King&Queen	-13.2	-10.3	-13.1	-2.6	4.2	-7.0	-2.1	-1.8	-1.5
Allsweet × Black Diamond	-0.1	-0.0	-0.0	-0.0	0.0	-0.0	-13.4	-11.5	-9.1
Peacock Shipper × Charleston Gray	0.5	1.6	0.1	0.4	0.1	0.5	0.6	0.5	0.4
Black Diamond × Charleston Gray	-0.1	-0.5	-0.0	-0.1	-0.0	-0.1	-0.1	-0.1	-0.1
King&Queen × Peacock shipper	0.2	2.2	0.2	0.5	0.1	0.7	1.0	0.9	0.7
Red-N-Sweet × King&Queen	2.0	54.2	2.0	13.6	1.1	14.6	0.3	0.3	0.2
Clinton									
PDS 808 × Red-N-Sweet	3.1	0.4	0.6	0.1	-0.1	0.8	3.7	3.2	2.5
Red-N-Sweet × Crimson Sweet	-1.6	-0.0	-0.0	-0.0	0.0	-0.3	-2.3	-2.0	-1.6
Red-N-Sweet × Allsweet	-1.3	0.0	-0.0	0.0	-0.0	-0.3	3.1	2.6	2.1
Red-N-Sweet × Black Diamond	0.1	0.3	0.1	0.1	0.0	0.1	3.6	3.1	2.4
Tendersweet OF × Red-N-Sweet	0.0	0.1	0.0	0.0	0.0	0.0	3.4	2.9	2.3
Red-N-Sweet × Charleston Gray	1.1	0.7	0.2	0.2	0.2	0.5	1.4	1.2	0.9
Crimson sweet × King&Queen	-2.8	-9.7	-2.8	-2.4	-3.3	-4.2	-1.5	-1.3	-1.0
Crimson sweet × Peacock Shipper	-2.8	-8.5	-2.5	-2.1	-3.0	-3.8	-1.4	-1.2	-0.9
Cream of Sask. × Red-N-Sweet	0.3	1.2	0.3	0.3	0.2	0.5	1.9	1.6	1.3
Allsweet × King&Queen	1.4	3.0	1.2	0.7	3.4	1.9	0.8	0.7	0.6
Allsweet × Black Diamond	-2.4	-0.7	-0.0	-0.2	-0.0	-0.7	-0.0	-0.0	-0.0
Peacock Shipper × Charleston Gray	-0.5	-3.3	-0.5	-0.8	-0.3	-1.1	-1.5	-1.3	-1.0
Black Diamond × Charleston Gray	0.2	-0.0	0.0	-0.0	0.0	0.0	-0.5	-0.4	-0.3
King&Queen × Peacock shipper	0.1	0.1	0.1	0.0	-3.5	-0.7	13.1	11.2	8.9
Red-N-Sweet × King&Queen	-1.2	-54.5	-1.0	-13.6	-0.5	-14.2	-0.2	-0.1	-0.1

a The number of effect factor are estimated by 5 different methods: Lande I, Lande II, Lande III, Mather, Wight.

b The gain from selection was calculated for 3 different selection intensities: 5%, 15%, 20%.

Gain= $k \times h_n^2 \times \sqrt{\sigma^2(P)}$.

Table 4-5. Generation Means by Set Family for Brix value in Watermelon.

Pedigree/ location	Mean					
	P_a	P_b	F_1	F_2	BC_1P_a	BC_1P_b
Kinston						
Crimson sweet × King&Queen	9.6	8.1	9.2	8.8	9.6	8.7
Allsweet × King&Queen	10.2	8.9	10.0	9.2	9.7	9.2
King&Queen × Peacock shipper	9.2	11.2	9.5	9.9	9.4	11.0
Red-N-Sweet × King&Queen	12.4	8.8	10.1	10.8	10.9	11.1
Clinton						
Crimson sweet × King&Queen	9.6	8.0	9.2	9.6	9.6	9.1
Allsweet × King&Queen	8.7	8.1	8.1	8.0	8.2	6.8
King&Queen × Peacock shipper	6.6	8.7	5.5	6.5	5.9	6.4
Red-N-Sweet × King&Queen	9.1	9.0	11.1	7.5	9.3	9.2

Table 4-6. Phenotypic variances by generation for watermelon Brix value in 2008 at Clinton and Kinston, North Carolina.

Pedigree/ location	Variance					
	$\sigma^2(P_a)$	$\sigma^2(P_b)$	$\sigma^2(F_1)$	$\sigma^2(F_2)$	$\sigma^2(BC_1P_a)$	$\sigma^2(BC_1P_b)$
Kinston						
Crimson sweet × King&Queen	1.41	3.81	1.31	1.29	1.18	0.85
Allsweet × King&Queen	0.62	1.88	0.68	1.30	1.54	1.20
King&Queen × Peacock shipper	0.84	0.62	0.47	2.75	1.94	1.32
Red-N-Sweet × King&Queen	0.93	1.73	0.47	2.05	3.27	0.41
Clinton						
Crimson sweet × King&Queen	0.78	1.00	0.77	1.87	1.09	0.91
Allsweet × King&Queen	0.75	0.86	1.50	3.82	1.26	2.79
King&Queen × Peacock shipper	0.93	1.90	1.41	2.97	2.11	3.08
Red-N-Sweet × King&Queen	8.14	0.50	0.91	2.78	8.37	1.46

Table 4-7. Variance and heritability estimates for the watermelon Brix value in 2008 at Clinton and Kinston, North Carolina.

Pedigree/ location	Variance				Heritability	
	$\sigma^2(P)$[a]	$\sigma^2(E)$[b]	$\sigma^2(G)$[c]	$\sigma^2(A)$[d]	H[e]	h^2_n[f]
Kinston						
Crimson sweet × King&Queen	1.29	1.96	-0.68	0.55	-0.53	0.42
Allsweet × King&Queen	1.30	0.97	0.33	-0.15	0.26	-0.11
King&Queen × Peacock shipper	2.75	0.60	2.14	2.23	0.78	0.81
Red-N-Sweet × King&Queen	2.05	0.90	1.14	0.42	0.56	0.20
Mean					**0.53**[g]	**0.48**[g]
Clinton						
Crimson sweet × King&Queen	1.87	0.83	1.04	1.73	0.56	0.93
Allsweet × King&Queen	3.82	1.15	2.67	3.59	0.70	0.94
King&Queen × Peacock shipper	2.97	1.41	1.56	0.77	0.52	0.26
Red-N-Sweet × King&Queen	2.78	2.62	0.16	-4.28	0.06	-1.54
Mean					**0.63**[h]	**0.94**[h]

a $\sigma^2(P)$ = phenotypic variance = $\sigma^2(F_2)$

a $\sigma^2(P)$ = phenotypic variance = $\sigma^2(F_2)$

b $\sigma^2(E)$ = environmental variance = $\dfrac{\sigma^2(P_a)+\sigma^2(P_b)+\left[2\times\sigma^2(F_1)\right]}{4}$

c $\sigma^2(G)$ = genetic variance = $\sigma^2(P)-\sigma^2(E)$

d $\sigma^2(A)$ = additive variance = $\left[2\times\sigma^2(F_2)\right]-\left[\sigma^2(BC_1P_a)+\sigma^2(BC_1P_a)\right]$

e H = broad-sense heritability

f h^2n = narrow-sense heritability

g The negative heritability was eliminated for calculation of the mean.

h The families King&Queen × Peacock shipper and Red-N-Sweet × King&Queen are excluded.

Table 4-8. Estimates of number of effective factors and predicted gain from selection under different selection intensities for the watermelon families tested for Brix value in 2008 at Clinton and Kinston, North Carolina.

Pedigree/ location	Effective number[a]						Gain from selection[b]		
	Lande I	Lande II	Lande III	Mather	Wight	Mean	5%	10%	20%
Kinston									
Crimson sweet × King&Queen	-0.4	2.0	-0.4	0.5	-0.1	0.3	1.0	0.8	0.7
Allsweet × King&Queen	0.8	-5.8	0.6	-1.5	0.3	-1.1	-0.3	-0.2	-0.2
King&Queen × Peacock shipper	0.3	0.9	0.2	0.2	0.2	0.4	2.8	2.4	1.9
Red-N-Sweet × King&Queen	1.5	15.5	1.4	3.9	0.9	4.6	0.6	0.5	0.4
Clinton									
Crimson sweet × King&Queen	0.3	0.7	0.3	0.2	0.9	0.5	2.6	2.2	1.8
Allsweet × King&Queen	0.0	0.0	0.0	0.0	0.0	0.0	3.8	3.2	2.6
King&Queen × Peacock shipper	1.1	2.9	0.4	0.7	0.2	1.1	0.9	0.8	0.6
Red-N-Sweet × King&Queen	6.3	-0.0	0.0	-0.0	0.0	1.3	-5.3	-4.5	-3.6

a The number of effect factor are estimated by 5 different methods: Lande I, Lande II, Lande III, Mather, Wight.

b The gain from selection was calculated for 3 different selection intensities: 5%, 15%, 20%.

Gain= $k \times h_n^2 \times \sqrt{\sigma^2(P)}$

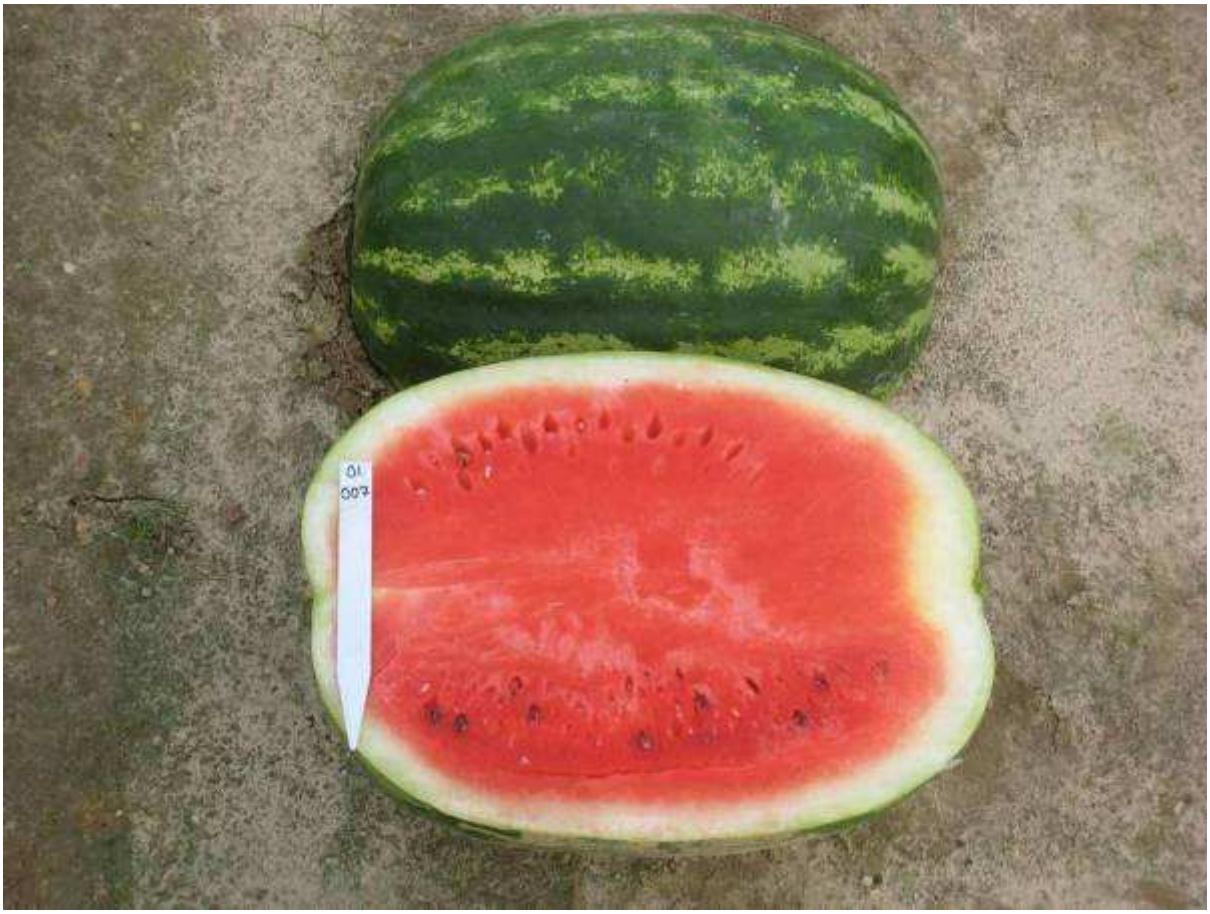

Figure 1. 'PDS 808' has rose flesh color, medium width medium green stripes with unclear margins on a light green background.

Figure 2. 'Red-N-Sweet' has scarlet flesh color, narrow width dark green stripes with clear margins on a light green background, long length and dotted seed, near round fruit shape, concave blossom end.

Figure 3. 'Crimson Sweet' has coral red flesh color. Medium width medium green stripes with unclear margins on a light green background, medium length seed size, near round fruit shape, thick rind, smooth rind surface.

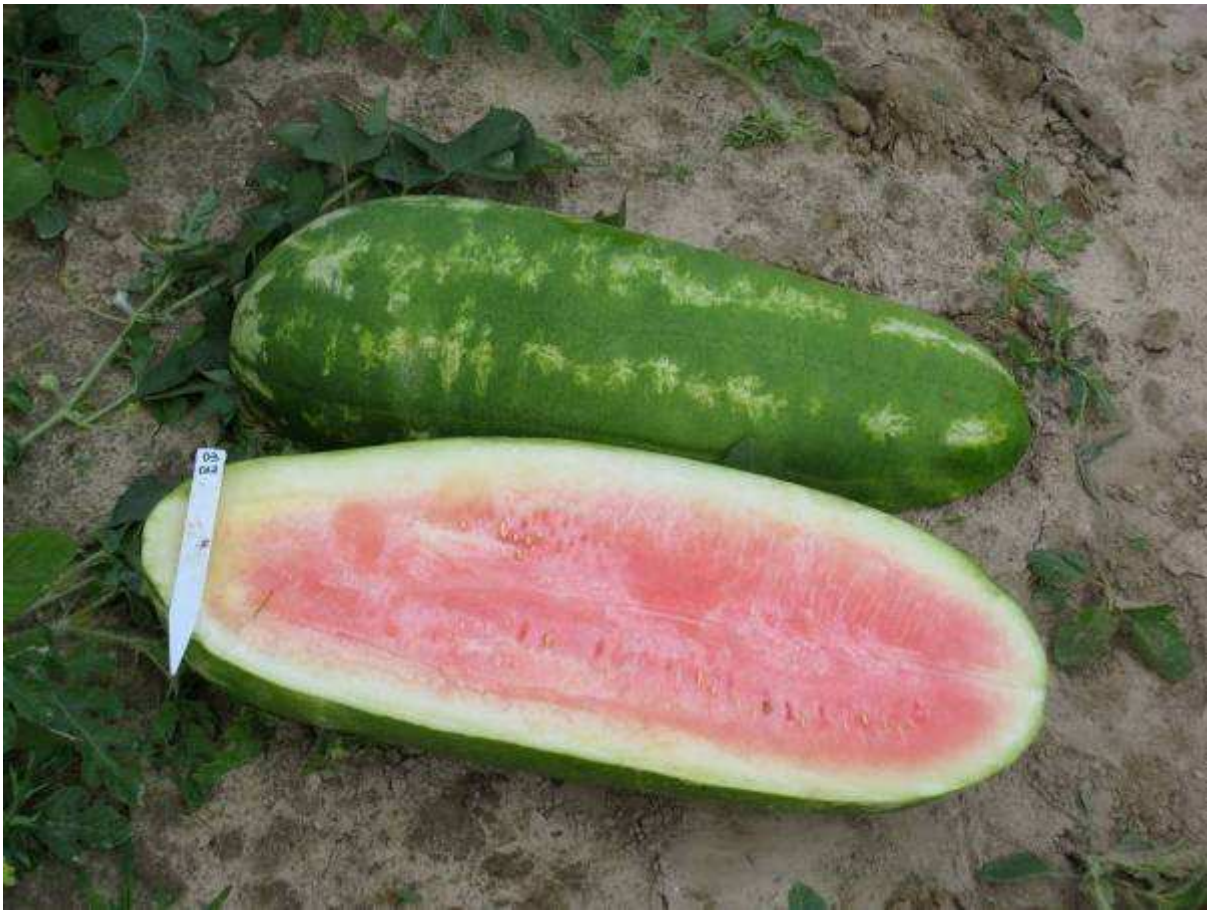

Figure 4. 'All Sweet' has coral red flesh color, wide width medium green stripes with unclear margins on a light green background, convex blossom end, elongate fruit and smooth fruit surface.

Figure 5. 'Black Diamond' has coral red flesh color, solid dark rind, concave blossom end, furrowed fruit.

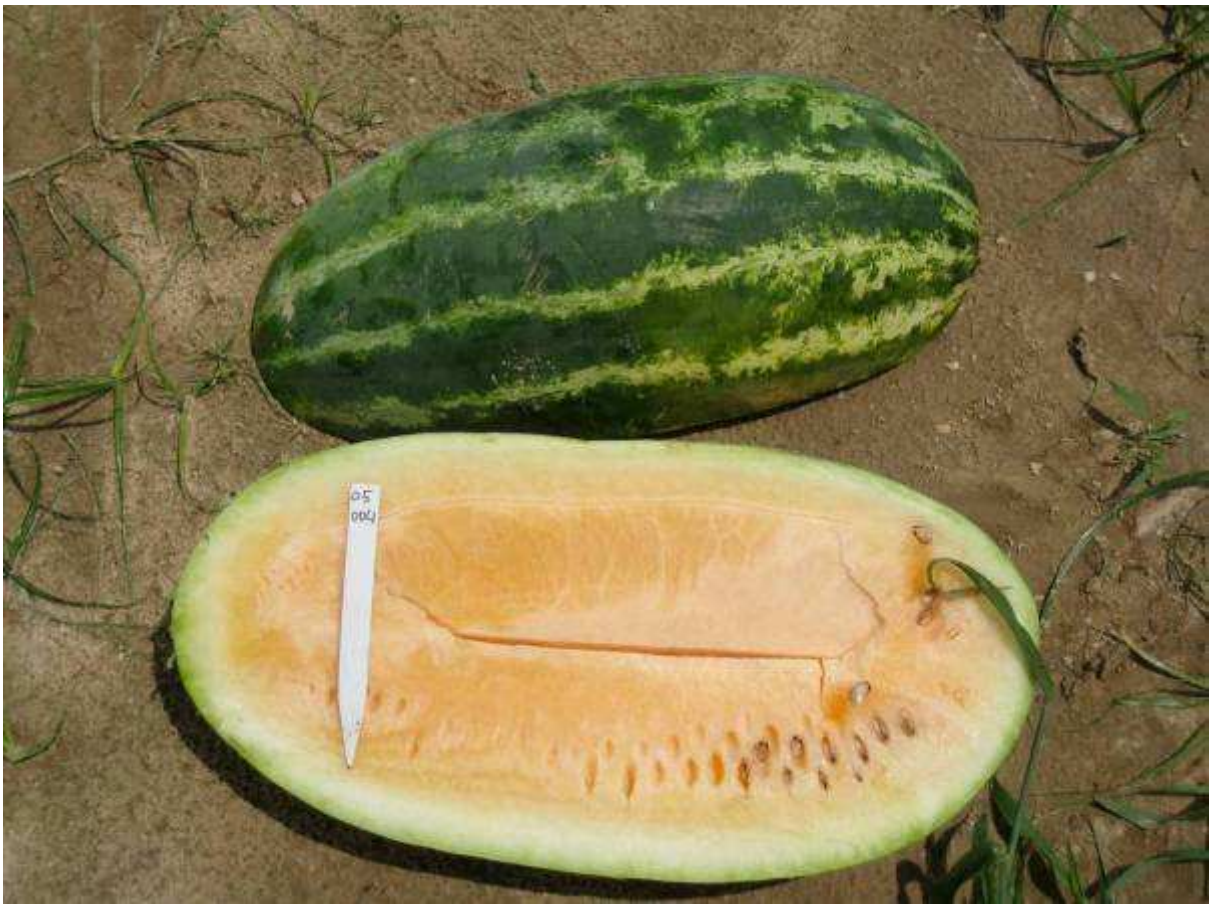

Figure 6. 'Tendersweet Orange Flesh' has orange flesh color, wide width medium green color stripes with unclear margins on a light green background, rimed tan seed, and oblong fruit.

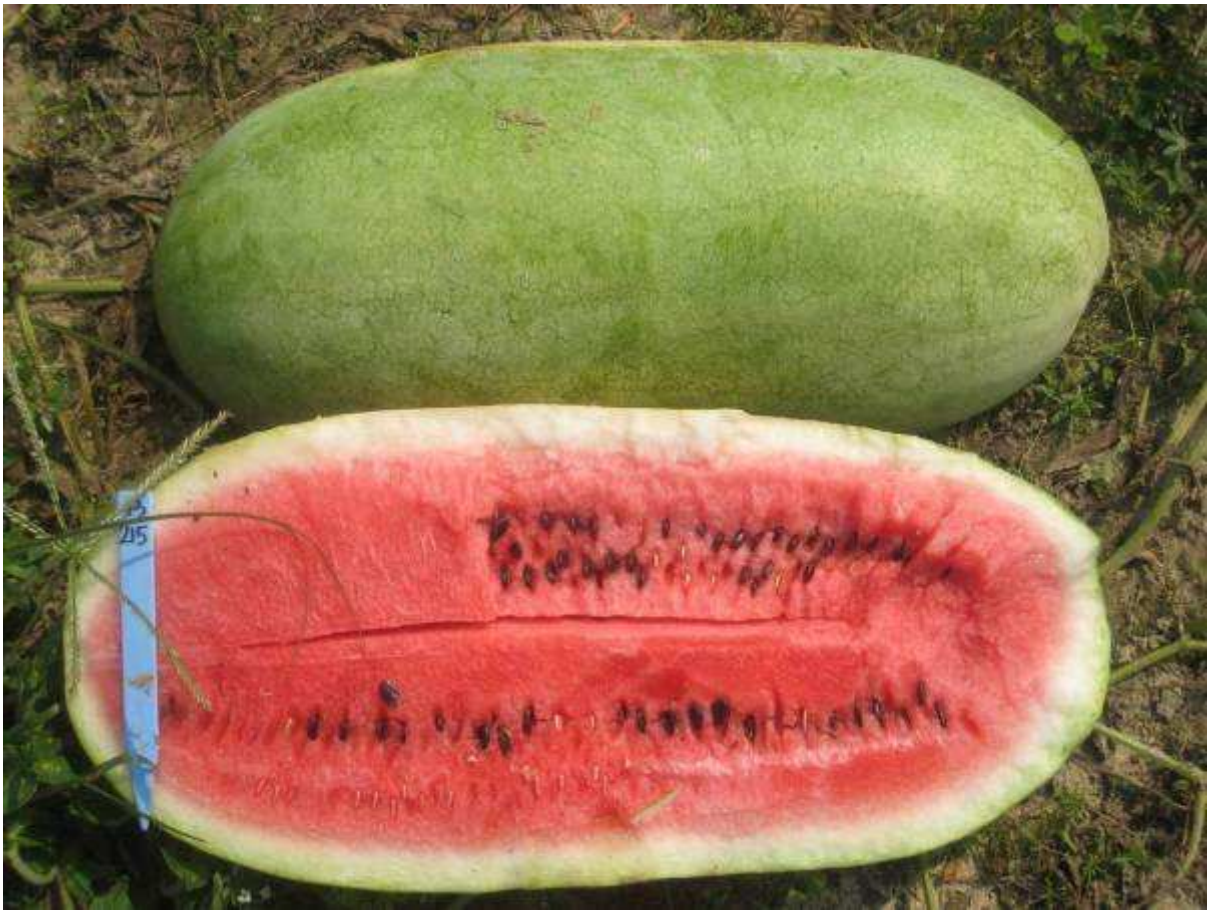

Figure 7. 'Charleston Gray' has coral flesh color, gray (light green with reticulations), long seed, convex blossom end, elongate fruit shape, smooth fruit surface, and hollow hearted endocarp.

Figure 8. 'King&Queen' has coral flesh color, solid light green (light green stripe on a light green fruit), medium seed length, round fruit weight.

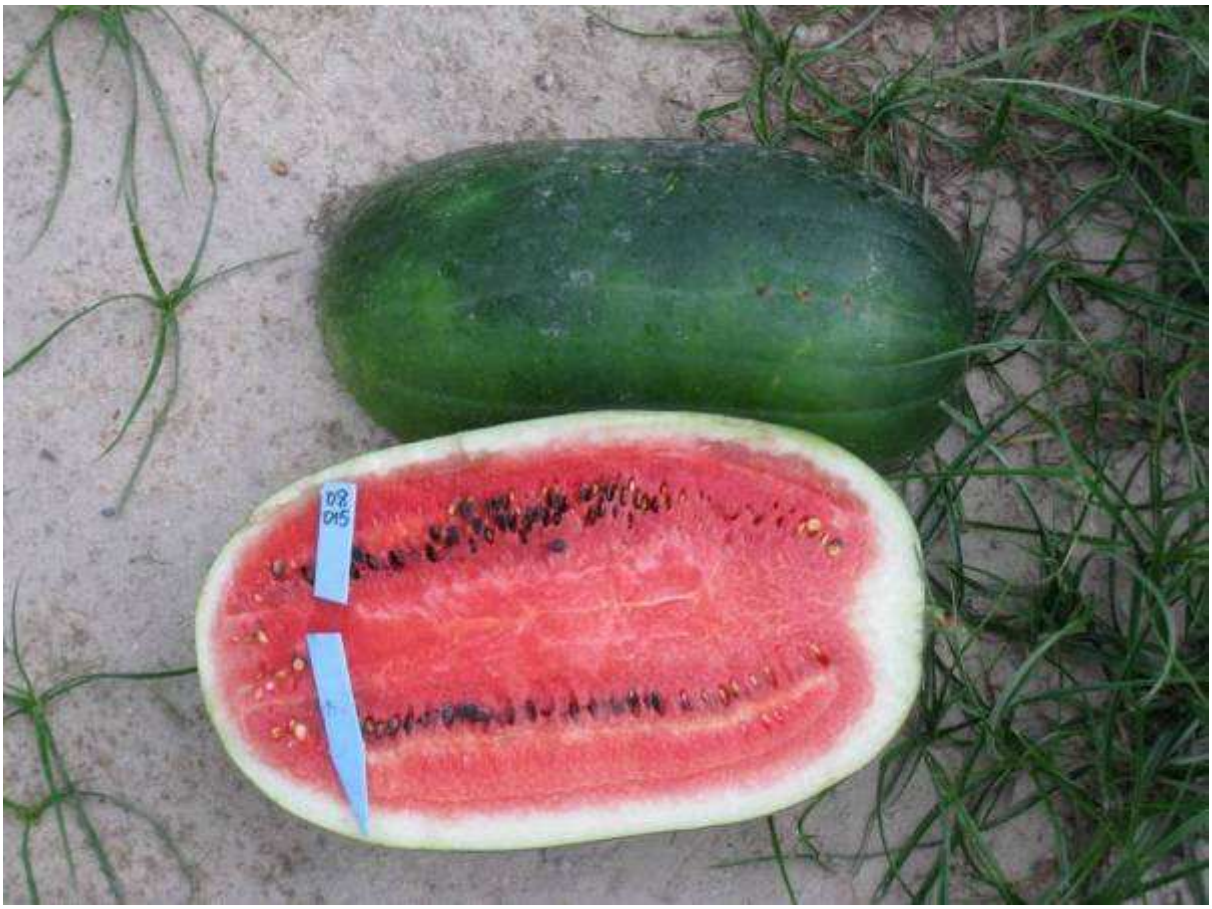

Figure 9. 'Peacock Shipper' has coral red flesh, solid medium dark green, medium length black seed, concave blossom end and oblong and furrowed fruit.

Figure 10. 'Cream of Saskatchewan' has white flesh color, narrow width narrow dark green stripes on a light green background, medium size and black seed.

Figure 11. Seedlings were held in the greenhouse at constant temperature (25-30 °C) until full emergence before transplanting.

Figure 12. In the field, raised beds were made up with drip irrigation tubes and covered with black polyethylene mulch. In order to keep families, generations, and plants separate for data collection, each plant was manually trained each week into a spiral shape by turning all the vines in a clockwise circle around the crown until about 70% of the plants in the field set fruit. The vine training allowed easy tracing of the fruit to the plant that produced it, giving high accuracy to the system.

Figure 13. F_1 fruit of 'Cream of Saskatchewan' and 'Red-N-Sweet' has a red center with yellow margin.

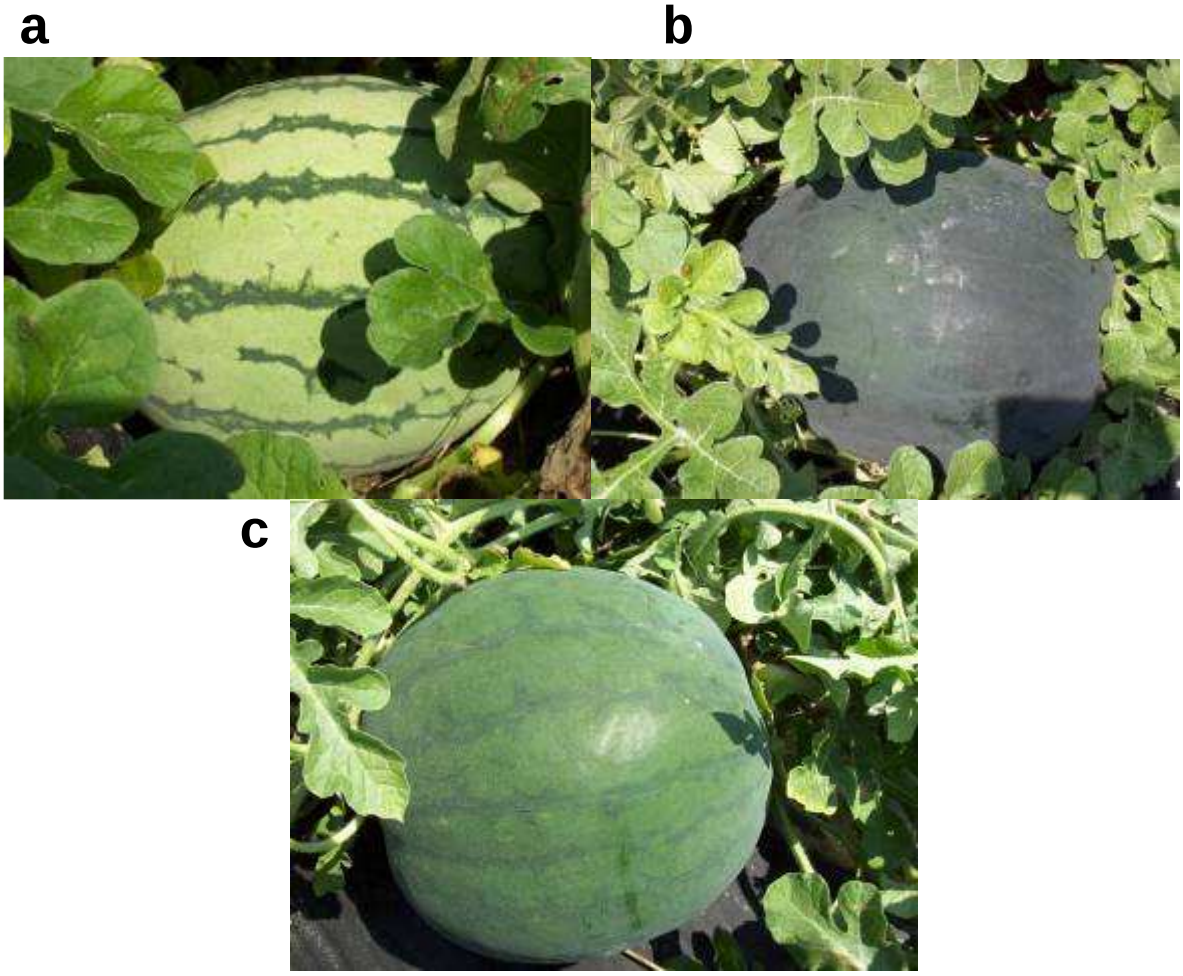

Figure 14. a: Narrow stripe on a 'Red-N-Sweet' fruit. b: The dark solid green rind on a 'Black Diamond' fruit. c: F_1 fruit of 'Red-N-Sweet' and 'Black Diamond' has intermediate medium green rind with inconspicuous stripes.

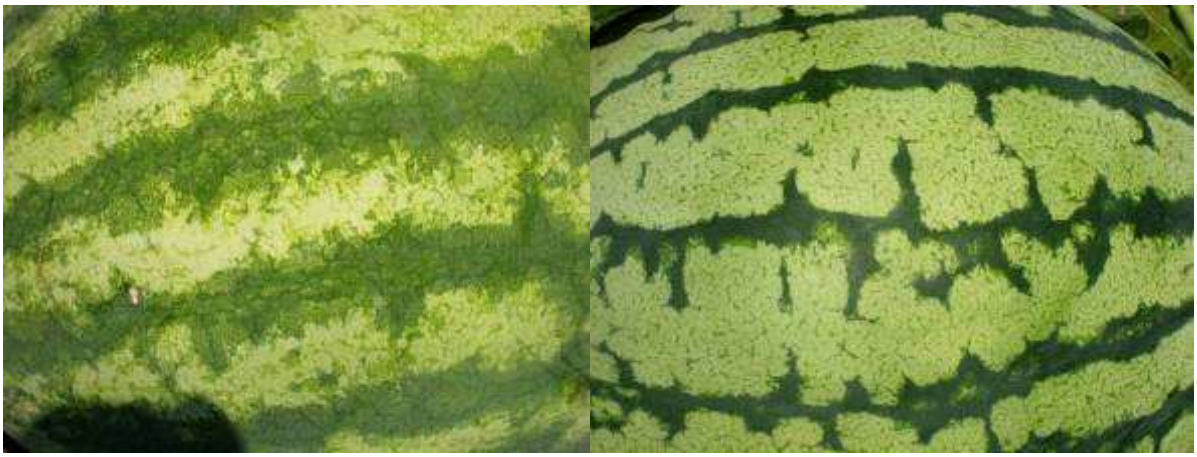

Figure 15. Two different stripe patterns: Blurred and clear.