# DEVELOPMENT OF TOMATO HYBRIDS (Lycopersicon esculentum
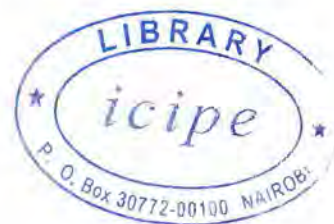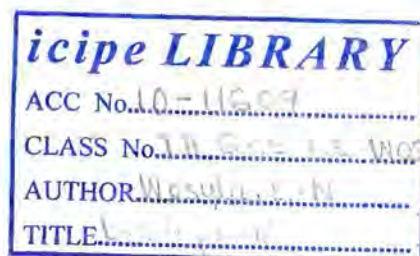
# x Lycopersicon hirsutum f. glabratum) RESISTANT TO TOBACCO

# SPIDER MITE (Tetranychus evansi)

## EVERLYNE NAFULA WOSULA

**A thesis submitted in partial fulfillment for the degree of Master of Science in Horticulture in the Jomo Kenyatta University of Agriculture and Technology**

**2007**

# DECLARATION

This thesis is my original work and has not been presented a degree in any other university.

Signature...~Nafula~............                    Date...05. 02. 2007

        Everlyne Nafula Wosula
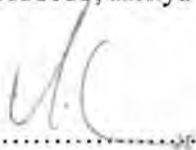
This thesis has been submitted for examination with our approval as University and institutional Supervisors.

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        Prof. Stephen G. Agong

        JKUAT, Kenya
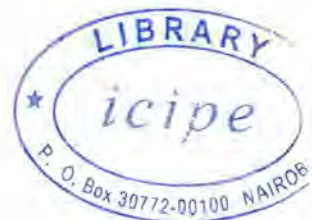
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        Dr. Markus Knapp

        ICIPE, Kenya

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# DEDICATION

This work is dedicated to my husband, our son Moses, my mother, sister, brother and my

aunt Charity, who have always inspired me to do my best.

## ACKNOWLEDGEMENT

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# LIST OF ABBREVIATIONS

AVRDC    Asian Vegetable Research and Development Centre

$BC_1$    First backcross generation

$BC_2$    Second backcross generation

FAO    Food and Agriculture Organization

$F_1$    First generation

$F_2$    Second generation

GTZ    German Development Cooperation

$H_0$    Null hypothesis

$H_A$    Alternative hypothesis

HCDA    Horticultural Crops Development Authority

ICIPE    International Center for Insect Physiology and Ecology

IPM    Integrated Pest Management

JICA    Japan International Cooperation Agency

JKUAT    Jomo Kenyatta University of Agriculture and Technology

MOA    Ministry of Agriculture

MOARD    Ministry of Agriculture Research and Development

SAS    Statistical Analysis Systems

# ABSTRACT

This study revealed that the mite resistance in *L. hirsutum* is heritable in *L. esculentum* and therefore can be utilized to improve tomato production by breeding mite resistant varieties. Glandular trichomes type IV may be responsible for high levels of resistance in accession LA 2204 to *T. evansi*. The study was to initiate inter-specific crosses between *Lycopersicon hirsutum* f *glabratum* C.H. Mull accession LA 2204 and the cultivated tomato *Lycopersicon esculentum* Mill. variety "Money Maker", and evaluate their resistance to tobacco spider mite *Tetranychus evansi* Baker and Pritchard. Screening studies carried out earlier revealed that accession LA2204 is resistant, while "Money Maker" is susceptible to mite damage. Trichome types that were identified on the abaxial and adaxial surfaces of both parent tomato plants and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations included types I, III, IV, V, VI and VII. Type II trichomes were completely absent on parents and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations. Type IV trichomes were absent on *L. esculentum* "Money Maker", while type V were absent on *L. hirsutum* accession LA 2204. The $F_1$, $F_2$, $BC_1$ and $BC_2$ generations possessed both type IV and V trichomes. Development from egg to adult and survival were significantly higher on "Money Maker" compared to LA 2204, and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations. Fecundity and longevity were significantly higher on "Money Maker" with average 57.9 eggs/mite and 13.1 days respectively compared to LA 2204, and the $F_1$, $F_2$, $BC_1$ and BC2 generations. Repellence studies revealed that leaves of accession LA 2204 and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations were more repellant to *T. evansi* than those of "Money Maker".

Shorter distances were covered on leaf surfaces in 20, 40 and 60 minutes respectively; and fewer mites attracted to accession LA 2204 and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations compared to "Money Maker" in thumbtack and slide bioassays. Greenhouse whole leaf bioassays showed that population densities of eggs/cm$^2$ and motiles/cm$^2$ leaf area were significantly higher on "Money Maker" than on $F_1$, $F_2$, $BC_1$ and $BC_2$ generations and accession LA 2204 eighteen days after infestation.

# CHAPTER ONE

## 1.0. INTRODUCTION

### 1.1. Background

Tomato, *Lycopersicon esculentum* Mill. is probably the most widely grown of all vegetables with annual world production of 114.51 million metric tonnes. Out of this, only about 10% is produced in Africa (FAO, 2003). Nevertheless, tomato holds a significant place in the ranking of vegetable crops in most of eastern and southern Africa, surpassed only by brassicas in some countries (GTZ, IPM Horticulture, 1994). It is a versatile vegetable for culinary purposes. Ripe tomato fruit is consumed fresh and is also used in cooking. In addition tomato is utilized in the manufacture of a range of processed products such as puree, paste, powder, ketchup, sauce, soup and canned whole fruits. Tomato contains vitamin A and C, potassium and lycopene the pigment that gives the fruit its red color a carotenoid that has an antioxidant property. Research has shown that tomatoes confer benefits against prostrate cancer, lung cancer and stomach cancer (Giovannucci, 1999).

In Kenya, tomatoes are usually grown in the field with limited production in the greenhouse and most of the tomatoes are for fresh market and processing (MOA, Kenya and JICA, 2000). However some varieties of tomatoes, such as cherry type, are now being grown for exports though their production is low (HCDA, 2002). Tomato is grown in all provinces with the highest production being from Central, Rift Valley and Nyanza provinces (MoARD, 2001).

Tomatoes are susceptible to a wide array of arthropod pests, particularly in tropical countries. The common ones according to Ministry of Agriculture, Kenya and JICA, (2000) and Varela *et al*, (2003) are; mites (*Tetranychus* spp.), African bollworms (*Helicoverpa armigera* Hübner), white flies (*Bemisia* spp.), leaf miners (*Liriomyza* spp), leaf hoppers (*Empoasca* spp.) and cutworms (*Agrotis* spp.).

Spider mites *(Tetranychus* spp) can become very destructive tomato pests when they find appropriate conditions for their development, such as high temperatures and low relative humidity. The intensive use of pesticides affects the populations of their natural enemies, often resulting in a significance increase in the spider mite populations. These mites feed on both sides of the leaves; their action reduces photosynthesis and also causes defoliation. Tomato yield and quality have been reported to reduce when 13% of plant leaflets are infested (Berlinger, 1986).

The tobacco spider mite *Tetranychus evansi* is a new pest in Kenya and was recorded for the first time at Mwea in 2001 (Knapp, 2002). It is a very invasive pest, and has a characteristic webbing pattern not common in other mite species (Knapp *et al.*, 2003). The mites cause white-silvery spots on tomato leaves that many farmers confuse for a tomato disease due to their small size. Control of mites with chemicals has not been easily achievable. The application of pesticides is not usually straightforward, for example the acaricide may not make direct contact with mites on the lower surfaces of leaves. It is known that pesticides may stimulate mite reproduction and populations may reach high levels of infestation (Meyer, 1996). The regular use of pesticides could lead to development of resistance, which will reduce choice of materials to be used for effective control of mites. New pests might also be induced or rare innocuous species may become abundant and very injurious.

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This may result when pesticides kill the natural enemies more effectively than the pest, hence permitting mites to breed uncontrolled (Meyer, 1996).

Spider mites are known to develop resistance to pesticides; this is especially true of economically important genera *Panonychus* and *Tetranychus*, to which many mite pests belong. Mites that are resistant to one acaricide are frequently cross-resistant to chemically related compounds and the pesticide industry is often under pressure to develop acaricides that are effective against resistant strains (Meyer, 1996).

A major difficulty in controlling an outbreak of spider mites is that they occur on the lower leaf surfaces where they are protected by webbing. Dense foliage and webbing hinders spray penetration. In practice, often less than 60% of the leaf surface is wetted after one spray application, whereas a minimum of 95% wetting is required for effective control (Meyer, 1996).

Mite resistance levels of current cultivars are not sufficiently high to permit a significant reduction in the amount of pesticides used in tomato production. Development of cultivars with increased levels of arthropod resistance would be an important component for integrated pest management (IPM) programs aimed at reducing the chemical sprays, leading to diminished environmental impact (Barbosa and Maluf, 1996). The incorporation of resistance to mites in commercial varieties would provide easy and economical protection (Gentile *et al.*, 1969). Small scale farmers in many parts of Africa utilize few external inputs in their food production practices, host plant resistance would therefore be appropriate as it comes as a package and needs little extra cost to make it work (Ampofo, 1995). Plant resistance should therefore be developed as a fundamental element of IPM (Kennedy and Farrar, 1987).

IPM methods used in tomatoes include; biological control, which involves conservation and importation of natural enemies (Meyer, 1996). *Phytoseiulus persimilis* Athias-Henriot has been used to effectively control *T. urticae* in greenhouse crops (Oomen, 1988). Mechanical control with help of screen houses has also been used (Meyer, 1996). Other methods include mixed cropping, plant breeding for increased genetic resistance, and pest avoidance by proper timing of planting and use of naturally occurring insecticides such as neem (Varela *et al.*, 2003).

There are three modes of resistance that can be utilized in breeding resistant crop cultivars. (1) Antibiosis, this is where plants contain unpalatable substances that reduce reproduction, survival, and can kill the pest. (2) Antixenosis is where plants contain substances that repel pests hence limiting the population build up. (3) Tolerance is where plants withstand pest damage and produce economic yield (Panda and Khush, 1995).

The genus *Lycopersicon* is characterized by great diversity within and among its nine species. Arthropod resistance has been associated with a diverse array of traits, including physical and chemical properties of glandular trichomes, constitutively expressed and wound induced chemical defenses associated with leaf lamellar exudates (Kennedy, 2003).

The wild tomato species: *Lycopersicon hirsutum* f. *glabratum* C.H. Mull., *Lycopersicon hirsutum* f. *hirsutum* Dunal, *Lycopersicon peruvianum* (L.) Mill. and *Lycopersicon pennellii* (Corr) D'Arcy are reported to be sources of resistance to many tomato pests (Gentile and Stoner, 1968; Rick, 1973; Kennedy and Yamamoto, 1979; Williams *et al.*, 1980; Ecole *et al.*, 1999).

However introgression of their arthropod resistance into the cultivated tomato is often limited by difficulty in maintaining the uniform infestations necessary to select for

resistance (Stevens and Rick, 1986). Direct selection for pest resistance is expensive and slow, but indirect selection techniques based on correlated traits with high heritability could be used to speed up introgression (Juvik *et al.*, 1982).

Amongst the most important resistance factors in tomato are trichomes that cover the leaves and stems of the plant. Luckwill (1943) and Reeves (1977) described several trichome types of *Lycopersicon* species. The resistance exhibited by wild *Lycopersicon* species has been attributed to trichomes, small-specialized hairs on the foliar surfaces of the plants. Glandular trichomes can operate by irritating, trapping, or poisoning arthropods and non-glandular trichomes can act as barrier to movement or to nutritional tissue (Simmons and Gurr, 2004). Some of the chemicals conferring toxicity in wild *Lycopersicon* taxa are; methyl ketones such as 2-tridecanone in *L. hirsutum* f. *glabratum* (Gonçalves *et al.*, 1998; Guo *et al.*, 1993; Weston *et al.*, 1989; Williams *et al.*, 1980); sequiterpenes in *L. hirsutum* f *hirsutum* (Eigenbrode *et al.*, 1994); acylsugars in *L. pennellii* (Goffreda *et al.*, 1989).

These compounds are found in glandular trichomes present on the leaf surfaces (Snyder and Carter, 1985; Carter *et al.*, 1989), and are often associated with moderately high or high heritability values (Maluf *et al.*, 1997). Allelochemical content could be useful clues to pest resistance (Juvik *et al.*, 1982). This has been demonstrated with 2-tridecanone or sesquiterpene (zingiberene) content and resistance to South American tomato pinworm *Tuta absoluta* Meyrick and spider mite repellency (Gonçalves *et al.*, 1998; Maluf *et al.*, 1997).

Resistance to several arthropods especially spider mites has been reported in wild tomato species including *L. hirsutum* f. *hirsutum*, *L. hirsutum* f. *glabratum*, *L. peruvianum* (L.) Mill and *L. pennellii* (Gentile *et al.*, 1969; Rick, 1973; Williams *et al.*, 1980) but these species do not have immediate commercial value.

Since *L. hirsutum* can easily be hybridized with cultivated tomato and presents a broad spectrum of arthropod resistance, it is ideally suited for breeding programs aimed at improving pest tolerance of tomato cultivars (Williams *et al.*, 1980; Zamir *et al.,* 1984; Kennedy and Farrar 1987). *L. hirsutum* is resistant to the red spider mite *Tetranychus urticae* Koch. (Weston *et al.*, 1989) as well as to other pest species such as green peach aphid, *Myzus persicae* Sulz. (Leite *et al.*, 1999); tomato pinworm *Keifera lycopersicella* Walshingham (Eigenbrode and Trumble, 1993); Colorado potato beetle *Leptinotarsa decemlineata* Say (Kennedy and Sorenson, 1985; Carter *et al.*, 1989) and corn ear worm *Helicoverpa zea* Boddie (Farrar and Kennedy, 1987).

The objective of this study was therefore to investigate whether tobacco spider mite (*T. evansi*) resistance in *L. hirsutum* accession LA2204 can be incorporated into the susceptible but widely cultivated tomato (*L. esculentum*) cultivar "Money Maker" through conventional backcross breeding.

The study was carried out at the International Centre of Insect Physiology and Ecology (ICIPE)-Nairobi and Jomo Kenyatta University of Agriculture and Technology (JKUAT) in Juja, Nairobi-Kenya.


## 1.2. Justification

Tomato is one of the most important vegetables in eastern and southern Africa yet yields are far below the crop's potential. Among the reasons for yield reduction is the large number of pests and diseases that attack this crop.

Pesticide-based methods for control of arthropod pests generally used in tomato production are time consuming, expensive and can have adverse effects on producers and the environment (Hond *et al.*, 2003).

Host-plant resistance could offer a better means of pest control, yet resistance exhibited by wild *Lycopersicon* spp., such as *L. hirsutum* and *L. pennellii*, is yet to be fully exploited as a source of resistance to many pest species (Simmons *et al.*, 2003). *T. evansi* is one of the most serious pests of tomatoes in southern Africa and semi-arid areas in eastern Africa. It has been reported to cause yield loss of up to 90% in smallholder production systems in Zimbabwe (Knapp *et al.*, 2003). Current control practices involve weekly application of highly toxic acaricides that result in pesticide contamination of the produce.

In addition, many acaricide treatments are inefficient due to poor application techniques and frequent treatments with same active ingredients increasing the risk of resistance development to the pesticides by the pests (Varela *et al.*, 2003). Moreover, acaricides do not target only pests but also kill natural enemies of pests. This could lead to uncontrolled pest population multiplication rate, new pests may be induced and rare innocuous species may become abundant and very injurious (Meyer, 1996).

The use of resistant plants will reduce pesticide usage and associated detrimental effects. Current levels of resistance in commercial tomatoes are not high enough to permit a significant decrease in the amount of acaricides applied (Maluf *et al.*, 2001). Small scale farmers in many parts of Africa utilize few external inputs in their food production practices, host plant resistance would therefore be reliable as it comes as a package with the seed and needs little extra cost to make it work (Ampofo, 1995).

## 1.3. Objectives of the study

### 1.3.1. Main objective

The main objective of the study was to develop $F_1$ hybrids from an inter-specific tomato cross (*L. esculentum* variety "Money Maker" x *L. hirsutum* accession LA 2204), and F2, BC1 and BC2 generations, and evaluate their resistance to tobacco spider mite (*T. evansi*).

### 1.3.2. Specific objectives

(i)     To determine trichome type and density on leaves of inter-specific generations ($F_1$, $F_2$, $BC_1$ and $BC_2$), and their parents, variety "Money Maker" and accession LA 2204.

(ii)    To determine the mite development, fecundity and longevity on inter-specific generations ($F_1$, $F_2$, $BC_1$ and $BC_2$) and their parents, variety "Money Maker" and accession LA 2204.

(iii)   To investigate mite repellency level on inter-specific generations ($F_1$, $F_2$, $BC_1$ and $BC_2$) and their parents, variety "Money Maker" and accession LA 2204.

(iv)    To determine mite population growth rate on inter-specific generations ($F_1$, $F_2$, $BC_1$ and $BC_2$), and their parents, variety "Money Maker" and accession LA 2204 under greenhouse conditions

## 1.4. Hypotheses

$H_0$  The inter-specific hybrids will be equally resistant to the tobacco spider

mite *T. evansi* as *L. hirsutum* accession LA2204.

$H_A$  The inter-specific hybrids will not be equally resistant to the tobacco spider

mite *T. evansi* as *L. hirsutum* accession LA2204.

# CHAPTER TWO
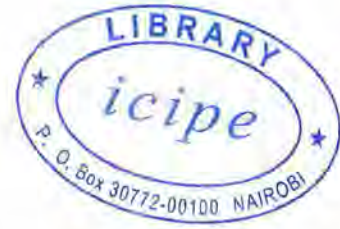
## 2.0. REVIEW OF LITERATURE

### 2.1. Tomato origin, taxonomy and botany

Tomato is believed to have originated from the Peru-Ecuador area due to the existence of greatest diversity in all the wild types of tomato in this region, but it was domesticated in Mexico. It is possible that the crop arrived in East Africa via Egypt or Sudan (Tindall, 1983). *L. esculentum* and to a lesser extent *Lycopersicon pimpinellifolium* Jusl., on account of their palatable fruits, have long been cultivated and are well distributed throughout the warmer parts of both South and North America and in tropics and sub-tropics. (Luckwill, 1943)

The commercial tomato belongs to the species *esculentum* in the genus *Lycopersicon*, the alternative names, *Solanum lycopersicon* L. or *Lycopersicon lycopersicon* (L.) Karsten have appeared in the literature. *Lycopersicon* is a relatively small genus within the extremely large and diverse family Solanaceae (Taylor, 1986).

Tomatoes are short-lived perennials cropped generally as annuals; both determinate and indeterminate cultivars have been developed. They are characteristically weak-stemmed plants, which form loose struggling bushes that grow up to 2m in height. All species are variably branched, and the auxiliary growth of the leaf immediately below each inflorescence is usually very strongly developed. All species are pubescent and the type and density of hairs present is one of the most valuable diagnostic characters for separation of species.

Tomato leaves are imparipinnate, the odd terminal leaflet usually being somewhat larger than the lateral leaflets, which are arranged, in two to six opposite pairs on the rachis. They are aromatic, the odors being due to oils secreted by special glandular hairs on the stems and leaves and sometimes fruits.

The inflorescence comprises of flower clusters that arise from internodes usually when the shoot has five to 10 leaves, morphologically it terminates the main growth. Flowers are lemon yellow to bright yellow in color (Luckwill, 1943).

The tomato fruit is botanically a berry. Fruit size varies from small cherry types with only two divisions of the ovary to large multi locular types. Fruit color can be green, yellow, orange, pink or red when ripe. The red color comes from the pigment lycopene, while orange and yellow colors come from beta-carotene pigments. Fresh market tomato shapes ranges from round to oblate, while processing tomatoes are more elongate or pear shaped (Peet, 2000). Tomato seeds are numerous, pear or kidney shaped. The size ranges from 1.5 mm – 5 mm in length. They are flat, hairy and vary in color from pale buff to brown (Pursglove, 1968).

### 2.1.1. Description of *Lycopersicon* species

*Lycopersicon esculentum* Mill. is villose especially towards the apex, glandular and strongly scented. The stem is first erect then decumbent. Leaves are large and more than 20 cm long, comprising of 7-9 leaflets that are ovate, acute to acuminate. (Plate 1a) Inflorescence is shorter than leaves with 3-20 flowers. Corolla is lemon yellow and up to 2.5 cm diameter. Fruits are densely villose and glandular when young becoming glabrous and shining when mature, red, yellow or pink when ripe (Plate 1b). Seeds are hairy pale buff in color and flat (Luckwill, 1943; Taylor, 1986).

*L. esculentum* is widely distributed all over the world due to its value as a crop. All its representatives are self compatible and inbreeding due to domestication, which has ensured progressive withdrawal of the stigma into the anther cone hence guaranteeing automatic self pollination (Rick, 1976).

**Plate 1a:** "Money Maker" plant six weeks after sowing

**Plate 1b:** "Money Maker" ripe fruit

*Lycopersicon hirsutum* Humb. and Bonpl. is bright green in color, densely large villose and glandular on all vegetative parts. Stems are stout, erect at first, later prostrate up to 1m long and woody towards the base. Leaves are ovate to oblong, up to 20 cm long and 16 cm broad. Leaflets are 7-9, bright green and hairy (Plate 2a). Inflorescence is forked monochasial thyme rarely simple, and 8-15 flowered with bright yellow corolla. Fruit is sub-spherical, laterally compressed, 2 cm diameter, finely mottled green and white, with an irregular streak of darker green down the centerline of each carpel (Plate 2b). Seeds are embedded in a bright green pulp, dark brown and glabrous except for a narrow apical wing (Luckwill, 1943). *L. hirsutum* consists of two sub species, *L. hirsutum* f. *hirsutum* Dunal and *L. hirsutum* f. *glabratum* C. H. Mull. *L. hirsutum* f. *hirsutum* has large showy flowers and strongly exerted stigma hence is an out breeder.

The majority of collections from this group have proven to be self incompatible and artificial self-fertilization lead to inbreeding depression (Martin, 1962). *L. hirsutum* f. *glabratum* has less showy flowers and can easily be self fertilized artificially without suffering inbreeding depression and easily hybridizes with *L. esculentum*.

It has been noted for resistance to several pests, hence is a suitable source of germplasm for pest resistance in cultivated tomato (Rick, 1973).



**Plate 2a:** LA2204 plant six weeks after sowing

**Plate 2b:** LA2204 ripe fruit

*Lycopersicon pennellii* (Corr.) D'Arcy is a green-fruited species, whose leaves are densely covered by glandular trichomes, found growing in hot dry areas of Peru. It consists of both self-compatible and self-incompatible types. It is readily crossable with *L. esculentum* and may prove to be a source of drought tolerance and insect resistance (Rick, 1960).

*Lycopersicon pimpinellifolium* (Jusl.), Mill. is a yellow/red fruited species typically encountered at low elevations in Peru. It is self-compatible and is the only wild species that naturally introgresses with *L. esculentum* (Rick, 1958). It has been utilized as a source of germplasm for resistance to fusarium wilts and bacterial speck (Bohn and Tucker, 1940; Pilowsky, 1982).

*Lycopersicon cheesmanii* Riley is an orange/red fruited species found only in the Galapagos Islands. All types are self compatible and exclusively inbreeding. This species easily hybridizes with *L. esculentum*, a number of genes have been transferred to the commercial tomato e.g. the jointless pedicel gene.

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It is not a source of pest and disease resistance genes because of its isolation but has salt tolerance genes (Rick, 1973).

*Lycopersicon parviflorum* Mill. is a green fruited species found in watershed regions of Peru. It is self compatible and highly self-pollinating. This species easily hybridizes with *L. esculentum* but little has been done to exploit its potential for high soluble solids and vitamin C content (Rick, 1973).

*Lycopersicon peruvianum* (L.) Mill. is a green fruited species found in Chile and Peru. It is the least thoroughly exploited wild tomato species due to severe barriers to interspecific hybridization with *L. esculentum* (Rick, 1973).

### 2.1.2. Description of interspecific hybrids

MacArthur and Chiasson (1947) emphasized de *L. hirsutum* x *L. esculentum* hybrids, because they might introduce valuable wild genes into the tomato. The $F_1$ hybrids are strongly *L. hirsutum* like with respect to the recessive mutant differences. They tend to be more nearly intermediate between parents in most of the normal specific and sub generic contrasts and dominance is often partial or lacking.

Such blending of characters is evident (Table 1) in various degrees in general habit of growth. The stem size and hairiness the development of pseudostipules and floral bracts and the shape, size and the number of leaflets. The flower size and shape and seed size, flatness and pubescence. The $F_1$ fruits are oblate 2-3 loculed, definitely smaller than intermediate, green in color and moderately or faintly stripped with purple, less leathery skinned than *L. hirsutum* and have tastes reminiscent of both species.

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The dried foliage has the "celery salt" odor of *L. hirsutum*. The $F_1$ hybrid fruit epidermis was reported to be pale yellow when that of *L. esculentum* parent is deep yellow, *L. hirsutum* being colorless. The $F_1$ hybrid is clear skinned when the *L. esculentum* parent is recessive clear skinned.

The hybrid fruit flesh is also nearly intermediate in degree of development of the two pigments from the red-fruited *L. esculentum* (lycopene and carotene) and the two from the green-fruited *L. hirsutum* (chlorophyll and anthocyanin). When the *L. esculentum* parent is tangerine fleshed, the $F_1$ hybrid is greenish yellow; when it is yellow, the hybrid is pale yellow or whitish with green around the seeds in the juice (Table 1) (MacArthur and Chiasson, 1947)

**Table 1: Species characters in *L. esculentum*, *L. hirsutum* and their F₁ hybrids**

| Character | *L. esculentum* | F₁ hybrids | *L. hirsutum* |
|---|---|---|---|
| Bracts and stipules | Absent | Present but not at every possible location | Present |
| Stem hairiness | Moderately hairy | Intermediate | Very hirsute |
| Leaf margins | Entire to lobed | *Hirsutum*-like | Many toothed, teeth entire or dentate |
| Fruit hairiness | Glabrous | Sparsely hirsute to glaborous when ripe | Very hirsute |
| Fruit markings | None | Purple midlocular stripe usually developed | Purple midlocular stripe |
| Fruit size (diameter) | 6-10 cm | About 2.5 cm | About 2 cm |
| Fruit flesh colors | Red | Ochraceous orange | Greenish white |
| | Tangerine | Primuline Yellow | Greenish white |
| | Yellow | Naples Yellow | Greenish white |
| Inflorescent | Simple, lemon yellow sparse flowers. | Intermediate | Forked monochasical cyme, crowded flowers |
| Seed size, shape and color | Light brown, kidney shaped and flat | Intermediate | Tiny, dark brown and glabrous |

Source: Modified from MacArthur and Chiasson, 1947 and Taylor, 1986

## 2.2. Reproductive biology in tomato

### 2.2.1. Floral Biology

Tomato produces bright yellow, hermaphrodite flowers with the pistil enveloped by a solid tube formed by stamens. This renders it an essentially self-pollinated crop with self pollination rates varying between 94 and 99%. However, some degree of natural cross-pollination does occur even though the flower is chasmogamous.

Floral anthesis starts very early in the morning around 6 a.m. and the flower continues opening until 11 a.m. The peak period of anther dehiscence is between 8 to 11 a.m. depending upon the initiation of sunshine, atmospheric temperature and humidity.

The pollen remains viable at temperatures ranging between 18°C to 25°C for 2 to 5 days. The stigma becomes receptive 16 to 18 hours before anthesis and retains the receptivity up to 6 days after anthesis, i.e., shortly before the flower withers (Kalloo, 1991)

### 2.2.2. Compatibility of *Lycopersicon* species

MacArthur and Chiasson (1947) made more than 1600 cross pollinations to intercross most of the species but did not include *L. cheesmanii* and varieties. Intra-subgeneric interspecific crosses between *L. esculentum* and *L. pimpinellifolium* were perfectly fertile. Hybrids from *L. peruvianum* as female and *L. glandulosum* as male produced viable seeds and vigorous hybrids were regularly obtained. Successful inter generic crosses between the green fruited and red fruited species have been reported between *L. esculentum* (female) and *L. hirsutum* (male); and *L. pimpinellifolium* (female) and *L. hirsutum* (male). Crosses between *L. esculentum* and *L. peruvianum* have been reported to be very difficult (Alexander *et al.*, 1942).

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On either red-fruited species *L. hirsutum* pollen produced viable seeds, which developed vigorous $F_1$ hybrids, but reverse pollination with *L. hirsutum* as female plant was incompatible, though one-way compatibility could not be assumed since *L. hirsutum* was female sterile with its own pollen under the prevailing conditions (MacArthur and Chiasson, 1947). Stevens and Rick (1986) also reported incompatibility when *L. hirsutum* was used as female with *L. esculentum* as male parent.

### 2.2.3. Hybrid sterility

The natural set of fruits was reported to be low both on plants isolated indoors, and those left to uncontrolled pollination outside. Making the diploid hybrids tetraploid did not restore, or even raise their fertility (MacArthur and Chiasson, 1947).

Germination ranged from 31-73% in the backcrosses with $F_1$ as males and *L. esculentum* as females, and from 50-90% in F2 samples tested, as compared with over 90% in *L. esculentum*. Collapsed seeds often greatly out number the filled ones, and a selective mortality may well affect segregation ratios in the F2 and backcross progenies. Many of the F2 plants were completely sterile, and plant fertility from the backcrosses ranged from nil to that of *L. esculentum* parent (MacArthur and Chiasson, 1947).

### 2.2.4. Transfer of economic attributes from wild species to commercial cultivars

Some notable examples of incorporation of resistance genes from wild species to true breeding cultivars are resistance to fusarium wilt, root knot nematodes and tomato mosaic virus (Bohn and Tucker, 1940; Pilowsky, 1982).

Recently resistance to tomato leaf curl virus was incorporated from *L. hirsutum* f. *glabratum* and *L. pimpinellifolium* into commercial cultivars (Kalloo and Banerjee, 1990). Resistance has been introgressed into cultivated tomato from *L. peruviannum* to *Verticilium dahliae* Reinke & Berhold (race 1); *Fusarium oxysporum* Snyder & Hansen (race 1); *Phytophthora infestans* Mont. (race T1) and Tomato mosaic virus (Saccardo *et al.*, 1981), and tolerance to *Alternaria solani* Ell. & Martin causing early blight has been introgressed from *L. hirsutum* f. *glabratum*. Resistance to *Septoria* spp. from *L. hirsutum* has been transferred to *L. esculentum* (Rick, 1979). The tomato variety H24 that is resistant to Tomato leaf curl virus was developed in Taiwan and the resistance was derived from an accession of *L. hirsutum* f. *glabratum* (AVRDC, 2002).

## 2.3. Tobacco spider mite (*Tetranychus evansi* Baker and Pritchard)

### 2.3.1. Origin

The tobacco spider mite, *T. evansi* belongs to family Acarina and genus Tetranychidae. It was first recorded as *T. marianae* McGregor from northeastern Brazil and Mauritius (Moutia, 1958) and later re-described as *T. evansi* (Baker and Pritchard 1960) from material collected in Mauritius It was reported from California in 1965, where it was found infesting nightshade, *Solanum* spp. In addition to nightshade, the mite was found on tomato, eggplant, *Artemisia douglasiana* Bess, *Nicotiana glauca* Graham, *Phacelia* spp, *Rosa* spp and lily of the valley vine *Salpichora rhomboidea* Miers (Oatman *et al.*, 1967). The species was known to exist in Mauritius, Texas and Brazil before it was discovered in California.

Recorded hosts were tomato, eggplant, peanut, nightshade, potato and sweet pepper (Baker and Pritchard, 1960; Moutia, 1958; Silva, 1954).

In Africa, the mite was first recorded in Zimbabwe in 1979 (Blair, 1983); and now exists in Zambia, Malawi, Namibia and Mozambique (Knapp and Luchen, 2000); South Africa (Meyer, 1996); Congo (Bonato, 1999); Morocco and Tunisia (Bolland *et al.*, 1998). In Kenya, the mite was recorded for the first time in May 2001 on tomato from Kirinyaga District (Knapp, 2002).

## 2.3.2. Life cycle

The life cycle of *T. evansi* is through five stages, the egg, larva, protonymph, deutonymph and adult (Plate 3). The first egg laid is deep orange, successive eggs are light orange and color fades with each additional egg until they turn colorless and transparent. As the embryo develops the egg becomes opaque, turning rusty red prior to hatching. The eggs are spherical, 0.12-0.14 mm in diameter with an incubation period of 2.5-3.5 days.

Newly emerged larvae are cream colored, six legged and turn greenish–yellow after starting to feed. They are 0.16-0.22 mm long and 0.15-0.18 mm wide, total larval period lasts 1.6-2.0 days. Feeding protonymphs are greenish-yellow; eight legged, 0.16-0.27 mm long and 0.13-0.19 mm wide. The total protonymph period lasts 1.6-1.9 days.

Feeding deutonymphs are greenish-yellow; eight legged, 0.28-0.37 mm long and 0.18-0.26 mm wide. The total deutonymph period is 2.1-2.8 days. The adult: adults have eight legs; the males are light orange, slender with long legs, 0.25-0.40 mm long and 0.15-0.24 mm wide.

The females are oval, orange red with an indistinct dark blotch on each side of the body; newly emerged females are 0.31-0.39 mm long and 0.19-0.28 mm wide, while ovipositing females are 0.41-0.49 mm long and 0.27-0.39 mm wide. This study was carried out at the temperature of 23.3±1 $^0$C and 40-50% relative humidity by Qureshi *et al.*, (1969).
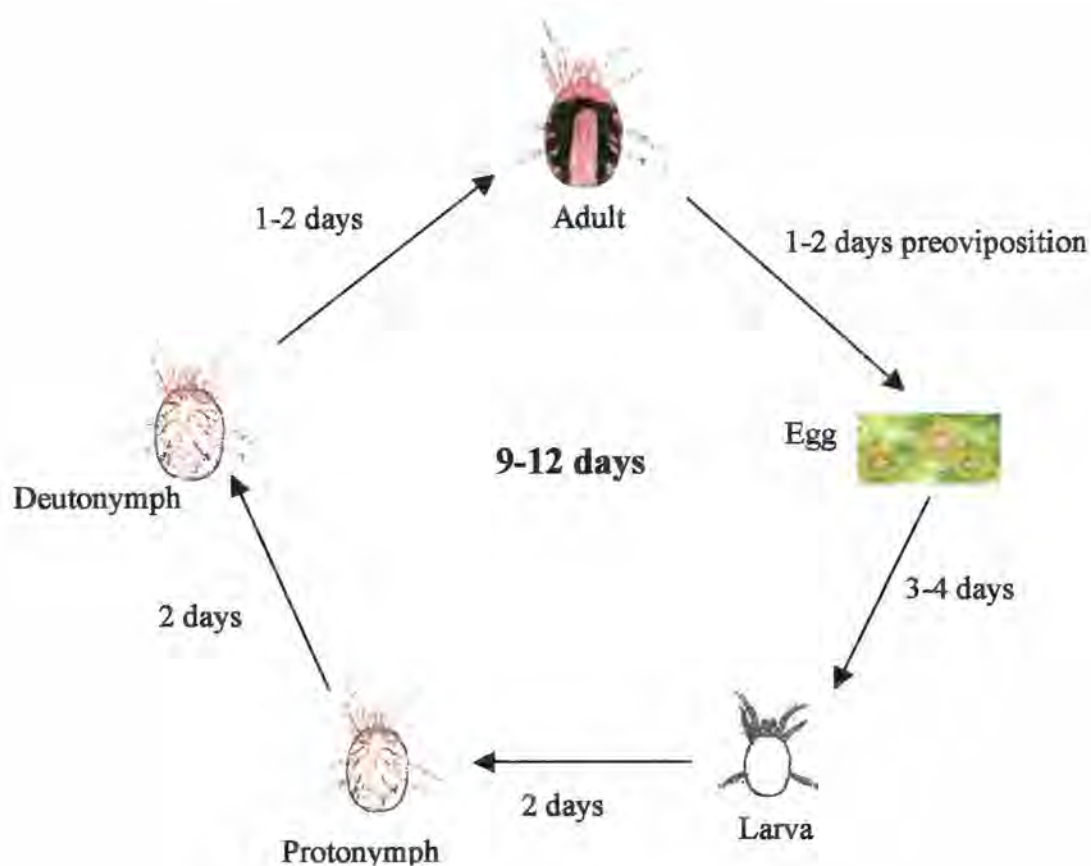


**Plate 3:** Life cycle of *T. evansi*
Source: Modified from Bonato, 1999

### 2.3.3. Biology

The tobacco spider mite *T. evansi* males do emerge earlier and keep watch over female deutonymphs; they copulate with them immediately after they emerge from the exuviae. Oviposition begins a day after emergence of females and they reach maximum egg laying capacity on the fourth day. Thereafter, the number of eggs laid per day reduces considerably with the female ovipositing daily until she dies. Individual mites may oviposit over 100 eggs during their lifespan (Meyer, 1996). Unfertilized females produce fewer eggs than fertilized ones and only males emerge from these eggs. However, unfertilized females tend to live longer than fertilized ones. The sex ratio tends to favor females, Moutia (1958) found a sex ratio of 1 male for every 3.3 females on tomato plants in the field, and Silva (1954) found a sex ratio 1 male for every 10 females. The lifecycle can be as short as 9-12 days, and reproduction continues throughout the year, resulting in 24-30 generations per year (Meyer, 1996; Qureshi *et al.*, 1969).

Field observations indicate that *T. evansi* prefers to oviposit on the lower, unexposed surface of the host leaf, although at high population eggs are laid also on the upper surface. The order of preference for oviposition site was; at the junctures of the main veins with the midrib; at the junctures of large veins and; at the inter-veinal areas. The fewest eggs are laid along the margins. Female mites prefer ovipositing on leaves with normal pubescence, than those with light pubescence, this helps to explain the mite preference for the lower leaf surface, which is more pubescent (Qureshi *et al.*, 1969).

### 2.3.4. Damage and dispersal

The tobacco spider mite, *T. evansi* feed by sucking sap from plants, they prefer the lower surface of leaves, but under severe attack, infestation will occur on both leaf surfaces as well as on stems and fruits. The damage first appears as stipples that later give the leaf a silvery or yellowish appearance (Plate 4a); as the population increases, the mites completely cover the plant with webbing (Plate 4b).

The leaves eventually turn entirely yellow or brown and die (Plate 4c). These mites can kill plants very rapidly. *T. evansi* has characteristic extensive webbing under high population not known to exist in other mite species in the genus *Tetranychus* (Knapp, 2002). The mites are spread by wind and the infestation often starts on the outside (border rows) of a plot. Therefore, other adjacent Solanaceae crops, wild plants and weeds can serve as sources of infestation. The mites can also be spread by irrigation water, dust storms, clothing and implements (Meyer, 1996).

**Plate 4a:** *T. evansi* yellow stipples
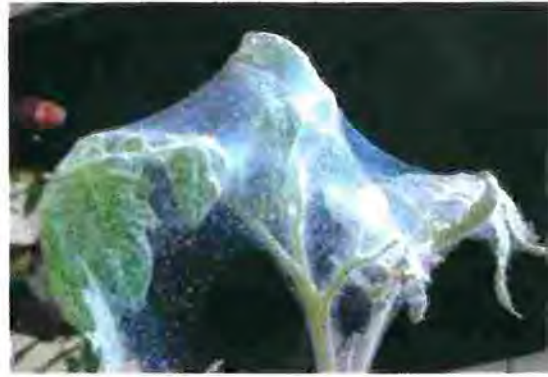


**Plate 4b:** *T. evansi* webbing



**Plate 4c:** *T. evansi* severe damage

Source: (Knapp, 2003)

### 2.3.5. Management of *T. evansi*

Mites can be controlled through biological control, cultural practices and chemical control. Biological control; in nature, there is usually balance between pests and their natural enemies. When natural enemies are not present, the balance is disturbed and the pest becomes a serious pest. In case of *T. evansi*, no suitable biological control agent is available yet in Africa since the mite was accidentally introduced to the continent recently (Meyer, 1996). Cultural practices are several techniques that are used to reduce mite populations.

Regular scouting of the crop to determine the presence of the pest and level of infestation, removal and burning of infested plants and separation of infected crops and newly planted crops help to minimize the problem. Dry hot conditions favor mite outbreak, therefore influencing the microclimate by reducing the planting distance and applying overhead irrigation has been said to repress mite populations. However, care should be taken as these can enhance fungal diseases. Water and nutrient stress should be avoided since this makes plants more susceptible to mite attack.

Chemical control so far is the major method of mite control. Care should be taken when considering chemical control and thorough understanding of different available chemical formulas and their cost-effectiveness is required. Some available pesticides have shown to increase mite reproduction. It is recommended to rotate acaricides with different chemical compositions. Spraying should be done weekly and at early stages of infestation to be effective. Care should be taken to ensure pesticides properly cover the entire plant. Farmers should use chemicals as a last resort and only if costs and risks involved do not out weigh benefits (Varela *et al.*, 2003).

## 2.4. Host plant selection

The host plant range of herbivorous arthropods is generally restricted to the small fraction of plant species that is available to them (Mitter, 1981). The host range of many herbivorous insects is determined by the oviposition preference of adult females for plants suitable to their progeny (Thompson, 1988).

The host plant range of the phytophagous spider mite *T. urticae* seems to be determined through different mechanisms, adult females reach potential host plants either by random walking or by passive wind dispersal (Kennedy and Smitley, 1985), though they readily escape from unfavorable ones (Fry, 1989)

The host plant range of *T. urticae* is determined through host plant acceptance, i.e. whether the adult female decides to settle on or leave the encountered host plant. The host plant suitability of *T. urticae* on different plant species can be expressed as the mean number of eggs produced by the females within five days. Positive correlation was reported between plant acceptance and fecundity in *T. urticae* (Yano *et al.*, 1998). The spider mite *T. urticae* has a broad range of host plants but it does not accept all plants at the same degree because of differences in nutritive and toxic constituents. Other factors, such as the induction of secondary metabolites, the morphology of the leaf surface and presence of natural enemies, also play an important role in plant acceptance. Boom *et al*, (2003) reported that acceptance of *T. urticae* varied among plants belonging to the families Fabaceae and Solanaceae families with the best accepted being tobacco and the worst accepted being sweet pepper.

## 2.5. Trichome types and description in *Lycopersicon* species

Amongst the most important resistance factors in tomato are trichomes. These are small-specialized hairs on the foliar surfaces of the plants that cover the leaves and stems of the plant. Luckwill (1943) and Reeves (1977) described several trichome types of *Lycopersicon* species. The resistance exhibited by wild *Lycopersicon* species has been attributed to trichomes that are either glandular i.e. possessing a small membraneous head containing toxins and/or adhesives, or non glandular.

Glandular trichomes can operate by irritating, trapping, or poisoning arthropods and non-glandular trichomes can act as barrier to movement or to nutritional tissue (Simmons and Gurr, 2004).

Trichomes are responsible for pubescence in *Lycopersicon* species, which is one of the most valuable diagnostic characters for separation of species.

According to Luckwill (1943), there are seven types of trichomes in the genus *Lycopersicon*, four of which are referred to as glandular, while three are non-glandular trichomes.

Type I: slender patent glandular hairs, 1.5-2.5 mm long, 6-10 celled, standing on a bulbous multicellular base of 4-5 cells, tip swollen in a small glandular vesicle (Fig 1a, b); Type II: similar to type I but shorter non glandular hairs, 0.2-1.0 mm long, 3-5 celled, standing on a 4-5 celled base, tip pointed lacking vesicle, under microscope walls appear punctuated; Type III: slender non glandular hairs, 0.4-1.0 long, 4-8 celled, standing on a large simple basal cell, tips pointed, walls not punctuated (Fig 1a); Type IV: similar to type III but shorter glandular hairs, 0.2-0.4 mm long with small vesicle at the tip (Fig 1b); Type V: short non glandular patent hairs, 0.1-0.3 mm long, 1-4 celled, often bend in the middle, tips pointed, walls punctuated, often densely packed, responsible for canescence shown by several species (Fig 1a); Type VI: glandular hairs, 0.1-0.5 mm long, standing on a large unicellular base, stalk of 1-2 cells, vesicle tip of 2-4 cells with diameter of 0.05-0.08 mm (Fig 1a, b); Type VII: glandular hairs, 0.05-0.1 mm long, standing on a single basal cell, an unicellular stalk, vesicle tip of 4-8 cells with diameter of 0.02-0.04 mm (Fig 1a).
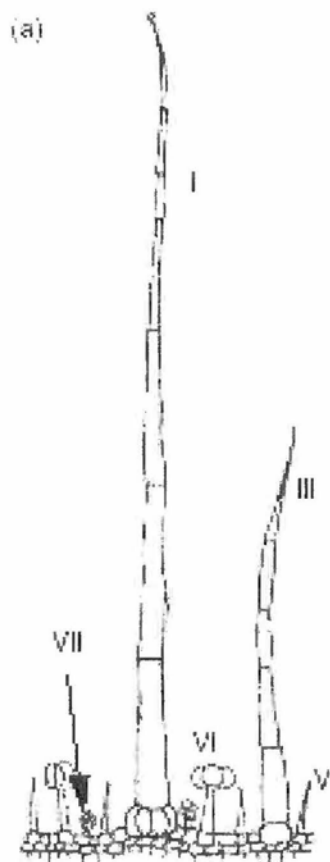
**Fig 1a:** Trichomes on *L. esculentum*

**Fig 1b:** Trichomes on *L. hirsutum*

Source: Simmons and Gurr (2005)

**Table 2: Trichome type and occurrence in *Lycopersicon* species**

| Species | Trichome types | | | | | | |
|---|---|---|---|---|---|---|---|
| | I | II | III | IV | V | VI | VII |
| *L. esculentum* | a | - | a | a | a | a | s |
| *L. pimpinellifolium* | - | v.s | - | - | a | a | - |
| *L. peruvianum* | a * | - | - | - | a | s | s |
| *L. pissisi* | - | v.s | - | - | a | a | s |
| *L. cheesmanii* | - | - | - | - | a | s | s |
| *L. hirsutum* | a | - | s | a | - | a | s |
| *L. glandulosum* | - | a | - | - | a | a | s |
| *L. pennelli* | v.s | - | v.s | a | - | s | v.s |

a- abundant (>5 mm$^2$), s- sparse (1-5 mm$^2$), v.s- very sparse (<1 mm$^2$),

*- absent from some individuals, - absent.
Source: (Luckwill, 1943)

### 2.5.1. Trichome based resistance of *Lycopersicon* species to arthropods

Glandular trichomes of *Lycopersicon* species are responsible for resistance to various insects (Gentile & Stoner, 1968; Gentile *et al.*, 1968; Dimock & Kennedy, 1983; Kennedy & Sorenson, 1985). Wild *Lycopersicon* spp are generally more resistant to arthropod pests than *L. esculentum*, although some *L. esculentum* cultivars have been shown to possess comparable resistance (Heinz and Zalom, 1995).

Several workers have reported resistance of *L. esculentum* and related species to the two spotted spider mite, *T. urticae*, and carmine spider mite, *T. cinnabarinus*. Stoner *et al*, (1968) and Gentile *et al*, (1969) found that resistance of *L. hirsutum* to these mite species was related to the densities of glandular trichomes.

Cantelo *et al*, (1974) reported that extracts of the glandular hairs of tomato are repellent to *T. urticae* and *T. cinnabarinus*. Aina *et al*, (1972) found that glandular exudates of the *L. hirsutum* accession of PI 251303 have acaricidal properties and are highly toxic to *T. urticae* when applied topically. Rasmy (1985) reported that two species of solanaceous plants, *L. hirsutum* f *glabrarum* and *Solanum sarachoides* Sendter were resistant to *T. urticae*. Leaves of both species have dense coverage of glandular trichomes and mites are quickly entrapped in their exudates. The leaf exudates of *L. hirsutum* f *glabratum* (PI134417) had an acaricidal effect at two levels tested. Research into trichome based host plant resistance has focused mainly on *L. hirsutum*, *L. hirsutum* f. *glabratum* and *L. pennellii*. The most studied aspect of trichomes on these species is their ability to confer antibiosis.

Removal of glandular exudates from *L. hirsutum*, *L. hirsutum* f. *glabratum*, *L. pennellii* and some accessions of *L. esculentum* was reported to have either increased survival, increased longevity, increased feeding, decreased mortality or decreased entrapment of the following pest species; *Manduca sexta* L., *K. lycopersicella*, *Phthorimaea operculella*, *H. armigera*, *Heliothis zea* Boddie, *Macrosiphum euphorbiae* Thomas, *Trialeurodes vaporiorium* Westwood., *Leptinotarsa decemlineata* Say and *Liriomyza trifolii* Burgess (Barbour *et al*., 1993; Dimock and Kennedy, 1983; Farrar and Kennedy, 1987; Gentile and Stoner, 1968; Gentile *et al*.,1968; Gurr and McGrath, 2002; Hawthorne *et al*., 1992; Kennedy and Sorenson, 1985; Lin and Trumble, 1986; Musetti and Neal, 1997; Simmons *et al*., 2003; 2004;).

Type IV trichomes on *L. hirsutum*, *L. hirsutum* f. *glabratum* and *L. pennellii* have been reported to be positively correlated with either entrapment, mortality, reduced adult emergence or decreased survival; and positively correlated with decreased survival of *H. armigera, S. exigua, P. opercullella, T. urticae* and *M. persicae* (Carter and Snyder, 1986; Eigenbrode and Trumble, 1993; Gurr and McGrath, 2002; Simmons *et al.*, 2003; 2004). Gurr and Mc Grath (2002) reported that type V trichome density is positively correlated with potato tuber moth, *Phthorimaea operculella* Zeller survival and development on abaxial leaf surfaces of five accessions of *L. hirsutum* f *glabratum*. This is similar to the trend observed for *Bemisia argentifolii* Perring and Bellows (Heinz and Zalom, 1995).

Type VI trichomes; are reported to be positively correlated with mortality of *P. operculella* in *L. hirsutum*, and negatively correlated with survival of *T. urticae* (Carter and Snyder, 1986; Gurr and McGrath, 2002).

The predominant trichomes associated with negative effects on pests (e.g. mortality, survival and entrapment) are the glandular trichomes types IV and VI. Correlation analysis has an advantage over exudates removal as the role of non-glandular trichomes in resistance can also be documented (Simmons and Gurr, 2005).

The chemical constituents of trichome exudates confer antibiosis; they have been reported to have antibiotic effects on *Helicoverpa zea* Boddie and *T. urticae* in *L. hirsutum* and *L. hirsutum* f *glabratum* (Aina *et al.*, 1972; Fery and Cuthbert, 1975); however the chemicals responsible were not identified. Research has subsequently established relationships between individual trichome types and the chemical component of their exudates. Two methyl ketones from type VI trichomes on *L. hisutum* f *glabratum*, 2-tridecanone and 2-undecanone are associated with numerous negative effects on several pests. 2-tridecanone was reported to cause mortality,

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increased time to pupation and decreased pupal weight of *Helicoverpa zea* Boddie. It has also been associated with increased mortality of *H. zea*, *Manduca sexta*, *Tuta absoluta* Meyrick, *Aphis gossypii* Glover and *Macrosiphum euphorbiae*; and is toxic and repellent to *T. urticae*.

2-undecanone has been reported to cause increased pupal deformity, pupal mortality and decreased pupal weight of *Heliothis zea*; and mortality of *T. absoluta* (Farrar and Kennedy, 1987; Fery and Kennedy, 1987; Leite *et al.*, 2001; Lundgren *et al.*, 1985; Musetti and Neal, 1997; Weston *et al.*, 1989; Williams *et al.*, 1980).

These two methyl ketones have been reported to be abundant in type VI trichomes of *L. hirsutum* f *glabratum*, but trace or absent in type VI trichomes of *L. esculentum* (Chatzivasileiadis *et al.*, 1999; Farrar and Kennedy, 1991; Kennedy, 2003).

Inheritance of high levels of 2 tridecanone is controlled by at least three independently assorting recessive genes (Fery and Kennedy, 1987). Zamir *et al.* (1984) found evidence that the gene for determinate growth habit has a pleiotropic effect for levels of 2 tridecanone. The introgression of high 2-tridecanone content into the cultivated tomato species *L. esculentum* could lead to improved insect tolerance of tomato cultivars (Barbosa and Maluf, 1996).

Zingiberene, a sesquiterpene found in the exudates of types IV and VI trichomes of *L. hirsutum* was reported to be toxic to *Leptinotarsa decemlineata*, repellent to *Tuta absoluta*, *Tetranychus urticae* and *Tetranychus evansi* (Carter *et al.*, 1989; Maluf *et al.*, 2001; Weston *et al.*, 1989). Another sesquiterpene, γ-elemene, is produced by type VI trichomes of *L. hirsutum* (Weston *et al.*, 1989), but is yet to be associated with resistance to arthropods. A range of unidentified sesquiterpenes produced by type VI trichomes may also play a role in resistance (Kennedy, 2003).

Patterson *et al*, (1975) found two unidentified sesquiterpenes in *L. hirsutum* PI 251303, with activity against *T. urticae*. The predominant toxins of *L. pennellii* are acylsugars, which are found in the exudates of type IV trichomes (Goffreda *et al.*, 1989; Hawthorne *et al.*, 1992). They have been reported to cause mortality of *M. euphorbiae*, *B. argentifolii* and *L. trifolii*; and are repellent to *Tetranychus evansi* (Goffreda *et al.*, 1989; Hawthorne *et al.*, 1992; Muigai *et al.*, 2002; Resende *et al.*, 2002). Two dominant genes control the presence of type IV trichomes; the presence of either results in the presence of type IV trichomes (Lemke and Mutschler, 1984).

Research on trichome based host plant resistance to arthropod pests has been done primarily to examine its suitability for use in pest control, should appropriate traits be transferred to *L. esculentum*. Snyder and Carter (1985), determined densities of types I, III, IV, V and VI trichomes on an $F_1$ *L. esculentum* x *L. hirsutum* and found that only densities of type III trichomes were greater on the hybrid than on the *L. esculentum* parent. They also reported that the type VI trichomes found on $F_1$ hybrids had a head morphology, lipid and phenol type and lipid content that was intermediate between the two parents. Carter and Snyder (1985) reported relationships between the densities of each trichome type and all other trichome types, leaflet surface and leaflet length for $F_2$ *L. esculentum* x *L. hirsutum* hybrids.

Densities and head morphology of the type VI trichomes on $F_1$ *L. esculentum* x *L. hirsutum* f. *glabratum* hybrids are also intermediate (Fery and Kennedy, 1987; Kauffman and Kennedy, 1989).

Although resistance exhibited by hybrids was not studied extensively, the small amount of literature available suggests that $F_1$ hybrids using *L. pennellii* as a wild parent may possess greater resistance to arthropods than the *L. esculentum* parent (Simmons and Gurr, 2005). Hawthorne *et al.* (1992) reported that the removal of

exudates from $F_1$ *L. esculentum* x *L. pennellii* progeny increased the number of punctures by *L. trifolii*. When *M. euphorbiae* were placed on leaflets of $F_1$ *L. esculentum* x *L. pennellii* progeny, the numbers of non-probing aphids on the $F_1$ were greater than the numbers on *L. esculentum*, and the same as on the *L. pennellii* parent. The time to first probe was also greater on the $F_1$ and the number of probes and time spent probing were reduced (Goffreda *et al.*, 1988). These authors also found that removal of exudates from the $F_1$ progeny, increased the number of probes, but the time to first probe, time spent probing and the average probe duration were unchanged.

The repellent effect reported by Goffreda *et al*, (1989) for *L. pennellii* may also be effective in $F_1$ *L. esculentum* x *L. pennellii* hybrids because $F_1$ progeny were infested with fewer *M. euphorbiae* than the *L. esculentum* parent, probably due to acylsugars in the exudates of type IV trichomes of $F_1$ hybrids (Goffreda *et al.*, 1990).

Simmons *et al*, (2005) reported high mortality and repellence of *M. persicae* on $F_1$ hybrids between *L. pennellii* x *L esculentum* and *L. cheesmanii* f. *minor* x *L. esculentum*, they attributed this to type IV trichomes inherited from the two wild parents.

$F_2$ genotypes of *L. esculentum* x *L. pennellii* were reported to have varied levels of acylsugars, and their repellence to *T. evansi* was positively correlated with the amount of the sugars (Resende *et al.*, 2002). Erb *et al*, (1993) reported that $F_1$ progeny produced by crossing *L. esculentum* x *L. cheessmanii* f. *minor* was highly resistant to *L. trifolii*. In a choice test, resistance of $F_1$ hybrids between *L. esculentum* x *L. cheessmanii* f. *minor* was similar to *L. pennellii*, *L. hirsutum* and *L. hirsutum* f. *glabratum*. These authors also reported that the removal of exudates decreased resistance, suggesting that glandular trichomes played a role.

Little research has been conducted on *L. esculentum* x *L. hirsutum* hybrids to determine the extent to which resistance is inherited. Carter and Snyder (1985) reported that the survival and fecundity of *T. urticae* on $F_2$ *L. esculentum* x *L. hirsutum* progeny was related to densities of types I, III, IV and VI trichomes and mortality was related to densities of type IV and VI trichomes. Maluf *et al*, (2001) reported that F2 genotypes of *L. esculentum* x *L. hirsutum* f *hirsutum* and a $BC_1$ to *L. esculentum* had varied levels of zingiberene inherited from the wild parent; it was positively correlated with *T. evansi* repellence. They also reported that type IV trichomes are the repositories of zingiberene since its amount increased with increase in density of these trichomes.

# CHAPTER THREE

## 3.0. MATERIALS AND METHODS

The experiments were carried out under greenhouse conditions at ICIPE on wooden benches measuring 2.0m long by 0.9m wide by 0.6m high. Each bench held twelve pots measuring 18 cm x 20 cm with 13 cm base diameter.

## 3.1. Establishment of parent plants

Seeds for the mite susceptible *L. esculentum* variety "Money Maker" were sourced from East Africa Seed Company, while those of the mite resistant *L. hirsutum* f *glabratum* accession LA 2204 where provided to ICIPE by the World Vegetable Center (AVRDC), Taiwan. Accession LA 2204 was used as the male parent, while "Money Maker" as the recurrent female plant. The morphological characteristics of the parent plants are as described in (Table 3). The planting media was prepared from soil, manure and sand in the ratio of 3:2:1 (v/v). Seedling trays used to raise seedlings had eighty holes each measuring 3 cm diameter and 5 cm depth. Two trays were used in this experiment. Plastic planting pots were measuring 18 cm x 20 cm with 13 cm base diameter and approximately 3 kg capacity. The pots had two holes of 5 mm diameter at the bottom to allow water drainage. The ratio of male to female plants was 1:2, and male plants were always established four weeks in advance so as to produce sufficient pollen.

Moist planting media was uniformly filled into seedling trays and 20 seeds each of accession LA 2204 and "Money Maker" were sown in individual holes and labelled. The seeds were watered moderately on daily basis to keep the soil moist. Seedlings were transplanted three weeks after sowing into pots.

Planting pots were filled with the planting media mixed with 3g of fertiliser Diammonium Phosphate per pot. A space of 2.5 cm was left from the soil level to allow for effective watering. The plants were watered moderately on daily basis to keep the soil moist. The plants were top dressed with 3g of Calcium Ammonium Nitrate (CAN, 26% N) two weeks after transplanting and again during the flowering stage. Weeds were uprooted as soon as they germinated. The pests that affected plants were the russet mites (*Aculops* spp), white flies (*Bemisia* spp); they were controlled using Dynamec (abamectin). The diseases were late blight caused by *Phytophthora infestans* Mont de bury and powdery mildew caused by *Erysiphe* spp; they were controlled using Benlate (Benomyl).

**Table 3: Characters of "Money Maker" and LA 2204**

| Character | "Money Maker" | LA 2204 |
|---|---|---|
| Stem hairiness | Moderately hairy | Very hirsute |
| Leaf margins | Entire to lobed | Many toothed, teeth entire or dentate |
| Fruit hairiness | Glabrous | Very hirsute |
| Fruit markings | None | Purple midlocular stripe |
| Fruit size (diameter) | 6-10 cm | About 2 cm |
| Fruit flesh colors | Red | Greenish white |
| Inflorescence | Simple, lemon yellow sparse flowers | Forked, monochasical cyme, crowded flowers |
| Seed size, shape and color | Light brown, kidney shaped and flat | Tiny, dark brown and glabrous |

## 3.2. Establishment of F₁ hybrid seed

Two healthy plants of accession LA 2204 were selected for pollen harvesting, while six uniform healthy plants of "Money Maker" were selected for pollination. All plants were properly labeled. Pollen from each of the male plants was used to pollinate three female plants.

### 3.2.1. Pollen collection

Mature flowers were collected from the two male plants separately to extract pollen during early morning hours before pollen was shed. The anther cones were removed, collected in envelopes and sun dried for 1-2 days.

The dried anther cones were put in a plastic cup with a fine mesh screen (200-300 mesh) and then sealed with a similar tight-fitting cup serving as a lid. The cup was shaken 10-20 times so that pollen was collected in the 'lid cup', after which it was transferred into a small convenient-to-handle container for pollination.

### 3.2.2. Emasculation

Emasculation is a process that involves removal of stamens from flower buds of the female line before they shed their pollen. This began about 45-55 days after sowing of the female parent plants "Money Maker". The flowers from the second cluster, which were expected to open within 2-3 days, were chosen for emasculation. The petals were slightly out of the flower bud but not opened. The corolla color was slightly yellow or even paler. Flowers from the first cluster were removed. Sharp pointed forceps dipped in 95% alcohol were used to split open the anther cones and remove them leaving the calyx, corolla and pistil. A few sepals were trimmed for easy identification of the hybrid fruits at the time of harvest.

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### 3.2.3. Pollination

The pollen from the two separate male plants was used to pollinate each three plants of "Money Maker". Flowers were artificially pollinated 2-3 days after emasculation, when the corolla turned bright yellow, signalling that the stigma is ready for pollination. Pollination was by touching the stigma with the tip of the index finger dipped in the pollen pool. Pollination process was done three times weekly over a 3-4 week period. Successful pollinations were easily seen within 4-5 days by the enlargement of the fruit. The second to fourth flower clusters were pollinated systematically as they became ready.

Four first flowers were pollinated from each cluster. All non-crossed flowers on the female plants were removed to lessen the chance of contamination from selfed seeds before harvest.

### 3.2.4. Fruit harvesting and seed extraction

The fruits were harvested separately from individual female plants, and put in nylon bags when fully ripe. The fruits were crushed to form a gel mass i.e. a mixture of pulp and seed and kept at room temperature for two days. Then, the mixture was placed into a clean fine mesh bag and washed thoroughly to remove the pulp. The seeds were suspended in the fine mesh bag to drain all the water and then sun-dried on a flat tray for 2-3 days.

### 3.3. Establishment of $BC_1$, $BC_2$ and F2 generations seed

The $F_1$ hybrid seed produced following the above procedures was used to establish $F_1$ hybrid male plants. The same procedures as in section (3.1) for establishment of male plants were followed after sowing to pollen harvesting with $F_1$ as the male plants.

The female plants "Money Maker" were established and managed following the same procedures as in section (3.1) after sowing to fruit harvesting and seed extraction. The $BC_1$ generation seed was established with the $F_1$ hybrid as the male parent and "Money Maker" as the female plant. Two $F_1$ hybrid plants were used to pollinate each three plants of "Money Maker".

The $BC_2$ generation seed was established with the $BC_1$ generation as the male parent and "Money Maker" as the female plant. Two $BC_1$ generation plants were used to pollinate each three plants of "Money Maker".

The $BC_1$ generation seed produced following the above procedures was used to establish $BC_1$ generation male plants. The same procedures as in section (3.1) for establishment of male plants were followed. The female plants "Money Maker" were established and managed following the procedures as in section (3.1). $F_1$ hybrid seed was used to establish six $F_1$ plants that were allowed to self and produce $F_2$ generation seed.

### 3.4. Mite rearing

The mite species used was *Tetranychus evansi*. The colony was maintained at the ICIPE rearing room and laboratory since 2001, when the species was first found attacking tomatoes in Kirinyaga District, Central Province. The mites were reared under controlled conditions of $25°$ C and a relative humidity of 50-70%, 12 hours light and 12 hours dark on "Money Maker" and "Cal J" tomato plants. The mites were supplied with fresh plants that were at least five to ten weeks old after sowing after every 3-5 days. Depleted plants appear silvery, extensively covered with mite webbing and mites aggregate at top portions of the plant in readiness to migrate.

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### 3.5. Data collection

### 3.5.1. Plant materials

The seeds of accession LA 2204, variety "Money Maker", $F_1$ hybrid, $BC_1$, $BC_2$ and $F_2$ generations were sown and transplanted as described above (3.1) to establish the respective plants. Ten healthy seedlings each for accession LA 2204, "Money Maker", $F_1$ hybrid, $BC_1$, $BC_2$ and $F_2$ generations were transplanted two weeks after sowing when seedlings were between 5-8 cm in height.

The plants were placed randomly on green house benches measuring 2.0 m x 0.9 m x 0.6 m, each bench held twelve plants. No pesticides were sprayed to the plants so as not to interfere with bioassays. Leaves at seven weeks after sowing were sufficiently expanded for mite bioassays in the laboratory.

Leaflets were randomly plucked from the ten plants each for accession LA 2204, "Money Maker", $F_1$ hybrid, $BC_1$, $BC_2$ and $F_2$ generations, on the 3-5th leaves from bottom of the plant. They were placed in labelled paper bags measuring 25 x 12 x 8 cm and taken to the laboratory for bioassay studies.

### 3.5.2. Trichome type and density

Six leaflets were randomly plucked from six plants selected randomly from the ten plants each for accession LA 2204, "Money Maker", $F_1$ hybrid. $BC_1$, $BC_2$ and $F_2$ generations and brought to the laboratory. In the laboratory, the leaflet petioles were immersed in water held on a petri dish to prevent rapid wilting.

The number and type of trichomes on the leaflets was counted with the aid of a dissecting microscope fitted with a square grid at magnification x32.

Fifteen squares each having an area of 0.11 mm$^2$ were randomly selected on each of the six leaflets, trichomes identified, counted according to each type on both abaxial and adaxial surfaces, and density calculated per mm$^2$.

### 3.5.3. Development time from egg to adult of *Tetranychus evansi*

Twenty leaflets were randomly plucked from the ten plants each of accession LA 2204, "Money Maker", $F_1$, $BC_1$, $BC_2$ and $F_2$, on the 3-5$^{th}$ leaves from bottom of the plant. They were placed in labelled paper bags and taken to the laboratory for mite development studies.

Small Petri dishes (55 mm diameter) were stuffed half with cotton wool and moistened by adding water. Twenty leaf discs with a diameter of 25 mm each from the selected lines were prepared using a leaf disc cutter. The leaf discs were placed in individual Petri dishes with the abaxial surface facing up (Plate 5).

Twenty female mites were taken from the colony using a camel hairbrush, put on leaflet for each tomato line separately and left for 2 hours to allow egg laying. Afterwards, one egg was transferred to each respective leaf disc using a camel hairbrush. Petri dishes containing leaf discs were then placed in open rectangular plastic dishes (32 × 22 ×6 cm) with wire gauze, each dish held 17-20 petri dishes. The leaf discs were checked every 24 hours with the aid of a dissecting microscope and development time from egg to larva, protonymph, deutonymph and adult, as well as adult survival and sex noted.

The cotton wool was kept wet by adding clean water to restrict mites on the leaf and keep the leaf discs fresh. Leaf discs were changed after every four days to provide fresh leaves for mites to feed on.

The rectangular plastic dishes containing the petri dishes with bioassays were placed in an incubator set at 25°C and 50-70% relative humidity.

The above experiment was repeated four times in a complete randomised design each time representing a set, hence four sets, and each set was carried out using new plants.
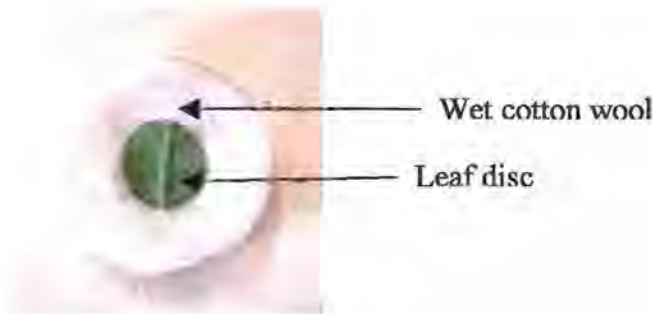


**Plate 5:** Leaf disc preparation

### 3.5.4. Fecundity and longevity of *Tetranychus evansi*

Twenty leaflets were randomly plucked from the ten plants each of all lines and as described above and taken to the laboratory for mite development studies.

Leaf discs were prepared and put into Petri dishes with cotton wool as described above. One female deutonymph and two males isolated from the colony using a camel hairbrush were placed on each leaf disc. The Petri dishes were placed in rectangular dishes then put in the incubator set at 25°C and 50-70% relative humidity. Males were removed 24 hours after the female had emerged. The number of eggs was counted after every 48 hours until the mite died, noting whether it died on the leaf disc or outside.

The cotton wool was kept wet and leaf discs changed every four days. The above experiment was repeated four times in a completely randomised design each time representing a set, hence four sets, and each set was carried out using new plants.

### 3.5.5. Repellence choice test

Two methods were used to determine mite repellence in "Money Maker", accession LA 2204, and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations.

### 3.5.5.1. Thumbtack bioassay method

This was set according to the procedures described by Weston and Snyder (1990). Six leaflets of similar size were randomly plucked from six plants randomly selected from the ten plants each for accession LA 2204, "Money Maker", $F_1$ hybrid, $BC_1$, $BC_2$ and $F_2$ generations and brought to the laboratory as described above One leaflet each of the parent plants and all crosses was attached to a sheet of Styrofoam with a metallic thumbtack (9 mm in diameter) placed in the centre of its abaxial surface (Plate 6). The leaflets were randomly placed on the Styrofoam sheet, and comprised one replication. Altogether six replications were used. Ten female mites from the colony were transferred with a camel hairbrush to the head of each thumbtack. The trial was carried out on a laboratory bench with estimated average temperature of $23^\circ$C.

Distances travelled by each mite onto the leaf surface were measured as the shortest distance between the mite and the thumbtack edge, and were recorded after 20, 40 and 60 minutes, respectively. Mites that stayed on the thumbtack were considered to have travelled a distance equal to zero.

Plate 6: Thumbtack bioassay

### 3.5.5.2. The slide method

Rectangular glass slides measuring 7.0 cm by 1.5 cm were prepared; a permanent marker pen was used to draw a line across the slide 1.0 cm from both edges of the slides, and to mark the centre of the slide i.e. 3.5 cm from both edges. The slides were dried and placed on a wet thin layer of cotton wool in a flat tray. Six leaflets of similar size were randomly plucked from six plants randomly selected from the ten plants of each line and brought to laboratory as described above. Twenty rectangular leaf portions measuring 1.5 cm by 1.0 cm were prepared excluding the midrib for accession LA 2204, "Money Maker", $F_1$ hybrid, $BC_1$, $BC_2$ and $F_2$ generations, two plant types were compared at a time for all the six types. The leaf portions for the two plant types to be compared were placed each at the opposite 1.5 x 1.0 cm marked portions at the slide edges (Plate 7). Twenty replications were used for each set of two plant types that were compared. Ten female mites from the colony were transferred with a camel hairbrush to the centre of the slide.

The set up was left to stand for 40 minutes, after which the number of mites settled on each leaf portion was recorded. Mites that remained on the slide or drowned were not included in the data analysis.

Wet cotton wool

Glass slide

Leaf portion
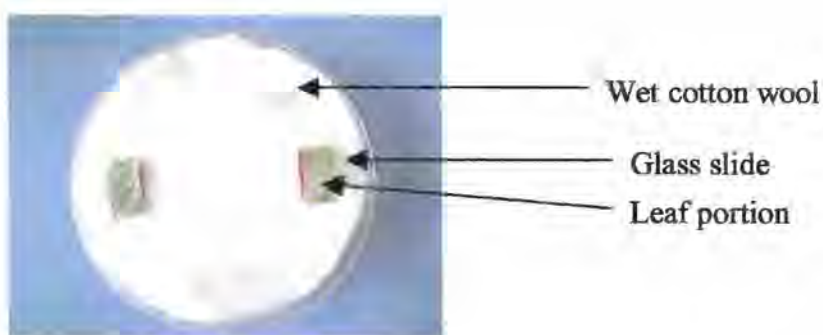
**Plate** 7: Slide bioassay

### 3.5.6. Greenhouse screening

Twenty seeds each of accession LA 2204, "Money Maker", and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations were sown in the greenhouse at ICIPE, following seedlings establishment procedures described in section (3.1). The seedlings were transplanted and managed following same procedures as in section (3.1).

Ten healthy plants each of accession LA 2204, "Money Maker", and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations were selected seven weeks after sowing and taken to JKUAT screen house where they were arranged in a complete randomised design on benches (3.0m x 1.2m x 0.6m). The leaves to be infested were randomly selected between $3^{rd}$ and $5^{th}$ leaf from the bottom. Cotton wool strings with insect glue on upper surfaces were tied around the petioles of selected leaves to prevent movement of mites (Plate 8). Ten female mites that were two days old were sourced from the colony. They were placed on each of the upper surfaces of isolated leaves using a camel hairbrush. 18 days after infestation, the leaves with mites were harvested into individual brown paper bags (25 x 12 x 8 cm) and placed in a cool box. The number of eggs and motile stages were counted with the aid of dissecting microscope. The leaf area of each harvested leaf was determined using a leaf area meter (Model LI-3100).

The density of eggs and motiles per cm$^2$ was then calculated by averaging number off eggs and motiles on each of the leaves with the respective leaf area. The average greenhouse temperature was 23$^{\circ}$C and average relative humidity was 68%.
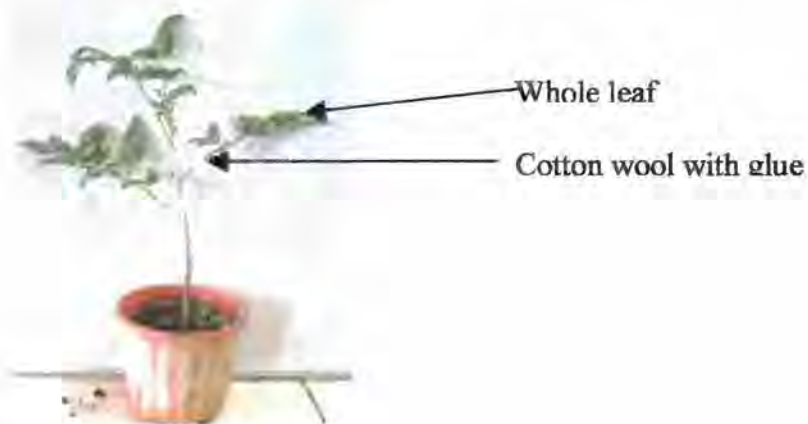


**Plate 8:** Whole leaf bioassay

## 3.6. Data analysis

Analysis of variance (ANOVA) was done using the General linear model (GLM) procedure analysis of SAS (2001). Means were separated with separation of means test following the procedures of Tukey's Studentized Range (HSD) Test. Means and standard errors on slide bioassay were calculated using SAS procedure Proc t-test.

Multiple regression and correlation analyses were out to establish the relationship between trichome types and mite behavior using SAS procedures Proc REG and Proc CORR.

# CHAPTER FOUR

## 4.0. RESULTS

### 4.1. Establishment of parents, and their $F_1$, $F_2$, $BC_1$ and $BC_2$ generations.

The parent plants *L. esculentum* "Money Maker" and *L. hirsutum* f *glabratum* accession LA 2204 produced flowers 10 weeks and 12 weeks after sowing, respectively. The cross breeding process commenced as soon as the flowers were ready for pollination, fruit set in successful crosses was visible 5-7 days after pollination. The first fruits matured in 55-65 days after pollination. A total of 48 flowers were cross pollinated on four plants of the female line "Money Maker" with accession LA 2204 as the pollen donor, out of which only 29 flowers successfully formed fruits. The whole period after sowing of female plants to production of mature ripe fruits lasted approximately four months. In crosses between $F_1$ hybrid plants as male parent and "Money Maker" as female parent, 32 flowers successfully produced fruits out of the 48 flowers that were pollinated. This lasted approximately four months after sowing of the female parents to the production of $BC_1$ seed. In crosses between $BC_1$ generation plants as male parent and "Money Maker" as the female parent, 39 flowers successfully produced fruits out of the 48 flowers that were cross pollinated. It took about four months after sowing of the female parent to the production $BC_2$ seed. Selfed $F_1$ hybrid plants produced $F_2$ seed approximately five months after sowing of the $F_1$ seed.

## 4.2. Description of parents, and their $F_1$, $F_2$, $BC_1$ and $BC_2$ generations.

*Lycopersicon hirsutum* accession LA 2204 and "Money Maker" had the stem, leaf, inflorescence, fruit and seed characteristics as described in Table 4.

The $F_1$ generation plants had stems, leaves, inflorescences, fruits and seeds that were morphologically more similar to accession LA 2204 than "Money Maker" (Table 4, Plate 9a, b). The $F_2$ generation plants had stems, leaves, inflorescences, fruits and seeds that were morphologically more similar to accession LA 2204 than "Money Maker" (Table 4, Plate 10a, b). The $BC_1$ generation plants had stems, leaves, inflorescences, fruits and seeds that were morphologically more similar to "Money Maker" than accession LA 2204 (Table 4, (Plate 11a, b). The $BC_2$ generation plants had stems, leaves, inflorescences, fruits and seeds that were morphologically more similar to "Money Maker" than accession LA 2204 (Table 4, Plate 12a, b).

**Table 4: Morphological characteristics of LA 2204, "Money Maker" and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations**

| Tomato line | Stem | Leaf | Inflorescence | Fruit | Seed |
|---|---|---|---|---|---|
| LA 2204 | Weak, more than 2 m height. | Bright green, many toothed, teeth entire or dentate margins | Forked monochasical cyme, bright yellow crowded flowers. | Green, less than 2 cm diameter, hairy, bilocular, dark green stripe. | Tiny, dark brown and glabrous |
| Money Maker | Strong, less than 2 m height | Dark green, entire to lobed margins | Simple, lemon yellow sparse flowers. | Red, more than 4 cm diameter, smooth, shiny and multilocular. | Light brown, kidney shaped and flat. |
| $F_1$ | Slightly weak, more than 2 m height. Vigorous | Bright green, narrow serrated margins, hairy. | Compound, bright yellow less crowded flowers. | Yellow/orange, 1.5-2 cm diameter, hairy, bilocular. | Tiny, brown and glabrous. |
| $F_2$ | Weak, more than 2 m height. | Bright green, narrow serrated margins, hairy. | Compound, bright yellow less crowded flowers. | Green/yellow, less than 2 cm diameter, hairy, bilocular, dark green stripe. | Tiny, dark brown and glabrous |
| $BC_1$ | Slightly strong, more than 2 m height. | Bright green, entire to lobed margins | Simple, lemon yellow sparse flowers. | Red, more than 2 cm diameter, smooth, shiny and 2-3 locules. | Tiny, light brown and glabrous |
| $BC_2$ | Strong, more than 2 m height | Green, entire to lobed margins | Simple, lemon yellow sparse flowers. | Red, more than 2 cm diameter, smooth, shiny and 2-3 locules. | Tiny, light brown and glabrous |

**Plate 9a:** $F_1$ plant six weeks after sowing



**Plate 9b:** $F_1$ ripe fruit



**Plate 10a:** $F_2$ plant six weeks after sowing



**Plate 10b:** $F_2$ ripe fruit

**Plate 11a:** BC$_1$ plant six weeks after sowing



**Plate 11b:** BC$_1$ ripe fruit



**Plate 11a:** BC$_2$ plant six weeks after sowing



**Plate 11b:** BC$_2$ ripe fruit

**4.3. General performance of parent plants, and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations**

Accession LA 2204 took longer to flower compared variety "Money Maker". The inflorescence comprised of 16 to 20 flowers with the first flower appearing ten weeks after sowing and the plant is perennial. Fruit set was not observed under natural conditions. This may be attributed to the fact that stigmas protrude through the anther cone. Seed germination was poor took five to seven days longer compared to "Money Maker", and less than 70% of the seeds germinated.

"Money Maker" germinated within seven days, and over 90% germination was observed, this variety was vigorous, produced inflorescences and fruits under prevailing conditions. The first inflorescence was noticed seven to eight weeks after sowing, and each cluster comprised of seven to nine flowers out of which only five to seven set fruit. Initial fruit set was ten weeks after sowing while the last fruit set was approximately eighteen weeks after sowing. In this tomato line flower stigmas do not protrude through the anther cones as in the case of *L. hirsutum*. The hybrid fruit produced with this variety as the female and accession LA 2204 as the male was similar to that of the female plant; produced many seeds though a small portion of less than 5% were immature or shrunken at time of extraction.

Seeds of $F_1$ germinated within seven days, and over 90% germination was observed. They were vigorous in growth compared to their parent plants; were uniform in appearance and produced flowers rapidly under prevailing conditions.

The first inflorescence was noticed eight weeks after sowing, each inflorescence comprised seven to nine flowers, though the first and in some cases the second inflorescence failed to set fruit; and fruit set in subsequent inflorescences was inconsistent under natural pollination. When artificially pollinated with pollen from other $F_1$ sibs, all flowers including those on the first inflorescence set fruit uniformly. The plants were perennial in nature.

Seeds of $F_2$ took more than seven days to germinate and less than 70% of seeds germinated. The first inflorescence appeared ten weeks after sowing, each inflorescence consisted of 14 to 16 flowers, and the plants were perennial. The plants produced flowers rapidly under cool conditions, but failed under dry hot conditions. These plants failed to set fruit under natural conditions, few fruits were produced under artificial pollination in some plants while other plants failed to set fruit completely.

Seeds of $BC_1$ germinated within seven days, and over 90% germination was observed. The plants were vigorous in growth, uniform in appearance and, produced flowers rapidly under prevailing conditions. The first inflorescence appeared after eight weeks after sowing; each inflorescence consisted of seven to nine flowers, while the last inflorescence appeared 20 weeks after sowing. Fruit set occurred under natural conditions beginning from the first inflorescence, though not uniformly as some flowers failed to produce fruits in some plants.

Seeds of $BC_2$ germinated within seven days, and over 90% germination was observed. The plants were vigorous in growth, uniform in appearance and produced flowers rapidly under prevailing conditions.

The first inflorescence appeared eight weeks after sowing; each inflorescence consisted of seven to nine flowers, while the last inflorescence appeared 18 to 20 weeks after sowing. Fruit set occurred uniformly under natural conditions beginning from the first inflorescence, with four to seven fruits per inflorescence.

### 4.4. Trichomes on parent plants, and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations

Trichome types V, IV and VI were the most dense trichome types on parent plants and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations, while trichome types I, II and VII were present in low densities. In *L. hirsutum* accession LA 2204, trichome types I, III, IV, VI and VII were present on both abaxial (lower) and adaxial (upper) leaf surfaces with type IV as the most dominant trichomes, while types II and V were absent. In *L. esculentum* "Money Maker", trichome types I, III, V, VI and VII were present on both leaf surfaces with type V as the most dominant trichomes; while types II and IV were absent. In the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations, trichome types I, III, IV, V, VI and VII were present on both leaf surfaces with type V as the most dominant trichome, while type II was absent (Table 5). Type VI trichome heads differed morphologically between the parent plants, "Money Maker" had four lobed heads, while LA 2204 had globular heads.

### 4.4.1. Trichome type comparison among parent plants, and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations.

The density of type I trichomes on abaxial surfaces was significantly higher on $BC_1$ and $BC_2$ tomato lines compared to $F_2$ and LA 2204 tomato lines, however they were not significantly different on "Money Maker" and $F_1$ tomato lines.

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Type III trichomes were significantly higher on the abaxial leaf surfaces of $BC_1$ generation than the $F_2$ generation, but not significantly different in "Money Maker", LA 2204, $F_1$ and $BC_2$ tomato lines. Type IV trichomes on both abaxial and adaxial leaf surfaces were significantly higher on accession LA 2204 compared to "Money Maker", $F_1$, $F_2$, $BC_1$ and $BC_2$ tomato lines. Type V trichomes on abaxial leaf surfaces were significantly higher on "Money Maker" compared to LA 2204, $F_1$, $F_2$, and $BC_2$, but there was no significance with the $BC_1$ generation. Type VI trichomes on abaxial leaf surfaces were significantly higher on $BC_2$, compared to $F_1$, $F_2$ and $BC_1$ tomato lines. Type VII trichomes on abaxial leaf surfaces were significantly higher on LA 2204 and $BC_2$ compared to $F_1$ generation, but no significant difference with "Money Maker", $F_2$ and $BC_1$ tomato lines (Table 5).

**Table 5: Trichome types among parent plants, and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations**

| Trichome type | Surface | LA 2204 | Money Maker | $F_1$ | $F_2$ | $BC_1$ | $BC_2$ |
|---|---|---|---|---|---|---|---|
| I | Abaxial | 0.20±0.14b | 0.91±0.20ab | 0.10±0.10ab | 0.10±0.10b | 1.82±0.41a | 1.41±0.35a |
| | Adaxial | 1.21±0.33b | 1.82±0.39ab | 0.91±0.29ab | 0.10±0.10b | 2.22±0.41ab | 2.83±0.45a |
| II | Abaxial | 0.00±0.00a | 0.00±0.00a | 0.00±0.00a | 0.00±0.00a | 0.00±0.00a | 0.00±0.00a |
| | Adaxial | 0.00±0.00a | 0.00±0.00a | 0.00±0.00a | 0.00±0.00a | 0.00±0.00a | 0.00±0.00a |
| III | Abaxial | 0.10±0.10ab | 0.81±0.27ab | 0.51±0.30ab | 0.00±0.00b | 1.01±0.17a | 0.91±0.20ab |
| | Adaxial | 0.40±0.20ab | 0.21±0.14b | 0.40±0.20ab | 0.30±0.17ab | 1.21±0.33a | 1.01±0.30ab |
| IV | Abaxial | 17.58±1.51a | 0.00±0.00d | 4.65±0.68bc | 4.14±0.66bc | 2.32±0.51cd | 2.93±0.47cd |
| | Adaxial | 7.47±1.3a | 0.00±0.00b | 1.11±0.40b | 0.81±0.27b | 0.81±0.27b | 1.21±0.33b |
| V | Abaxial | 0.00±0.00d | 28.38±1.84a | 18.69±1.82bc | 18.99±1.89bc | 23.54±1.75ab | 19.70±1.66bc |
| | Adaxial | 0.00±0.00c | 9.60±1.30a | 4.55±0.99b | 5.96±1.33ab | 7.47±1.22ab | 4.75±0.94b |
| VI | Abaxial | 4.85±0.54ab | 5.15±0.66ab | 3.94±0.54b | 4.34±0.60b | 4.04±0.54b | 7.27±0.78a |
| | Adaxial | 4.44±0.54a | 3.23±0.48a | 3.74±0.57a | 3.84±1.61a | 3.43±0.67a | 3.84±0.63a |
| VII | Abaxial | 1.31±0.34a | 0.51±0.22ab | 0.10±0.10b | 1.01±0.30ab | 0.71±0.26ab | 1.41±0.35a |
| | Adaxial | 0.33±0.17a | 0.00±0.00a | 0.20±0.14a | 0.10±0.10a | 0.40±0.20a | 0.30±0.17a |

Means with same letter notation within rows for same surface are not significantly different (Tukey test, $p > 0.05$)

Correlation analysis of trichomes types revealed a significant negative relationship between type IV and type V trichomes; trichome types I and IV; and trichome types III and IV. Correlation between types I and VII; types III and VII; types IV and VI; and types V and VII was not significant. There was a significant positive relationship between trichome types VI and VII; types I and III; types I and V; types III and V; and types III and VI, while a non significant positive relationship existed between trichome types I and VI; types III and VII; types IV and VII; and types V and VI (Table 6).

**Table 6: Trichome types correlation coefficients on abaxial leaf surfaces**

| Variable | Correlation coefficient | | | | |
|---|---|---|---|---|---|
| | Type I | Type III | Type IV | Type V | Type VI |
| Type III | $0.38^*$ | - | - | - | - |
| Type IV | $-0.35^*$ | $-0.39^*$ | - | - | - |
| Type V | $0.49^{**}$ | $0.47^{**}$ | $-0.84^{***}$ | - | - |
| Type VI | $0.29^{ns}$ | $0.38^*$ | $-0.12^{ns}$ | $0.32^{ns}$ | - |
| Type VII | $-0.02^{ns}$ | $-0.04^{ns}$ | $0.28^{ns}$ | $-0.23^{ns}$ | $0.55^{***}$ |

Non significant (ns) or significant (*, **, ***) at 5%, 1%, 0.1% levels

### 4.4.2. Glandular and non-glandular trichomes

The density of glandular trichomes (type I+IV+VI+VII) on both abaxial and adaxial leaf surfaces was significantly higher on accession LA 2204 compared to $F_1$, $F_2$, $BC_1$, $BC_2$ and "Money Maker", while the density of non-glandular trichomes (type III+V) was significantly higher on "Money Maker" compared to LA 2204, $F_1$, $F_2$ and $BC_2$ on abaxial surfaces. On adaxial surfaces the density was significantly higher on "Money Maker" compared to LA 2204 and $F_1$. The total number of trichomes (I+III+IV+V+VI+VII) was significantly lower on accession LA 2204 compared to "Money Maker", $F_1$, $F_2$, $BC_1$ and $BC_2$ (Table 7).

**Table 7: Glandular and non-glandular trichomes on abaxial and adaxial leaf surfaces**

| Trichome type | Surface | LA 2204 | Money Maker | $F_1$ | $F_2$ | $BC_1$ | $BC_2$ |
|---|---|---|---|---|---|---|---|
| Glandular | Abaxial | 23.93±1.65a | 6.56±0.69c | 12.22±0.98b | 9.59±1.01bc | 8.89±0.70bc | 13.03±0.91b |
| | Adaxial | 13.43±1.41a | 5.05±0.56b | 6.97±0.63b | 5.65±0.67b | 6.86±0.72b | 8.18±0.73b |
| Non Glandular | Abaxial | 0.10±0.10d | 29.19±1.88a | 17.07±1.78c | 18.99±1.89bc | 24.54±1.74ab | 20.61±1.70bc |
| | Adaxial | 0.40±0.20c | 9.79±1.29a | 4.94±0.99b | 6.26±1.35ab | 8.68±1.23ab | 5.76±0.97ab |
| Total | Abaxial | 24.04±1.64b | 35.76±2.08a | 29.29±2.09ab | 28.59±2.05ab | 33.43±1.95a | 33.64±1.82a |
| | Adaxial | 13.84±1.38a | 14.85±1.37a | 11.92±1.14a | 11.92±1.43a | 15.56±1.29a | 13.94±1.16a |

Means with same letter notation within are not significantly different (Tukey test, $p > 0.05$).

## 4.5. Development time of mites from egg to adult

The development of the mite from egg to adult was through five stages, egg, larva, protonymph, deutonymph and adult. The period from egg to larva was significantly lower in "Money Maker" compared to LA 2204, $F_1$ and $F_2$, but not significantly different from $BC_1$ and $BC_2$. The larval, protonymph and deutonymph periods for "Money Maker" were not significantly different from LA 2204, $F_1$, $F_2$, $BC_1$ and $BC_2$. However the shortest lifecycle was on "Money Maker" (11.3 days) compared to 13.2, 13.4, 12.9, 12.3 and 11.6 days on LA 2204, $F_1$, $F_2$, $BC_1$ and $BC_2$ respectively. The adult mites lived significantly longer on "Money Maker" compared to LA 2204, $F_1$, $F_2$, $BC_1$ and $BC_2$. Survival was 52.5% on "Money Maker", but less than 25% on LA 2204 $F_1$, $F_2$, $BC_1$ and $BC_2$ (Table 8).

**Table 8: Development time from egg to adult of *T. evansi***

| Plant | Egg | | Larva | | Protonymph | | Deutonymph | | Adult | | Sex | | Survival |
| | n | Duration (days) | n | Duration (days) | n | Duration (days) | n | Duration (days) | n | Duration (days) | M | F | (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MM | 80 | 4.2±0.16c | 69 | 2.7±0.14b | 60 | 2.4±0.10a | 48 | 2.0±0.09a | 43 | 9.3±1.26a | 13 | 29 | 52.5 |
| LA 2204 | 80 | 5.1±0.19ab | 40 | 3.1±0.21ab | 9 | 3.0±0.37a | 2 | 2.0±0.00a | 0 | 0.0±0.00b | 0 | 0 | 0.0 |
| $F_1$ | 80 | 5.3±0.21a | 44 | 3.4±0.26a | 18 | 2.4±0.16a | 11 | 2.3±0.14a | 10 | 1.1±0.36b | 4 | 6 | 12.5 |
| $F_2$ | 80 | 5.1±0.21ab | 56 | 3.0±0.16ab | 36 | 2.8±0.12a | 25 | 2.0±0.11a | 12 | 2.4±0.56b | 5 | 7 | 15.0 |
| $BC_1$ | 80 | 4.5±0.12bc | 67 | 3.0±0.19ab | 27 | 2.8±0.13a | 20 | 2.0±0.09a | 16 | 2.0±0.54b | 4 | 13 | 21.3 |
| $BC_2$ | 80 | 4.5±0.14bc | 62 | 2.5±0.13b | 28 | 2.4±0.16a | 17 | 2.2±0.16a | 13 | 1.1±0.30b | 5 | 8 | 16.3 |

Means with same letter notation within columns are not significantly different. (Tukey test, $p > 0.05$)

F = Female, M = Male, MM= Money Maker.

### 4.6. Fecundity and longevity of mites

The mean number of eggs laid per female mite was significantly higher on "Money Maker" compared to LA 2204, $F_1$, $F_2$, $BC_1$ and $BC_2$. Longevity was significantly higher on "Money Maker" compared to LA 2204, $F_1$, $F_2$, $BC_1$ and $BC_2$ (Table 9). Multiple regression analyses with various combinations of trichomes showed that types IV and V are responsible for most of the variation in fecundity and longevity. Their exclusion from the analyses reduced the 55% variation in fecundity due to the effect of all trichomes to 38%, while in longevity variation reduced from 66% to 47% (Table 10).

**Table 9: Fecundity and longevity of *T. evansi***

| Tomato line/generation | Eggs/mite | Longevity (days) |
|---|---|---|
| Money Maker | 57.9±4.46a | 13.1±1.06a |
| LA 2204 | 0.04±0.02d | 4.5±0.23d |
| $F_1$ | 10.5±1.94c | 8.7±0.43bc |
| $F_2$ | 5.4±0.94c | 6.9±0.38cd |
| $BC_1$ | 26.5±2.25b | 9.2±0.49bc |
| $BC_2$ | 26.4±2.32b | 9.4±0.49bc |

Means with same letter notation within columns are not significantly different. (Tukey test, $p > 0.05$)

**Table 10: Multiple regression of trichomes with fecundity and longevity of *T. evansi***

| Multiple variables | Egg | | | Longevity | | |
|---|---|---|---|---|---|---|
| | $R^2$ | p value | Trichomes p <0.05 | $R^2$ | p value | Trichomes p <0.05 |
| I, III, IV, V, VI, VII | 0.55 | <0. 0001 | Non | 0.66 | <0. 0001 | Non |
| I, III, V, VI, VII | 0.54 | <0. 0001 | V | 0.64 | <0. 0001 | V |
| I, III, IV,VI, VII | 0.52 | 0.0003 | IV | 0.63 | <0. 0001 | IV |
| I, III, VI, VII | 0.38 | 0.0004 | I | 0.47 | 0.0004 | I, VII |
| Glandular | 0.21 | 0.01 | - | 0.29 | 0.007 | - |
| Non glandular | 0.50 | <. 0001 | - | 0.60 | <0. 0001 | - |

Correlation analysis revealed that trichome types IV and V had a significant relationship with fecundity and longevity. Type IV trichomes were negatively correlated with fecundity and longevity, while type V had a highly significant positive correlation with fecundity and longevity. Type I and III trichomes had a significant positive relationship with fecundity and longevity. Correlation of fecundity and longevity with glandular trichomes revealed a significant negative relationship, while non-glandular trichomes showed a significant positive relationship (Table 11).

**Table 11: Correlation coefficients of trichomes with fecundity and longevity**

| Trichome | Correlation coefficient | |
|---|---|---|
| | Egg | Longevity |
| Type I | 0.49** | 0.51** |
| Type III | 0.51** | 0.51** |
| Type IV | -0.61*** | -0.69*** |
| Type V | 0.69*** | 0.76*** |
| Type VI | $0.30^{ns}$ | $0.32^{ns}$ |
| Type VII | $-0.08^{ns}$ | $-0.20^{ns}$ |
| Glandular | -0.46** | -0.50** |
| Non glandular | 0.70*** | 0.78*** |

Non significant (ns) or significant (*, **, ***) at 5%, 1%, 0.1% levels

## 4.7. Repellence choice tests

### 4.7.1. Thumbtack bioassay method

The distance covered by the mites on abaxial leaf surfaces in the first 20 minutes was significantly higher on "Money Maker" compared to all other lines. However, after 40 and 60 minutes the difference between" Money Maker" and $BC_1$ was not significant.

The shortest distance was covered on accession LA 2204, while the longest distance was (Table 12).

**Table 12: Distance traveled by mites on leaf surfaces in 20, 40 and 60 minutes**

| Tomato line | Distance traveled by mites on to leaf surface in mm | | |
| --- | --- | --- | --- |
| | 20 minutes | 40 minutes | 60 minutes |
| Money Maker | 8.83±1.27a | 10.10±1.19a | 11.80±1.28a |
| LA 2204 | 0.12±0.05d | 0.20±0.06d | 0.65±0.19d |
| $F_1$ | 3.12±0.47bc | 5.02±0.66c | 5.44±0.68c |
| $F_2$ | 2.20±0.30cd | 6.57±0.74bc | 7.48±0.86c |
| $BC_1$ | 5.17±0.56b | 8.55±0.56ab | 10.98±0.67ab |
| $BC_2$ | 2.58±0.37cd | 4.77±0.71c | 8.00±0.93bc |

Means with same letter notation within columns are not significantly different (Tukey test, $p > 0.05$)

Multiple regression analyses with various combinations of trichomes showed that types IV and V are responsible for most of the variation on distances covered in 20, 40, 60 minutes, respectively. Their exclusion from the analyses reduced the variation in distance covered due to effect of all trichomes from 61% to 35% in 20 minutes; 74% to 23% in 40 minutes and 76% to 34% in 60 minutes. Type V seems to have a higher variation effect because most of the significant effect is due to the presence of this trichome. Effects of type IV are only significant in analyses where type V is excluded from the multiple regression models except for 60 minutes (Table 13).

**Table 13: Multiple regressions of trichomes with distance covered by mites in 20, 40 and 60 minutes**

| Multiple variables | Distance (mm) (20 minutes) | | Distance (mm) (40 minutes) | | Distance (mm) (60 minutes) | |
|---|---|---|---|---|---|---|
| | $R^2$ | Trichomes $p < 0.05$ | $R^2$ | Trichomes $p < 0.05$ | $R^2$ | Trichomes $p < 0.05$ |
| I, III, IV, V, VI, VII | 0.65*** | V | 0.74*** | V, VI | 0.76*** | V, VI |
| I, III, V, VI, VII | 0.61*** | V | 0.73*** | V, VI | 0.74*** | V, VI |
| I, III, IV, VI, VII | 0.48** | IV | 0.62*** | IV | 0.69*** | IV |
| I, III, VI, VII | 0.35** | VII | $0.23^{ns}$ | non | 0.34** | I |
| Glandular | 0.26** | - | 0.50** | - | 0.49** | - |
| Non glandular | 0.60*** | - | 0.65*** | - | 0.66*** | - |

Non significant (ns) or significant (*, **, ***) at 5%, 1%, 0.1% levels

Correlation analysis of trichomes with distance covered by mites on abaxial leaf surfaces in 20, 40 and 60 minutes revealed a strong significant relationship with trichome types IV and V. The type IV trichomes had a highly significant negative relationship with distance covered in 20, 40 and 60 minutes, respectively.

However type V trichome had a highly significant positive relationship with distance covered in 20, 40 and 60 minutes, respectively Trichomes type I and III had significant positive relationship with distance covered. Glandular trichomes had a significant negative relationship with distance covered, while non-glandular ones had a positive relationship with distance covered by the mites (Table 14).

**Table.14: Correlation coefficients of trichomes with distance covered in by mites in 20, 40 and 60 minutes.**

| Trichome | Correlation coefficient | | |
|---|---|---|---|
| | 20 minutes | 40 minutes | 60 minutes |
| Type I | 0.36* | 0.39* | 0.51** |
| Type III | 0.46** | 0.33* | 0.39* |
| Type IV | -0.61*** | -0.77*** | -0.79*** |
| Type V | 0.76*** | 0.81*** | 0.81*** |
| Type VI | $0.23^{ns}$ | $0.05^{ns}$ | $0.08^{ns}$ |
| Type VII | $0.23^{ns}$ | $-0.21^{ns}$ | $-0.19^{ns}$ |
| Glandular | -0.51** | -0.71*** | -0.71*** |
| Non glandular | 0.77*** | 0.80*** | 0.81*** |

Non significant (ns) or significant (*, **, ***) at 5%, 1%, 0.1% levels

### 4.7.2. The slide method

This method was used to determine number of mites attracted to either tomato line in a set of two tomato lines. The t-values obtained using the Student t-test analysis revealed significant difference in number of mites attracted to either tomato line ($p < 0.05$) in all sets of tomato lines that were compared except for $F_1$ and $F_2$.

Majority of the mites i.e. more than 60% were attracted to "Money Maker" compared to LA 2204, $F_1$, $F_2$, $BC_1$ and $BC_2$; while the minority i.e. less than 15% were attracted to LA 2204 compared to "Money Maker", $F_1$, F2, $BC_1$ and BC2 (Table 15).

**Table 15: The number of mites attracted in paired tomato plants**

| Tomato line | Number of mites | t-value |
|---|---|---|
| Money Maker | 156 | 12.34* |
| LA 2204 | 14 | |
| Money Maker | 128 | 6.17* |
| $F_1$ | 37 | |
| Money Maker | 138 | 6.75* |
| $F_2$ | 45 | |
| Money Maker | 138 | 7.82* |
| $BC_1$ | 49 | |
| Money Maker | 155 | 9.23* |
| $BC_2$ | 38 | |
| LA 2204 | 25 | 4.44* |
| $F_1$ | 70 | |
| LA 2204 | 20 | 3.9* |
| $F_2$ | 60 | |
| LA 2204 | 11 | 7.23* |
| $BC_1$ | 81 | |
| LA 2204 | 8 | 12.05* |
| $BC_2$ | 89 | |
| $F_1$ | 37 | $1.7^{NS}$ |
| $F_2$ | 56 | |
| $F_1$ | 36 | 4.6* |
| $BC_1$ | 76 | |
| $F_1$ | 35 | 2.97* |
| $BC_2$ | 65 | |
| $F_2$ | 36 | 5.51* |
| $BC_1$ | 82 | |
| $F_2$ | 41 | 5.69* |
| $BC_2$ | 104 | |
| $BC_1$ | 38 | 3.45* |
| $BC_2$ | 74 | |

*- Significantly different (Student t-test $p < 0.05$), $^{NS}$- Not significantly different

($N = 200$ mites)

## 4.8. Greenhouse screening for egg and motiles density

This was carried out to determine population establishment of the mites on the two parent tomato lines and their hybrids/generations under greenhouse conditions. The densities of eggs and motile stages on the selected leaves after 18 days were significantly higher on "Money Maker" compared to LA 2204, $F_1$, $F_2$, $BC_1$, and $BC_2$. No eggs were laid on LA 2204; $F_1$, $F_2$, $BC_1$ and $BC_2$ had less than one egg/$cm^2$, while on "Money Maker" an average of 2.3/$cm^2$ eggs were laid (Table 16).

**Table 16: Number of eggs and motiles on leaves after 18 days**

| Tomato line/generation | No of eggs/$cm^2$ | No of motiles/$cm^2$ |
|---|---|---|
| Money Maker | 2.31±0.24a | 0.86±0.13a |
| LA 2204 | 0.00±0.00c | 0.01±0.00c |
| $F_1$ | 0.50±0.17bc | 0.21±0.07bc |
| $F_2$ | 0.33±0.16bc | 0.32±0.08bc |
| $BC_1$ | 0.72±0.20b | 0.41±0.07b |
| $BC_2$ | 0.67±0.12bc | 0.30±0.06bc |

Means with same letter notation within columns are not significantly different (Tukey test, $p > 0.05$)

Correlation analysis of trichomes with density of eggs and motiles revealed a significant relationship with trichome types IV and V. The type IV trichomes had a highly significant negative relationship with eggs/$cm^2$ and motiles/$cm^2$. However, type V

trichome had a highly significant positive relationship with eggs/cm$^2$ and motiles. Trichomes type I and III had a significant positive relationship with eggs/cm$^2$ but type I had no significant effect on motiles, while trichomes types VI and VII had no significant effect on eggs/cm$^2$ and motiles/cm$^2$. Correlation of motiles/cm$^2$ and eggs/cm$^2$ with glandular trichomes revealed a significant negative relationship, while with non-glandular trichomes there was a significant positive relationship (Table 17).

**Table 17: Correlation coefficients of trichomes with greenhouse fecundity and motiles**

| Trichome | Correlation coefficient | |
|---|---|---|
| | Motiles | Fecundity |
| Type I | $0.25^{ns}$ | $0.41**$ |
| Type III | $0.49**$ | $0.41**$ |
| Type IV | $-0.62***$ | $-0.69***$ |
| Type V | $0.78***$ | $0.76***$ |
| Type VI | $0.26^{ns}$ | $0.25^{ns}$ |
| Type VII | $-0.09^{ns}$ | $-0.16^{ns}$ |
| Glandular | $-0.51**$ | $-0.50**$ |
| Non glandular | $0.79***$ | $0.77***$ |

Non significant (ns) or significant (*, **, ***) at 5%, 1%, 0.1% levels

# CHAPTER FIVE

## 5.0. DISCUSSION

### 5.1. Establishment and description of parents and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations

*Lycopersicon esculentum* variety "Money Maker" easily hybridized with *L. hirsutum* f. *glabratum* accession LA 2204 and produced plenty of viable $F_1$ seeds. Rick (1973) reported that *L. hirsutum* f. *glabratum* could be a source of valuable traits to improve the cultivated tomato since it easily hybridizes with *L. esculentum*. Other authors also have successfully established hybrids of these two species and worked on them (Erb *et al.*, 1993; Fery and Kennedy, 1987; Snyder and Carter, 1985). Accession LA 2204 failed to produce flowers under dry hot conditions and did not set fruit under prevailing conditions in the greenhouse; artificial pollination brought little success in terms of fruit set. This failure to reproduce could be attributed to two factors; either lack of insect pollinating agents since plants were in the greenhouse or unfavourable climatic conditions. *L. hirsutum* f. *glabratum* is known to be highly out crossing. This is evident from the flower morphology as stigmas protrude outside the anther cones and flower corollas are bright yellow (Taylor, 1986) and establishment in the greenhouse could have led to lack of fruit set due to absence of natural pollinating agents. However, this factor might not be the reason in our case, since artificial pollination failed to yield fruits especially under dry hot conditions. *L. hirsutum* has been reported to flower and set normal seeded fruits in South America its native habitat, where temperatures are cool (MacArthur and Chiasson, 1947).

The poor seed germination could also be attributed to climatic conditions especially temperature (Picken *et al.*, 1986).

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This response might vary amongst accessions of *L. hirsutum* f. *glabratum*. Accessions L06219 and PI134417, were established together with LA 2204, to access a better pollen donor, but these two species performed poorly in terms of flower production. They could therefore not produce sufficient pollen for cross breeding; this was the reason why LA 2204 was used as the male plant and not the widely studied accession PI134417.

*Lycopersicon esculentum* variety "Money Maker" performed well in all growth parameters i.e. seed germination, flower production and fruit set. This could be attributed to the fact that "Money Maker" is a commercial variety adapted to wide climatic conditions. Fruit set occurred well in the greenhouse conditions since plants are highly inbreeding, this is evident by stigmas enclosed inside anther cones and dull yellow corollas (Taylor, 1986).

The $F_1$ hybrids were vigorous in growth compared to the parent plants accession LA 2204 and "Money Maker", good seed germination and flower set were observed, but fruit set was poor. This could be attributed to the genetic influence of accession LA 2204 which failed to set fruit completely under greenhouse conditions. MacArthur and Chiasson (1947) reported vigour in $F_1$ hybrids between *L. esculentum* and *L. hirsutum*. $F_2$ generation plants were closely similar to the parent *L. hirsutum* accession LA 2204 in growth and development, especially regarding failure to set fruit under natural conditions. MacArthur and Chiasson (1947) reported a high number of sterile plants in the $F_2$ segregating population between *L. esculentum* and *L. hirsutum*; they attributed this to genetic factors. However, in our case the environmental conditions may also have played a role in poor reproduction of $F_2$ generation.

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The performance of backcrosses, $BC_1$ and $BC_2$ was comparable to $F_1$ hybrids except for fruit set which was higher and fruits were bigger and red when ripe. MacArthur and Chiasson (1947) reported that fertility in backcrosses ranged from nil to that of the *L. esculentum* parent.

## 5.2. Trichome type and density

Glandular and non-glandular trichomes of types I, III, IV, V, VI and VII were present on leaf surfaces of LA 2204 and "Money Maker", and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations: while trichomes type II were completely absent. Luckwill (1943) reported that the tomato species *L. hirsutum* and *L. esculentum* do not possess type II, and that they lack type V and type IV trichomes respectively (Table 5). Type II trichomes, according to Luckwill (1943) are found in *L pimpinellifolium* (Jusl.) Mill, *L. pissisi* Phil. and *L. glandulosum* C.H. Mull. Trichome types IV, V and VI had higher densities compared to trichome types I, III and VII. Other authors have also reported similar findings on *L. hirsutum*, *L. hirsutum* f *glabratum*, *L. esculentum* and $F_1$ hybrids (Eigenbrode and Trumble, 1993; Weston *et al.*, 1989; Snyder and Carter, 1985; Gurr and McGrath, 2002; Simmons *et al.*, 2004; 2005). Snyder and Carter (1984) reported that $F_1$ hybrids of *L. hirsutum* and *L. esculentum* possessed all trichome types of parent plants; they concluded that trichome characteristics are inherited from both parents. Average densities of trichome types I, IV, V, VI and VII, were within ranges that have been reported by other authors on leaf surfaces of *L. hirsutum* f *hirsutum*, *L. hirsutum* f *glabratum*, *L. esculentum* and $F_1$ hybrids (Good and Snyder, 1988; Maluf *et al.*, 2001; Snyder and Carter, 1985).

Glandular heads of type VI trichomes differed morphologically between LA 2204, "Money Maker" and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations. "Money Maker" trichomes appeared to have four lobes, due to marked divisions between the four tip cells, while on accession LA 2204 the divisions were less apparent, resulting in a globular appearance of the tip, the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations had an intermediate morphology. This agrees with the findings of Fery and Kennedy (1987); Kauffman and Kennedy (1989) and Snyder and Carter (1985). Type IV and V trichomes had the highest negative correlation between trichomes than any other trichome correlations (Table 6), this was also reported by Good and Snyder (1988).

Glandular trichomes were denser on LA 2204 and non-glandular trichomes were denser on "Money Maker" respectively. Luckwill (1943) reported similar results and attributed host plant resistance to glandular trichomes. Toxic methyl ketones such as 2-tridecanone are found in high levels in type VI glandular trichomes present on the leaf surface of *L. hirsutum* f *glabratum* (Williams *et al.*, 1980; Carter *et al.*, 1989; Maluf *et al.*, 1997) and are associated with moderately high to high heritability values (Maluf *et al.*, 1997). In our results, densities of type VI trichomes were not significantly different between accession LA2204 and variety "Money Maker". Though they have been reported to contain higher methyl ketones in *L. hirsutum* compared to *L. esculentum*, our study did not establish this. These methyl ketones are toxic to *T. urticae* (Chatzivasileiadis *et al.*, 1999; Farrar and Kennedy, 1991; Kennedy, 2003).

Type I, III and VII trichomes were sparse in both accession LA 2204 and "Money Maker", though according to Luckwill (1943), type I and III are abundant in *L. esculentum*, and type I are abundant on *L. hirsutum*.

These differences may have resulted from accessions used or part of organ sampled. Snyder and Carter (1985) reported findings similar to our case.

## 5.3. Development time, fecundity and longevity of mites

The total period from egg to adult in "Money Maker" was 11.3 days. Silva (1954) reported that the life from egg to adult on tomato leaves ranged from 6.5 to 11.5 days. Meyer (1996) reported that the life cycle is as short as 9 to 12 days resulting to 24-30 generations in a year.

The differences in time taken for eggs to hatch and mites to complete development indicated that development and population increase of *T. evansi* depends on host type.

In this case "Money Maker" is a more suitable host compared to accession LA 2204, and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations because it had the shortest egg period and 52.5% of the eggs reached the adult stage. However, the protonymph and deutonymph stages were significantly higher on "Money Maker". This could be explained by the fact that most larvae on accession LA 2204, and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations died before reaching the adult stage (Table 8). Host plants can exert profound effects on the biology of spider mites including *T. evansi* (Jeppson *et al.*, 1975).

The short life cycle, high fecundity and longevity on "Money Maker" indicate that on a suitable host and under favourable climatic conditions *T. evansi* can reproduce rapidly and cause severe crop losses (Qureshi *et al.*, 1969). Low survival rates, fecundity and longevity at all stages on accession LA 2204, $F_1$, $F_2$ $BC_1$ and $BC_2$ compared to "Money Maker" indicated that they are unsuitable for *T. evansi* hence more resistant (Table 8, 9).

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Trichomes do affect mite fecundity and longevity as revealed in regression and correlation analyses (Table 10, 11).

Type IV trichomes could be responsible for the low fecundity and longevity since they have a negative relationship with these two parameters. Type IV trichomes are inversely correlated with survival of *T. urticae* and probably related with host plant resistance of *L. hirsutum* to mites. Type VI trichomes have no significant correlation, while type V trichomes are positively correlated with mite survival (Carter and Snyder, 1985; 1986; Good and Snyder, 1988; Snyder and Carter, 1984). Carter and Snyder (1985) reported that type IV trichome density greater than 0.6 $mm^2$ had an effect on resistance to *T. urticae*, in our case the $F_1$, $F_2$ $BC_1$ and $BC_2$ had type IV trichome densities greater than 0.6 $mm^2$.

Gurr and Mc Grath (2002) reported that type V trichome density is positively correlated with potato tuber moth, *Phthorimaea operculella* Zeller survival and development on abaxial leaf surfaces of five accessions of *Lycopersicon hirsutum* f *glabratum*. This is similar to the trend observed for *Bemisia argentifolia* (Heinz and Zalom, 1995)

High densities of glandular trichomes compared to non-glandular trichomes may be responsible for high levels of resistance in accession LA 2204. Rasmy, (1985) reported that mite oviposition is deterred by high density of glandular trichomes on *L. hirsutum* f *glabratum* and *Solanum sarachoides* Sendter compared to *L. esculentum* that had lower density of the trichomes.

A positive relationship has been reported between the density of type IV trichomes and mortality of mites but not type VI on *L. hirsutum*, *L. esculentum* and their $F_2$ generation sibs (Snyder and Carter, 1985), and this agrees with our findings. Type IV trichomes in *L.*

*pennellii* are known to contain acylsugars that are responsible for high levels of resistance to *T. evansi* (Goffreda *et al.*, 1990; Resende *et al.*, 2002)

In *L. hirsutum* f *hirsutum* they are known to contain the sesquiterpene zingeberene responsible for high levels of resistance to *T. evansi* (Maluf *et al.*, 2001), but no literature was available on what they contain in *L. hirsutum* f *glabratum* to which accession LA 2204 belongs.

## 5.4. Repellence choice test

## 5.4.1. Thumbtack bioassay method

*Tetranychus evansi* prefers "Money Maker" to accession LA 2204, and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations. Line differences were evident with measures taken as early as 20 minutes after placement of mites on to the thumbtack. The reluctance of mites to move on accession LA 2204; and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations compared to "Money Maker" could be attributed to presence of type IV trichomes, they were absent in "Money Maker". Type IV trichomes possess exudates or volatiles that could have impaired mite movement (Maluf *et al.*, 2001; Resende *et al.*, 2002). Other glandular trichomes may have contributed to this especially type VI which have been reported to posses high levels of 2-tridecanone in *L. hirsutum* f *glabratum* but trace amounts in *L. esculentum* (Chatzivasileiadis *et al.*, 1999; Farrar and Kennedy, 1991; Kennedy, 2003; Williams *et al.*, 1980).

Multiple regression and correlation analyses showed that trichomes affect mite host preference in terms of distance covered (Table 13, 14).

Type IV trichomes are inversely while trichomes type V are positively correlated to distance covered on leaf surfaces of the six lines.

Maluf *et al,* (2001) reported a high negative correlation between type IV trichome densities and distances traveled by *T. evansi* onto leaves of $F_2$ generation (*L. hirsutum* f *hirsutum* and *L. esculentum*) they attributed these to presence of zingiberene which had a positive correlation with density of these trichomes.

### 5.4.2. The Slide method

Results indicate that "Money Maker" is preferred by mites to accession LA 2204 and $F_1$, $F_2$, $BC_1$ and $BC_2$ generations, as demonstrated in (Table 15).

Therefore $F_1$, $F_2$, $BC_1$ and $BC_2$ generations are more resistant than "Money Maker", this could be probably attributed to volatiles emitted by glandular trichomes, especially types IV which were abundant on accession LA 2204, present on $F_1$, $F_2$, $BC_1$ and $BC_2$ generations, but completely absent on "Money Maker". Type VI trichomes could also play a role if they contain higher concentrations of 2-tridecanone in *L. hirsutum* than *L. esculentum* as reported by Kennedy (2003). Lin *et al,* (1987) reported that 95% of type VI trichome gland contents consisted of the methyl ketones 2-tridecanonone (146ng), 2-undecanone (47ng) and a sesquiterpene (5ng) in *L. hirsutum* f *glabratum,* while in *L. esculentum* only small amounts of a monoterpene and a sesquiterpene were found. The reluctance of mites to settle on accession LA 2204, $F_1$, $F_2$, $BC_1$ and $BC_2$ generations showed that they prefer a specific host that is suitable for feeding and development.

The host plant range of herbivorous arthropods is generally restricted to the small fraction of plant species that is available to them (Mitter, 1981).

Host plant acceptance is described as the proportion of adult females settling on the test plant on which they have been placed. The host plant range of the phytophagous spider mite *T. urticae* seems to be determined through different mechanisms. Adult females reach potential host plants either by random walking or by passive wind dispersal (Kennedy and Smitley, 1985), though they readily escape from unfavorable ones (Fry, 1989). The host plant range of *T. urticae* is determined through host plant acceptance, i.e. whether the adult female decides to settle on or leave the encountered host plant.

*Tetranychus urticae* has a broad range of host plants. However, the spider mite does not accept all plants at the same degree because of differences in nutritive and toxic constituents. Other factors, such as the induction of secondary metabolites, the morphology of leaf surface and presence of natural enemies, also play an important role in plant acceptance. Boom *et al*, (2003) reported that acceptance of *T. urticae* varied among plants belonging to *Fabaceae* and *Solanaceae* families with the most well accepted being tobacco and the most poorly accepted being sweet pepper.


## 5.5. Greenhouse screening for mite population density

The results of the greenhouse screening indicate that the resistance expressed in the laboratory, was expressed in the greenhouse (Table 16).

The densities of eggs/cm$^2$ and motiles/ cm$^2$ were significantly higher on "Money Maker" compared to accession LA 2204; and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations.

Fecundity and population density can be used to determine suitability of host plant (Yano *et al.*, 1998). In this case "Money Maker" is a suitable host to *T. evansi* than accession LA 2204; and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations.

The host plant suitability of different plant species to *T. urticae* species is expressed as the mean number of eggs produced by the females within a fixed number of days. Positive correlation has been reported between plant acceptance and fecundity in *T. urticae* (Yano *et al*, 1998). The host range of many herbivorous insects is determined by the oviposition preference of adult females for plants suitable to their progeny (Thompson, 1988).

# CHAPTER SIX

## 6.0. CONCLUSIONS AND RECOMMENDATIONS

*Lycopersicon esculentum* variety "Money Maker" easily hybridized with *Lycopersicon hirsutum* accession LA 2204 and produced viable $F_1$ seeds. Therefore valuable traits especially for pest resistance can be incorporated in the cultivated tomato from this wild species. The hybrid plants are intermediate to their parents in morphological and pest resistance attributes.

Trichome types I, III, IV, V, VI and VII do exist on these two species and their $F_1$, $F_2$, $BC_1$ and $BC_2$ generations, glandular type IV trichomes were completely absent on "Money Maker" which had abundant non-glandular type V trichomes. On accession LA 2204, glandular type IV trichomes were abundant, but type V were completely absent, while the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations possessed both type IV and V trichomes in addition to types I, III, VI and VII. Trichome types IV, V and VI are abundant on these species and their $F_1$, $F_2$, $BC_1$ and $BC_2$ generations, while types I, III and VII are sparse. Trichome types IV, V, VI and VII are denser on abaxial than adaxial leaf surfaces, whereas types I and III are denser on adaxial than abaxial leaf surfaces. Correlation analyses between trichomes revealed that trichome types can either be positively or negatively related and this affects the behaviour of *T. evansi*. Type IV and V trichomes are the most dominant trichomes, they are negatively correlated such that increase in one leads to decrease of the other. Trichome types are inherited by the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations from both parents, though the non-glandular type V seems to be inherited more dominantly than the glandular type IV.

The developmental characteristics, fecundity and longevity studies of *T. evansi* on *L. hirsutum* accession LA 2204, *L. esculentum* variety "Money Maker" and their $F_1$, $F_2$, $BC_1$ and $BC_2$ generations reveal that accession LA 2204 and the respective generations are resistant to the mite compared to "Money Maker". The low fecundity, survival and longer life cycle of the mite on LA 2204 and the generations indicate that mite population growth can be suppressed the resistance is effectively incorporated in cultivated varieties. The trichome type that seems to be associated with resistance is type IV since it is the most dominant in accession LA 2204 and present on the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations. It also has a highly significant negative correlation with fecundity and longevity. The positive relation between fecundity and longevity with type V trichomes may be due to absence or sparse type IV trichomes. Alternatively mites may prefer surfaces with type V trichomes due to their villose nature. Research has shown that mites prefer to oviposit on candescence surfaces (Carter and Snyder, 1985). Types I and III trichomes also do affected mite behaviour as demonstrated by their significant effect in multiple regressions, and positive correlation with all parameters investigated. The high percent of mites that reached adult stage and shorter egg emergency period show that "Money Maker" is a suitable host for *T. evansi* compared to accession LA 2204; and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations.

Repellency choice tests estimated by distances covered by mites revealed that mites prefer "Money Maker" to accession LA 2204 and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations. In the slide method bioassay mites were significantly repelled by accession LA 2204 and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations, but were attracted to "Money Maker".

Repellence is therefore another mechanism of resistance to *T evansi* in accession LA 2204 in addition to antibiosis; these mechanisms are inherited by $F_1$, $F_2$, $BC_1$ and $BC_2$ generations as demonstrated by the results.

Whole leaf bioassays in greenhouse screening showed that mite population build up was faster on "Money Maker" than on LA 2204 and the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations, this indicates that the later are resistant to *T. evansi*.

This study reveals that the glandular type IV trichomes could be the source of resistance to *T. evansi* in *L. hirsutum*, since they are the only trichomes that were significantly negatively correlated with all parameters of mite behavior. These trichomes are heritable and therefore can be utilized to improve tomato production by breeding mite resistant varieties, which will posses these trichomes and fewer type V trichomes, which were positively correlated with all parameters investigated. This will minimize pesticides application hence lowering production cost and reducing their negative effect on the environment and human health. Small scale farmers in many parts of Africa utilize few external inputs in their food production practices, host plant resistance would therefore be reliable as it comes as a package and needs little extra cost to make it work (Ampofo, 1995).The resistance to *T. evansi* in LA 2204 is inherited by its hybrids with "Money Maker" as revealed by our study. This mechanism of host plant resistance can therefore be fully exploited in management of *T. evansi*.

Further research work should be carried out to establish, the contents of type IV glandular trichomes in *L. hirsutum* f. *glabratum* in which accession LA 2204 belongs; they have been reported to possess zingiberene in *L. hirsutum* f. *hirsutum* and acylsugars in *L. pennellii* (Goffreda *et al.*, 1990; Maluf *et al.*, 2001; Resende *et al.*, 2002)

Methyl ketones content in type VI trichomes should also be studied, though there is no difference in their abundance in density/mm$^2$ between LA 2204 and "Money Maker" in this study, literature reveals that they differ in methyl ketones level (Williams *et al.*, 1980).

Further research should be carried out to establish the inheritance of the genes responsible for type IV trichomes expression so that they can be effectively incorporated in cultivated tomato to improve resistance to *T. evansi*.

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