AHMED YOUSSEF ABDELNABI MOHAMED ELSAYED

INHERITANCE OF RESISTANCE TO TOMATO LATE BLIGHT IN A POPULATION OF *Solanum lycopersicum* X *Solanum habrochaites*

A thesis submitted to Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Doctor Scientiae* in Genetics and Breeding

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To .....

My Family,

Parents

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First of all, to God who enabled me to realize and finish my study until this moment. To University Federal of Viçosa and Postgraduate program in Genetics and Breeding for this opportunity. I also wish to acknowledge to The National Council for Scientific and Technological Development (CNPq), Brazil and The Academy of Science for the Developing World (TWAS), Italy for the fellowship during the period of course and I greatly appreciate your confidence and financial support for opportunity to study in Brazil and attain scientific and cultural benefits.

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BIOGRAPHY

I was born in Dakahlia (Egypt) on the 09th of October, 1977. In July 1995, concluded second grade at Ali Mobarak School. After that, joined course in Agronomy, Faculty of Agriculture, Mansoura University, Egypt from September, 1995 to June, 1999 graduated in Horticultural Science with ranked general grade very good.

In July, 2000 I got my first government employment as Agricultural Specialist in Horticulture Research institute, Agriculture Research Center, Giza, Egypt. After I got my position I intended to start my postgraduate study and registered to Master degree under supervision of Professor Kauthar Sad Kash, Department of Genetics, Mansoura Uni. concluded in January, 2004.

In December, 2005, I was accepted in a full time doctorate program fellowship under the agreement established by the Academy of Science for the Developing World (TWAS), Italy and the National Council for Scientific and Technological Development (CNPq), Brazil in tomato breeding under supervision of Prof Derly da Silva, Universidade Federal de Viçosa.

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A requeima causada por *Phytophthora infestans* (Mont.) De Bary, é uma séria doença que afeta a produção de tomateiros especialmente em regiões tropicais e subtropicais. No Brasil, cerca de 20% do custo da produção de tomate é devido ao controle químico da requeima. A ausência de cultivares resistentes a requeima é devido à dificuldade de trabalhar com este patógeno em programas de melhoramento, pois as raças do patógeno possuem alta variabilidade e a resistência a este é associada com uma herança quantitativa. No desenvolvimento de cultivares competitivas o estudo da capacidade de combinação é extremamente importante para auxiliar o melhorista na escolha dos pais e combinações híbridas superiores. Este trabalho teve como objetivo estudar herança a resistência na população F_2 e estimar a capacidade geral (CGC) e específica (CEC) de combinação para resistência à requeima e qualidade de frutos de tomate. Foi realizado dialelo parcial obtendo vinte e cinco combinações híbridas, provenientes de cruzamentos entre variedades de tomate e cinco linhagens F_9 como fontes de genes de resistência a requeima. As combinações híbridas foram avaliados para resistência à requeima e qualidade de frutos em dois experimentos simultâneos, no delineamento em blocos casualizados com três repetições e 3 plantas por parcela. Os parentais e os cruzamentos F_1, mais duas variedades industriais 'Nova York' e 'Caline' como padrões de susceptibilidade contendo o gene de resistência *ph*-1 foram artificialmente inoculadas em condições de campo com mistura de isolados de *Phytopthora infestans* a uma concentração de 10^3 esporângios/mL. Severidade da doença foi determinada pela estimativa três variáveis da doença, a severidade na metade

epidemia (Y50), a severidade no final da epidemia (Ymax) e área abaixo da curva de progresso da doença (AACPD). Para a qualidade dos frutos, estimaram-se as seguintes características: peso médio do fruto, tamanho do fruto, o índice de tamanho de frutos, pH, % de acidez titulável, sólidos solúveis totais, firmeza e sabor. Análise de variância mostrou alta diferenças significativas entre os genótipos para os três parâmetros e alto correlação positiva (0,949) foi observada entre as variáveis da doença Y50, Ymax e AACPD. No controle da resistência a requeima, estiveram envolvidos efeitos genéticos aditivos e não aditivos, sendo o efeito aditivo mais importante. Os pais de maior potencial em relação a resistência a requeima foram as cultivares NC 2 CELBR e NC1 CELBR, do Grupo I, 133A e 163A do grupo II, respectivamente. As melhores combinações híbridas foram NC 2 CELBR x 64B e NC 1 CELBR x 64B. No entanto, os pais selecionados para resistência à requeima foram inferiores para a qualidade dos frutos, especialmente os pais do Grupo II. A combinação NC 2 CELBR x 163A foi mais promissora para o programa de melhoramento visando resistência intrapoulacional a requeima. Vale ressaltar que todas as cinco linhagens foram altamente estável com relação à resistência à requeima, confirmando a presença de resistência poligênica. A herança da resistência a requeima em duas populações F_2 segregantes (IKR4 e HEN4) foi estudada. A análise genética da resistência na população F_2 indicaram que a resistência parcialmente recessivo com heterose de 32,97 e 26,76 para as duas populações. Considerando do HEN4 foi mais resistente à *P. infestans* do que população IKR4. A análise genética da herança da resistência indicou que a resistência nas linhagens foi controlada por genes recessivos. Assim, apenas os melhores pais do grupo I podem ser selecionados com base na capacidade geral de combinação. Considerando que, a seleção baseada em capacidade específica de combinação poderia ser uma opção viável para a seleção da geração segregante para evitar perder os genes recessivos resistentes que estão nas linhagens avançadas.

ABSTRACT

ELSAYED, Ahmed Youssef Abdelnabi Mohamed, D.Sc. Universidade Federal de Viçosa, March, 2010. **Inheritance of resistance to tomato late blight in a population of *Solanum lycopersicum* x *Solanum habrochaites*.** Advisor: Derly José Henriques da Silva. Co-Advisors: Eduardo Seiti Gomide Mizubuti and Pedro Crescêncio Souza Carneiro.

Late blight caused by *Phytophthora infestans* (Mont.) De Bary, is a serious disease affecting tomato production worldwide especially in tropical and subtropical regions. In Brazil, about 20% of the tomato production cost is due to the chemical control of late blight. The absence of tomato cultivars resistant to this disease is related to the high variability of the pathogen and the quantitative inheritance of the resistance. In the development of competitive cultivars, estimating the combining ability is extremely important to assist the breeder in the choice of parents and hybrid combinations. The aim of this research was to study the inheritance of late blight resistance in both fresh and processing tomato varieties through analysis of inheritance in both half-diallel and F_2 segregant populations. A half-diallel set of crosses was generated from ten diverse parents comprising two groups, I and II as varieties and testers, respectively. The first group included three commercial tomato hybrids 'Ikram', 'Alambra F_1' and 'Heinz H7155', that were considered as susceptible in the current study and two resistant varieties NC1 CELBR and NC2 CELBR possessing *Ph*-2 and *Ph*-3 resistant genes to late blight. Group II (testers) included five inbred lines derived from the interspecific cross *S. lycopersicum* L. cv. Santa Clara x *S. habrochaites* f. *glabratum* accession BGH 6902. The parents and F_1 crosses in addition to two standard susceptible varieties 'New York' and 'Caline' processing *Ph*-1 resistance gene were artificially inoculated with mixed isolates of *Phytopthora infestans* in a field experiment. The hybrid combinations were evaluated for resistance to late blight and fruit quality in two simultaneous experiments, in a randomized block design with three replications. The plants were inoculated with a mixture of sporangia of *P. infestans* at concentration 10^3 sporangia.mL^{-1}. Disease severity was determined by estimating three disease variables: severity at

halfway epidemic (Y_{50}), severity at the end of the epidemic (Y_{max}) and area under disease progress curve (AUDPC). The following characteristics were determined for fruit quality: average fruit weight, fruit size, fruit size index, pH, % titratable acidity, total soluble solids, firmness and flavor. Analysis of variance showed high significant differences among the genotypes for the three parameters and strong positive correlation (0.949) was observed among the disease variables Y_{50}, Y_{max} and AUDPC. Both the additive and non-additive genetic effects contributed in controlling the resistance. Predominance of GCA effects suggested that additive effects were more important than non-additive effects and that simple selection or backcrossing would be useful for improving the resistance in these varieties. The best donor parents for resistance to late blight were cultivars NC 2 CELBR and NC 1 CELBR (Group I) and 133A and 163A (Group II). The best combinations were NC 2 CELBR x 64B and NC 1 CELBR x 64B. However, the parents selected for resistance to late blight, were inferior in terms of fruit quality especially the parents of Group II. The cross CELBR NC 2 x 163A was the most suitable for intra-population breeding programs to late blight. It is worth mentioning that all the five inbred lines were highly stable with respect to late blight resistance, confirming the presence of polygenic resistance. The genetic analysis of the resistance in the F_2 population indicated that resistance is inherited as a partially recessive trait. The heterosis scores were 32.97 and 26.76, respectively for the two populations whereas HEN4 was more resistant to *P. infestans* than IKR4 population. Most fruit quality traits had significant variation in both GCA and SCA except for pH and titratable acidity, where no significant difference was observed. Both the additive and non-additive genetic effects were included in controlling these traits. The inbred line 163A proved its superiority with regard to AFW, FS, pH and firmness when compared to other lines. The genetic analysis of the inheritance to resistance indicated that the resistance in the inbred lines was controlled by recessive genes. Hence, only the best parents of group I could be selected based on general combining ability. Whereas, selection based on specific combining ability could be a viable option for selecting the segregating generation to avoid losing the recessive resistant genes that exit in the advanced inbred lines.

1. INTRODUCTION

Tomato (*Solanum lycopersicum*) is one of the most important vegetables in the world including Brazil. It is a rich source of lycopene, beta-carotene, folate, potassium, vitamin C, flavonoids, and vitamin E (Willcox et al., 2003; Bose and Agrawal, 2007). Worldwide production of fresh market and processing tomatoes has steadily increased during the last decade and reached an annual production of 124.4 million tons in 2004, with an average yield of 27.5 ton/hectare (FAOSTAT 2004) and world fresh tomato trade grew 45% over the last 5 years (USDA-FAS 2009). The tomato growing area has increased by 38% and production by 42% worldwide in the past 10 years. Most of the increase came from China, where the growing area nearly tripled from 0.47 million ha in 1995 to 1.26 million ha in 2004, and production more than doubled from13.2 million ton to 30.1 million ton. More than half of the total tomato production was from the six top producing countries: China, USA, Turkey, India, Egypt, and Italy (USDA-FAS 2007).

Tomato cultivars suffer from as many as 200 diseases worldwide of which 30 are routinely important (Watlerson, 1986). Out of these diseases, late blight, caused by the oomycete *Phytophthora infestans* Mont. De Bary, is a destructive disease of tomatoes, and approximately 15-20 % of fresh tomato production costs in Brazil are for late blight control (Mizubuti, 2001), while worldwide losses due to late blight

and control measures are estimated to exceed $5 billion annually. *P. infestans* is thus regarded as a threat to global food security (Duncan, 1999). A 80-90% of tomato production may be damaged by this disease if control measures are not applied on the time (Zahid et al., 1993).

Cultural and physical methods of control are of limited efficiency and have serious operational implementation constraints as high costs and labor demands. The control of late blight heavily relies on the frequent application of protecting fungicides, which are applied every 5-14 days (Wang, 2003). This is expensive and undesirable for the ecosystem and lead to emergence of resistant isolates with increased fitness and aggressiveness (Ko, 1994). Late blight control is increasingly difficult due to changes in *P. infestans* pathogenicity, the introduction of new pathogen isolates, and increased resistance of the pathogen to fungicides (Kato et al., 1997). For healthy tomato cultivation, using resistant cultivars is a desirable alternative to chemical control. The development of crops that possess durable genetic resistance provides the best prospect for efficient, economical and environmentally safe control of late blight (Bonnet et al., 2007).

Attempts to breed late blight resistant tomato lines started since 64 years ago (Richards and Barratt, 1946) ultimately resulting in the identification of three dominant genes: *Ph*-1 on chromosome 7 (Clayberg et al., 1965; Peirce, 1971), *Ph*-2 on chromosome 10 (Moreau et al., 1998) and *Ph*-3 on chromosome 9 (Chunwongse et al., 1998). Tomato varieties carrying the resistance genes *Ph*-1 or *Ph*-2 provide inadequate control against the local population of the pathogen (Cohen, 2002). Whereas, *Ph*-3 is a strong resistance gene and has been incorporated into many breeding lines of fresh market and processing tomato. However, new P. infestans isolates have been identified which overcome *Ph*-3 resistance (Chunwongse et al., 2002).

Race-specific and polygenic resistance have been characterized and exploited in breeding, providing an efficient control of disease severity (Thabuis et al., 2004). The high variability in P. infestans populations throughout the world, especially for

virulence, has made race-specific resistance genes almost useless in disease control (Andrivon, 1994). With the lack of durability of resistance with single dominant genes that result in hypersensitive resistance (HR), it is probable that new resistance genes that result in HR will not be durable. More emphasis is being given to transfer of quantitative trait resistance to commercial cultivars of tomato.

Wild *S. pimpinellifolium* is the original source of the race-specific resistance genes *Ph*-1, *Ph*-2 and *Ph*-3 (Gallegly, 1960; Ignatova et al., 1999). Resistance to late blight has also been observed in wild *S. habrochaites* (Lobo and Navarro, 1987; Kim and Mutschler, 2000; Abreu, 2005). An interspecific F1 progeny from *S. lycopersicum* L. cv. Santa Clara x *S. habrochaites* f. *glabratum* accession BGH 6902 exhibited resistance to numerous *P.infestans* isolates under the field conditions of Viçosa, MG state (Abreu, 2005).

The choice of parents for use in a plant breeding program is one of the most important decisions that a breeder makes (Borem and Miranda, 2005). In tomato, the methodology presented by Griffing (1956) is quite used. This methodology which estimates the general and specific combining abilities of the parents in a diallel cross was developed for four types of diallel tables corresponding to four methods. The most commonly used is method 2 which includes the n parents and the [n(n-1)/2] crosses in the generation F1 without reciprocal crosses and the second in use is method 4 which involves only the group of F1s without parents and reciprocal.

In a hybridization program, selection of parents on the basis of per se performance alone is not a sound procedure since superior lines identified on the basis of per se performance may result in poor recombinants in the segregating generations. Therefore, parents should be chosen on the basis of their combining ability. The general combining ability (GCA) characterizes the average performance of a genotype in a series of hybrids combinations and is mainly associated with additive gene action. While, the specific combining ability (SCA) is used to characterize the performance of a specific hybrid combination in relation to the average of its parents and is predominantly associated with genetic effects involving

dominance. Ramalho et al. (1993) mentioned GCA as a parameter of larger practical importance for breeder since it gives information about the participation of additive gene effects in the variation range of the segregating generations of a cross allowing to trace the best strategies for the breeding program.

The main objectives of the current study were to study the inheritance of resistance to late blight in two segregating populations, develop durable resistance to late blight in tomato using different sources and levels of resistant genotypes; estimation the components of genetic variation and general and specific combining ability through half dialel analysis; combining both fruit quality and high level of resistance within the resistant individual and recovering the quality factors through further studies using backcross method.

2. Literature Review

2.1 Tomato production in Brazil

Brazil takes the eighth place in tomato production worldwide (USDA-FAS 2007). Although tomatoes can be grown in many regions of Brazil, and favorable weather allows for production throughout the year in many areas, the main season runs from June to September. Yields are highest in regions with milder winters and low chance for frost while summer production poses greater risks for disease and fruit set problems. The states with the largest tomato production are Goiás, São Paulo and Minas Gerais.

According to Global Agricultural Information Network (GAIN) report in 2009, Brazilian tomato production declined significantly in 2009 dropping 9 percent to 3.58 million metric tons (mmt) from 2008's harvest of 3.94 mmt. Production is expected to fall in terms of both area planted (from 62,100 to 59,100 hectares) and average yield (from 63.35 to 60.65 kg/hectare). Area planted is expected to decline over 20 percent in the state that is the major producer of tomatoes for industrial use. Excessive heat and humidity in the major fresh tomato producing state has reduced fresh tomato yields and led to a price spike.

Due to adverse weather conditions, the yields have declined in the major fresh tomato producing state of São Paulo. Excessive heat and humidity caused the

fruit to be smaller and green and therefore not marketable. Besides creating quality issues, the hot weather in February and March increased the incidence of Tospovirus, reducing average yields in key São Paulo growing areas by as much as 14 percent. In March 2009 this drop in production caused the price of tomatoes to double temporarily. The price of a kilo of tomatoes in the supermarket went from R$2 to R$5.

According to industry contacts, tomatoes for fresh consumption accounted for 60% of total Brazilian tomato production. The percentage of production for processing tomatoes is steadily increasing. Most of the country's processing tomato products are located in Goias creating a strong vertical production system in the state. Modernization continues as late last year a new plant opened up that can harvest, pack and ship in the same day.

Per capita tomato consumption is fairly low in Brazil, particularly for fresh tomatoes. According to a São Paulo-based Agricultural Institute, Brazilian per capita tomato consumption is 6.5 kilos per year, while per capita consumption in Norway, Greece, Switzerland, and other countries exceeds 40 kilos per year.

2.2 Tomato Late Blight

Late blight is best known as a disease responsible for the Irish potato famine during the 1840s. The disease essentially destroyed the potato crop in Ireland during 1845 and 1846, when over one million people died and 1.5 million Irish citizens emigrated (Large 1940). In 2004, late blight was confirmed in at least 26 counties in USA, which completely destroyed some commercial organic plantings and many home garden tomatoes (Foolad *et al*., 2006). The disease occurs in a wide range of places where tomatoes are grown, being more severe in cold and humid periods. It is favored by moderate temperatures, 12 - 20 °C and leaf wetness than 10 hours and can occur in warm climates, where the nights are cold (Vale et al. 2000). At temperatures above 30 °C the pathogen lose its pathogenicity, but the fungus

remains alive and can cause damage as soon as weather conditions are favorable (Lopes and Santos 1994).

The use of pathogen free seed tubers, application of fungicides, and elimination of other pathogen harboring sources helped to reduce late blight effects in the middle of the twentieth century (Fry and Goodwin 1997a). However, devastating outbreaks of the disease during the 1980s and 1990s throughout the world have led to renewed efforts to understand the pathogen nature and to develop novel methods of late blight control (Fry and Goodwin 1997b).

2.2.1 Taxonomy and morphology of pathogen

The genus *Phytophthora* was first described by Anton de Bary in 1876, the name derived from the Greek; phyto = plant, pthora = destroyer. *Phytophthora* is a member of the kingdom Chromista, phylum Oomycota, order Peronsporales, family Pythiaceae (Hawksworth *et al*., 1995). There are 60 described species within *Phytophthora*, which affect many plant species (Erwin and Ribeiro, 1996). Although originally classified as a fungus, oomycetes have been re-classified in the kingdom Chromista. Oomycetes are distinguishable from fungi based on metabolism (Pfyffer *et al*., 1990), cell wall composition (Bartnicki-Garcia and Wang 1983), rRNA sequence (Cooke *et al*., 2000), and zoospore motility (Zentmyer, 1983). The mycelium characterized by the absence of cross walls, zoospores with heterokont flagella (one whiplash, one tinsel) borne in sporangia, diploid nuclei in vegetative cells, and sexual reproduction via antheridia and oogonia, Heterothalic (Zentmyer 1983).

2.2.2 Symptoms and signs

Late blight symptoms can develop on leaves, stems, green and ripe fruit. Leaf symptoms begin as small, water-soaked spots, generally at the tips or edges of lower leaves. These spots can grow quickly into large pale green to brown lesions. Under

favorable weather, gray to white mycelia growth may occur on the undersides of foliar lesions. Foliage infected with late blight eventually turns brown, shrivels, and dies (Agrios 2005). Symptoms on stems resemble leaf symptoms. Stem lesions are typically dark patches or brown spots, leading to brittleness and plant death (Blancard 1994).

Tomato fruit symptoms begin as dark, greasy spots on the fruit surface. These spots may increase in size to cover the entire fruit. Under environmental conditions conducive to late blight sporulation, white mycelium may be visible on fruit (Stevenson, 1991). Lesions on tomato fruit may establish a ringed pattern. Late blight fruit infection is often followed by soft rot leading to total fruit decay (Watterson 1986). *P. infestans* fruit infection can penetrate the seed, oospores were detected inside the embryo resulting in infected tomato seedlings (Rubin *et al*., 2001).

2.2.3 Primary inoculum

The primary inoculum of tomato late blight is airborne sporangia from infected plants left in fields or gardens, infected volunteer potato plants, and infected transplants (Agrios, 2005). Since sporangia can be transported over large distances by wind, the pathogen can move south to north in the spring if cool moist conditions prevail. In regions where *P. infestans* reproduces sexually, oospores in the soil or on debris also serve as a source of primary inoculum. While soil-borne sporangia remain viable for a maximum of 77 days, oospores have been shown to remain viable for eight months even in extreme temperatures (Pittis and Shattock 1994).

The life cycle can be completed in 3–4 days and rapid inoculum build up commonly occurs in fields during favorable conditions (average temperature between 20 and 22 °C and high relative humidity or in rainy weather), which leads to high progress rate epidemics but the high humidity play a major role in the reproduction especially in sporulation stage (Mizubuti and Fry, 2006).

2.2.4 Reproduction

P. infestans has the ability to reproduce by both types of asexual and sexual reproduction. In the case of asexual reproduction, in cool moist weather, numerous sporangiophores bearing sporangia may emerge within four days after infection (Agrios, 2005). Sporangia are dispersed via wind or water splash. Each sporangium contains between three and eight zoospores which are released upon bursting of the sporangial wall (Agrios 2005). Upon coming to rest, and in the presence of cool temperatures and adequate water, sporangia germinate by the production of zoospores. Late blight lesions have been found to produce up to 30,000 sporangia per day (Legard et al., 1995). Furthermore, foliar disease has been noted to increase from 1 to 75 % in a period of two weeks under favorable environmental conditions (Turkensteen 1973).

In the sexual reproduction, *P. infestans* is a heterothallic organism defined as the requirement of two different mating types A1 and A2 for sexual reproduction. Individual genotypes of *P. infestans* produce both antheridia and oogonia and some genotypes are capable of self-fertilization in culture (Frinking et al. 1987). These self-fertile types only produced oospores in vitro and did not produce oospores in vivo. When growing in close proximity, each mating type (compatibility type) produces a hormone which induces mycelia of the opposite mating type to form antheridia and oogonia (Smart et al. 1998). Initial interaction between mating types occurs between diploid mycelium. Upon recognition of the other mating type, haploid antheridia and oogonia are formed (Smart et al., 1998). An antheridium can fertilize an adjacent oogonium, yielding a diploid oospore (Agrios, 2005). Germination of oospores occurs through a germ tube and results in the production of a sporangium (Agrios 2005). The presence of both *P. infestans* mating types and the subsequent potential for sexual reproduction raises several concerns with respect to disease variability and survivability. Sexual recombination provides the potential or new, more adapted or aggressive isolates (Gavino et al., 2000). In Brazil to date, all the detected isolates in tomato are of the A1 mating type and all the potato isolates

are of the A2 mating type (Reis et al., 2006) and A1 and A2 isolates were never found in the same field (Reis et al., 2003).

2.3 Disease management

Commercial tomato varieties with effective general late blight resistance against all extant strains are not available (Mizubuti, 2005). Primary use of disease free transplants, preventative fungicide application along with appropriate cultural practices, including sanitary field practices, crop rotation, and removal of diseased material and weed hosts (Agrios, 2005; Stevenson, 1991) means are employed to control late blight. Low levels of late blight are difficult to detect in the field and may remain unnoticed until substantial damage occurs. Currently, most effective fungicides labeled for use are protectants and must be applied prior to infection, since they lack therapeutic activity (Fry and Goodwin 1997a).

Chemical control is complicated by the rapid development of late blight epidemics in wet conditions. Since fungicides cannot be applied and spray residues may wash off in rain, crops are often unprotected under ideal conditions for pathogen reproduction, dispersal, and infection (Gallegly, 1960). In addition, strains of late blight resistant to the fungicide metalaxyl have been developed (McLeod et al., 2001; Mukalazi et al., 2001; Reis et al., 2003) and resistance to other fungicides may emerge in the future. Due to these problems with chemical late blight control, the development and utilization of late blight resistant cultivars is highly desirable. In comparison with susceptible cultivars, resistant cultivars may require fewer fungicide applications for effective late blight control (Agrios 2005).

2.4 Breeding for late blight resistance in tomato

Breeding for resistance to *P. infestans* in tomato began more than 64 years ago (Richards and Barratt 1946). In the early 1950s, a screening of many cultivars led to the discovery of a single dominant resistance gene, *Ph-1*, conferring resistance to late blight race T_0 (Gallegly, 1952). Subsequent linkage tests indicated that *Ph-1* is located at chromosome 7 (Peirce, 1971). *Ph-1* existed originally in two cultivars, 'West Virginia 36' and 'West Virginia 106', and was later integrated into 'Geneva 11', 'Rockingham', and 'New Hampshire Surecrop' (Walter, 1967). A new race of *P. infestans*, T1, which overcame the resistance conferred by *Ph-1* was observed shortly thereafter (Conover and Walter, 1953).

A second tomato resistance gene was found in a late blight resistant wild relative, *L. pimpinellifolium*, accession 'West Virginia 700'. This resistance was originally documented by Gallegly in 1960. However, at the time, the inheritance was unknown (Gallegly, 1960). Consequently, partial resistance to *P. infestans* in line WVa 700 was redefined to be controlled by a single incompletely dominant gene named *Ph-2* (Laterrot 1975). *Ph-2* maps to the long arm of chromosome 10 (Moreau *et al*., 1998).

Two types of resistance to late blight have been identified in tomato. The first is specific or qualitative resistance this resistance shows a discontinue range of variation in resistance, susceptible and resistant genotypes can be easily discerned. It's effect against specific races or biotypes of a pathogen (Thurston, 1971). It is usually characterized by a hypersensitive response to late blight and frequently confers immunity (Black, 1952).

According to Kuc´ *et al*. (1976), expression of specific resistance against *P. infestans* is associated with rapid localized cell death in the resistant plant, browning of the affected area, and the accumulation of at least 16 terpenoids. Specific late blight resistance so far identified has been monogenic. These genes are often dominant, but a few are partially dominant. The high variability in *P. infestans*

populations throughout the world, especially for virulence, has made race specific resistance genes almost useless in disease control (Andrivon, 1994).

The second type of resistance is general or quantitative resistance in which host shows a continuous range of variation in resistance from extremely susceptible to fairly resistant. The effect of this resistant is against all known pathogen strains or biotypes (Vale *et al*., 2001). General resistance is controlled by multiple genes, each with a small effect. General resistance consists of a number of complementary resistance components (host-parasite interactions) which can be individually measured (Thurston 1971). These resistance components are infection efficiency, lesion growth rate, latent period, sporulation capacity, and sporulation period. It is difficult to assess general resistance accurately, as it has been reported to be influenced by plant age, nutrition, day-length, leaf position (Thurston, 1971). Breeding for general resistance is also challenging due to frequent decreases in the level of resistance in crossing and backcrossing (Douches *et al*., 2001).

Black *et al* (1996a) reported that resistance in *L. pimpinellifolium* accession L3708 possessed a single dominant resistance gene *Ph-3*. This was confirmed and the locus was mapped to chromosome 9 (Chunwongse *et al*., 1998). L3708 has been further investigated in virulent California fields, and quantitative trait loci aside from *Ph-3* were identified on chromosomes 6 and 8, although the effect of the QTL on chromosome 6 is hypothesized to be a pleiotropic effect of the *sp* locus (Frary *et al*., 1998).

Other studies have identified tomato resistance sources to late blight, however the mode of inheritance of resistance in these sources is unknown. In 1951, Barham and Ellis screened all tomato plant introduction accessions using a seedling greenhouse inoculation, and found 28 of the 909 available lines to possess some resistance. A collection of heirloom cultivars was screened in a field trial with natural US-11 strain inoculation. ‘Matt’s Wild Cherry’ was identified as possessing resistance relative to the other varieties (Inglis *et al*., 2000).

Black *et al*., (1996b) screened lines with Taiwanese *P. infestans* isolates and found four accessions, L3707, L3708, L3683, and L3684, with some resistance. Continuous variation of this character suggested that the resistance is quantitative, presumably polygeneic in nature.

Kim *et al*., (2005) identified the resistance to late blight in an accession L3708. This resistance has been transferred to processing tomato lines, which are resistant to multiple *P. infestans* isolates. Lab trails, inoculated field trials in New York, and naturally infested field trails in Mexico indicate that these processing tomato lines are fixed late blight resistance. Segregation data do not support the hypothesis of single gene control of the full resistance trait, but suggest that more than one gene is involved, and these genes interact in an epistatic manner. Tomato genotypes carrying the *Ph-2* gene of resistance to late blight and sensitive genotypes which have good yield and quality were hybridized by Mijatovic et al. (2007) who found the new lines and hybrids of tomato were more resistant than their sensitive parents and showed intermediate type of heredity to late blight.

2.5 Heterosis (Over dominance)

The choice of germplasm source determines the potential improvement for traits under selection in the breeding programme (Fountain and Hallauer 1996). The parents used in a plant breeding programme generally fall into two categories: locally adapted varieties and varieties chosen for a particular attribute without regard to local adaptation (Simmonds, 1979). All programmes concentrate upon economical means of exploiting the genetic variability of unrelated foreign parents and locally well-adapted genetic backgrounds. In addition, the utilization of heterosis improves the performance of varieties through developing high-yielding single-cross hybrids in allogamous or autogamous species. The literature includes many estimates advantages of hybrids relative to the mid-parent (heterosis), the high parent (heterobeltiosis), or the best standard (inbred or open-pollinated varieties; Wehner, 1999).

Heterosis is a biological phenomenon manifesting itself in hybrids that are more vital, adaptive and productive than their parents (Bai and Lindhout 2007). Heterosis has been explained by over-dominance and by additive effects. However, it is still unclear how much each of these effects contributes to the total heterosis effect (Birchler et al., 2006; Semel et al., 2006). Heterosis has a dual influence in the breeding procedure: firstly, it enriches the cultivation categories of varieties with single-cross hybrids; commercial single cross hybrid-varieties are often the major component of seed companies' catalogues, as for example in maize (Troyer, 1996), or in tomato (Scott and Angell, 1998). Secondly, it creates a new gene pool by using the F_2 generation as germplasm; for example, in maize, an increased use of F_2 and backcrosses for second-cycle inbred development programmes was reported (Jenkins, 1978).

Even though benefits of heterosis in tomato have long been recognized and some hybrid varieties were available in the 1940s, widespread use of hybrids has occurred only since the 1970s. The use of hybrids is not due so much to the benefits of heterosis *per se*, such as increased earliness and greater yields, but has more to do with several other factors. A primary benefit is the protection of parental inbreds used in the production of elite hybrids. This is important, since there has been an increase in the involvement of private companies in tomato breeding research (Scott and Angell, 1998). A second important benefit of hybrids is the uniformity of trait expression among plants of a variety (Wehner, 1999). Hybrids offer additional advantages when important traits are controlled by dominant genes (Kalloo, 1993), which need not be fixed in all breeding lines. Examples include resistance to Fusarium wilt races 1, 2 and 3, Fusarium crown and root rot, Verticillium wilt race 1, root-knot nematodes, tobacco mosaic virus and spotted wilt virus (Scott and Angell, 1998). Also, there are cases where hybrids may offer benefits that are not possible in inbred or open-pollinated varieties, as for example, the ripening inhibitor (rin) gene or the non ripening gene (nor), which in the heterozygous form can reduce postharvest damage if fruit is harvested at more mature stages of development (Tigchelaar et al., 1978). Finally, heterosis may be sufficient by itself to justify the

production of hybrids. In tomato, hybrid advantage ranges from 0 to 300% over the best inbreds (Wehner, 1999). The average turnover time of commercial tomato cultivars is approximately 5 years.

Tomatoes are heterotic for vigour, increased growth and development, earliness, yield, uniformity, or adaptability to a range of environments (Scott and Angell, 1998). Several theories have been proposed to account for heterosis. Griffing (1990) showed that heterosis in a cross of two tomato inbreds was due to increased nutrient uptake, as opposed to being more efficient at utilizing limited nutrients. In spite of commercial hybrid-varieties, a number of local varieties or open-pollinated varieties are cultivated by farmers, which are mainly grown in the open-field under lower-input systems.

As the inbred-hybrid system still remains the most important breeding scheme for the commercial production of hybrid seeds (Miranda Filho, 1999), the narrowing of the genetic base and the genetic vulnerability to abiotic and biotic stresses, as well as limited future gains from selection (Taller and Bernardo, 2004) are matters of concern. The maize paradigm showed that among the maize inbreds available in 2001 from foundation seed companies, most derived from only eight inbreds (Lu and Bernardo 2001). This point attracted the attention of tomato breeders, although tomato has three advantages: (i) in temperate zones, the proportion of natural out crossing has been between 0.005 and 0.04 (Rick, 1949), because there is a requirement for physical movement of flowers for pollination to take place (Jones, 1999), and the stigma receptivity begins 1–2 days before anthesis (Scott and Angell, 1998); (ii) there are many well-adapted varieties that complement the source germplasm, and they are themselves either at or near local varietal standard in performance; and (iii) in self-fertilized crops, like tomato, additive genetic variation predominates, and it is always feasible to fix and transgress heterosis (Burdick, 1954; Christakis and Fasoulas, 2001).

New traits are rarely introduced from wild germplasm as it may take many generations to remove the deleterious genes that go along with the introduced genes

due to linkage drag. When the parental lines are more fixed (F4 to F6), crosses are made to produce test hybrids. After several generations of testing at the breeders site and eventually at the farmers' sites, the best hybrids are selected for commercial usage. Hybrids of tomato show some heterosis, but this is only selected for at the latest stage of the breeding programme, when test hybrids are generated. In earlier generations, the parent lines are selected at a single plant basis but not for combining abilities or heterosis. So, recurrent selection programmes to select parents with the best combining abilities, like that used in field crops, is not a common practice in tomato breeding (Bai and Lindhout, 2007).

2.6 Diallel analysis

One of the most important factors in an breeding program is selection of the parents (Borem and Miranda, 2005). When choosing parents, the objective is to maximize the probability of generating new lines that will perform better than the best pure line that are currently in use. The parents chosen should generate a population for selection that will meet the criterion of usefulness described by Schnell (1983), as discussed in Lamkey *et al*. (1995). The usefulness of a segregating population was described by Schnell as the mean of the upper α% of the distribution expected from the population. Mathematically, $U\alpha = Y G\alpha$, where $U\alpha$ is usefulness, Y is the mean of the unselected population and $G\alpha$ is gain from selection of the upper α% of the population. This statistic takes into account both the mean and the genetic variability, thus emphasizing a basic axiom in plant breeding: a population that will produce an improved cultivar will have both a high mean and an adequate genetic variability.

In the vegetable species, countless lines exist and cultivate that could be participate in the hybridization programs to obtain segregated populations, is being necessary using criteria for selection. The identification of efficient methodologies for that choice has been received great attention (Charcosset et al., 1998). Among

the available methods, the dialel crossing has been the more thoroughly used in almost cultivated species. Griffing proposed a dialel technique for determining the combining ability of lines and characterizing the nature of extent of gene action in both plants and animals. His approach has also been adapted to assess competition. Griffing's analysis allows the option to test for fixed (model 1) or random (model 2) effects. Griffing (1956) proposed four methods of diallel crossing; method 1 (full dialle), the P, F_1 and F_1r are included; method 2 (half dialle), P and F_1's included only; method 3 includes F_1 and F_1r but no P and finally method 4 where F_1 included, but no reciprocal or parents. Total entries are (P^2), [p(p+1)/2], (P^2-P) and [p(p-1)/2] respectively. Experimental material and the objective of the experiment are the main factors that determine the appropriate method that could be used. The reciprocal effects can be usefully employed to detect variation due to sex-linked genes and maternal effects (cytoplasmic inheritance). So, method 3 would be most useful. While in most combining ability analysis in which a chosen set of lines is used, the interesting is concentrated on the performance of F1's. Therefore, there is no necessary to include the parental lines. But in some cases, it's important to include the parents when the breeder want to synthesize new variety and if there is inbreeding occurs in the species, so it is advisable to use method 1 or 2. In plant and animal breeding, when a random set of lines is used, dialle crossing method 3 or 4 is again the most applicable.

The term general combining ability (GCA) is the average performance of a parent in a series of hybrid combinations and is associated with the presence of additive effects of alleles and associations of the epistatic additive effect. While the specific combining ability (SCA) refers to those instances in which the performance of a hybrid is relatively better or worse than would be expected on the basis of the average performance of the parents involved (Sprague and Tatum 1942). The SCA shows the deviation on the average of their parental GCA and associated with dominance effect and epistasis involving dominance (Cruz and Vencovsky 1989). Through using these estimates, we can identify the best parents and hybrids for use in breeding program (Cruz and Regazzi 2001).

By calculating the proportion GCA/SCA, a relatively large variance ratio suggests the importance of additive gene effects while a low ration implies the presence of dominant and epistatic gene effects. It should also be noted that if additive x additive effects are present, the GCA component will contain some of these effects in addition to additive effects.

The diallel analysis is widely used in breeding programs, providing information about the predominant type of gene action and heterosis and to estimate the GCA and SCA which aid as tools in choosing the best strategy for improvement (Oliveira, 2005).

2. MATERIALS AND METHODS

2.1 Experimental location

The field experiments were conducted at *Horta de Pesquisa da Universidade Federal de Viçosa* (UFV). Viçosa belongs to Minas Gerais state (MG), southeastern Brazil. It has a subtropical highland climate, and is situated at an altitude of 689 m above sea level and is located in the co-ordinates of 20° 45′ 14″ latitude S and 42° 52′ 54″ longitude W. The annual average minimum and maximum temperatures are 15.63 and 26.82 °C respectively and the annual average precipitation is 1,440 mm with relative humidity of 80% (average annual).

2.2 Plant materials

In the current study, five inbreed lines of F_9 generation (127F, 64B, 73A, 163A and 133A) were used from the breeding program against late blight resistance in tomato, Universidade Federal de Vicosa (UFV). These lines resulted from interspecific cross between *Solanum lycopersicum L.*cv. Santa Clara x *Solanum habrochaites f. glabratum.* They were selected from previous work by Abreu (2005) followed by Fiorini (2008) who produced F_8 generation. These lines had confirmed polygenic resistant genes to late blight, and were used as a source of pollens (♂)**.** These lines are indeterminate in growth habit**,** with small green and inferior quality fruits**.** Seed duplication of these lines was done during October, 2007 to February,

2008 in order to increase the amount of seeds and in addition to obtain the F8 lines by self-pollination.

2.2.1 Genetic resource of *Ph-2* and *Ph-3* resistant genes

The following advanced inbred varieties; NC 1 CELBR, NC 2 CELBR and NC 25P were received from Prof. R. Gardner, North Carolina State University. They are homozygous, with determinate growth habit, heavy foliage and large, red-fruited tomato. NC 1 CELBR and NC 2 CELBR incorporate combined early blight resistance (Campbell 1943 and PI 126445 origin) and have late blight resistance genes (*Ph-2* and *Ph-3*). It is also resistant to Verticillium wilt (*Ve* gene) and races 1 and 2 of Fusarium wilt (*I* and *I-2* genes). NC 1 CELBR bear deep oblate to flattened globe fruit are firm and highly crack resistant, late in maturity and has larger fruits than NC 2 CELBR. NC 25P is a fresh market plum tomato line with the *Ph-3* gene for late blight resistance and crimson gene for increased lycopene. It has early blight and Verticillium wilt resistance (Ve gene) and resistance to races 1 and 2 of Fusarium wilt (I and I-2 genes) determinate in habbit with heavy foliage cover. Fruits are intermediate in length with 2-3 (mostly 3) locules and jointless pedicels. Immature fruits are uniform, light green. Fruit are highly resistant to gray wall and fruit cracking. Besides, the following commercial hybrids were used in our current study:

'Ikram' (*Solanum lycopersicum* L.): indeterminate growth habit, round slightly flattened; long life, fruit weight 130-150 grams, fresh market variety and resistance to Fusarium 1 e 2, Verticilium 1, T.M.V.

'Heinz H7155' (*Solanum lycopersicum* L.): is processing tomato, oval fruit shape, resistant to *Fusarium* (race 1), *Verticillium* (race 1).

'Alambra' F_1 (*Solanum lycopersicum* L.): indeterminate growth habit, fresh market tomato; fruit weight 200-250 grams; open field, fresh market variety, resistant to *Fusarium* (race 1), *Fusarium* (race 2), *verticillium*, tomato mosaic virus (ToMV) and nematodes.

To study the inheritance in the F_2 population, F_2 seed of the crosses were Ikram x inbred line 163A and Heinz H7155 x inbred line 163A were included with 77 and 95 plants of each F_2 population respectively. These materials were used from the previous work of Fiorini (2008).

In addition to the previous materials, 'New York' and 'Caline' which have only the *Ph*-1 resistance gene to late blight were used as standard varieties susceptible control.

2.3 Mating design

Thirty seedlings of each of the 10 selected parents were grown in the greenhouse during winter 2008 at Horta Velha, Vicosa, MG. Pollens from each inbred line plants originated from the crossing (*Solanum lycopersicum L.*cv. Santa Clara x *Solanum habrochaites f. glabratum*) were collected and bulked into plastic plate, 4cm in diameter with the aid of vibration tool to help pollen-dispersal. Each of the 3 commercial hybrids (Ikram, Heinz H7155 and Alambra) and three advanced inbred lines (NC 1 CELBR, NC 2 CELBR and NC 25P) were crossed separately to each of the five inbred lines following the II mating design (half dialle) where the P and F_1's were included only. Twenty pollinations for every cross was accomplished during June/July, 2008. The fruit set of the cross NC 25P x inbred lines was low and in addition a majority of fruits did not produce sufficient seeds (Table 1) so this cross was eliminated from the field experiment evaluation. Table 1, shows the names of parents and the amount of seed of each cross. Seed extraction was done through fermentation for 48 h according to Giordano et al. (2003).

2.4 Field design

Seeds of F_1 were sown in 2nd of March, 2009 in 200-cell trays using commercial peat moss mixture as growing media fertilized once a week with 0.5% solution of N:P:K (15:15:20). Thirty five day-old seedlings were transplanted in the field. The applied experiment design was randomized complete block design (RCBD) with 3 replicates, 5 plants per plot with distance 60 cm intra-row and 100

cm inter-row. The experiment was surrounded from outside by a border of tomato plants to prevent the other plants into the blocks and to insure that the amount of relative humidity and the spraying is distributed equally over the plants as possible. Not all the seeds of the hybrids were equal in amount since there were certain ones with few seeds due to the difficulty and incompatibility of interspecific cross between *S. lycopersicum* and *S. habrochaites* and as a result of missing cross combinations with the female parent NC 25P, Design II analyses of 5 x 5 was applied.

Table 1. The amount of seeds obtained and the % of fruit set of thirty crosses conducted in the current study during June/July 2008. Viçosa-MG, 2008.

♀ \ ♂	Inbred line 127F		Inbred line 64B		Inbred line 73A		Inbred line 163A		Inbred line 133A	
	seeds	% of F.set	seeds	% of F.set	seeds	% of F.set	seeds	% of F.set	seeds	% of F.set
Ikram	++	85	++	90	++	90	++	95	++	85
Heinz H7155	40	80	++	100	++	95	++	100	++	100
Alambra F_1	+	90	+	90	20	35	+	65	+	75
NC1 CELBR	++	90	++	85	++	90	++	80	++	80
NC2 CELBR	+	85	+	90	+	80	25	25	+	75
NC25 P	20	3	18	5	30	45	30	4	0.0	6

++: more than 100 seeds; +: around 50 seeds;

2.5 Pathogen isolates

To avoid the specific-race resistance and to eliminate possible epistatic effect genes of vertical resistance, selection upon the horizontal resistance phenotypes was considered through applied inoculum of mixture isolates of *P. infestans* collected from different regions from several production fields of tomato during 28 and 29 of May 2009 as follow: 5 isolates from Coimbra and 1 isolate each from Ervalia, Paula Cândido and Viçosa respectively. We could not reach any field of tomato in the city São Miguel do Anta since the most of producers replaced tomato with coffee,

Eucalyptus and other cultivars. At early morning, infected leaves of late blight were collected from the commercial fields of tomato and put in polyethylene cases saved in ice tank until reaching the laboratory.

2.5.1 Preparation of inoculum

After reaching the laboratory, the infected leaves were placed in 30 x 40 x 5 cm plastic trays in order to multiply the inoculum. A single ply of facial tissue paper was plastered with water on the bottom of the tray to maintain high humidity. The trays were kept in a dark chamber at 18–20 °C for 24 h. After 24 h, the surface of fresh mycelium on the underside of leaves was very lightly brushed with a toothpick, and the toothpick was whisked in chilled, distilled water in a 100-mL beaker to loosen the sporangia. The suspension of each isolate was prepared separately to adjust its concentration. After that equal volume of every suspension was taken and mixed together. The sporangia suspension was kept in the dark at 11–12 °C for 90–100 min to release the zoospores (Nilson, 2006). A uniform suspension was used to obtain an accurate sporangia count. The concentration was determined with a hemacytometer and adjusted to 10^3 sporangia mL^- .The inoculation was accomplished in 1st of June 2009 at 7:30 PM after about 2 hours of sunset using manual backpack sprayer (20 litre volume) applying 20 mL of the sporangia suspension per plant with total volume of 16.50 litres applied for 817 plants. The time between the preparation of the suspension and inoculation did not exceed two hours to keep the culture vigorous and maintain infectivity (Abreu, 2005).

2.5.2 Quantify the resistance

Thirty five genotypes of the half-diallel in addition to standard susceptible varieties were screened against late blight disease under field conditions. The first observation was recorded after 4 days of inoculation and then every 4 days during June 2009. The disease severity was recorded based on the proportion of area or amount of plant tissue that is diseased. To insure optimal conditions for germination of the zoospores, a level of humidity was provided on the leaves to keep a thin film of water using Micro Sprinklers (full-circle 5 m, 325ml/mint/micro sprinkler). The

spray system was adjusted to turn on 15 minutes each 3 h over the 24 h beginning after the inoculation on 1st June to 23 June 2009. Before applying the inoculation, the micro sprinklers were kept turned on for approximately 2 hours to provide a thin film of water to aid the spores to penetrate the plant tissues. After 4 days of inoculation, the first evaluation of disease severity was started and repeated over time every 4 days for a total of 6 times. During this period of disease development (1st to 23 June) the average maximum and minimum temperature was 25.2 and 13.7 °C, respectively and average relative humidity was 85.7. On an average 31.21 mm of rainfall occured during the evaluation period while was 267.0 and 157 mm on 6th and 18th of June, respectively.

2.5.3 Data collection

Foliar data were converted using the area under the disease progress curve (AUDPC) model to account for foliar disease, which progressed over time as follow:

$$AUDPC = \sum_{i=1}^{n} \left[\frac{R_{i+1} + R_i}{2}\right] \left[(t_{i+1} - t_i)\right]$$ (Tooley and Grau 1984).

Where:

R= rating (estimated proportion of affected tissue) at the *i*th observation.

t_i= time (days) since the previous rating at the *i*th observation.

n = total number of observations.

The AUDPC was first calculated for each plant per plot and the final value of each plant was taken by calculating the mean of all the plant leaves. To evaluate the disease severity of late blight, the estimators were submitted to training, to use the software 'severity Pro' (Nutter, 1997), a computerized disease assessment training program for foliar diseases. At field, it was evaluated for every leaf on the plant for

9 plants for each F_1 and their parents. In addition, 95 and 77 plants the two F_2 populations was evaluated. It was best to record readings independently (i.e., without knowing the value given at the previous reading) at each date, such as having someone else write in the field book or by using a cassette recorder (Henfling, 1987). The selection to the resistance to late blight was done based on the negative values, or in other words, the plants which had minimum values of AUDPC were considered as resistant. In addition to the previous disease variable, it was estimated the percentage of severity at the halfway epidemic (Y_{50}) and at the percentage of severity at the end of epidemic (Y_{max}).

2.5.3.1 Disease rating

To classify the individuals in order to study the genetic inheritance in the segregating populations, a disease rating was used as shown in Table 2.

Table 2. Four ratings, numeric scores, and descriptions utilized in evaluating the F_2 populations. Inbred line 163A is resistant, *L. esculentum* 'Ikram' is highly susceptible, and F_2 individuals displayed intermediate symptoms development.

Rating	Score	% Severity rang	Description
Resistant	1	10-25	Few restricted non-sporulating lesions
Moderately Resistant	2	25-40	Several restricted non-sporulating lesions
Moderately Susceptible	3	41-60	Several expanding lesions, reduced sporulation
Susceptible	4	> 60%	Extensive Lesions

2.6 Evaluation of fruit quality

To evaluate the characters that determine fruit quality of the parents and F_1, three lateral shoots were collected from every genotype from the previous evaluation experiment before inoculation and was then planted in 72 tray-cells until rooting. The clones were transplanted in the field after 30 days of the rooting. The applied

experimental design was randomized block with 2 replicates, 60 cm intra-row and 100 cm inter-row.

The following traits were used in the evaluation; average fruit weight (AFW), fruit size (FZ), fruit shape index (FSI), firmness (F), total soluble solids (TSS), pH, % titratable acidity (TA) and flavor. Fruit volume was determined by the water displacement method.

Average fruit weight in grams was taken by random sample of the two first clusters and average fruit weight was calculated by dividing the weight of sample with the number of fruits in the sample. To evaluate TSS, pH and TA, the fruits of each genotype were crushed in a multi brand 'ARNO'. The TSS was estimated using digital refractometer 'QUIMIS' apparatus Científicos Ltd. The refractometer was washed with distilled water each time after use and dried with blotting paper. The total acidity (pH) was estimated using pH meter 'MS TECNOPON instrumentações Cientifica' after standardization with buffer solutions of 7.0 and 10.0 pH. The % titratable acidity (TA) was determined using 0.05 $mol.L^{-1}$ of NaOH solution and using 5 grams of the crushed pulp transferred to 100ml-standard flask diluted to 100 mL with distilled water. 10 ml of this diluted solution was used for titration using phenolphthalein indicator (1%). Appearance of pink colour was taken as end point of titration. The titratable acidity was expressed in terms of mg anhydrous citric acid in 100 ml of juice and calculated as given below:

% Acidity = M=(V x N x meqAc.Citr. x F x 100)/Y

Where:

V=volume (ml) of NaOH used in titratable;

N= concentration of NaOH solution (=0.005)

meq citric acid=0.064

F= correction factor of NaOH=1.04

Y=volume (ml) or weight (g) of sample

The flavor was obtained by proportion between TSS and TA (Kader et al. 1978). For fruit shape index (FSI): Polar (P) and equatorial (E) diameters of five

fruits per entry per replication were measured by digital Vernier Calliper and fruit shape index was calculated as an average of the ratio (P/E) of five fruits per entry per replication.

2.7 Statistical analysis

2.7.1 Analysis of variance

Randomized block design experiment was analyzed by standard analyses of variance and tests of significance at P< 0.05 for each trait.

Table 3. The scheme of analysis of variance of a randomized complete block design with within-plot individuals information.

S.V.	DF	M.S.	E(M.S.)
Blocks	b-1	$M.S_B$	$\sigma_p^2 + n\sigma_e^2 + ng\sigma_b^2$
Genotypes	g-1	$M.S._T$	$\sigma_p^2 + n\sigma_e^2 + nb\phi_g$
Residual	(b-1)(g-1)	$M.S._E$	$\sigma_p^2 + n\sigma_e^2$
Within plots	(n-1)bg	$M.S._W$	σ_p^2

The statistical model:

$$Y_{ijk} = \mu + G_i + B_j + \varepsilon_{ij} + \delta_{ijk}$$

Y_{ijk} = The observe obtained from the *k* individual of *i* genotype evaluated in *j* block ;

μ= General mean;

G_i= Effect of i genotype considered fixed;

Bj= Effect of j block considered random;

ε_{ij}= Random effect of the variance among plots;

δ_{ijk}= Random effect of variance within the plants among the plots.

In this model, the following components of variance can be obtained:

σ_p^2: Phenotypic variance among plants within the families;

σ_b^2: Component of variance of environmental factors, that measures the variations among blocks

ϕ_g: Squares component associated with families' variability

σ_e^2: Component of environmental variance that measures the variations among plots

σ_p^2: Component of phenotypic variance that measures the variations among plants within plots.

2.7.1.1 Dunnett's test

Dunnett's test was applied (Dunnett, 1955) at P<0.05 for comparing each disease variable mean with the control mean. Dunnett's test controls the experimental error and is more powerful than tests designed to compare each mean with each other mean. Dennett's test is conducted by computing *a t-test* between each genotype and the control group using the formula:

$$t_d = \frac{M_i - M_c}{\sqrt{\frac{2MSE}{n_h}}}$$

Where:

Mi is the mean of the ith genotype group, Mc is the mean of the control group, MSE is the mean square error as computed from the analysis of variance, and n_h is the harmonic mean of the sample sizes of the experimental group and the control group

2.7.1.2 Cluster analysis

Three disease variables Y_{50}, Y_{max} and AUDPC were used to calculate squared Euclidean distances. The distances were used to group the genotypes into clusters according to the method outlined by Johnson (1967). When all variables are continuous, the most commonly used distance between two individuals (observations) is the Euclidean distance or the Manhattan distance. The Euclidean distance (*di j*) between individuals *i* and *j* is

$$d_{ij} = ||y_{ik} - y_{jk}|| = \left[\sum_{k=1}^{p}(y_{ik} - y_{jk})^2\right]^{1/2}$$

2.7.2 Diallel analysis

For the determination of combining abilities and gene effects, both disease variables AUDPC and Y_{max} were used in the statistical analysis. The GCA and SCA were determined according to the Griffing (1956) diallel crossing system analyses: Method 2, with parental values but without reciprocal crosses. Crosses were considered as fixed effects, so the GCA mean square was tested against SCA mean square for estimating the significance of F values.

The genotypic value G*ij* of the single cross hybrid obtained by pollinating maternal parent *i* by paternal parent *j* is:

G*ij* = μ + gca*i* + gca*j* + sca*ij*

where

μ = the overall mean

gca*i* = the general combining ability of parent P*i*

gca*j* = the general combining ability of parent P*j*

sca*ij* = the specific combining ability of parents P*i* and P*j*

Half diallel involving two groups of parents and their crosses closed to the factorial model proposed by Comstock and Robinson (1948) (Model II). Adjustments to the Griffing model (1956) and Gardner and Eberhart (1966) for this type of diallel have maximum possible information on the groups with few crosses than that required in complete diallel.

The following model was carried out:

Analysis of Parents and F_1's- (Geraldi and Miranda Filho, 1988)

$$Y_{ij} = \mu + \frac{1}{2}(d_1 + d_2) + g_i + g_{\cdot j} + s_{ij} + \bar{\varepsilon}_{ij}.$$

Where:

Y_{ij}: The mean crossing involving the i-*th* and j-*th* parents of groups I and II;

Y_{i0}: The mean i-*th* parent of group I (i = 0,1,...p)

Y_{0j}: The mean of the j-*th* parent of group II (j = 0,1,...q)

μ : The diallel general mean

d_1 , d_2: Contrasts involving means of groups I and II and the general mean

g_i : Effect of general combining ability of the i-*th* parent of group I

g_j : Effect of general combining ability of the j-*th* parent of group II

s_{ij} : Effect of specific combining ability

$\bar{\varepsilon}_{ij.}$: Mean of the experimental error

All the statistical analyses, analysis of variance, cluster analysis, comparing between the means and estimation of genetic parameters in the half diallel and segregating populations were applied using GENES software program (Cruz, 2008).

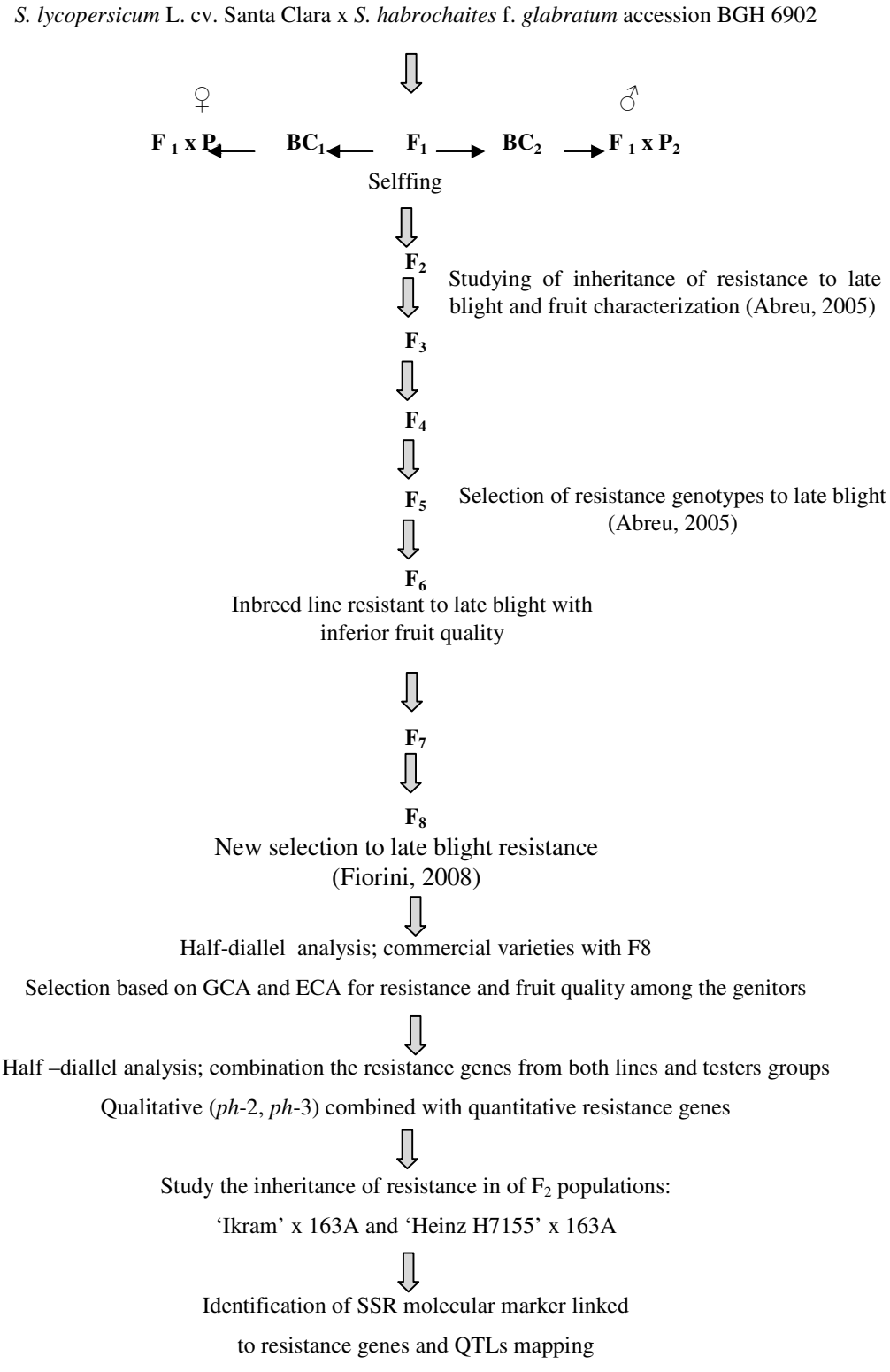

Figure 1. The main procedures related to the breeding program of late blight during 2005 to 2010 at UFV. Viçosa, MG, 2010.

3. RESULTS AND DISCUSSIONS

3.1 The inheritance analysis of resistance to late blight

After four days of the inoculation, the disease symptoms began to show up and were very slight. In the following days, heavy rain and low temperature which is considered favorable and optimal natural conditions for disease development followed and from the second evaluation, the lesion expansion of the infected plants was obvious and the symptoms were extreme.

Out of the thirty five genotypes (parents and their progenies), none exhibited immune reaction. The females varieties (group I) differed in their resistance expression and susceptibility (Figure 2) while the testers (group II), all the inbred lines were closed in their expression in respect of AUDPC and the 73A recorded the highest values comparing with other testers. All of the crosses between varieties parents and inbred lines are represented in Figures 3, 4, 5, 6 and 7. However, two crosses resulted from crossing both NC 1 CELBR and NC 2 CELBR as females parent to the five inbred lines as source of pollens were found to be resistant in all the three experimental plots. In these crosses, the lesions were very small and there was less sporulation as compared with the susceptible varieties 'New York' and 'Caline', where the lesions were large with heavy sporulation. The variable behavior of these crosses may be attributed to the differences in the genetic background and

the types of the resistant genes they possess which transmitted from the parents to their progeny.

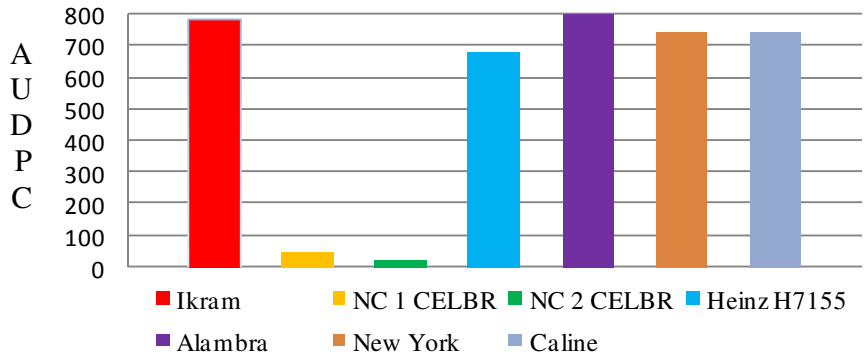

Figure 2. The mean values of the area under disease progress curve (AUDPC) of the female parents commercial hybrids (Ikram, Heinz H7155, Alambra) and NC 1, NC 2 CELBR possessing the resistance genes *Ph-2* and *Ph-2* + *Ph-3,* respectively, and 'New York' and 'Caline' as susceptible control.

The commercial female parents (Figure 2) showed divergence in respect of resistance to late blight comparing with NC 1 CELBR and NC 2 CELBR. The Alambra cultivar had the maximum value of AUDPC (801.90) and was grouped in the same group of the cultivar Ikram despite it not having significant differences between its group and control group (Caline and New York) in Dunnett's test at $P<0.05$ (Table 5). While the other parents showed no statistically significant difference. The both NC 1 and NC 2 scored the minimum values of AUDPC and had high sufficient vertical analysis probably due to their content of monogenic resistance genes *Ph*-2 and *Ph*-3.

Certain genotypes were maintained after the last field evaluation on 23rd June since these genotypes had slight symptoms and showed high level of resistance over all the replicates. These genotypes (F_1) resulted from the crosses NC 1 CELBR and NC 2 CELBR with the inbreed lines (127F, 64B, 73A, 163A and 133A). However,

they differed in respect of the % of severity but in general they were considered resistant. Although it remains disputable as to what extent plant age may affect the resistance of tomato to late blight, leaf position definitely has an effect. Young leaves towards the apex have been observed to be more resistant to attack by *P. infestans* than older leaves near the base, on both tomato (Mills 1940; Enkerli et al., 1993) and potato (Carnegie and Colhoun, 1982; Visker et al., 2003; Nilson, 2006).

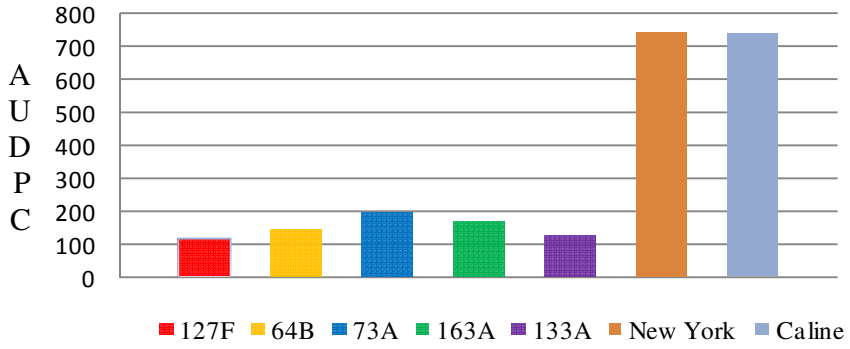

Figure 3. The mean values of the area under disease progress curve (AUDPC) of the five inbred lines F_9 generation as source of pollens originated from the cross: *S. lycopersicum* L. cv. Santa Clara x *S. habrochaites* f. glabratum accession BGH 6902 and 'New York' and 'Caline' as susceptible control.

The five inbred lines (Figure 3) which were used as male parents showed similar expression in respect of the degree of resistance to late blight. This may be due to the fact that they share the same genetic factors responsible of resistance trait with high homozygousity. The inbred line 73A had the maximum value of AUDPC (192.50) and was grouped together with the inbred line 163A and the cross NC 1 CELBR x 73A (Figure 9). The group of these lines had significant differences in comparison with control group (Caline and New York) in Dunnett's test at $P<0.05$ (Table 5).

Three well-defined types of host-pathogen interactions occur for the *P. infestans* in tomato: highly compatible, partially compatible, and incompatible interactions (Gallegly and Marvel 1955). It was further observed that the moderately resistant commercial hybrids 'Ikram', 'Heinz H7155' and Alambra F_1' exhibited susceptibility and the disease progress rate was higher comparing with the other genotypes. In contrast some of these varieties; 'Ikram' and Heinz H7155 were recorded to be moderately resistant in another study (Fiorini, 2008). This discrepancy in the type of reaction may be due to racial differences of the pathogen and structural change in the virulence genes of the pathogen or environmental factors interactions.

3.1.1The analysis of variance for Y_{50}, Y_{max} and AUDPC

The analysis of variance of the three disease variables Y_{50}, Y_{max} and AUDPC, showed that the great part of variation was attributed to genotypes that had highly significant differences for these traits (Table 4) whereas there were no significant differences for replicates (blocks) or between/within the plots. Analysis of variance showed highly significant differences among the genotypes indicating the occurrence of broad range of variability in the expression of resistant.

It can be observed from the analysis of variance that the coefficient of variance in the case of severity at halfway epidemic (Y_{50}) had the highest value (33.16) than the other traits; severity at the end of the epidemic (Y_{max}) and area under disease progress curve (AUDPC). This was expected during the period of evaluation, due to the difficulty of having homogeneity of the scores over all the plants of the same treatment and at the same time, and may be attributed to the disease progress rate, that was not equal over the replicates.

Table 4. Analysis of variance (mean squares) of disease variables: Y_{50}, Y_{max} and AUDPC of half diallel and two susceptible varieties 'New York' and 'Caline' inoculated with *P. infestans*. Viçosa, MG. 2009

S.V	D.F	Y_{50}	Y_{max}	AUDPC
Blocks	2	1102.63	986.35	325331.65
Genotypes	36	683.84**	11452.92**	810607.01**
Residual	72	69.60	113.78	16666.18
Within plots	222	27.65	73.58	6406.55
Mean		14.53	57.63	423.37
CV (%)		33.16	10.69	17.61

** *F-test* significant at the 1% significance level.

The five crosses resulting from the cross of Ikram with the five inbred lines (Figure 4) showed similar expression level of resistance to late blight. This may be due to the fact that these lines have a high homogenseity-homozygousity as an advanced generation (F9). The cross Ikram x 64B had the maximum value of AUDPC (694.37) located together with the cross Ikram x 127F (Figure 9). There was no differences between the crosses of this group and the control group (Caline and New York) in Dunnett's test at P<0.05 (Table 5).

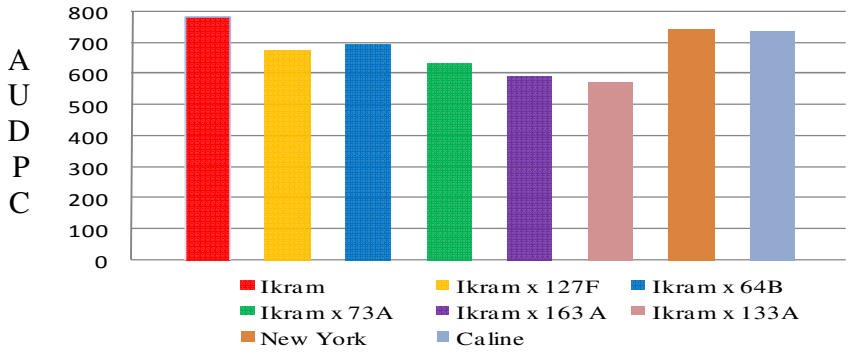

Figure 4. The mean values of the area under disease progress curve (AUDPC) in five crosses between 'Ikram' female progenitor and 5 inbred lines as male progenitor.

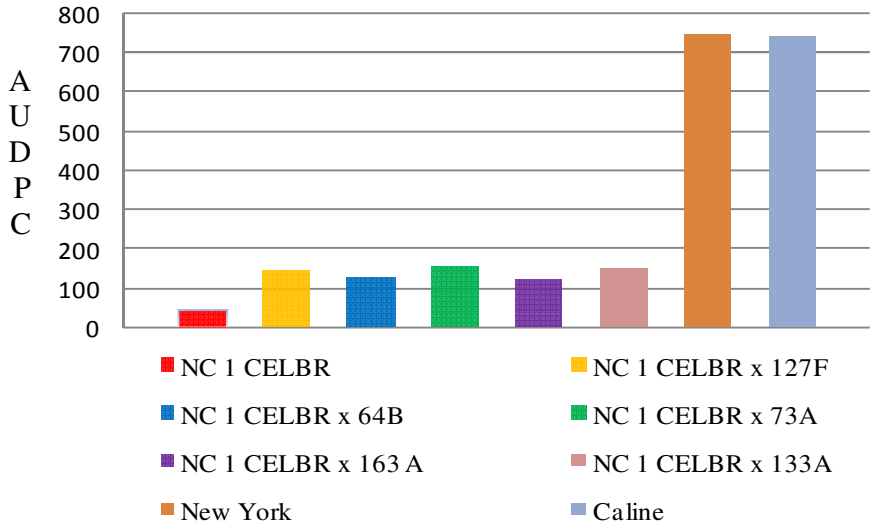

Figure 5. The mean values of the area under disease progress curve (AUDPC) in five crosses between NC 1 CELBR as female progenitor and 5 inbred lines as male progenitor.

The five crosses resulted from the cross NC 1 CELBR with the five inbred lines (Figure 5) showed closed level of resistance to late blight. This may be due to that the testers sharing the same ancestor which they resulted from interspecific cross. The cross NC 1 CELBR x 73A had the maximum value of AUDPC (153.06) located together in the same cluster of the line 163A (Figure 9). While the cross NC 1 CELBR x 163A had the minimum value of AUDPC (119.30). The group of these crosses differed than the control group (Caline and New York) in Dunnett's test at $P<0.05$ (Table 5).

With regards to the cross of NC 2 CELBR with the five inbred lines (Figure 6), the results were similar to that obtained from the last cross of NC 1 CELBR; whoever their crosses showed least values of AUDPC as compared to crosses using NC 1 CELBR parent. This may be because NC 2 CELBR possesses the resistant genes *Ph*-3, besides the *Ph*-2. In general all the crosses had similar resistant level due to the same ancestor of testes. The cross NC 2 CELBR x 127F had the maximum value of AUDPC (85.89) located together in the same cluster as its tester 127F (Figure 9). While the cross NC 2 CELBR x 64B had the minimum value of

AUDPC (52.02). The group of these crosses differed from the control group (Caline and New York) in Dunnett's test at P<0.05 (Table 5).

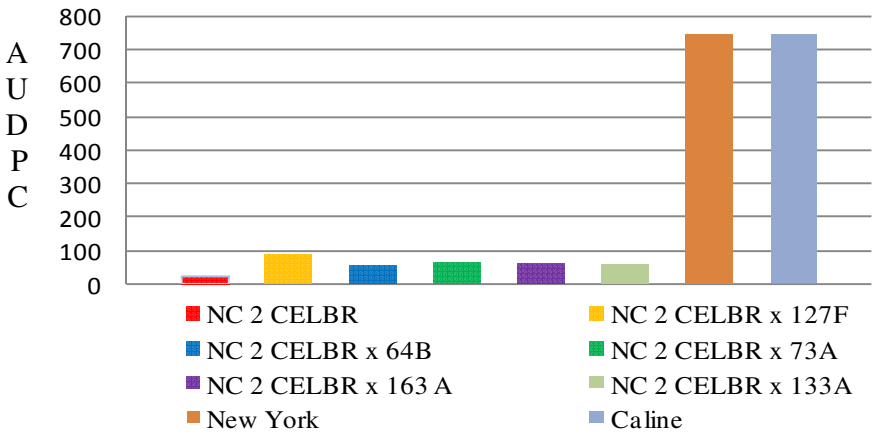

Figure 6. The mean values of the area under disease progress curve (AUDPC) in five crosses between NC 2 CELBR x 5 inbred lines as a source of pollens.

The cross commercial variety Heinz H7155 x the five inbred lines (Figure 7) had high values of AUDPC and were considered as susceptible to late blight in current study. The cross Heinz H7155 x 73A had the maximum value of AUDPC (756.17) located together with the susceptible control Caline in the same cluster (Figure 9). While the cross Heinz H7155 x 64B had the minimum value of AUDPC (644.18).

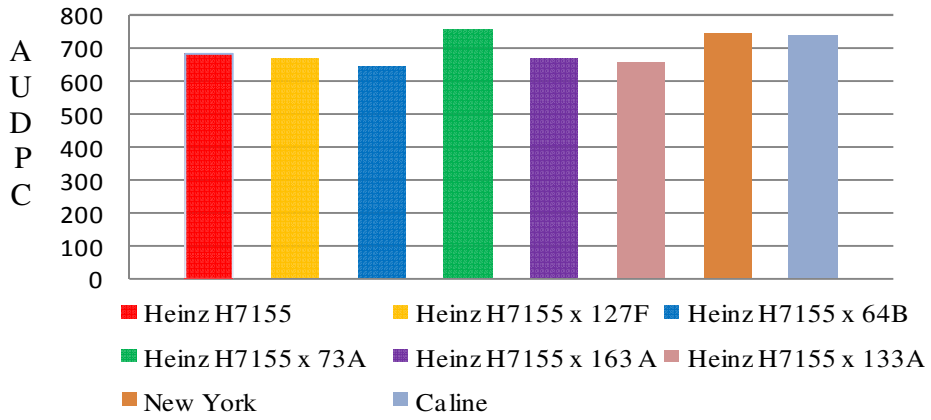

Figure 7. The mean values of the area under disease progress curve (AUDPC) in five crosses between Heinz H7155

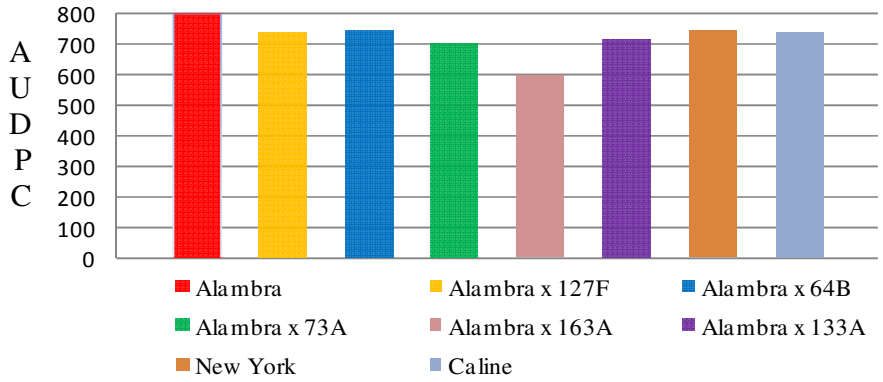

Figure 8. The mean values of the area under disease progress curve (AUDPC) in five crosses between Alambra as female progenitor and 5 inbred lines as male progenitor.

The crosses between the commercial variety Alambra and the five inbred lines (Figure 8) was similar to the previous crossing where the expression of all the crosses had a high values of AUDPC and were considered as susceptible to late blight in current study. The cross Alambra x 64B had the maximum value of AUDPC (745.89) located together with the susceptible control 'New York' in the same cluster (Figure 9). While the cross Alambra x 163A had the minimum value of AUDPC (603.06). There was no significant differences between this group of

crosses and the control group (Caline and New York) in Dunnett's test at $P<0.05$ (Table 5) demonstrated their closed behavior compared to the susceptible control.

"Dunnett's test" was applied to compare each experimental mean with the control mean. A t-test was used to compare the differences in means between each experimental group and the control group for all the three disease parameters Y_{50}, Y_{max} and AUDPC. Significant differences were found among the genotypes. The genotypes NC 2 and NC 1 CELBR had the least values of severity at halfway epidemic (Y_{50}), 0.00 and 0.56 without significant differences between them and was found to be resistant at the end of the epidemic (Y_{max}). They scored the least values of area under disease progress curve (AUDPC) (25.16 and 48.55, respectively) (Table 5). Besides, it was observed that the crosses resulting from both the cultivars NC 1 and NC 2 recorded to be more resistance than the crosses resulting from the hybridization between the commercial hybrids varieties (Ikram, Heinz H7155 and Alambra F_1) as female parents. The cultivar ‘Alambra’ was recorded to be a more susceptible genotype through the severity at halfway epidemic (Y_{50}), at the end (Y_{max}) and for the area under disease progress curve (AUDPC) scored the values 24.35, 98.56 and 801.90, respectively (Table 5).

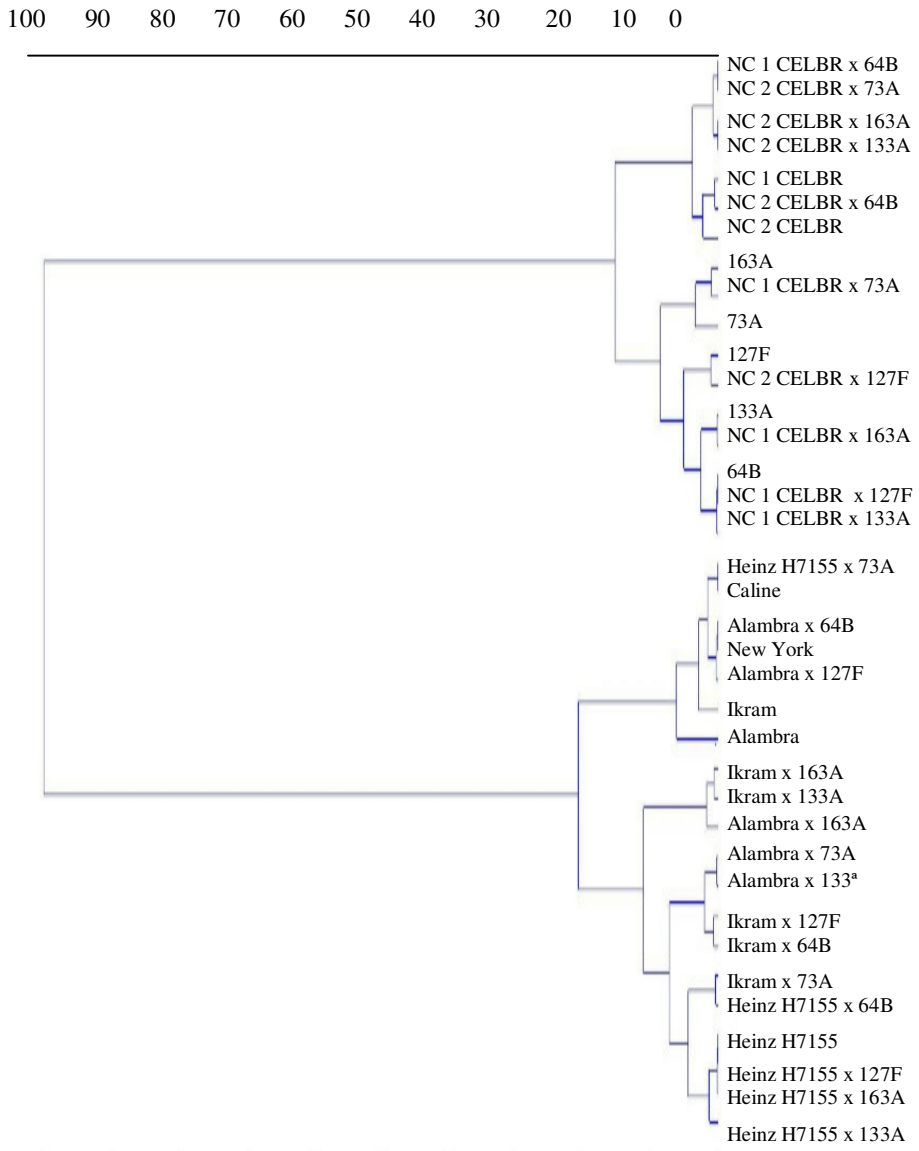

Figure 9. Dendrogram for the 35 genotypes in addition to tow standard susceptible varieties based on the cluster method of Word using AUDPC, Y_{50} and Y_{Max} disease variables discriminated the genotypes into two main groups of resistance and susceptible categories.

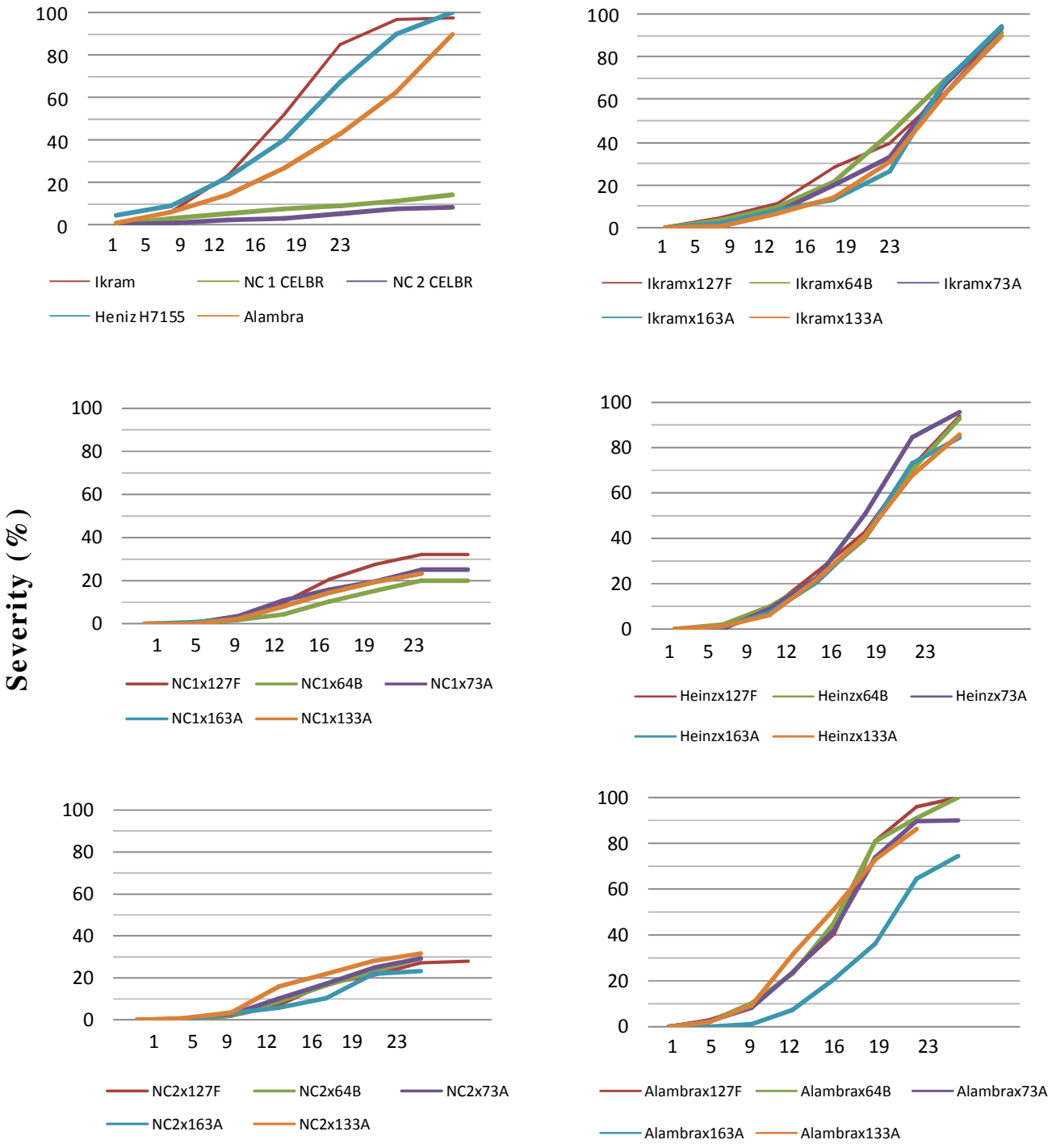

Figure 10. The area under disease progress curve of late blight (*P. infestans*) in tomato during June 2009 for twenty five crosses and their female genotypes. Viçosa, MG, 2009.

Table 5. The mean performance and Dunnett's test at (P<0.05) compares genotypes mean of disease variables Y_{50}, Y_{max} and AUDPC of the half diallel design and two standard susceptible varieties 'New York' and 'Caline'. Viçosa, MG. 2008

Genotype	Y_{50}		Y_{max}		AUDPC	
Ikram	23.62	ab	97.89	ab	784.74	Ab
NC 1 CELBR	0.56		9.73		48.55	
NC 2 CELBR	0.00		5.42		25.16	
Heinz H7155	22.58	ab	90.53	ab	683.77	
Alambra	24.35	ab	98.56	ab	801.90	
127F	1.56		22.84		117.91	
64B	0.80		25.02		139.96	
73A	8.20		23.16		192.50	
163A	5.92		24.83		167.32	
133A	2.18		23.29		126.22	
Ikram x 127F	24.09	ab	92.67	ab	677.70	a
Ikram x 64B	20.98	ab	91.44	ab	694.37	
Ikram x 73A	19.89	ab	94.64	ab	635.69	
Ikram x 163A	13.07	a	94.33	ab	595.27	
Ikram x 133A	13.74	a	89.78	ab	575.44	
NC 1 CELBR x 127F	7.01		24.12		145.29	
NC 1 CELBR x 64B	8.88		27.84		125.83	
NC 1 CELBR x 73A	10.07		14.26		153.06	
NC 1 CELBR x 163A	5.77		18.66		119.30	
NC 1 CELBR x 133A	15.90	a	20.93		148.64	
NC 2 CELBR x 127F	9.79		21.59		85.89	
NC 2 CELBR x 64B	4.40		20.03		52.02	
NC 2 CELBR x 73A	10.82		19.42		67.09	
NC 2 CELBR x 163A	5.93		20.93		59.61	
NC 2 CELBR x 133A	8.08		17.70		60.54	
Heinz H7155 x 127F	18.00	a	84.18	ab	665.15	
Heinz H7155 x 64B	18.86	ab	77.18	ab	644.18	
Heinz H7155 x 73A	22.66	ab	86.13	ab	756.19	ab
Heinz H7155 x 163A	20.80	ab	84.44	ab	668.20	
Heinz H7155 x 133A	22.04	ab	85.84	ab	653.41	
Alambra x 127F	23.85	ab	96.00	ab	739.21	ab
Alambra x 64B	23.21	ab	91.00	ab	745.89	ab
Alambra x 73A	23.76	ab	89.73	ab	703.43	ab
Alambra x 163A	20.78	a	74.44	b	603.06	
Alambra x 133A	20.21	a	86.36	ab	715.30	ab
New York	26.12	a	94.07	a	746.17	a
Caline	29.03	b	92.82	b	740.70	b

* Genotypes that have no significant differences regard to the control group share the same letters by Dunnett's test at 5 % of probability.

3.1.2 Pearson's correlations between disease variables

The main objective of this part of results was to assess the accuracy of the variables that could reveal and discriminate the levels of resistance among the different genotypes. Since the standardized methods for determining the level of resistance and susceptibility to *P. infestans*, is traditional and semi quantitative and is not based on a true interval scale (Yuen and Forbes, 2009).

Strong positive correlation (over 0.94) was observed between the different resistant traits; Y_{50}, Y_{max} and AUDPC. However there was high significant variation in the correlation among variables according to the degree of resistance over the genotypes. Based on the current results, the variable AUDPC is more reliable and accurate than the other indicators (Y_{50} and Y_{max}). As such, it combines information of all epidemic aspects, including inoculum, environment, and host susceptibility (Yuen and Forbes, 2009). So the disease variables Y_{max} and AUDPC were only included in the further genetic analysis to estimate different genetic parameters. The variable Y_{50} was discarded from further analyses.

3.2 Evaluation of resistance in F_2 population

The inbred line 163A was considered as resistant to late blight, producing a mean DI (Disease Index rating) of 1 whereas the cultivar ' Ikram' was fully susceptible, scored DI = 4. The inbred line 163A (served as male parent) was crossed with the susceptible cultivars Ikram and Heinz H1755. Offspring progeny plants at the F_1 and F_2 generations were inoculated at the 10-leaf stage with a mixture of isolates of *P. infestans*. All the plants of inbred line 163A were resistant showing DI of 1 (Table 6), whereas Heinz H1755 was susceptible with DI of 4. The F_1 plants showed various levels of moderate to susceptible resistance with DI ranging between 2 and 4. The moderate level of resistance in F_1 plants indicates that resistance in 163A is partially recessive.

3.2.1 Genetic analysis of resistance in F_2 population

Evaluation of resistance to *P. infestans* was performed on two populations F_2 IKR4 and HEN4 with 77 and 95 individual respectively. The plants of F_1 generation showed susceptibility in general with 5 plants scoring a moderately susceptible (41-60%) and 4 plants scoring susceptible (> 60%) (Table 6), indicating that resistance is inherited as a partial recessive trait. There was no genotype 100% free of any symptoms, so, in the progeny screening, the phenotypic class 1 could be assigned as resistant (10-25%). With this criterion, the F_2 population IKR4 plants segregated 10 resistant and 67 susceptible in two classes moderately resistant and moderately susceptible. The F_2 individuals of second population (HEN4), 95 plants were tested against *P. infestans.* Eleven individuals had few restricted non-sporulating lesions and were considered as resistant. On the other hand, 45 plants of F_2 population showed severe symptoms, consistent with the proportion of homozygous susceptible plants expected for the inheritance of an incompletely dominant gene.

Table 6. Evaluation of the parents, F_1 and F_2 populations against *Phytopthora infestans* and their plants per class observed on the leaves. Inbred line 163A is resistant, *L. esculentum* 'Ikram' is highly susceptible, and F_2 individuals displayed intermediate symptoms development.

Cross[†]	Parent or generation	Disease index[††]				Total
		1	2	3	4	
		Number of plants per class				
IKR4	Ikram				9	9
	163A	9				9
	F_1			5	4	9
	F_2	10	7	24	36	77
HEN4	H7155				9	9
	163A	9				9
	F_1		5	3	1	9
	F_2	11	4	34	45	95

[†] IKR4 and HEN4 are Ikram x Inbred 163A and Heinz H7155x Inbred 163A respectively crosses
[††] as % severity, 1: 10-25; 2: 26-40; 3: 41-60; 4: > 60%

The parents, susceptible, 'Ikram' and resistant, 163A, were at or near the distribution extremes for susceptibility and resistance respectively. The F_1 individuals fell between the parental means but with more in the direction of

susceptibility. The genetic parameters of the F_2 segregating populations are showed in Table 6.

The HEN4 population had higher phenotypic variation than the other population while the IKR4 had the great part of genetic variability. In general, the HEN4 population was more resistant to *P. infestans* than the IKR4 population (Table 7). In general, heritability was 96.75 and 61.41% for IKR4 and HEN4 respectively. In a similar study, Irzhansky and Cohen (2005) found that F_1 plants exhibited various levels of moderate resistance and F_2 plants segregated 3:6:7 resistant : moderately resistant : susceptible. The data support the hypothesis that race-non-specific resistance in *S. pimpenellifolium* L3707, is controlled by two independent genes: a partially-dominant gene and a dominant epistatic gene.

Table 7. The means and variances of the final severity (Y_{max}) for parents (P), F_1 and F_2 generations (G) for the two crosses Ikram x 163A and Heinz H7155x 163A.

P/G	Population					
	IKR4			HEN4		
	No.of ind	Mean	variance	No. of ind	Mean	Variance
P_1	9	97.89	10.11	9	90.53	119.66
P_2	9	24.83	26.74	9	24.83	26.74
F_1	9	94.33	51.00	9	84.44	301.53
F_2	77	70.53	567.27	95	56.08	781.34

The low number of highly resistant plants in the evaluation test for the F_2 population and the wide range in disease reactions of this population in the field indicate that more than two genes likely contribute to late blight resistance. For two genes, assuming dominant gene action for resistance, 25 percent of the population should have been in the most resistant class in the F_2 population in the field. Resistance has also been associated with reduction in the time course of development of symptoms (partial resistance) is desirable trait for plant breeder since it is often effective across a broad range of pathogen races or strains (Parleviet, 1979)

The heritability estimates showed that 96.75% and 61.41% of the total variation in the F_2 populations IKR4 and HENZ4 respectively is attributed to genetic causes and that 3.17% and 38.59% of the total phenotypic variation is attributed to environmental factors (Table 8). A normal consistency of low heritability was observed in quantitative traits, which is due to the large interference of the environment on the expression of the trait studied (Ramalho et al., 2000). The difference between the two populations in their degree of heritability may be because both Ikram and Heinz female parents have different levels of heterozygosity, since they are commercial hybrids and in segregating generation, the individuals have broad range of variability and so the response of each genotype to the environmental factors are not the same.

Table 8. The genetic parameters of final severity (Y_{max}) for the F_2 segregating populations IKR4 and HEN4.

Parameter	Population	
	IKR4	**HEN4**
Phenotypic var.	567.27	781.34
Environment var*.	18.43	301.53
Genotypic var.	548.84	479.81
H_b (%)	96.75	61.41
Heterosis	32.97	26.76
Degree of dominance	0.90	0.81

The average degree of dominance was 0.90 and 0.81 towards the susceptibility indicating partial recessive gene action controlling the resistant. Whereas, the inheritance of resistance to other pathogens such as *Ralstonia solanacearum*, and *Colletroctichum coccodes* in tomato are quantitative with partial dominance of the alleles in tandem with the higher AUDPC (Neto et al., 2002, De Castro et al., 2007).

There was a wide distance between the parents regarding the severity. The minimum severity was 71.45% for the susceptible parent Ikram while the minimum

value for the resistant parent 163A was 15.68%. In the F_2 generation, there was wide variation, however the lowest value (17.21) was not less than the lowest value of 163A, but the highest value (100%) exceeded the highest value of Ikram.

The continuous distribution of the F_2 individual from the resistance to the susceptibility of the severity values showed that the resistance to *P. infestans* is polygenic and genetic analysis suggest that this resistance is quantitatively inherited. The F_2 population demonstrated that the gene action controlling the resistance to late blight in 163A is recessive.

As the ultimate goal is obtain a population genetically improved, for that the prediction of the selection gain is an important factor to realize this objective. For evaluation of disease severity, the selection should be negative, or harvest, the lower the note for the disease, the greater the degree of resistance of the individual. Therefore, negative selection aims to reduce the disease severity in the next generation of each selection cycle. In study of Abreu (2005), selected 25 individuals in the population F_2 for the lower levels of severity of late blight, it was observed that there should be little gain after one cycle of selection. In the population F_2, the mean value of AUDPC was 273.6. Selection the 50 best resistance individuals, the mean reduced to125.56 with reduction of 13.41 is equivalent to 4.9% of disease. The mean for AUDPC predicted after one cycle of selection was 260.19.

Regarding field evaluation, about 12 percent of the plants were in the most resistant class. This is in agreement with previously studies on late blight resistance in *S. habrochaites* appears to be under polygenic control (Saccardo et al., 1975). The authors used leaf discs to evaluate the inheritance of resistance in *S. habrochaites* accessions for F_1 and F_1BC_1 progeny. They concluded that the resistance was polygenic but did not indicate the number of genes involved (Saccardo et al., 1975). Abreu (2005), demonstrated that a high number of genes (28) are controlling resistance in respect of AUDPC, confirming that resistance to *P. infestans* in tomato is polygenic inheritance, confirming results of previous research. The majority of genes controlling quantitative traits cannot have their effects independently without gene-environment interaction.

3.3 Half diallel analysis of inheritance to resistance

Major resistant genes to late blight are associated with field resistance presumably by genetic linkage (Tereshonkova et al., 2003). This observation is important as continuing to include defeated major genes and combine different resistance will be important to breed for durable resistance. In this study we selected promising genotypes which were developed by combining different sources of resistance that show high resistance after artificial inoculation and natural late blight epidemics with aggressive *P. infestans* strains.

Both fresh market tomato varieties 'Ikram' and 'Alambra F_1' and processing 'Heinz H 7155' were included in the half-diallel cross. As it was mentioned previously, not all the seeds of the hybrids were equal in amount since there were certain ones with few seeds due to the difficulty and any possible incompatibility mechanism between cross *S. esculentum* and *S. habrochaites.* Design II analyses of 5 x 5 was applied to study the inheritance of resistance to late blight in tomato.

Through the results obtained from the genetic analysis of F_2 populations and the mean performance of the parents and their progenies in the half diallel indicating that the resistance in the inbred lines is controlled by recessive genes. This mode of gene action that was observed in the half F_1 diallel implied that the homozygote effects were more important than heterozygote effects. This case was demonstrated by Heun, (1987) who found that in the commercial cultivars the frequencies of dominant genes are higher than in the inbred lines, with incomplete dominance in both cases. Only a slightly higher mean resistance in generation F_1 was observed as compared to the parents, and no or very little variance was attributable to specific combining ability effects. However, significant differences existed in the average heterosis without their being correlated to the general combining abilities of the common parents. Therefore, it could be conclude that part of the genes conferring quantitative resistance act dominantly and a part act recessively.

3.3.1 Combining ability analysis of late blight resistance

Analysis of parents and F_1's using Griffing's approach as modified by Geraldi and Miranda Filho (1988) were employed to study the GCA, SCA, the nature of gene action and their interactions for exploring the possibilities of isolating useful recombination related to resistance to late blight. Mean squares of GCA (group I only) and SCA were significant for Y_{max} and AUDPC at 1% of probability (Table 9) indicated that both the additive and non-additive genetic effects are included in controlling these traits. The high values of mean squares of GCA over the SCA is evidence that the importance of the additive genetic effect is more than the non-additive one. Similar results were found by Raj and Pandey (2007) and Nkalubo et al., (2009)

3.3.1.1 The GCA effects (gi)

A great variability of GCA was observed between different parents (Table 10). The least values of GCA (gi) positive or negative effects indicate that these genotypes do not differ from the general mean of the half diallel population. Whereas, the highest values of (gi) wether, positive or negative, indicate that the parent is superior or inferior than the others parents in the diallel, with regard to the average performance of the progeny (Cruz and Regazzi, 2001; Sprague and Tatum, 1942). It indicates the importance of additive genes in controlling the trait under study.

The interpretation of GCA (gi) effects depends on the breeder´s interest. Since the selection to late blight resistance is towards the negative or in other words, the least values of Y_{max} or AUDPC indicate highest level of resistance, so, the high negative values of gi are most important to the breeder. It indicates that the general mean of crosses that included these parents is less than the general mean of crosses in the diallel. In addition, these values indicate the importance of additive genetic effect with regard to the genetic variability in the population.

Table 10, shows that, for the $Y_{max,}$ the cultivars NC 1 CELBR and NC 2 CELBR (group I) had significant negative GCA effects (-33.368 and -35.008 respectively) and the inbreed lines 163A and 133A (group II) had significant negative ones (-1.103 and –0.577, respectively). AUDPC, was similar to Y_{max} (-262,931 and -308.903 for NC 1 and NC 2, respectively and -15.048 and -12.194 for 163A and 133A respectively). The negative highest values of gi indicate the superiority of these parents compared to the others.

Genetic component of variance for general combining ability and specific combining ability were 686.2805, -14.8498 and 49299.916, -3608.3003 for Y_{max} and AUDPC respectively (Table 14). General combining ability variance was greater than the specific ability variance indicating that additive gene action was more important for expression in both disease parameters. Fiorini (2008) also report similar findings. Based on the previous observations, we can say that additive type of gene action was dominant over non-additive effect because specific combining ability variance is less than those of general combining ability. However, both additive and non-additive genes action were involved in the expression for resistance. Similar findings have also been observed by various authors (Ghanadha et al, 2000; Jagadeesha and Wali, 2006; Singh and Singh, 2008).

3.3.1.2 The SCA effects (Sij)

The positive values of specific combining ability effect (Sjj) imply negative unidirectional dominance and the negative sjj values are observed when the deviations due to dominance are positive (Viana, 2000). Moreover, when the SCA effect of a population with itself is null, the population has the same gene frequencies as the average frequencies in the group of the diallel's parents. Furthermore, higher the absolute value of sjj, the greater the differences between the gene frequencies in the population and the average frequencies in the diallel's parents.

Table 9. Partitioning of genotypes variance (mean squares) in GCA and SCA of the parents and their half diallel crosses for Y_{max} and AUDPC and fruit quality characters. Viçosa, MG, 2009.

S.V.	D.F.	Mean squares[(1)]									
		Y_{max}	AUDPC	AFW	FS	FSI	pH	TA	TSS	Firmness	Flavor
Genotypes	34	3802.70**	266984.24**	7879.24**	3604.48**	0.067**	0.043*	0.013 *	1.8497**	4.8569**	17.0122**
Groups	1	10045.60**	768201.61**	130487.17**	61051.25**	0.341**	0.025^{NS}	0.039^{NS}	38.4199**	67.3445**	110.0743**
GCA Group I	4	26458.17**	1853654.7**	1165.15**	645.78**	0.021^{NS}	0.136**	0.013 **	2.8987**	1.9475**	18.2559**
GCA Group II	4	24.67^{NS}	5535.76^{NS}	156.98**	305.72**	0.037**	0.031^{NS}	0.017^{NS}	0.2001*	1.0198*	17.8704**
SCA I x II	25	532.60**	34900.01**	5284.74**	2307.80**	0.068**	0.031^{NS}	0.011^{NS}	0.4830**	3.4369**	12.9535**
Error	68/34[(2)]	115.06	15047.58	20.15	13.82	0.008	0.020	0.010	0.0748	0.3548	0.7206
Mean		57.617	423.37	39.281	32.564	1.026	4.028	0.404	4.824	2.900	12.279
SD		1.846	21.113	0.946	0.783	0.172	0.009	0.003	0.057	0.126	0.179

[(1)] NS: not significant, significant; * and ** significant and high significant at 1% and 5% of probability respectively; Ymax: severity at the end of the epidemic; AUDPC: area under disease progress curve; AFW: average fruit weight; FS: fruit size (mL); FSI: fruit size index ; pH; TA: total acidity ; TSS: total soluble solids; SD: standard division of the difference between two estimations. (2) Degree of freedom is 68 for the Y_{max} and AUDPC; and 34 for the other variables based on the analysis of variance in each case.

Table 10. Estimation of general combining ability (GCA) effects (gi) of a half diallel mating design involving ten genotypes (group I and II) for Ymax, AUDPC and nine fruit quality characters in tomato. Viçosa, MG, 2009.

	Genotypes	Effects[(1)]									
		Y_{max}	**AUDPC**	**AFW**	**FS**	**FSI**	**pH**	**TA**	**TSS**	**Firmness**	**Flavor**
Group I	Ikram	25.896	176.9278	-11.565	-6.939	-0.0042	-0.067	0.026	-0.209	0.136	-1.315
	NC 1 CELBR	-33.368	-262.931	6.448	5.372	-0.0037	-0.080	-0.017	0.250	-0.314	1.214
	NC 2 CELBR	-35.008	-308.903	4.640	6.261	0.0241	0.059	0.024	0.585	0.305	0.645
	Heinz H7155	19.250	177.6744	-5.327	-5.200	0.0358	0.121	-0.036	-0.305	-0.391	0.109
	Alambra	23.230	217.2322	5.804	0.506	-0.052	-0.067	0.002	-0.321	0.264	-0.653
	SD (G_i-$G_{i'}$)	1.8464	21.1153	0.9464	0.7839	0.0192	0.029	0.0211	0.0577	0.126	0.179
Group II	127F	1.3173	3.7271	-2.507	-0.717	-0.012	0.003	0.050	0.005	-0.131	0.356
	64B	0.5718	2.966	-1.065	-1.928	0.028	-0.037	-0.012	0.050	0.046	1.188
	73A	-0.2093	20.5493	-0.080	-0.489	0.059	0.043	-0.033	0.068	-0.246	0.478
	163A	-1.1027	-15.0484	5.050	6.978	-0.059	-0.046	-0.007	0.060	0.380	-0.726
	133A	-0.5771	-12.194	-1.398	-3.844	-0.017	0.038	0.002	-0.184	-0.048	0.356
	SD (G_i-$G_{i'}$)	1.8464	21.1153	0.9464	0.7839	0.0192	0.029	0.0211	0.0577	0.126	0.179

[(1)]Y_{max}: severity at the end of the epidemic; AUDPC: area under disease progress curve; AFW: average fruit weight; FS: fruit size (mL); FSI: fruit size index; TA: total acidity ; TSS: total soluble solids; SD: standard division of the difference between two estimations.

Table 11. Estimation of specific combining ability (SCA) effects (Sij) of twenty five crosses for Y_{max}, AUDPC and nine fruit quality characters in tomato. Viçosa, MG, 2009.

Genotypes	Effects[1]									
	Y_{max}	**AUDPC**	**AFW**	**FS**	**FSI**	**pH**	**TA**	**TSS**	**Firmness**	**Flavor**
Ikram x 127F	9.8883	91.9654	-14.23	-9.41	-0.105	-0.044	0.079	0.58	-1.01	-0.42
Ikram x 64B	9.4038	109.3965	-17.65	-9.70	-0.105	0.016	0.000	0.48	-1.08	0.97
Ikram x 73A	13.385	33.1332	-15.59	-4.64	-0.066	0.026	-0.029	0.42	-0.19	1.78
Ikram x 163A	13.9683	28.311	-22.07	-14.10	-0.093	0.010	0.106	-0.33	-1.22	-3.24
Ikram x 133A	8.8927	5.6265	-14.52	-11.28	-0.005	0.081	-0.033	0.62	-0.49	2.60
NC 1 CELBR x 127F	0.6016	-0.5857	-29.05	-15.22	-0.156	-0.069	-0.039	-0.23	0.34	-0.11
NC 1 CELBR x 64B	5.0671	-19.2846	-35.16	-19.51	-0.066	0.081	-0.028	0.03	-0.28	0.75
NC 1 CELBR x 73A	-7.7317	-9.6379	-33.05	-21.45	0.004	-0.094	0.083	-0.04	1.01	-3.07
NC 1 CELBR x 163A	-2.4384	-7.8001	-42.48	-25.61	-0.079	-0.060	0.018	-0.13	-0.82	-1.34
NC 1 CELBR x 133A	-0.694	18.6854	-35.06	-26.09	-0.096	-0.159	0.119	0.00	-0.44	-3.17
NC 2 CELBR x 127F	-0.2884	-14.0135	-27.14	-22.11	0.021	-0.066	0.080	0.04	0.08	-1.83
NC 2 CELBR x 64B	-1.1029	-47.1224	-31.80	-20.20	-0.184	-0.011	0.121	0.19	-0.35	-2.66
NC 2 CELBR x 73A	-0.9317	91.9654	-32.51	-23.54	-0.219	-0.087	-0.088	-0.42	-0.79	2.33
NC 2 CELBR x 163A	1.4716	109.3965	3.35	25.65	0.199	0.128	-0.083	0.23	2.37	3.53
NC 2 CELBR x 133A	-2.284	33.1332	-29.13	-20.13	-0.089	-0.137	-0.012	-0.28	0.09	-0.18

[1] Y_{max}: severity at the end of the epidemic; AUDPC: area under disease progress curve; AFW: average fruit weight; FS: fruit size (mL); FSI: fruit size index; A: total acidity ; TSS: total soluble solids;

Table 11. Cont.

Genotypes	Effects									
	Y_{max}	**AUDPC**	**AFW**	**FS**	**FSI**	**pH**	**TA**	**TSS**	**Firmness**	**Flavor**
Heinz H7155 x 127F	8.0438	78.668	-20.84	-15.15	-0.130	-0.131	-0.010	-0.87	-0.33	-2.03
Heinz H7155 x 64B	1.7893	58.459	-24.27	-15.04	-0.145	-0.046	-0.029	-0.12	-0.76	0.71
Heinz H7155 x 73ª	11.5205	152.886	-25.16	-13.63	-0.016	-0.126	-0.028	0.06	-0.46	1.49
Heinz H7155 x 163ª	10.7238	100.494	-29.85	-25.84	0.097	0.058	-0.043	-0.13	-1.19	1.11
Heinz H7155 x 133ª	11.5982	82.849	-23.97	-15.52	-0.030	-0.051	0.008	0.26	-0.66	0.44
Alambra x 127F	15.8838	113.171	-34.15	-21.35	0.097	-0.052	0.072	-1.01	-1.18	-3.68
Alambra x 64B	11.6294	120.612	-34.36	-21.64	-0.133	-0.222	-0.067	-0.20	-0.41	1.55
Alambra x 73ª	11.1405	60.568	-30.31	-25.08	-0.313	0.182	-0.066	-0.22	-1.52	1.44
Alambra x 163ª	-3.2562	-4.203	-37.54	-31.55	-0.095	0.067	-0.081	0.34	-1.29	3.27
Alambra x 133ª	8.1382	105.182	-30.80	-20.73	-0.143	-0.103	-0.050	0.53	-0.97	2.72

(1)Ymax: severity at the end of the epidemic; AUDPC: area under disease progress curve; AFW: average fruit weight; FS: fruit size (mL); FSI: fruit size index; TA: total acidity ; TSS: total soluble solids;

The effects of specific combining ability (Sij) refers to those instances in which the performance of a hybrid is relatively better or worse than would be expected on the basis of the average performance of the parents involved (Sprague and Tatum, 1942). The best parents and hybrids can be identified by combination of a cross with highest value of Sij with the more favorable GCA effect for use in breeding program (Cruz and Regazzi, 2001). The Sij values reflect the importance of genes with dominance and epistasis effects.

Table (11) shows the specific combining ability effects (Sij) including the Ymax and AUDPC as indicators for screening late blight resistance with the observance that they differ in the hybrid combinations that captured the highest values of Sij. In the case of Ymax, the crosses NC 1 CELBR x 73A and Alambra x 163A had the two first maximum values of Sij (-7.7317 and -3.2562, respectively). The best combination is NC 1 CELBR x 73A since one of its parents; NC 1 CELBR had high combining ability whereas the other cross had not. In contrast, AUDPC in the crosses NC 2 CELBR x 64B and NC 1 CELBR x 64B had the maximum values of Sij (-47.1224and -19.2846 respectively). The best combination is NC 2CELBR x 64B since one of its parents, NC 2 CELBR had the highest combining ability value (-308.903).

It can be observed that the best crosses, with regard to the resistance, were that involved the cultivars NC 2 and NC 1. These are exotic in relation to Brazilian germplasm, a fact that can indicate a favorable contribution of the genetic diversity among the parents for high values of SCA. Crosses between divergent parents with high values of SCA can be explored through breeder by selection for favorable segregated individuals that lead to obtain superior lines (Sharma and Phul, 1994). These crosses have additional advantage that they combine both the vertical resistant genes *Ph-2* and *Ph-2, Ph-3* from the female parents (NC 1 CELBR and NC 2 CELBR, respectively) and the horizontal quantitative resistant genes that are including in the inbred lines resulted from the interspecific cross between *S.*

lycopersicum L. cv. Santa Clara x *S. habrochaites* f. *glabratum* accession BGH 6902 (Tables 12 and 13).

Table 12. Summary of the best values of combining ability effects (group I and II) for Y_{max}, AUDPC and nine fruit quality characters in tomato. Viçosa, MG, 2009.

Character	Group I (lines)					Group II (tester)				
	Ikram	Heinz H7155	Alambra	NC 1 CELBR	NC 2 CELBR	127F	64B	73A	163A	133A
Y_{max}					-35.0				-1.103	
AUDPC					-308.9				-15.04	
AFW				6.448					5.050	
FS	-6.93				6.26				6.978	
FSI		0.036						0.059		
pH				-0.080					-0.046	
TA	0.026					0.050				
TSS					0.585			0.068		
Firmness					0.305				0.380	
Flavor				1.214			1.188			

Y_{max}: severity at the end of the epidemic; AUDPC: area under disease progress curve; AFW: average fruit weight; FS: fruit size (mL); FSI: fruit size index; TSS: total soluble solids;

Table 13. The best combinations of twenty five crosses in respect of resistance to *P. infestans* and fruit quality characters in tomato. Viçosa, MG, 2009.

Group I (lines)	Group II (tester)				
	127F	64B	73A	163A	133A
Ikram					TSS
Heinz H7155					
Alambra					
NC 1 CELBR			Y_{max}		
NC 2 CELBR		AUDPC		AFW/ FS Firm/Flavor	

Y_{max}: severity at the end of the epidemic; AUDPC: area under disease progress curve; AFW: average fruit weight; FS: fruit size (mL); TSS: total soluble solids; Firm: Firmness

Table 14. Genetic components combing ability variance in half diallel cross of tomato for Ymax, AUDPC and nine fruit quality characters in tomato. Viçosa, MG, 2009.

S.V.	Trait									
	Y_{max}	AUDPC	AFW	FS	FSI	pH	TA	TSS	Firmness	Flavor
GCA (I)	1365.68	98336.45	6.644	23.616	0.0013	0.0064	0.0010	0.1556	0.2856	-0.481
GCA (II)	-1.116	263.39	-1.465	7.279	-0.0021	-0.0002	0.0019	-0.0031	-0.0684	2.518
GCA (mean)	686.28	49299.92	2.590	15.448	-0.0004	0.0031	0.0015	0.0763	0.1086	1.019
SCA	-14.851	-3608.30	58.138	120.610	0.0083	-0.0003	-0.0002	0.1136	0.4380	4.633

(1) Y_{max}: severity at the end of the epidemic; AUDPC: area under disease progress curve; AFW: average fruit weight; FS: fruit size (mL); FSI: fruit size index; TA: total acidity ; TSS: total soluble solids;

3.3.2 Combining ability analysis of fruit quality traits

By estimation of the nature of gene action and their interactions, there is a possibility of isolating useful recombination related to quality traits in tomato fruits associated with the resistance to late blight. Viana (2007) demonstrated that the general combining ability effect is an indicator of the superiority of the population, in terms of frequency of the favorable genes. Mean squares of GCA for group I (lines) for all the estimated quality traits were highly significant at 1% of probability except for fruit shape index (FSI) that has no significant differences between the parents of group I in this trait. While the mean squares of GCA in respect of group II (testers), the AFW, FS, FSI and flavor had highly significant differences between the parents of this group and for both TSS and firmness at 5% probability. While with the traits, pH and titratable acidity, there was no significant differences between the testers in respect to these traits and also interaction line x tester (SCA) (Table 9).

These results implying that the distribution of alleles and their frequencies were similar among the parents of this group in respect to these traits. In contrast for the others traits, it was observed that from the analysis of variance (Table 9) the SCA had highly significant differences at 1% of probability for most quality traits expect pH and titratable acidity. The results indicate that both the additive and non-additive genetic effects are included in controlling traits under study. The high values of mean squares of SCA over the GCA show the importance of the non-additive genetic affect was more than the additive, for the traits such as AFW, FS, FSI and firmness. In contrast, the additive gene effect for pH, titratable acidity, TSS and flavor, was superior than the non-additive effect for the genes controlling these traits. While there were no significant differences for both pH and titratable acidity in both GCA (group I) and SCA mean squares.

TSS, and flavor had significant differences and the mean squares of GCA were higher than the mean squares of SCA indicating that the importance of additive effect of the genes controlling these traits were more than the non-additive effects. In contrast, Garg et al. (2008) found that the additive gene action was predominant

for average fruit weight, fruit shape index and lycopene in two different environments, whereas non-additive genetic variance predominated in controlling firmness index, number of locules, pericarp thickness, alcohol insoluble solids (AIS), dry matter, total soluble solids (TSS), titratable acidity, TSS: Acid ratio, pH, ascorbic acid and shelf life.

In most crops including tomato, there is a high positive / negative correlation between the quality traits. So it is easy to observe that both additive and non-additive gene actions are important in controlling these traits, implying that the selection may be effective in providing high level of genetic variability.

3.3.2.1 GCA effects (gi)

Highly significant effects were detected for GCA and SCA in most of fruit quality traits. The relative contribution of individual parents to quality traits was estimated by comparison of GCA effects (Table 10). A great variability was observed among the parents in both groups I and II over the most quality traits. The least values of GCA (gi) effects positive or negative indicate that these genotypes do not differ than the general mean of the half diallel population. Whereas, the highest values of (gi), wether positive or negative indicate that the parent is superior or inferior than the other parents in the diallel with regard to the average performance of the progeny (Cruz and Regazzi, 2001; Sprague and Tatum, 1942) indicating the importance of additive genes controlling the trait under study.

The interpretation of GCA (gi) effects in the case of fruits quality traits depends on the breeder interest and the classification of tomato fruits whether for fresh market or processing. For the traits fruit size (FS), the inbred line 163A (group I) had the highest positive values of GCA effects (gi) 6.978 (Table 10). Whereas, the cultivar NC1 CELBR showed highest positive value GCA effects for AFW (6.448). Since the high level of total acidity (pH) is desirable especially for processing tomato, so the selection for the combining ability is toward negative values; but in the current study we could not observe significant differences for both GCA (for group II only) while the cultivars Ikram and Alambra had the highest negative

values of GCA effects (-0.067). The SCA effect for pH and titratable acidity did not show any significant differences. The positive highest values of gi for TSS, firmness and flavor were recorded by NC 2 CELBR, 163A and NC 1 CELBR respectively indicate the superiority of these parents compared with the others.

Tomato quality is a complex character due to its number of components and because it is dependent on conditions throughout the entire process of plant and fruit development (Chittaranjan, 2007). A few mutations along wild tomato species have been shown to be involved in fruit quality, particularly in ripening (Hobson and Grierson, 1993) and QTL studies have revealed a number of genomic regions involved in the variation of quality traits.

3.3.2.2 SCA effects (Sij)

The genetic quality of a genotype appears often poorly from the phenotype of the plant(s) representing the genotype. An alternative way of assessing the genetic quality of the genotype is by means of evaluation of progeny obtained from it. To identify the best parents and hybrids combination, the specific combining ability effects (Sij) for the twenty five crosses was estimated. Since a cross with high value of Sij involving at least one of its parents with more favorite GCA effect is a promising way for genetic improvement (Cruz and Regazzi, 2001). The Sij values reflect the importance of genes with dominance and epistasis effects. Besides, when the SCA effect of a population with itself is null, the population has the same gene frequencies as the average frequencies in the group of the diallel's parents, reflecting the inferiority of the population in the respect of genetic variability among its individuals (Viana, 2000).

Table 11, shows that the cross NC 2 CELBR x 163A captured the highest positive value of specific combining ability effects (Sij) for the AFW and FS (3.35 and 25.65 respectively). The best combination is NC 2 CELBR x 163A since one of its parents, 163A, had high general combining ability whereas the rest of the crosses had negative values of sij with regard to these traits. Many studies on tomato fruit size inheritance have seldom positive heterosis. In general, fruit size in the F_1

generation is smaller than the arithmetical mean of the parents (Larson and Currence, 1944; Maluf et al., 1982b). For TSS, the following crosses: Ikram x 133A, Ikram x 127F and Alambra x 133A had better Sij values (0.62, 0.58 and 0.53 respectively). For firmness, the crosses NC 2 CELBR x 163A and NC 2 CELBR x 73A had highest positive values (2.37 and 1.01 respectively): so it can be predicted that the first combination NC 2 CELBR x 163A could be used to improve this trait since both the parents involved in this cross had high GCA effect.

The flavor depends on the ratio between total soluble solids and the titratable acidity content. Flavor was highly significant in both GCA and SCA mean squares. The cultivar: NC 1 CELBR and 64B had high positive GCA (1.214 and 1.188, respectively) while for SCA effect, the crosses NC 2 CELBR x 163A, Alambra x 163A and Alambra x 133A had the highest values (3.53, 3.27 and 2.72, respectively). Among the previous crosses it was not clear to select the better combinations since they did not share any one of the parents that had the best GCA effect. This may be due to the fact that titratable acidity trait did not show any significant differences for both GCA and SCA.

It was observed that in the genetic component of variance for general combining ability, specific combining ability for quality traits of tomato, the variance of SCA was greater than the GCA in current study, except pH and % titratable acidity (Table 14), indicating that non-additive gene action was more important for expression of these traits while in both pH and titratable acidity, the additive gene action was more important for expression of these traits. From these results, it was concluded that non-additive type of gene action was dominant over additive effect because specific combining ability variance is greater than those of general combining ability. However, both additive and non-additive genes action were involved in the expression for this trait. Similar findings have also been observed by various research workers (Makesh et al., 2002 and 2003; Atanassova et al., 2003; Arun, 2006).

It was observed that certain crosses with the largest values of SCA involved parents contrasting in GCA (TSS and flavor traits) i.e. one or the both parents presenting high values and inverse gi sign (Table 10 and 11). Such combinations can result in transgressive segregation if the genes with additive effects are complementary and act in the same direction of maximum expression of the trait (Gadag et al., 1999). Viana (2007) noted that the hypothesis that the specific combining ability effects of the populations of the two groups are equal to zero is not rejected, showing little divergence between them, a result corroborated by the test on the differences of the mean gene frequencies of the groups. Do Rego et al. (2009) also report similar findings on a diallel study of yield components and fruit quality in chilli pepper and observed significant variation for fruit quality and yield components among parents and F_1 generation. Analysis of variance for the combining ability showed that GCA and SCA effects exhibited significant difference for the most traits. It has been reported that both additive and non-additive effects influenced the performance of hybrids for most studied traits.

The present evaluation through mating designs showed that the genotypes NC 1 CELBR and NC 2 CELBR produced the best performing offspring and had the highest combining ability with regard to high level of resistance to late blight in both Y_{max} and AUDPC due to desirable load of resistant genes *Ph-2* and *Ph-2* + *Ph-3* respectively to *P. infestans* with low recorded values of AUDPC (Tables 13). Besides, the highest negative values of gi indicate the superiority of these cultivars when compared with the other parents from the two groups. Regarding quality traits of tomato fruits, the results indicated that both the additive and non- additive genetic effects are included in the gene expression of these traits.

The current results indicate that there was no significant change in the fruit of the F_9 generation of the inbreed lines (group I) as it was estimated in other study (Fiorini, 2008). In other word, fruit quality traits are similar after one generation of self-pollination, meaning that the genetic background of these lines did not reveal unexpected traits, although the heterozygosity decreased by one half.

However, based on the results of the diallel analysis, using the cultivar NC 2 CELBR as maternal source of resistance is not supported by negative GCA (-308.9) and the positive SCA (109.39) (Tables 10 and 11), provided that single-cross hybrids with low inbreeding depression. The positive GCA and negative SCA have a desirable assemblage of genes that correspond to a F_2 generation capable of developing elite recombinant lines. The trustworthiness of the proposed pattern of mating design was applied in maize commercial hybrids (Koutsika-Sotiriou, 1999; Koutsika-Sotiriou and Karagounis, 2005), and demonstrated that the process for the choice of the certain germplasm was acceptable.

The hybrids: 'Ikram', 'Heinz H7155' and 'Alambra', despite the fact they are well- adapted varieties grown in a large scale in Brazil, but their mean performance relating to the resistance to *P. infestans* was inferior. However, the hybrids are more stable than standard varieties under stress (Janick, 1999). Partly, this advantage may be due to disease resistance, which is easier to combine in hybrids than in pyramiding genes using conventional breeding strategies. This emphasizes the importance of genetic materials at the inbred-line level in selection programs for resistance to *P. infestans*, such as open-pollinated varieties. In a comparison of modern varieties and long-established landraces, Ceccarelli and Grando (1996) reported that new varieties selected under well-managed conditions were superior to local varieties only under conditions of improved management, but not under extreme low-input conditions. Nevertheless, introgression of exotic germplasm into adapted maize breeding populations has been proposed as a guard against genetic vulnerability and selection plateaus (Hallauer and Miranda Filho, 1995; Sfakianakis et al., 1996; Goodman and Brown, 1998; Evgenidis et al., 2001).

The Genetic variation of *P. infestans* has intensified in recent years mainly due the sexual reproduction of this pathogen via mating of A1 and A2 (Cohen, 2002; Gavino et al., 2000; Rubin and Cohen, 2004a). Some recombinant isolates might be more aggressive than their ancestor isolates (Gavino et al., 2000) thus rendering host resistance genes and chemical control (Gisi and Cohen, 1996) inefficient. Searching

for durable resistance in tomato against late blight is therefore an important need for the tomato industry.

In the present study, the assessment of both commercial hybrids and inbred lines showed that cv. Ikram, Heniz H7155 and Alambra had significant positive GCA effects for Y_{max} and AUDPC (Table 10). This implies susceptibility to late blight and is of concern. Whereas they were superior with regard to most of the fruit quality traits. In cvs. Alambra and Ikram, it appears to have a close disagreement between the resistance to late blight and fruit quality. This suggests that the better quality trait varieties will probably be inferior in resistance to late blight. However the both cultivars CN1 CELBR and CN2 CELBR can be used as a good example for explaining the recovery of recombinant inbreds in tomato by applying selection in the F_2 generation (Christakis and Fasoulas, 2002), or fixing and transgressing heterosis (Burdick, 1954). In the assessment of certain fruit descriptives (AFW, FS, LDF and TDF) and qualitative traits of the parents and simple diallel crosses some significant differences were observed mainly in the descriptive traits, without any degradation of the fruit quality in any trait (Table 14).

A diallel analysis of eight tobacco accessions demonstrated that general combining ability (GCA) effects accounted for the majority of variation observed among crosses (Hayes et al., 1995) and suggested that additive gene action plays a significant role in the inheritance of resistance to *Globodera tabacum solanacearum*. Whereas, specific combining ability (SCA) effects, which correspond to non-additive gene action were not significant in the same study.

It should thus be clear that the main interest in applying a GCA and SCA analysis is not in the progenies but in their parents (Bos and Caligari, 2008). So, an analysis of a diallel cross in these terms is, indeed, a special way of progeny testing. Most of the resistant varieties identified in the present study are small fruited. Earlier workers (Bond and Murphy, 1952; Abreu, 2005; Fiorini, 2008) also observed that small fruited varieties possess high level of resistance. Such small fruited types have been used as donors of late blight resistance to develop commercial varieties. The

genotypes identified as resistant in the present study cannot be exploited for commercial cultivation due to their small fruit size in addition to the inferiority of quality of their fruits.

With conventional breeding schemes, the genetic variation of breeding populations is estimated (and selected) by means of the phenotypic performance only. Even though this process has proven to be very effective, a selection procedure directly at the genotype level would greatly increase the efficiency of breeding efforts (Dekkers and Hospital, 2002). This is due to environmental influence on the phenotypic measurements, resulting in a biased measure of the true genetic potential of an individual.

Studies of *P. infestans* on potato (Carnegie and Colhoun, 1982; Stewart, 1990) have shown effects of plant age on the rate of lesion growth or the type of lesion formed. In general, the youngest plants tended to have more extensive lesion development, i.e. to be more susceptible than older plants, although the reactions were not always consistent. Visker *et al*. (2003) found older plants to be more resistant than younger plants, although they did not find plant age to have a great effect on lesion growth rate.

Tomato genotypes carrying the *Ph-2* gene of resistance to late blight and sensitive genotypes which have good yield and quality were hybridized by Mijatovic et al. (2007) who found that the new lines and hybrids of tomato were more resistant than their sensitive parents and showed intermediate type of heredity to late blight.

Both cultivars NC 1 CELBR and NC 2 CELBR showed good acceptable degree of adaptation under the current experimental conditions of our study with respect to resistance to late blight, *P. infestans* isolates. Besides, their production and quality of fruits as compared to the other commercial cultivars (Ikram, Heinz 7155 and Alambra F_1) was better. In respect to fruit quality traits, they were better than the inbred lines testers. It is necessary to ensure that the resistance recorded for the crosses resulted from the hybridization between both NC 1 and NC 2 CELBR with

the different inbred lines, is quantitative resistance or field resistance (against broad range of pathogen isolate).

Besides the cultivars NC 1 CELBR and NC 2 CELBR possess the resistant genes *Ph-2* and *Ph-3* and their crosses had both these genes of resistant and the other resistant genes from the tester parents (inbred lines). So it can be said that they have different genetic back ground in respect to resistance to this disease. However, the NC1 CELBR and NC2 CELBR presented acceptable level in most of fruit quality traits except in firmness. The fruits lost their firmness very fast and did not have good storage ability or did not withstand exposure to pressure. This could be the reason for its decrease in commercial value in addition to the determinate growth habit with heavy foliage and consequently low yield. The progeny result from the crosses between these lines x testers can be explored and the crosses having highest SCA (Sij) effect may be select. This would result in high frequency of favorable alleles in respect of resistance, indeterminate growth habit and at the same time provide a acceptable level of variability in the segregating population that aid in selection to traits of interest. Using back cross method to recover the fruit quality traits is a common approach in this context since the resistant genes have to be selected during each round of back crossing and furthermore the possibility to recover the genetic factors responsible of quality especially average fruit weight, pigments, acidity, TSS, flavors and the other quality traits is bleak.

4. CONCLUSIONS

The three commercial tomato hybrids `Ikram`, `Alambra $F_1$` and `Heinz H 7155` showed high level of susceptibility along with their F_1 progeny. While, the varieties NC 1 CELBR and NC 2 CELBR and their F_1 progeny showed high level of resistance to late blight, under field conditions of current study.

The crosses Heinz H7155 x 73A and Alambra x 64B scored the highest values of AUDPC indicating their overall susceptibility, while the crosses NC 2 CELBR x 64B and NC 2 CELBR x 163A had the first two minimum values of AUDPC reflect their overall resistance among all the genotypes.

The best combinations with respect to the resistance to late blight were the crosses NC 2 CELBR x 64B and NC 1 CELBR x 64B indicating that higher frequency of favorable alleles were found in their parents which were responsible for the resistance that could be useful in the breeding programs to late blight.

The cross NC 2 CELBR x 163A embraced high level of resistant to late blight combined with some fruit qualities of tomato. This cross is promising for genetic improvement of synthetic new cultivar with regard to resistant and fruit quality.

However, the NC 1 and NC 2 CELBR presented acceptable level in most of the fruit quality traits except in firmness. The fruits lost their firmness very fast and did not have good ability to storage or could not withstand exposure to pressure. This may be important factor that reduce its commercial value in addition to its low yield.

The genetic analysis of the F_2 populations indicated that the resistance in the inbred lines was controlled by recessive genes. The values of disease rating indicated that HEN4 population was more resistant to *P. infestans* than IKR4 population.

The stable performance regards of resistance for the five inbred lines in the current and previous studies insure that the resistance in these lines is polygenic and that could be exploited in genetic improvement programs.

Figure 11. The photos of fruits and plant in the for NC 2 CELBR, respectively possesses the resistant genes (*Ph*-2, *Ph-3*) against *P. infestans* and resistant to late blight exhibited high resistance under Brazilian conditions however their yield and quality traits are not fit for the commercial production.

Figure 12. Fruits resulted from the cross between NC 1 CELBR x 73A, combined two sources of resistant genes, *Ph*-2 with dominant effect combined with polygenic recessive resistant genes of 73A inbred line to late blight (*P. infestans*).

Figure 13. Plants hold numbers 12, 8, 43, and 36 are NC 2 CELBR x 64B, NC 1 CELBR x 73A, 64B and Alambra F_1 respectively show different levels of resistance and susceptibility to late blight (*P. infestans*) at the end of evaluation period (Y_{max}).

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