GENETIC ANALYSIS AND HERITABILITY ESTIMATES FOR HEAT-TOLERANCE TRAITS IN TOMATO (*Solanum lycopersicum* L.)

A Thesis

by

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ABSTRACT

High temperature is a major limiting factor for tomato production in subtropical and tropical regions. Traditional breeding of heat tolerant crops is mainly based on phenotypic analysis and selection of individuals or lines with higher yield. Most abiotic stress tolerance traits are polygenic and inherited in a complex fashion. Studying correlation and the genetic control for heat-tolerance traits under high temperature stress facilitates tomato breeding for heat tolerance. In the first experiment, the main gene effects for heat-tolerance traits were determined by generation mean analysis of six genetic generations of two crosses 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' in two locations, College Station. TX and Waller, TX. For 'Freshmarket 9' x 'Black Sea Man', dominance effects were significant for all traits except pollen viability in Waller. For T215VR x 'Manyel', significant additive effects were found in all traits, with pollen viability showing significance in both additive and dominance effects in College Station. In Waller, significant dominance effects were found in fruit number per cluster and fruit set. Narrow-sense heritability estimates for the heat-tolerance traits were low to moderate in both locations. The low narrow-sense heritability for most traits implied that single plant selection in the F_2 will not be effective, and that alternative approaches such as mass or recurrent selection should be considered in early generations.

In the second experiment, Design II and combining ability analysis revealed that both additive and dominance gene action contributes to the expression of heat-tolerance traits with additive effects being the primary role in the expression of pollen viability,

days to flower and flower number per cluster, and with dominance effects being predominant in the expression of days to first fruit, fruit number per cluster, fruit set and yield. The parent lines ‘Homestead’, T214, and ‘Freshmarket 9’ were identified as good general combiners and ‘Homestead’ x ‘Freshmarket 9’ as the most favorable hybrid combination which can be used in developing heat tolerant hybrids. The findings of this study should be able to provide information to breeders for parent selection and hybrid development in tomato breeding for heat tolerance.

DEDICATION

I dedicated this thesis to my mother (Li-Ying Chen), father (Mu-Shui Chi), brother (Ting-Yen Chi) and twin sister (Yu-Ning Chi) for their unconditional love, support and inspiration.

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The method of Generation Mean Analysis and significance tests of heritability estimates in Chapter III was provided by Dr. William Rooney. All the data analyzed for the thesis was completed by the student independently.

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CHAPTER I

INTRODUCTION

Tomato (*Solanum lycopersicum L.*) is one of the most economically important and widely consumed vegetable crops grown around the world. In the United States, there were 404,900 acres of tomatoes harvested in 2016, producing 29 billion pounds valued at $0.9 billion dollars (USDA-ERS, 2016). California and Florida are the two leading producers of all tomatoes in the United States, producing fresh-market tomatoes on 32,200 and 30,400 acres, respectively, and accounting for almost two-thirds of total U.S. fresh-tomato acreage (USDA-ERS, 2015).

In tropical and sub-tropical climates, excess radiation and high temperatures are often a major limiting factor in tomato production. High temperatures adversely affect both vegetative and reproductive development of tomatoes, and thus directly reduce final yield. In tomato, fruit set is interrupted when day/night temperatures exceed 26 and 20°C, respectively, which leads to a reduction of yield (Lohar and Peet, 1998). Therefore, breeding for heat tolerant tomatoes is a relatively important priority.

Traditional breeding of heat tolerant crops is mainly based on phenotypic analysis and selection of individuals or lines with higher yield. However, most abiotic stress tolerance traits are controlled by more than one gene and highly influenced by uncontrollable environmental factors and large genotype by environment interactions. Studying the correlation and the genetic control for heat-tolerance traits under high temperature stress

could provide valuable information to enhance the efficiency in selection for heat tolerance. The objectives of this study were to a) evaluate tomato genotypes for their response to high temperatures under field conditions and b) to elucidate the inheritance and the genetic effects controlling the traits related to heat tolerance in tomato by estimating heritability and gene effects including additive, dominance and epistasis effects and c) to identify the best general combiner for selection of favorable parent lines and the best specific combiner as the desirable hybrid combination for heat tolerance.

CHAPTER II

LITERATURE REVIEW

Plant Description

Tomato (*Solanum lycopersicum* L.) belongs to the genus *Solanum*, in the Solanaceae family. The center of origin of tomato and its wild relatives is the Andean region of South America (Rick, 1973). Wild cherry tomato (*S. lycopersicum* var. *cerasiforme*) is considered the most likely ancestor of tomatoes, which was possibly domesticated from the red-fruited wild tomato *Solanum pimpinellifolium* (Ranc et al., 2008), and was distributed into Mexico and other countries in South America (Rick and Holle, 1990)

Tomato is often consumed directly as a fresh vegetable and in addition, it is also used in a multitude of processed forms, including juice, sauces and soups (Foolad, 2007). Tomato and tomato-based products are rich in various antioxidant compounds and are considered an important source of nutrient and antioxidant molecules such as carotenoids, in particular lycopene, ascorbic acid, vitamin E, as well as phenolic compounds (Abushita et al., 1997; Vinson et al., 1998). The composition of antioxidant compounds in tomato fruit depends upon its genotype, stage of ripeness and the condition under which it was cultivated and processed. (Abushita et al., 2000; George et al., 2004). A number of epidemiologic studies have associated decreased risk of various types of cancers, such as prostate cancer, and cardiovascular diseases with intake of tomatoes and tomato-based products or lycopene (Clinton, 1998; Giovannucci et al., 2002). The observed positive

effects are attributed to the presence of antioxidants in tomato, in particular, lycopene. Therefore, consumption of tomato is considered an indicator of good dietary habits and health.

In terms of production and consumption, tomato ranks second among vegetable crops in the world. World production of tomatoes was 163.9 million tonnes in 2013 (FAOSTAT, 2013). China is the main producer of tomato, contributing 30.83% of the total production, followed by India (11.14%), the U.S. (7.67%), Turkey (7.21%) and Egypt (5.20%). The United States produced about 129 billion pounds of commercial vegetables and pulses, with a value of 19 billion dollars and area harvested of 7.4 million acres in 2016 (USDA-ERS, 2016). In the U.S., 404,900 acres of tomatoes were harvested in 2016, producing 29 billion pounds. Tomato also claimed the second highest price among fresh market vegetables, creating 0.9 billion dollars of farm value (USDA-ERS, 2016). California is the leading producer of tomatoes in the United States, accounting for 96% of U.S. processing tomato production and one-third of fresh-market tomato production. Across the State, fresh-market tomatoes are produced in each season except winter. Florida and California produce fresh-market tomatoes on 32,200 and 30,400 acres, respectively, contributing almost two-thirds of total U.S. fresh-tomato acreage (USDA-ERS, 2015).

Heat-Stress Threshold

In the tropics, high temperature is known to cause significant losses in tomato yield due to reduced fruit set (Kuo et al., 1979), size and quality (El Ahmadi and Stevens, 1979a; Levy et al., 1978). Climatic analysis of tomato-growing areas suggests

that the intensity and frequency of above-optimal temperatures will rise in the coming decades (Bell et al., 2000). In such conditions, tomato cultivars that are tolerant to heat are required.

A threshold temperature is the value of the mean temperature in which a detectable reduction in crop growth occurs. Upper and lower developmental threshold temperatures have been determined for various crop genotypes through controlled laboratory and field experiments. Upper threshold temperatures differ for different plant species and genotypes within species. Identifying upper threshold temperatures is difficult because the plant behavior may differ depending on other environmental situations (Miller et al., 2001). In tomato, when day/night temperatures exceed 26 and 20°C, respectively, fruit set is interrupted, which leads to a marked reduction in yield (Lohar and Peet, 1998). Heat tolerance in tomato is defined by Villareal et al. (1978) as "the ability to set fruits under night temperatures not lower than 21°C."

Responses of Tomato to Heat Stress

Physiological Responses

In tropical climates, excess radiation and high temperatures are often a major limiting factor affecting plant growth and final yield. High temperatures can cause remarkable pre- and post-harvest damage, including burning of leaves and twigs, sunburn on leaves, stems and branches, leaf abscission and senescence, inhibition of shoot and root development, fruit discoloration and reduced yield (Ismail and Hall, 1999; Vollenweider and Gunthardt-Goerg, 2005). Photosynthesis is a heat-sensitive physiological process and it can be completely inhibited by high temperatures before

other stress symptoms are detected (Berry and Bjorkman, 1980). This makes it a good indicator of heat tolerance as it is directly related to growth. Photochemical reactions in thylakoid lamellae and metabolism of carbon in chloroplast stroma have been suggested as the primary sites of injury at high temperatures (Wise et al., 2004).

Water relations is the most imperative variable under changing environmental temperatures (Mazorra et al., 2002). In tomato, heat stress has been shown to disturb osmotic adjustment, root hydraulic conductivity and leaf water relationships (Morales et al., 2003). In general, during the daytime, increased transpiration induces water deficiency in plants and causes a reduction in water potential and disturbance of many physiological processes (Tsukaguchi et al., 2003). High temperatures seem to cause more water loss in plants during daytime compared to nighttime (Wahid et al., 2007).

An imperative adaptive mechanism in many plants developed under abiotic stress, including water deficit, salinity and extreme temperatures, is accumulation of certain organic compounds of low molecular mass, commonly referred to as compatible osmolytes (Hare et al., 1998; Sakamoto and Murata, 2002). Under stress, different plant species may accumulate different varieties of osmolytes including sugar and sugar alcohols (polyols), proline, and tertiary sulphonium compounds (Sairam and Tyagi, 2004; Wahid, 2007).

Stability of cellular membranes under stress is fundamental for processes including respiration and photosynthesis (Blum, 1988). The integrity and function of biological membranes are sensitive to high temperatures due to the accelerated kinetic energy and motion of molecules across membranes, which lose chemical bonds in biological

membrane molecules. This causes the lipid bilayer of biological membranes to be more fluid by either protein denaturation or an increase in unsaturated fatty acids (Savchenko et al., 2002). The changes increase the permeability of the membrane, as evident from increased loss of electrolytes. The increased solute leakage, as an indicator of diminished cell membrane thermostability (CMT), has long been applied as an indirect estimation of heat stress tolerance in different plant species, including potato and tomato (Chen et al., 1982), cotton (Ashraf et al., 1994), cowpea (Ismail and Hall, 1999), and barley (Wahid and Shabbir, 2005).

Plants have the capability to adjust to adverse environmental conditions, though the degree of adaptability or tolerance to specific stresses differs among species and genotypes. Hormones play a crucial role in this issue. Under heat stress, hormonal homeostasis, stability, content, biosynthesis and compartmentalization are altered (Maestri et al., 2002). Abscisic acid (ABA) and ethylene (C_2H_4), as stress hormones, are involved in the regulation of various physiological properties by functioning as signal molecules. Diverse environmental stresses, such as high temperatures, result in enhanced ABA levels (Larkindale and Huang, 2005). In tomato, brassinosteroids (BRs) have been found to confer thermo-tolerance. The potential roles of other phytohormones involved in thermo-tolerance of tomato are yet unknown.

Anatomical and Morphological Responses

Alterations in tomato anatomy under high temperatures have not been fully explored in detail and limited information is available. In general, anatomical changes under high temperatures are similar to those under drought stress. At the whole plant

level, there's a common trend of reduced cell size, closure of stomata and curtailed transpiration, enhanced stomatal and trachomatous densities, and greater xylem vessel numbers of both shoot and root (Bañon et al., 2004).

Susceptibility of plant species and cultivars to high temperatures may vary with the stage of plant growth, but all growth stages are affected by heat stress to some degree. Studies have shown that reproductive development in tomato is more affected by high temperatures than vegetative development (Sato et al., 2002; Abdelmageed et al., 2003). During reproduction, high temperatures affect meiosis in male and female organs, germination of pollen and development of pollen tubes, ovule viability, stigmatic and style positions, number of pollen grains retained by the stigma, fertilization and post-fertilization processes, endosperm development, pre-embryo and fertilized embryo development (Foolad, 2005). In some cases, high temperatures in tomato resulted in an exserted style (i.e., stigma is elongated beyond the anther cone), which hinders self-pollination (Golam et al., 2012).

Peet et al. (1998) compared the effect of heat stress on both male and female gametes in tomato; heat stress was more damaging to pollen development than ovule development. Heat reduced pollen, pollen shed, pollen viability, germination capability, and fruit set in tomato under high temperature conditions (Peet et al., 1997; Sato et al., 2000). Apart from pollen shed, differences between cultivars in pollen germination under heat stress affect fertilization and fruit set (Sato et al., 2000). For germination, pollen grains depend on sugars as metabolic substrates (Stanley, 1971). Pressman et al. (2002) found that the deleterious effects of heat stress on pollen quality of tomato were

associated with decreased starch concentration and thus led to decreases in the concentration of soluble sugars in the anther walls and the mature pollen grains. Firon et al. (2006) studied the correlation between carbohydrate concentrations in the developing and mature pollen grains, pollen quality and fruit set in tomato cultivars that are different in their sensitivity to high temperatures. The results confirmed the association in the previous study (Sato et al., 2000) and showed that pollen release and quality are the most important factors that affect fruit set under heat stress. However, the reason for decreased starch concentration in tomato pollen grains developing under high temperatures is still unknown (Firon et al., 2006). Release of pollen and capability of germination can be reliable indicators for identifying plant reactions to high temperatures, and are applied as criteria for selection in breeding programs to choose heat tolerant varieties (Comlekcioglu and Soylu, 2010)

Molecular Responses

Expression of stress proteins is an important mechanism of adaptation to deal with environmental stresses. Synthesis and accumulation of specific proteins are induced during a rapid heat stress and these proteins are identified as heat shock proteins (HSPs), which are exclusively implicated in response to heat stress. In higher plants, HSP induction seems to be a worldwide reaction to heat stress at any stage of development and the major HSPs are highly homologous among eukaryotes, and in some cases, homologous proteins have been identified in prokaryotes as well (Vierling, 1991). HSP-triggered thermo-tolerance is attributed to the observation that their induction coincides with organisms under stress, that their biosynthesis is extremely intensive and

rapid, and that they are induced in a broad variety of cells and organisms (Wahid et al., 2007). The presence of HSPs can hinder denaturation of other proteins caused by high temperatures. In tomato plants developed under heat stress, HSPs aggregate into a granular structure in the cytoplasm, possibly protecting the protein biosynthesis machinery (Miroshnichenko et al., 2005).

Inheritance of Heat Tolerance

Traditional breeding of heat tolerant plants is based on selection, and a common method of selecting plants for heat stress tolerance has been to grow breeding materials in a hot target production environment and identify individuals/lines with higher yield potential (Ehlers and Hall, 1998). In tomato, a strong positive correlation has been perceived between fruit set and yield under high temperatures. Therefore, evaluation of germplasm to identify sources of heat tolerance has regularly been performed by screening for fruit set under high temperatures (Berry and Rafique-Uddin, 1988). Moreover, decreases in pollen germination and/or pollen tube growth are among the most commonly reported factors for reduced fruit set under high temperatures. Hence, pollen viability has been suggested as an indirect selection criterion for heat tolerance. In addition, production of viable seed is reduced under heat stress and thus high seed set has been reported as an indicator of heat tolerance (Berry and Rafique-Uddin, 1988).

El Ahmadi and Stevens (1979b) found that the inheritance of fruit set under high temperatures of heat-tolerant genotypes under greenhouse conditions is additive with moderate heritability. The heritability was low for seed set, but high for stigma exsertion. It was also reported that additive gene action seems to be more important than

non-additive gene action for fruit set, fruit drop and undeveloped ovaries under high temperatures in field conditions (Hanna et al., 1982)

In tomato, adaptation to higher temperatures has occurred mainly by human selection, but requires constant efforts. Studies of heat tolerance in tomato have been the focus of the extensive breeding programs in Texas, Florida and Taiwan (Leskovar et al., 2014). Despite all the complexities of heat tolerance and difficulties confronted during transfer of tolerance, several heat-tolerant inbred lines and hybrid varieties with commercial acceptability have been developed and released in tomato (Leeper and Cox, 1986; Scott et al., 1995)

CHAPTER III

GENERATION MEAN ANALYSIS

Generation mean analysis is a useful technique that provides the estimation of main genetic effects such as additive, dominance and their allelic interactions involved in the expression of quantitative traits (Mather and Jinks, 1982). A number of models of generation mean analysis have been developed over time (Hayman, 1958; Hayman, 1960; Van der Veen 1959). Generation mean analysis has been applied successfully for studying inheritance of various tomato traits such as yield (Bhatt et al., 2001), cold tolerance (Foolad and Lin, 2001) and salt tolerance (Foolad, 1996).

Mather and Jinks (1971) derived individual scaling tests (A, B, and C) to test the adequacy of the additive-dominance model in explaining variation among the generation means. The first assumption of the test is that the genes exhibit simple autosomal inheritance, i.e., there are no maternal effects or sex-linkage in determining the character, and second, the genes involved are independent, i.e. total effect of genes affecting the trait is the sum of their individual effects (Singh and Chaudhary, 1985). A joint scaling test is based on combining all the scaling tests into one and comparison of experimental mean generation values and expected generation values that indicate epistatic effects (Cavalli, 1952).

The errors of estimate of generation mean analysis are smaller since means are used instead of variances. Moreover, generation mean analysis is applicable to

cross-pollinating and self-pollinating crops, and requires a smaller experiment scale to obtain a good degree of precision (Hallauer and Miranda, 1981)

Materials and Methods

Plant materials

For this study, two breeding lines 'Freshmarket 9' (Leeper and Cox, 1986) and T215VR and two heirloom cultivars 'Black Sea Man' and 'Manyel' were used in the original crosses. 'Freshmarket 9' and T215VR were used as the females and were crossed to 'Black Seaman' and 'Manyel', respectively, to produce F_1 hybrid, 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel'. A heat tolerant F_1 hybrid tomato cultivar Hot-Ty was used as a control.

Both F_1 populations were planted in three-gallon, black plastic, self-draining pots with growing medium of Sunshine mix #4 (Sun Gro Horticulture Inc., Bellevue, WA). The greenhouse care consisted of watering twice a day as needed and fertilizing biweekly with an application of 1 tablespoon per gallon of Peters 20-20-20 water soluble fertilizer. F_1 populations were self-pollinated to produce F_2 seeds and were crossed back to both parents to produce backcrosses (BC_1P_1 and BC_1P_2) in a greenhouse at College Station, Texas in the spring of 2016.

In summer 2016, 150 F_2 seeds of both hybrids, 12 F_1 , 20 BC_1P_1, 20 BC_1P_2 and 12 parents were sown on July 13th, 2016 in a greenhouse in multi-pot trays (72 pots per tray) with a mixture of growing medium consisting of Sunshine mix #4 (Sun Gro Horticulture Inc., Bellevue, WA) and vermiculite (1:1). On August 24th, 100 F_2 transplants, 10 BC_1P_1, 10 BC_1P_2, 8 F_1 and 8 parents of both genotypes and 6 controls were transferred to the

field in College Station, Texas. On August 30th, 23 ‘Freshmarket 9’ x ‘Black Sea Man’ F_2 transplants, 41 T215VR x ‘Manyel’ F_2 transplants, 10 BC_1P_1, 10 BC_1P_2, 4 F_1 and 4 parents of both genotypes and 4 controls were transferred to the field in Waller, Texas.

Phenotypic Evaluation

The pollen grains were sampled from two random completely opened flowers per plant on October 14th, 2016 in College Station and October 18th, 2016 in Waller. The pollen grains were collected in an eppendorf tube with a modified electronic toothbrush. The pollen was stored under dry conditions in a -18°C freezer and pollen viability was identified within a week after sampling. A hanging drop pollen assay protocol was modified and used (Abdul-Baki, 1992; Zlesak, 2004). A small drop of 10% sucrose solution with 0.4% boric acid was placed on a cover slip. The pollen grains were picked up with a needle and placed on the drop on the cover slip. Then the cover slip was picked up and inverted without letting the drop slide off and placed over the well of the concave microscope slide. A drop of sucrose solution was placed along the outside edge of the cover slip to seal off the well. The pollen grains were incubated for 3 hours at room temperature and assessed under a light microscope. Pollen grains with pollen tubes that were at least the length of the grain were counted and pollen viability (PV) was estimated as a percentage of total grains that had germinated.

Flower number was counted during mid-September and late-October. Flower number per cluster (FLC) was measured as the total number of flowers from the second to sixth cluster on each plant tagged during anthesis. All flowers were counted, including abscised flowers. Fruit number was counted during October 1st to November 4th. Fruit

number per cluster (FRC) was measured as the total number of fruit from the second to sixth cluster on each plant. A fruit is considered set if it enlarged to > 1 cm in diameter. Fruit set (FS) was calculated by dividing the total fruit number by the total flower number on each plant.

Statistical Analysis

All data were analyzed using JMP software (Version 12.0; SAS Institute, Cary, N.C., 2016). Analysis of variance (ANOVA), least significant difference (LSD) Student's t test, and Pearson's correlation coefficients were obtained. The ANOVA and LSD Student's t tests were performed to determine differences among genotypes. Pearson's correlation coefficients were used to determine the relationships between the traits.

Generation Mean Analysis

Individual scaling tests (A, B, and C) were performed to provide information on the presence or absence of allelic interaction, for which the additive and dominance components of variances were sometimes estimated by assuming the absence of gene action.

The scaling tests involved in the test of three scales with the following equations, using the mean values: $A = 2\ BC_1P_1 - P_1 - F_1$, $B = 2\ BC_1P_2 - P_2 - F_1$, and $C = 4\ F_2 - 2\ F_1 - P_1 - P_2$; where P_1, P_2, F_1, F_2, BC_1F_1, and BC_2F_1 are the means of parents, F_1 crosses, F_2, and backcross generations, respectively. The respective variances were calculated according to the following equations:

$$V_A = 4V_{BC1P1} + V_{P1} + V_{F1}$$

$$V_B = 4V_{BC1P2} + V_{P2} + V_{F1}$$

$V_C = 16V_{F2} + 4V_{F1} + V_{P1} + V_{P2}$

where V_{P1} is the variance of parent 1 (female parent), V_{P2} is the variance of parent 2 (male parent), V_{F1} is the variance of the derived progeny, V_{BC1F1} is the variance of the backcross of the recurrent parent (P_1) with the respective F_1, V_{BC2F1} is the variance of the backcross of the recurrent parent (P_2) with the respective F_1.

The standard error (SE) was determined from the square root of the respective variance, and Student's t test was performed by dividing the value by the SE: $SE_{(A)}=(V_A)^{1/2}$, $t_{(A)}=A/SE_{(A)}$, where V_A is the variance of scale A. A similar procedure was used to calculate the standard errors of B and C and their t values. The calculated t values were compared with the tabulated values at the 5% and 1% levels of significance.

Generation mean analysis was used to determine the gene actions of heat-tolerance traits in tomato (P_1, P_2, F_1, F_2, BC_1P_1, BC_1P_2), using additive/dominance model, i.e., the three-parameter model (Mather and Jinks, 1982). The effects of genes were calculated as:

$(m) = 0.5\ P_1 + 0.5\ P_2 + 4F_2 - 2\ BC_1P_1 - 2\ BC_1P_2$

$(a) = 0.5\ P_1 - 0.5\ P_2$

$(d) = 6\ BC_1P_1 + 6\ BC_1P_2 - 8\ F_2 - F_1 - 1.5\ P_1 - 1.5\ P_2$

where (m) represents the mean, (a) is the additive effect and (d) is the dominance effect. The standard errors were calculated using the following formulas:

$SE^2_{(m)} = 0.25\ SE^2_{(P1)} + 0.25\ SE^2_{(P2)} + 16\ SE^2_{(F2)} + 4\ SE^2_{(BC1P1)} + 4\ SE^2_{(BC1P2)}$

$SE^2_{(a)} = 0.25\ SE^2_{(P1)} + 0.25\ SE^2_{(P2)}$

$SE^2_{(d)} = 36\ SE^2_{(BC1P1)} + 36\ SE^2_{(BC1P2)} + 64\ SE^2_{(F2)} + SE^2_{(F1)} + 2.25\ SE^2_{(P1)} + 2.25$

$SE^2_{(P2)}$

The significance of the genetic effects were tested with Student's t test by dividing the value by the SE: $t_{(m)}= (m)/SE_{(m)}$; $t_{(a)}= (a)/SE_{(a)}$; $t_{(d)}= (d)/SE_{(d)}$. The calculated t values were compared with the tabulated values at the 5% and 1% levels of significance.

If at least one value from the A, B, and C sets turns out statistically significant, the three-parameter model is declared inadequate. In these instances, Hayman's six-parameter model (1958) was used to determine the type and the magnitude effects of epistasis.

$(m) = F_2$

$(a) = BC_1P_1 - BC_1P_2$

$(d) = F_1 - 4F_2 - 0.5\ P_1 - 0.5\ P_2 + 2\ BC_1P_1 + 2\ BC_1P_2$

$(aa) = 2\ BC_1P_1 + 2\ BC_1P_2 - 4\ F_2$

$(ad) = BC_1P_1 - 0.5\ P_1 - BC_1P_2 + 0.5\ P_2$

$(dd) = P_1 + P_2 + 2\ F_1 + 4\ F_2 - 4\ BC_1P_1 - 4\ BC_1P_2$

where (m) is the mean, (a) is the additive effect, (d) is the dominance effect, (aa) is the additive x additive effect, (ad) is the additive x dominance effect and (dd) is the dominance x dominance effect.

The standard errors were calculated with the following formula:

$SE^2_{(m)} = SE^2_{(F2)}$

$SE^2_{(a)} = SE^2_{(BC1P1)} + SE^2_{(BC1P2)}$

$SE^2_{(d)} = SE^2_{(F1)} + 16\ SE^2_{(F2)} + 0.25\ SE^2_{(P1)} + 0.25\ SE^2_{(P2)} + 4\ SE^2_{(BC1P1)} + 4SE^2_{(BC1P2)}$

$SE^2_{(aa)} = 4\ SE^2_{(BC1P1)} + 4\ SE^2_{(BC1P2)} + 16\ SE^2_{(F2)}$

$SE^2_{(ad)} = SE^2_{(BC1P1)} + 0.25\ SE^2_{(P1)} + SE^2_{(BC1P2)} + 0.25\ SE^2_{(P2)}$

$$SE^2_{(dd)} = SE^2_{(P1)} + SE^2_{(P2)} + 4\,SE^2_{(F1)} + 16\,SE^2_{(F2)} + 16\,SE^2_{(BC1P1)} + 16\,SE^2_{(BC1P2)}$$

The significance of the genetic effects were tested with Student's t test by dividing the value by the SE: $t_{(m)} = (m)/SE_{(m)}$; $t_{(a)} = (a)/SE_{(a)}$; $t_{(d)} = (d)/SE_{(d)}$; $t_{(aa)} = (aa)/SE_{(aa)}$; $t_{(ad)} = (ad)/SE_{(ad)}$; $t_{(dd)} = (dd)/SE_{(dd)}$. The calculated t values were compared with the tabulated values at the 5% and 1% levels of significance.

Heritability estimates

Broad-sense heritability (H^2) of those phenotypes was calculated as the ratio of genotypic variance (V_G) to phenotypic variance (V_P). The environmental control 'Hot-Ty' was considered genetically uniform, therefore its variance for the traits was considered the environmental variance (V_E). The variation of the F_2 population was assumed to be the phenotypic variance of the population. By subtracting V_E from V_P, the genetic variance (V_G) was determined (Napier, 2006).

Narrow-sense heritability (h^2) was calculated with data collected from the parents, the backcross generations (BC_1P_1 and BC_1P_2), F_1, and F_2 individuals. Narrow-sense heritability was estimated using the variances of the F_2 and backcross generations (Warner, 1952) as:

$$h^2 = [V_{F2} - (V_{BC1P1} + V_{BC1P2})/2]/V_{F2}$$

with V representing corresponding variances. F-tests and standard errors of the heritability estimates were calculated as described by Ketata et al. (1976). A standard error for h^2 was derived as the square root of the following:

$$V(h^2) = 2\,\{\,[\,(V_{BC1P1} + V_{BC1P2})^2/df_{F2}] + (V_{BC1P1}{}^2/df_{BC1P1}) + (V_{BC1P2}{}^2/df_{BC1P2})\} / V_{F2}{}^2$$

In the formula df_{F2}, df_{BC1F1} and df_{BC2F1} refer to the degrees of freedom associated with

V_{F2}, V_{BC1P1} and $V_{BC1P2,}$ respectively. Significance of h^2 was evaluated with the mean and standard error. If the estimated mean exceeded two times the value of standard error, then it is significant at $P \leq 0.05$. And if the estimated mean exceeded three times the value of standard error, then it is significant at $P \leq 0.01$.

Result and Discussion

Traits Evaluations

The mean values and the standard errors of the four traits studied for six genetic generations of the crosses 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' in College Station are listed in Table 1 and Table 2, respectively. In 'Freshmarket 9' x 'Black Sea Man', most heat-tolerance traits showed no significances among generations, indicating that the population means between the generations were not significantly different. Pollen viability of the F_1 was significantly higher than both parents, which suggested that there might be heterosis for the trait. The fruit set of the F_1 and BCP_1 exceeded mid parent values and were not significantly different from those of 'Freshmarket 9', indicating a dominance effect toward the female parent might play a role in the inheritance of fruit set. In the cross T215VR x 'Manyel', the population means for most traits showed significant differences between the generations. Flower number per cluster of the F_1 was found to be significantly higher than both parents, indicating possible expression of heterosis for the trait. The female parents of the crosses 'Freshmarket 9' and T215VR generally performed better with higher values of all traits than the male parents 'Black Sea Man' and 'Manyel'.

Table 1 Means and the standard errors of six generations of 'Freshmarket 9' x 'Black Sea Man' for heat-tolerance traits at College Station.

	PV (%)	FLC	FRC	FS (%)
Generation				
Freshmarket 9 (P_1)	0.50 ± 0.07 b	4.25 ± 0.76 a	2.25 ± 0.57 a	0.53 ± 0.10 a
Black Sea Man (P_2)	0.55 ± 0.05 b	3.44 ± 0.46 a	1.13 ± 0.35 a	0.35 ± 0.06 a
F_1	0.72 ± 0.05 a	4.11 ± 0.49 a	1.96 ± 0.37 a	0.46 ± 0.07 a
F_2	0.54 ± 0.03 b	3.80 ± 0.30 a	2.24 ± 0.23 a	0.49 ± 0.04 a
BC_1P_1	0.54 ± 0.07 b	3.33 ± 0.76 a	1.58 ± 0.57 a	0.46 ± 0.10 a
BC_1P_2	0.55 ± 0.07 b	3.08 ± 0.76 a	1.5 ± 0.57 a	0.44 ± 0.10 a

* Means were separated by LSD Student's t test at α=0.05 level. Means with same letter indicate no significant differences.

Table 2 Means and the standard errors of six generations of T215VR x 'Manyel' for heat-tolerance traits at College Station.

	PV (%)	FLC	FRC	FS (%)
Generation				
T215VR (P_1)	0.61 ± 0.06 ab	3.95 ± 0.59 ab	1.75 ± 0.44 ab	0.42 ± 0.08 a
Manyel (P_2)	0.44 ± 0.05 c	2.57 ± 0.45 c	0.64 ± 0.37 c	0.21 ± 0.07 b
F_1	0.60 ± 0.05 ab	4.21 ± 0.53 a	1.46 ± 0.40 abc	0.33 ± 0.07 ab
F_2	0.56 ± 0.02 ab	3.26 ± 0.16 ab	1.21 ± 0.12 bc	0.34 ± 0.02 a
BC_1P_1	0.70 ± 0.07 a	3.83 ± 0.76 abc	1.58 ± 0.57 abc	0.41 ± 0.10 a
BC_1P_2	0.63 ± 0.06 ab	3.56 ± 0.65 abc	1.56 ± 0.49 abc	0.44 ± 0.09 a

* Means were separated by LSD Student's t test at α=0.05 level. Means with same letter indicate no significant differences.

The same four traits were evaluated in Waller and the mean values and the standard

errors for six generations of the crosses ‘Freshmarket 9’ x ‘Black Sea Man’ and T215VR x ‘Manyel’ are listed in Table 3 and Table 4, respectively. In ‘Freshmarket 9’ x ‘Black Sea Man’, significant differences among most traits were found. The mean values of different generations in flower number per cluster suggested the occurrence of heterosis for the trait. The mean values of fruit number per cluster and fruit set of the F_1 and BCP_1 exceeded mid parent values and were not significantly different from those of ‘Freshmarket 9’, indicating dominance effects for fruit number per cluster and fruit set toward the heat-tolerant female parent ‘Freshmarket 9’. The population means of the heat-tolerance traits evaluated in T215VR x ‘Manyel’ in Waller were significant among generations except flower number per cluster (Table 4). Flower number per cluster of the F_1 and BCP_1 exceeded mid parent values and were not significantly different from those of T215VR, which suggests a dominance effect for flower number per cluster toward the female parent T215VR. Interestingly, fruit number per cluster and fruit set of the F_1 and BCP_1 exceeded mid parent values, but the values of BCP_1 were significantly higher than both of the parents. The result indicated that there might be some expression of heterosis in the backcross generation.

According to the results from the two environments, generation means for the heat-tolerance traits showed significance in T215VR x ‘Manyel’, but not in ‘Freshmarket 9’ x ‘Black Sea Man’. In ‘Freshmarket 9’ x ‘Black Sea Man’, the female parent in general had higher values in flower number per cluster, fruit number per cluster and fruit set, and ‘Black Sea Man’ only performed better in pollen viability. The result is as expected since ‘Freshmarket 9’ is a heat-tolerant cultivar (Leeper and Cox, 1986). In T215VR x ‘Manyel’,

the female parent outperformed the male parent in all traits except pollen viability and flower number per cluster in Waller.

Table 3 Means and the standard errors of six generations of 'Freshmarket 9' x 'Black Sea Man' for heat-tolerance traits at Waller.

	PV (%)	FLC	FRC	FS (%)
Generation				
Freshmarket 9 (P_1)	0.57 ± 0.04 b	6.83 ± 0.90 ab	3.67 ± 0.64 a	0.53 ± 0.08 ab
Black Sea Man (P_2)	0.72 ± 0.04 a	5.58 ± 0.90 ab	2.58 ± 0.64 ab	0.49 ± 0.08 ab
F_1	0.58 ± 0.05 b	7.86 ± 1.10 a	4.50 ± 0.78 a	0.55 ± 0.10 ab
F_2	0.61 ± 0.02 b	4.51 ± 0.32 b	1.89 ± 0.23 b	0.36 ± 0.03 b
BC_1P_1	0.58 ± 0.04 b	7.08 ± 0.90 a	4.33 ± 0.64 a	0.61 ± 0.09 a
BC_1P_2	0.58 ± 0.04 b	6.94 ± 0.78 a	4.31 ± 0.55 a	0.62 ± 0.07 a

* Means were separated by LSD Student's t test at α=0.05 level. Means with same letter indicate no significant differences.

Table 4 Means and the standard errors of six generations of T215VR x 'Manyel' for heat-tolerance traits at Waller.

	PV (%)	FLC	FRC	FS (%)
Generation				
T215VR (P_1)	0.74 ± 0.04 ab	5.17 ± 0.90 a	2.83 ± 0.64 abc	0.55 ± 0.09 ab
Manyel (P_2)	0.76 ± 0.03 a	5.35 ± 0.69 a	2.5 ± 0.50 bc	0.45 ± 0.07 b
F_1	0.62 ± 0.04 bc	5.58 ± 0.90 a	3.17 ± 0.64 abc	0.55 ± 0.09 ab
F_2	0.68 ± 0.02 abc	5.17 ± 0.40 a	2.35 ± 0.27 c	0.48 ± 0.04 b
BC_1P_1	0.69 ± 0.03 abc	6.04 ± 0.64 a	3.63 ± 0.45 a	0.60 ± 0.06 a
BC_1P_2	0.61 ± 0.03 c	5.04 ± 0.64 a	2.83 ± 0.45 abc	0.56 ± 0.06 ab

* Means were separated by LSD Student's t test at α=0.05 level. Means with same letter indicate no \ significant differences.

Phenotypic Correlations

The phenotypic correlation coefficients among traits in 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' from College Station are given in Table 5 and Table 6, respectively. In the cross 'Freshmarket 9' x 'Black Sea Man', all correlations were positive and highly significant, except pollen viability (Table 5). Flower number per cluster was highly correlated to fruit number per cluster (0.94) and fruit set (0.82). Fruit number per cluster was highly correlated to fruit set (0.88). In the cross T215VR x 'Manyel', the correlations of all traits were positive and significant (Table 6). Moderately high correlations were found between flower number per cluster and fruit number per cluster (0.74), and between flower number per cluster and fruit set (0.63). Fruit number per cluster was highly correlated to fruit set (0.93).

Table 5 Phenotypic correlation among 4 traits in the F_2 population from 'Freshmarket 9' x 'Black Sea Man' at College Station.

	PV (%)	**FLC**	**FRC**	**FS (%)**
PV (%)	1.0000	0.2058	0.3177	0.3334
FLC	--	1.0000	0.9442**	0.8165**
FRC	--	--	1.0000	0.8769**
FS (%)	--	--	--	1.0000

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 6 Phenotypic correlation among 4 traits in the F_2 population from T215VR x 'Manyel' at College Station.

	PV (%)	FLC	FRC	FS (%)
PV (%)	1.0000	0.4435**	0.3004*	0.3314**
FLC	--	1.0000	0.7400**	0.6322**
FRC	--	--	1.0000	0.9260**
FS (%)	--	--	--	1.0000

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$ respectively.

The phenotypic correlation coefficients among traits in 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' from Waller are given in Table 7 and Table 8, respectively. In the cross 'Freshmarket 9' x 'Black Sea Man', pollen viability was found to be significantly correlated with fruit set only (Table 7). Flower number per cluster was correlated to fruit number per cluster (0.79) and fruit set (0.63). Fruit number per cluster was highly correlated to fruit set (0.88). For the cross T215VR x 'Manyel', only the correlation between fruit number and fruit set was found to be significant (0.82) (Table 8). The results showed flower number per cluster, fruit number per cluster and fruit set are highly correlated with each other, with values varying from 0.6 to more than 0.9, depending on the environments and the genotypes.

Table 7 Phenotypic correlation among 4 traits in the F_2 population from 'Freshmarket 9' x 'Black Sea Man' at Waller.

	PV (%)	FLC	FRC	FS (%)
PV (%)	1.0000	0.2192	0.3723	0.4193*
FLC	--	1.0000	0.7867**	0.6307**
FRC	--	--	1.0000	0.8769**
FS (%)	--	--	--	1.0000

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 8 Phenotypic correlation among 4 traits in the F_2 population from T215VR x 'Manyel' at Waller.

	PV (%)	FLC	FRC	FS (%)
PV (%)	1.0000	0.2101	0.3263	0.3845
FLC	--	1.0000	0.4294	0.4015
FRC	--	--	1.0000	0.8228**
FS (%)	--	--	--	1.0000

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Hazra and Ansary (2008) reported that pollen viability and flowers/truss were significantly and positively correlated to fruit set. In our study, lack of significant correlations between pollen viability and all other traits under high temperature across different environments suggests that different mechanisms might contribute to heat tolerance in these genotypes. Stevens and Rudich (1978) reported various mechanisms of conditioning heat tolerance, including pollen viability as well as dehiscence, ovule viability and stigma and style exsertion. Shelby et al. (1978) found a slight but significant

decline in pollen viability from plants grown under high temperatures. They concluded that insufficient pollination was more likely a major factor of reduced fruit set under high temperature rather than reduced pollen viability. The results in our experiment also suggest that using pollen viability as an indirect selection criterion for heat tolerance is genotype specific, which is in accordance with the result obtained by Abdul-Baki and Stommel (1995)

Gene effects

The generation mean analysis for the four traits in 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' in College Station are listed in Table 9 and Table 10, respectively. For both crosses, the individual scaling tests (A, B and C) were not significant for all traits, implying the absence of non-allelic interactions. Therefore, the three-parameter additive/dominance model was adequate in explaining the gene effects of the traits in both crosses. The results of generation mean analysis indicated that in 'Freshmarket 9' x 'Black Sea Man', none of the traits showed significance for additive or dominance gene effects. For pollen viability in T215VR x 'Manyel', both additive and dominance effects were significant, with a higher estimated value for dominance effect (Table 10.). For the other three traits in T215VR x 'Manyel', flower number per cluster, fruit number per cluster and fruit set, additive gene effects were found to be significant. Preponderance of additive gene effects for flower number per cluster (Hanson et al., 2002), fruit number per cluster (Zdravkovic et al., 1998; Zdravkovic et al., 2011) and percent fruit set (El-Ahmadi and Stevens, 1979b) under high temperatures were supported by the present results.

Table 9 Generation mean analysis of gene effects of 'Freshmarket 9' x 'Black Sea Man' for heat-tolerance traits at College Station.

	PV (%)	FLC	FRC	FS (%)
Gene effect estimated form three-parameter model				
(m)	0.51 ± 0.24 **	6.22 ± 2.49 ns	4.47 ± 1.88 *	0.58 ± 0.33 ns
(a)	-0.02 ± 0.04 ns	0.41 ± 0.44 ns	0.56 ± 0.33 ns	0.09 ± 0.06 ns
(d)	-0.08 ± 0.69 ns	-7.56 ± 6.99 ns	-6.42 ± 5.27 ns	-0.30 ± 0.93 ns
Scaling test				
A	-0.13 ± 0.17 ns	-1.69 ± 1.76 ns	-1.05 ± 1.37 ns	-0.06 ±0.23 ns
B	0.55 ± 0.16 ns	-1.38 ± 1.65 ns	-0.09 ± 1.25 ns	0.09 ± 0.22 ns
C	-0.31 ± 0.18 ns	-0.69 ± 1.79 ns	1.64 ± 1.35 ns	0.17 ± 0.24 ns

ns, *, ** Nonsignificant or significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Table 10 Generation mean analysis of gene effects of T215VR x 'Manyel' for heat-tolerance traits at College Station.

	PV (%)	FLC	FRC	FS (%)
Gene effect estimated form three-parameter model				
(m)	0.12 ± 0.21 ns	1.51 ± 2.14 ns	-0.25 ± 1.60 ns	-0.03 ± 0.28 ns
(a)	0.08 ± 0.04 *	0.69 ± 0.38 *	0.55 ± 0.29 *	0.11 ± 0.05 *
(d)	1.29 ± 0.62 *	4.30 ± 6.28 ns	4.15 ± 4.71 ns	1.12 ± 0.83 ns
Scaling test				
A	0.19 ± 0.17 ns	-0.49 ± 1.71 ns	-0.04 ± 1.29 ns	0.07 ± 0.23 ns
B	0.22 ± 0.15 ns	0.35 ± 1.50 ns	1.02 ± 1.13 ns	0.34 ± 0.20 ns
C	0.01 ± 0.14 ns	-1.89 ± 1.46 ns	-0.47 ± 1.10 ns	0.07 ± 0.19 ns

ns, *, ** Nonsignificant or significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

The analysis of gene effects for the four traits in 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' in Waller are listed in Table 11 and Table 12, respectively. The

individual scaling tests (A, B and C) were not significant for all traits in both crosses. Therefore, the three-parameter model was sufficient in explaining the gene effects of the traits in both crosses. In ‘Freshmarket 9’ x ‘Black Sea Man’, there was no gene effect found significant for pollen viability, while dominance effects were found significant in all other traits (Table 11). In T215VR x ‘Manyel’, no gene effects were found significant for pollen viability and flower number per cluster. The results indicated that dominance effects were significant for fruit number per cluster and fruit set, which were in accordance with the results given by Hanson et al. (2002).

Compared to Waller, lack of significance of gene effects for the traits of ‘Freshmarket 9’ x ‘Black Sea Man’ grown in College Station might be due to the high environmental variances, which might mask the gene effects and their significances. Also, the experimental errors resulting from the small sample size in the F_2 generation of ‘Freshmarket 9’ x ‘Black Sea Man’ could have affected the result. The sample size of the F_2 population of T215VR x ‘Manyel’ was larger, so the result of the generation mean analysis might not be as much affected as the result analyzed from the cross ‘Freshmarket 9’ x ‘Black Sea Man’.

The results of the generation mean analysis signified the importance of dominance gene effects for most of the traits under high temperatures, while additive gene effects were also involved. The dominance effects were higher in magnitude for all traits, especially for flower number per cluster and fruit number per cluster. The importance of dominance gene effects for traits influencing heat tolerance in the present investigation is supported by earlier reports (Hazra and Ansary, 2008; Shelby et al., 1978)

Table 11 Generation mean analysis of gene effects of 'Freshmarket 9' x 'Black Sea Man' for heat-tolerance traits at Waller.

	PV (%)	FLC	FRC	FS (%)
Gene effect estimated form three-parameter model				
(m)	0.77 ± 0.14 **	-3.79 ± 2.78 ns	-6.60 ± 1.98 ns	-0.48 ± 0.26 ns
(a)	-0.07 ± 0.03 ns	0.63 ± 0.64 ns	0.54 ± 0.45 ns	0.02 ± 0.06 ns
(d)	-0.43 ± 0.38 ns	21.54 ±7.90 **	22.87 ±5.62 **	2.34 ± 0.75 **
Scaling test				
A	0.02 ± 0.11 ns	-0.54 ± 2.29 ns	0.50 ± 1.63 ns	0.13 ± 0.22 ns
B	-0.14 ± 0.10 ns	0.42 ± 2.11 ns	1.54 ± 1.50 ns	0.19 ± 0.20
C	-0.004±0.14 ns	-10.12±2.85 ns	-7.68 ± 2.03 ns	-0.66 ± 0.27 ns

ns, *, ** Nonsignificant or significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Table 12 Generation mean analysis of gene effects of T215VR x 'Manyel' for heat-tolerance traits at Waller.

	PV (%)	FLC	FRC	FS (%)
Gene effect estimated form three-parameter model				
(m)	0.84 ± 0.12 **	3.74 ± 2.12 *	-0.84 ± 1.72 ns	0.08 ± 0.21 ns
(a)	-0.005±0.03 ns	-0.09 ± 0.57 ns	0.17 ± 0.40 ns	0.05 ± 0.05 ns
(d)	-0.44 ± 0.32 ns	3.85 ± 6.05 ns	8.76 ± 4.61 *	1.11 ± 0.58 *
Scaling test				
A	0.02 ± 0.09 ns	1.33 ± 1.80 ns	1.25 ± 1.28 ns	0.10 ± 0.17 ns
B	-0.15 ± 0.08 ns	-0.85 ± 1.71 ns	-0.00 ± 1.21 ns	0.12 ± 0.16 ns
C	-0.03 ± 0.13 ns	-1.04 ± 2.34 ns	-2.25 ± 1.86 ns	-0.20 ± 0.23 ns

ns, *, ** Nonsignificant or significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Inheritance of Heat-Tolerance Traits

Broad-sense heritability and narrow-sense heritability estimates for heat-tolerance traits for the crosses in College Station and in Waller are listed in Table 13 and Table 14, respectively. The broad-sense heritability estimates indicated that the performance of most traits in T215VR x 'Manyel' was more affected by the environment in College Station than 'Freshmarket 9' x 'Black Sea Man' (Table 13). In College Station, narrow-sense heritability estimates in 'Freshmarket 9' x Black Sea Man' were not significant for all trait. The narrow-sense heritability estimates were low for pollen viability (0.39) and fruit set (0.25), and moderate for flower number per cluster (0.66) and fruit number per cluster (0.62). In T215VR x 'Manyel', narrow-sense heritability estimates for pollen viability and fruit set were found significant. The narrow-sense heritability estimates for all traits were low, with values ranged from 0.11 to 0.25. The low narrow-sense heritability estimates indicated that additive gene action does not play a major role in the inheritance of those traits. In Waller, the narrow-sense heritability estimate was found significant in fruit set only in 'Freshmarket 9' x 'Black Sea Man' (Table 14). The narrow-sense heritability estimates were low for pollen viability (0.15) and fruit number per cluster (0.15), and moderate for flower number per cluster (0.60) and fruit set (0.72). In T215VR x 'Manyel', the narrow-sense heritability estimate was found significant in fruit set only. The narrow sense heritability estimates were low for pollen viability (0.36), flower number per cluster (0.14) and fruit number per cluster (0.45), and moderate for fruit set (0.58) Moderate narrow-sense heritability estimate in high temperature fruit set was also reported by Wessel-Beaver and Scott (1992).

The narrow-sense heritability estimates for 'Freshmarket 9' x 'Black Sea Man' for

the heat-tolerance traits at College Station were moderate but the mean and standard errors of the traits for 'Freshmarket 9' x 'Black Sea Man' in Table 1 didn't showed significant differences. The reason might be due to different effects on different loci, which can be revealed by estimating heritability based on variances and be masked by analysis based on population means.

Table 13 Broad-sense and narrow-sense heritability for heat-tolerance traits of 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' at College Station.

Cross	'Freshmarket 9' x 'Black Sea Man'		T215VR x 'Manyel'	
	H^2	h^2	$H^{2.}$	h^2
PV (%)	0.58	0.39 ± 0.46	0.66	0.11± 0.05 *
FLC	0.89	0.66 ± 0.63	0.64	0.09 ± 0.52
FRC	0.91	0.62 ± 0.73	0.59	0.11 ± 0.21
FS (%)	0.60	0.28 ± 1.17	0.44	0.25 ± 0.03 **

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Table 14 Broad-sense and narrow-sense heritability for heat-tolerance traits of 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' at Waller.

Cross	'Freshmarket 9' x 'Black Sea Man'		T215VR x 'Manyel'	
	$H^{2.}$	h^2	$H^{2.}$	h^2
PV (%)	0.91	0.15 ± 1.24	0.94	0.36 ± 0.81
FLC	0.96	0.60 ± 0.44	0.78	0.14 ± 1.23
FRC	0.96	0.15 ± 0.74	0.91	0.45 ± 0.52
FS (%)	0.93	0.72 ± 0.05 **	0.74	0.58 ± 0.14 **

** Significant at $P \leq 0.01$.

The results of broad-sense heritability estimates at the two locations showed that the genetic variance of the traits at Waller was higher than at College Station. Therefore, there was less environment variation at Waller than at College Station. A number of studies have reported low or moderate heritability of the complex traits related to heat tolerance (El Ahmadi and Stevens, 1979b; Villareal and Lai, 1979). Narrow-sense heritability estimates for pollen viability and flower number per cluster were low to moderate at both locations. For fruit set, narrow-sense heritability estimates were low at College Station and moderate at Waller. Narrow-sense heritability estimates for most of the traits were low, indicating that single plant selection is ineffective unless heritability for the specific trait is high (Nyquist and Baker, 1991)

The low narrow-sense heritability estimates for most of the traits under high temperatures imply that single plant selection in the F_2 will not be effective, and that alternative approaches such as mass or recurrent selection should be considered in early generations.

Conclusion

The findings of the generation mean analysis indicate that both additive and dominance gene actions contribute to the expression of the heat-tolerance traits. Dominance effects were higher in magnitude, suggesting dominance gene action being the major contributor to the expression of the traits studied. Narrow-sense heritability

estimates were low to moderate for the heat-tolerance traits, indicating little additive gene action in the inheritance of the traits. It might also be due to the large environmental effects on the expression of the traits under high temperature conditions. A previous study on high temperature fruit set (Hanson et al., 2002) supported this proposition. It also implies that single plant selection in the F_2 for heat tolerance will not be effective. Reciprocal recurrent selection should hold some promise for improving heat tolerance in tomato (Hazra and Ansary, 2008). Based on the results of the present study and on some previous studies (Villareal and Lai, 1979; Hanson et al., 2002), it can be concluded that selection for fruit set under high temperature conditions should be primarily based on replicated family testing in the F_3 and later generations.

CHAPTER IV

DESIGN II ANALYSIS

For plant breeders, heritability in narrow sense is important because it measures the additive portion of genetic variance, which is the foundation of effective selection in plant breeding. Various mating designs are used by breeders to estimate narrow sense heritability. Selection of suitable parents and mating designs in conventional plant breeding are the keys to successful plant breeding programs (Nduwumuremyi et al., 2013).

The design II mating design, also known as North Carolina design II or factorial design, is a reliable design to evaluate narrow sense heritability. The assumptions for this mating design are that there are no maternal effects, no linkage equilibrium, and no epistasis. The design II is more applicable to self-pollinated crops and provides a direct estimate of dominance effects (Hallauer and Miranda, 1981). The design II can handle more parents and produce considerably fewer crosses than a diallel mating design, yet still allows estimation of narrow sense heritability for both males and females, which is an advantage of design II over the diallel (Hallauer and Miranda, 1981).

Design II also allows breeders to measure general combining ability (GCA) and specific combining ability (SCA). GCA was described as the general performance of a line in a series of hybrid combinations and SCA was described as those cases in which certain hybrid combinations outperform or perform poorer than would be expected on

the basis of the average performances of the parental lines involved (Sprague and Tatum, 1942). Parents with a high average combining ability in crosses are considered to have high GCA, while if their potential to combine well is restricted to a particular cross, they are considered to have high SCA. According to Hallauer and Miranda (1981), male and female effects, and the male x female interaction effects in a design II mating design are equivalent to GCA and SCA effects in a diallel mating design. Two independent estimates of GCA allow calculation of narrow sense heritability based on male variance, which is free from maternal effects (Fasahat et al., 2016). The aforementioned advantages lead to the use of design II mating design in this study.

Materials and Methods

Plant Materials

Seven tomato lines were selected as parents with different degrees of heat tolerance. The parental lines include heirloom cultivars 'Rutgers', 'Homestead', 'Black Sea Man', and breeding lines 'Freshmarket 9', T135VR, T214, and BL58.

In December, 2015, seed of all seven parental lines were planted in Sunshine mix #4 (Sun Gro Horticulture Inc., Bellevue, WA) in three-gallon, black plastic, self-draining pots in a greenhouse in College Station. In spring, 2016, crosses were made using North Carolina Design II mating design (Comstock and Robinson, 1952). In the mating design, 'Rutgers', 'Homestead' and 'Black Sea Man' were used as females and were mated to ' Freshmarket 9', T135VR, T214, and BL58 which were used as males. The crosses were made by brushing anther cones of newly opened flowers of male parents against emasculated flowers of female parents. F_1 hybrid seeds were collected after fruit maturity.

The F_1 hybrid seeds were planted in March, 2017. The seedlings were transplanted in the experimental plots in the field in College Station on March 30th, 2017. The twelve hybrid crosses were arranged in a randomized complete block design (RCBD) with three replications. Each unit plot contained a single row with 5 plants per line.

Phenotypic Evaluation

Data on days to flower (DFL), flower number per cluster (FLC), pollen viability (PV), days to fruit (DFR), fruit number per cluster (FRC), fruit set (FS) and yield (YD) were recorded. For days to flowering, flowers were tagged during anthesis and days from transplant to first flower opened were counted from April 21th to June 20th. Days to fruit were counted as the days from transplant to first fruit formed. Fruits were harvested from June 26th to July 17th and the total fruit weights per plant were recorded as yield. Data on flower number per cluster, pollen viability (%), and fruit set (%) were collected as described in Chapter III

Statistical Analysis

All data were analyzed using JMP software (Version 12.0; SAS Institute, Cary, N.C., 2016). Analysis of variance (ANOVA) and Pearson's correlation coefficients were obtained. The ANOVA were performed to indicate the significance of male, female and male x female effects. Pearson's correlation coefficients were used to determine the correlation between the traits.

Described by Hallauer and Miranda (1981), the ANOVA procedure was used to estimate sources of variation and main effects due to male, female and female-male interaction (female x male). The form of ANOVA when *f* females are crossed with *m*

males and evaluated in *r* replications in one environment is shown in Table 15. The expectations of females and males for design II are equivalent to GCA, and the female x male source is equivalent to SCA. There were two sets of parents in design II, so there are two independent estimates of GCA. F-tests are made to test for the differences among males and among females and for male x female.

Table 15 Sources of variation, degrees of freedom and expected mean square of Design II mating design in one environment (reprinted from Hallauer and Miranda, 1981).

Source of variation	Degrees of Freedom	Expected Mean Squares
Replications	*r*-1	
Females (F)	*f*-1	$\sigma^2 + r\,\sigma^2_{fm} + rm\,\sigma^2_f$
Males (M)	m-1	$\sigma^2 + r\,\sigma^2_{fm} + rf\,\sigma^2_m$
M x F	(*m*-1)(*f*-1)	$\sigma^2 + r\,\sigma^2_{fm}$
Error	(*r*-1)(*mf*-1)	σ^2

Additive and dominance variances were estimated using the equations according to Hallauer and Miranda (1981). Estimates of additive variance from the female source of variation were estimated as: $\sigma^2_{Af} = 2\sigma^2_f$. Estimates of additive variance from the male source of variation were estimated as: $\sigma^2_{Am} = 2\sigma^2_m$. Dominance variances were estimated as $\sigma^2_D = 2\sigma^2_{fm}$.

Estimates of narrow-sense heritability were calculated from the estimates of σ^2_A from female sources of variation described by Hallauer and Miranda (1981) as follows:

$$h^2_f = \sigma^2_f / [(\sigma^2/r) + \sigma^2_{fm} + \sigma^2_f]$$

where standard error was calculated as follows:

$$SE(h^2_f) = SE(\sigma^2_f) / [(\sigma^2/r) + 4\sigma^2_{fm} + 4\sigma^2_f]$$

Similar estimates of heritability and standard errors were calculated from male sources of variation. Significance of h^2 was evaluated with the mean and standard error. If the estimated mean exceeded two times the value of standard error, then it is significant at $P \leq 0.05$. And if the estimated mean exceeded three times the value of standard error, then it is significant at $P \leq 0.01$.

The GCA estimates for females (g_i) and male (g_j) and SCA estimates for all hybrid genotypes (s_{ij}) were calculated according to Beil and Atkins (1967) as follows:

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

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

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

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

Results and Discussion

Phenotypic Correlation

The phenotypic correlation coefficients among traits in the tomato progeny are shown in Table 16. Correlations between all traits were found significant except for correlation between fruit set and days to flower, days to fruit and flower number per cluster. Days to flower was negatively correlated with all other traits except days to fruit. Similarly, days to fruit was negatively correlated with all other traits except days to

flower. Pollen viability, flower number per cluster, fruit number per cluster, fruit set and yield were positively correlated. Days to flower and days to fruit were highly and positively correlated (0.77). Flower number per cluster was found highly correlated with fruit number per cluster (0.62). Fruit number per cluster was highly correlated to fruit set (0.82) and yield (0.75). Fruit set was highly correlated to yield (0.69).

Table 16 Phenotypic correlation of seven heat-tolerance traits in tomato progeny from the North Carolina Design II mating design.

	PV	DFL	DFR	FLC	FRC	FS	YD
PV	1.0000	-0.2146**	-0.2768**	0.3057**	0.3504**	0.2224**	0.3340**
DFL	--	1.0000	0.7698**	-0.4387**	-0.3238**	-0.0926	-0.3243**
DFR	--	--	1.0000	-0.4488**	-0.3432**	-0.0909	-0.3018**
FLC	--	--	--	1.0000	0.6224**	0.0925	0.3812**
FRC	--	--	--	--	1.0000	0.8151**	0.7549**
FS	--	--	--	--	--	1.0000	0.6922**
YD	--	--	--	--	--	--	1.0000

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Design II Analysis

The ANOVA in Table 17 indicated significance was found in the mean squares due to female and female x male interactions for all traits and in the mean squares due to male in all traits except days to flower and days to fruit. There were more significant differences for the females than the males. The significance of mean squares due to female and male both represent GCA variances while female x male interaction designates SCA variance,

suggesting that both additive and non-additive genes were important in the expression of the traits studied. However, the GCA effects were higher than the SCA effects for all traits, which indicated prevailing additive gene action with contribution of dominance or epistatic gene action in the expression of the traits.

Table 17 Analysis of variance for seven heat-tolerance traits in tomato progeny from the North Carolina Design II analysis.

Source of Variation	df	Mean Squares						
		PV	DFL	DFR	FLC	FRC	FS	YD
Rep	2	0.02ns	1603.05**	1963.55*	10.65**	0.76ns	0.05ns	35892.45 ns
Male (GCA)	3	0.18**	48.95ns	146.68ns	4.80**	4.54**	0.17**	627668.47 **
Female (GCA)	2	0.10**	863.13**	550.05**	17.56**	12.25**	0.28**	902557.25 **
M x F (SCA)	6	0.03**	155.05**	173.98*	2.36**	4.45**	0.24**	547812.95 **
Error	130	0.01	45.81	70.32	0.54	0.29	0.02	25800
Total	143							

ns, *, ** Nonsignificant or significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Inheritance of Heat-Tolerance Traits

The additive variance from the females for days to flower, days to fruit, flower number per cluster, fruit number per cluster, fruit set and yield were larger than the additive variances from the males (Table 18). For pollen viability and yield, the additive variances from the males were larger than the additive variances from the females. The

additive variances from the male were smaller than the additive variances from the females for all the other traits. The additive variances were larger than the dominance variances for pollen viability, days to flower and flower number per cluster. Hence, the additive gene action was the major contribution in traits expression. The dominance variances were larger than the additive variances for days to fruit, fruit number per cluster, fruit set and yield, indicating dominance effects as the prevailing gene action in the expression of these traits.

Narrow-sense heritability estimates from both female and male variances were calculated and listed in Table 18. Narrow-sense heritability from the female variance for days to flower, days to fruit, flower number per cluster, fruit number per cluster and yield was found significant. Fruit set had the lowest heritability estimates (0.04) while flower number per cluster had the highest heritability estimates (0.66). Narrow-sense heritability from the male variance for flower number per cluster and yield was found significant. Days to flower had the lowest heritability estimates (-0.41), which was not different from zero in this study, while pollen viability had the highest heritability estimates (0.71). The estimates of narrow-sense heritability from the male variance for days to flower, days to fruit and fruit set were found negative due to the negative signs of their σ^2_{Am}. The negative values were not different from zero in this study, so the values were marked zero in Table 18 with the original estimated values in the parentheses. The results also indicated that heritability from female variances were much higher than those from male variances for all traits except pollen viability.

Table 18 Estimates of additive and dominance variance, and narrow sense heritability from the male and female sources of variation.

	σ^2_{Af}	σ^2_{Am}	σ_D^2	$h_f^2 \pm$ SE	$h_m^2 \pm$ SE
PV	0.01	0.04	0.01	0.47 ± 1.49	0.71 ± 1.35
DFL	118.02	0 (-23.58)	72.83	0.59 ± 0.02 **	0 (-0.41)
DFR	62.68	0 (-6.07)	69.11	0.44 ± 0.02 **	0 (-0.08)
FLC	2.54	0.55	1.22	0.66 ± 0.15 **	0.29 ± 0.14 *
FRC	1.3	0.02	2.77	0.32 ± 0.10 **	0.007 ± 0.01
FS	0.01	0 (-0.02)	0.15	0.04 ± 0.19	0 (-0.11)
YD	59124.05	17745.67	348008.65	0.14 ± 0.00 **	0.05 ± 0.00 **

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Combining Ability

The GCA component is a function of the additive variance, which indicates additive gene action in the expression of the traits. A parent with higher positive values of GCA effects is considered as a good general combiner. The GCA effects of seven parents for seven different traits are presented in Table 19. For pollen viability, the male parent T214 showed the highest positive GCA effect (0.05) while T135VR showed the highest negative GCA effect (-0.07). Therefore, T214 was the best general combiner for pollen viability. For days to flower, 'Homestead', 'Black Sea Man', T135VR and T214 had higher negative GCA effects while the others had positive GCA effects.
Hence, 'Homestead' performed as the best general combiner for earliness of flowering followed by 'Black Sea Man', T135VR and T214. For days to fruit, T214 and 'Homestead' and 'Black Sea Man' showed higher negative GCA effects while the others

showed positive GCA effects, indicating that T214 was the best general combiner for earliness of fruit followed by ‘Homestead’ and ‘Black Sea Man’. For flower number per cluster, T214, ‘Black Sea Man’ and ‘Homestead’ demonstrated higher GCA effects than the others. Thus, T214 was the best general combiner for flower number per cluster followed by ‘Black Sea Man’ and ‘Homestead’. For fruit number per cluster, ‘Homestead’, T214 and ‘Freshmarket 9’ had higher positive GCA effects while the others had negative GCA effects. Therefore, ‘Homestead’ performed as the best general combiner for fruit number per cluster followed by T214 and ‘Freshmarket 9’. For fruit set, ‘Homestead’, ‘Freshmarket 9’ and T214 showed positive GCA effects while the others showed negative GCA effects. Thus, ‘Homestead’ was the best, followed by ‘Freshmarket 9’ and T214 with respect to higher fruit set. For yield, highest positive GCA effects were found in T214, ‘Homestead’, ‘Freshmarket 9’ and ‘Black Sea Man’. Therefore, T214 was the best general combiner followed by ‘Homestead’, ‘Freshmarket 9’ and ‘Black Sea Man’

It was observed from the results that for all seven traits studied, T214 was identified as the best general combiner among the male parents, with the highest GCA values in pollen viability, days to fruit, flower number per cluster and yield. And ‘Homestead’ was identified as the best general combiner among the female parents, with the highest GCA values in days to flower, fruit number per cluster and fruit set. ‘Freshmarket 9’ would be a good combiner as well, with high positive GCA values in fruit number per cluster, fruit set and yield.

Table 19 Estimates of GCA effects for seven traits of the seven parents.

Parents	PV	DFL	DFR	FLC	FRC	FS	YD
Male							
Freshmarket 9	-0.01	0.19	0.76	-0.25	0.11	0.07	63.77
T135VR	-0.07	-0.92	1.01	-0.09	-0.34	-0.09	-149.96
T214	0.10	-0.84	-3.01	0.54	0.45	0.04	148.07
BL58	-0.02	1.58	1.24	-0.20	-0.22	-0.03	-61.88
Female							
Homestead	0.05	-3.24	-2.91	0.30	0.50	0.09	136.71
Rutgers	-0.03	4.80	3.72	-0.70	-0.51	-0.04	-137.54
Black Sea Man	-0.02	-1.56	-0.81	0.39	0.003	-0.04	0.84

The SCA effects related to a specific cross signify the role of non-additive gene action in the expression of the traits. High SCA effects lead to the best performance of some particular cross combinations. High SCA effects may arise not only in crosses with good combiners but also in poor combiners with non-additive gene actions involved. The SCA effects of 12 crosses for seven different traits are presented in Table 20. For pollen viability, six hybrids showed positive SCA values. 'Rutgers' x BL58 had the highest positive SCA value (0.06) followed by 'Black Sea Man' x T214 (0.05) and 'Homestead' x T135VR (0.03). For days to flower, of the twelve cross combinations, seven showed negative SCA values, indicating that these hybrids flowered earlier than the other hybrids. 'Homestead' x 'Freshmarket 9' showing the highest SCA value (-6.06), seems to be the best specific combiner for early flowering, followed by 'Rutgers' x BL58 (-2.16) and 'Black Sea Man' x T135VR (-1.81). For days to fruit, six hybrids had negative SCA

values, suggesting that these hybrids set fruits earlier than the others. ‘Rutgers’ x BL58 had the highest negative SCA value (-4.97), indicating the best specific combiner for early fruit setting, followed by ‘Black Sea Man’ x T135VR (-3.64) and ‘Homestead’ x ‘Freshmarket 9’ (-2.53). For flower number per cluster, seven out of twelve hybrids had positive SCA values. ‘Black Sea Man’ x T214, as the best specific combiner, showed the highest positive SCA value (0.54), followed by ‘Rutgers’ x ‘Freshmarket 9’ (0.40) and ‘Homestead’ x ‘Freshmarket 9’ (0.21). For fruit number per cluster, seven hybrids showed positive SCA values. ‘Black Sea Man’ x T135VR had the highest SCA value (0.65) followed by ‘Homestead’ x ‘Freshmarket 9’ (0.55) and ‘Rutgers’ x ‘Freshmarket 9’ (0.31). For fruit set, six out of twelve hybrids had positive SCA values. ‘Black Sea Man’ x T135VR with the highest SCA value of 0.17 would be a most desirable combination to enhance fruit set under high temperatures, followed by ‘Homestead’ x ‘Freshmarket 9’ (0.11) and ‘Rutgers’ x T214 (0.08). For yield, four hybrids had positive SCA values. ‘Homestead’ x ‘Freshmarket 9’, showing the highest SCA value (268.02) performed as the best specific combiner for yield improvement, followed by ‘Black Sea Man’ x BL58 (150.97) and ‘Rutgers’ x T214 (117.16).

According to previous studies (Verma and Srivastava, 2004; Dey et al.,2014), high SCA effects resulting from crosses including both parents with good GCA (i.e. good GCA x good GCA) may be ascribed to additive x additive gene action, while the high SCA effects derived from crosses where one parent is a good general combiner and one is a poor general combiner (i.e. good GCA x poor GCA) may be ascribed to favorable additive effects of the good general combiner parent and epistatic effects of the poor general

combiner. High SCA effects resulting from crosses where both parents are poor general combiners (i.e. poor GCA x poor GCA) may be due to presence of non-additive gene action especially complementary epistasis (Dey et al., 2014). High SCA effects in crosses involving both parents with poor GCA effects like 'Rutgers' x BL58 for pollen viability, 'Rutgers' x BL58 for days to fruit and 'Black Sea Man' x T135VR for fruit number per cluster and fruit set might be due to the presence of complementary epistasis. For days to flower, high SCA effects derived from one good general combiner and one poor general combiner such as 'Homestead' x 'Freshmarket 9' indicated possible additive and non-additive gene action are involved in the expression of the trait. As a result, the traits mentioned above would be difficult to fix due to the involvement of non-additive gene action, but might be useful in heterosis breeding along with recurrent selection. High SCA effects in the crosses involving both parents with good GCA such as 'Black Sea Man' x T214 for flower number per cluster and 'Homestead' x 'Freshmarket 9' for yield suggested the role of cumulative effect of additive and additive x additive gene action, and that these traits might be easier to fix. Therefore, 'Black Sea Man' x T214 and 'Homestead' x 'Freshmarket 9'crosses may be exploited to improve flower number per cluster and yield in hybrid breeding for heat tolerance.

Table 20 Estimates of SCA effects of the cross combination for seven traits of the twelve F_1 hybrids.

Cross	PV	DFL	DFR	FLC	FRC	FS	YD
'Homestead' x 'Fm 9'	-0.02	-6.06	-2.53	0.21	0.55	0.11	268.02
'Homestead' x T135VR	0.03	1.88	2.30	0.09	-0.10	-0.0035	74.09
'Homestead' x T214	0.003	1.55	-0.92	-0.10	0.02	-0.01	-134.96
'Homestead' x BL58	-0.02	2.63	1.16	-0.21	-0.48	-0.10	-207.16
'Rutgers' x 'Fm 9'	0.01	3.23	3.92	0.40	0.31	0.04	-16.00
'Rutgers' x T135VR	-0.02	-0.08	1.34	0.03	-0.55	-0.17	-157.35
'Rutgers' x T214	-0.06	-0.99	-0.30	-0.45	0.01	0.08	117.16
'Rutgers' x BL58	0.06	-2.16	-4.97	0.02	0.22	0.05	56.19
'Black Sea Man' x 'Fm 9'	0.01	2.83	-1.39	-0.61	-0.86	-0.15	-252.02
'Black Sea Man' x T135VR	-0.02	-1.81	-3.64	-0.12	0.65	0.17	83.25
'Black Sea Man' x T214	0.05	-0.56	1.22	0.54	-0.04	-0.06	17.80
'Black Sea Man' x BL58	-0.04	-0.47	3.81	0.18	0.25	0.04	150.97

*'Fm 9' indicates the male parent line 'Freshmarket 9'.

Conclusion

It was observed from the results of the Design II analysis that both additive and non-additive gene action contributes to the expression of the traits studied. Additive gene action was the prevailing gene action for the expression of pollen viability, days to flower and flower number per cluster while dominance gene action was the major contribution in the expression of days to fruit, fruit number per cluster, fruit set and yield. Narrow-sense heritability from the female variance for days to flower, days to fruit, flower number per cluster, fruit number per cluster and yield was found significant, while for narrow-sense heritability from the male variance, only flower number per cluster and yield was found significant. The narrow-sense heritability estimates from the

female and from the male variance were low to moderate.

The results of GCA and SCA analysis suggested that the parents ‘Homestead’, T214 and ‘Freshmarket 9’ showed relatively higher GCA effects for heat tolerance and yield-related traits. ‘Homestead’ x ‘Freshmarket 9’ was identified as the best specific combiner for days to flower and yield. ‘Rutgers’ x BL58 performed as the best specific combiner for pollen viability and days to fruit. ‘Black Sea Man’ x T214 was identified as the best specific combiner for flower number per cluster. ‘Black Sea Man’ x T135VR had the highest SCA values for fruit number per cluster and fruit set. Overall, the best hybrid combination was found to be ‘Homestead’ x ‘Freshmarket 9’, which was identified as a good specific combiner for days to fruit, flower number per cluster, fruit number per cluster and fruit set and as the best specific combiner for earliness of flowering and yield. The parental lines ‘Homestead’, T214 and ‘Freshmarket 9’ can be used extensively in hybrid breeding programs for deriving desirable lines in the segregating generations. The findings of this study, along with other studies on combining ability in heat-tolerant tomato will help breeders establish efficient breeding programs to develop heat-tolerant tomato hybrids.

CHAPTER V

SUMMARY

In the study of generation mean analysis, I found that both additive and dominance effects play a role in contributing to the expression of pollen viability, flower number per cluster, fruit number per cluster and fruit set. The dominance effects were higher in magnitude for all traits, especially for flower number per cluster and fruit number per cluster, which imply that dominance effects were the predominant gene action in the expression of the traits. The result also implies that the later generations derived from the F_2 may not necessarily be heat tolerant due to the reduction in dominance gene action associated with increased inbreeding. Narrow sense heritability estimates of the heat-tolerance traits including pollen viability, flower number per cluster, fruit number per cluster and fruit set are low to moderate, suggesting that the improvement of the traits studied will be slow through selection and that single plant selection is ineffective unless heritability for the specific trait is high. The incidents of heterosis found in 'Freshmarket 9' x 'Black Sea Man' for flower number per cluster and T215VR x 'Manyel' for fruit number per cluster in the backcross generation suggest that heterosis breeding might hold some potential for improving heat tolerance in tomato based on these traits.

It was observed from Design II analysis that additive gene action was the major contributor in the expression of pollen viability, days to flower and flower number per

cluster, while dominance gene action was prevailing in the expression of earliness of fruit, fruit number per cluster, fruit set and yield. Narrow-sense heritability from the female variance for days to flower, days to fruit, flower number per cluster, fruit number per cluster and yield was found significant, while for narrow-sense heritability from the male variance, only flower number per cluster and yield was found significant. The narrow-sense heritability estimates from the female and from the male variance were low to moderate.

According to the combining ability analysis, the parent lines 'Homestead', T214, and 'Freshmarket 9' have been identified as good general combiners and can be used in deriving favorable lines in the segregating generations. Comparing the results from GCA and SCA analysis, I conclude that 'Rutgers' x BL58 can be used to improve pollen viability and days to fruit, and 'Homestead' x 'Freshmarket 9' can be used to improve earliness of flowering, and 'Black Sea Man' x T135VR can be used to improve fruit number per cluster and fruit set in heterosis breeding due to the presence of non-additive gene action. On the other hand, 'Black Sea Man' x T214 and 'Homestead' x 'Freshmarket 9' may be exploited to improve flower number per cluster and yield in hybrid breeding for heat tolerance. Being identified as a good specific combiner for flower and fruit number per cluster, earliness of fruit and fruit set and as the best specific combiner for earliness of flowering and yield, 'Homestead' x 'Freshmarket 9' was found to be the most desirable hybrid for overall performance, which can be exploited to develop a high yielding, heat tolerant F_1 hybrid. The findings of this study should be useful for parent selection and hybrid development in tomato breeding for heat tolerance.

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