

# Molecular mapping and marker assisted selection for trichome mediated insect resistance in tomato

G.M. SAJJANAR AND R.A. BALIKAI\*

U.A.S. (D) Regional Agricultural Research Station, BIJAPUR (KARNATAKA) INDIA

## ABSTRACT

Control of insect pests is an important factor in the productivity of cultivated crops. Applied breeding for quantitative traits like insect resistance is difficult. The availability of high density molecular linkage maps and QTL mapping technology permit the dissection of quantitative traits and thus making marker assisted selection feasible. A high level of resistance to number of insects has been found in the wild species of tomato. An association between insect resistance and the presence and density of glandular trichomes has been reported by several researchers. The primary components of exudates from glandular trichomes viz., the acylsugars and 2-tridecanone secreted by type IV trichomes of *Lycopersicon pennellii* and type VI trichomes of *L. hirsutum*, respectively mediate the insect resistance. The genetics of these characters in tomato appears to be complex. This paper reviews on mapping and marker assisted introgression of QTLs associated with trichome densities, acylsugar accumulation and expression of 2-tridecanone mediated insect resistance. The development of tomato cultivars with the ability to synthesize sugar esters and increased 2-tridecanone content may substantially increase the level of insect resistance in cultivated tomato. Marker assisted breeding will enable introgression of multiple QTLs of inheritance of insect resistance in tomato via gene pyramiding.

**Key words :** Molecular mapping, Marker assisted selection, Insect resistance, Tomato

## INTRODUCTION

Cultivated crops are attacked by large number of insect pests which damage plants and reduce yields. The use of resistant varieties can be regarded as the most efficient method of biological control considering adverse effects of use pesticides. In tomato, the damage caused by is substantial (Schwartz and Klassen, 1981) and result

in a significant economic loss to market and processing tomato industry. To develop tomato cultivars with reduced susceptibility to insect pests, early studies identified *Lycopersicon pennellii* (Corr.) D'Arcy and *L. hirsutum* f. *glabratum*, wild relatives of the cultivated tomato as a source of resistance to several important pests (Table 1).

In common with many members of solanaceae the

**Table 1 : Wild sources of resistance to different insect pests in tomato**

Insects	References
<i>Lycopersicon pennellii</i> (Corr.) D'Arcy	
Potato aphid ( <i>Macrosiphum euphorbiae</i> )	
Green peach aphid ( <i>Myzus persicae</i> )	
Leaf minor ( <i>Liriomyza trifolii</i> )	
Silver leaf white fly ( <i>Bemisia argentifolii</i> )	
Tomato fruit worm ( <i>Helicoverpa zea</i> )	(De Ponti <i>et al.</i> ,1975; Gentile and Stoner, 1968; Gentile <i>et al.</i> ,1969; Goffreda <i>et al.</i> ,1989; Hawthorne <i>et al.</i> ,1992; Liedl <i>et al.</i> ,1995, Rodriguez <i>et al.</i> ,1993)
Beet army worm ( <i>Spodoptera exiqua</i> )	
White fly ( <i>Trialeurodes vaporariorum</i> West W.)	
Carmine spider mite ( <i>Tetranychus cinnabarius</i> )	
Two spotted spider mite ( <i>T. urticae</i> Koch.)	
<i>L. hirsutum</i> f <i>glabratum</i>	
Glass house white fly ( <i>Trialeurodes vaporariorum</i> West W.)	
Army worm	
<i>Heliothis armigera</i>	
<i>Helicoverpa sps</i>	De Ponti <i>et al.</i> ,1975; Juvick <i>et al.</i> ,1982; Gentile <i>et al.</i> ,1969;
Carmine spider mite ( <i>Tetranychus cinnabarius</i> )	Kennedy and Sorenson 1985; Kenndy and Henderson, 1978;
Two spotted spider mite	Fery and Curth bert, 1975; Dimock and Kennedy, 1983;
Colarado potato beetle	Gentile and Stoner, 1968; Gentile <i>et al.</i> ,1969; Webb <i>et al.</i> ,1971; Schuster,1977)
Tobacco hornworm	
Tobacco flea beetle	
Vegetable leaf minor	
Tomato pin worm	

foliage of some *Lycopersicon* species is provided with a vesture of glandular trichomes that freely secrete mucilaginous substance, these sticky exudates may help entrap or otherwise deter potential predators (Mckinney, 1938; Dimock and Kennedy, 1983). The studies have suggested that the exudates of type IV glandular trichomes in *L. pennelli* primarily composed of acylsugars that mediate resistance mechanism to several insect species. It is showed that 2-tridecanone in type VI trichome glands of *L. hirsutum f. glabratum* had an insecticide activity to *Manduca sexta* L., *Heliothis zea* (Boddie) and *Aphis gossypii* Glover (Williams *et al.*, 1980; Zamir *et al.*, 1984).

While acylsugars and other chemical trichome exudates are primarily found in wild species, their transfer to cultivated species promises to contribute greatly to an improvement of resistance to insect pests and thus a reduction in the dependence on synthetic chemicals for insect control. Effects of linkage drag, non-fecundity and segregation inherent in the interspecific crosses impede breeding when a desired trait must be transferred from a wild to domesticated species. The use of molecular markers has been effective in identifying and mapping quantitative trait loci (QTL) in several crop plants and expedites the transfer of important genes from wild species into elite lines. In tomato, the availability of high density linkage map permits systematic dissection of quantitative traits and further identification and transfer of chromosomal regions associated with such traits (Tanksley, 1993).

The genetics of trichomes and their exudates is complex. The integration of marker technology and traditional breeding could be more beneficial in studying and transferring such complex traits. In this paper, the mechanisms resistance, inheritance of resistance traits, mapping and marker assisted introgression of QTLs associated trichome mediated insect resistance in tomato are reviewed.

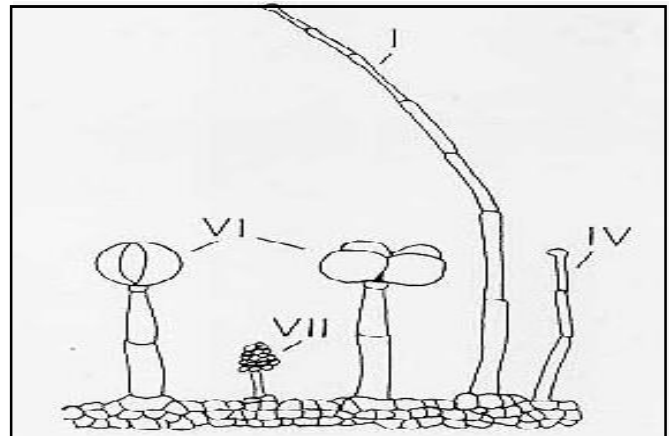
#### **Trichomes and mechanisms of action:**

A central dogma in the study of plant/insect interaction is that plants utilize natural products to defend against herbivorous insects. Some of the clearer examples of plant products providing resistance/defense to insects come from work on trichomes (Levin, 1973). The gross morphology of trichomes and their defense reaction in *Lycopersicon* are discussed below.

#### **Morphology of trichomes:**

The gross morphology of the glandular trichomes of species of *Lycopersicon* and *Solanum* has been studied

in some detail (Luck Will, 1943). In species of *Lycopersicon* there are four major types of glandular trichomes (Fig 1). While, in cereals like sorghum trichomes are non-glandular and microscopic (Sajjanar, 2002).



Type I: a tall elongated multicellular stalk with a multicellular base.  
 Type IV: a short multicellular stalk with a multicellular base.  
 Type VI: a short multicellular stalk with 2-4 celled glandular head and multicellular base.  
 Type VII: a very short unicellular stalk with a 4-8 celled glandular head.

**Fig. 1: Four of the most common cellular trichomes found on members of the genus *Lycopersicon* (Luck Will, 1943)**

#### **Trichomes and defense**

The defense action dependent upon plant/insect system arises from a diversity of causes and effects such as,

- Highly trichotomous state acts as physical barrier for the insect to gain access to the plant surface and thus to feed, seek shelter and/or oviposition.
- Ability of trichomally contained chemicals to poison the insects by contact, ingestion and/or inhalation.
- Ability of insect fractured trichomes to exude gummy, sticky or polymerising chemical mixture that severely impedes the insect's ability to feed, to move and/or survive.

In many plant species, there is negative correlation between trichome density and insect feeding preferences, survival, oviposition and/or larval nutrition (Levin, 1973). The higher trichome densities play an important role in resistance against sorghum shoot fly as evidenced by higher correlations with deadheart percentage (Sajjanar, 2002). In tomato, an association between insect resistance and the presence and density of type IV and type VI glandular trichomes in *L. hirsutum f. glabratum* and *L. pennellii* has been reported by several authors (Snyder

and Carter, 1984; Fery and Kennedy, 1987, Goffreda *et al.*, 1988, 1990a, 1990b; Weston *et al.*, 1989). Trichome type IV present in *L. pennellii* and *L. hirsutum f. glabratum* but absent in *L. esculentum*. Trichome VI is present in all *Lycopersicon* species (Luckwill, 1943) but more abundant in *L. hirsutum f. glabratum* than *L. esculentum*. Non-significant correlations between type IV and type VI trichome density measurements suggested that a relationship does not exist between the two types of trichomes (Lemke and Mutschler, 1984).

The insects like aphids (*Myzus persicae* and *Aphis crossivora*) were unable to effectively colonize tomato plants because the migrants tarsi become bagged down with a gum like exudates from the foliage which caused the insects either to fall off the plant because of loss of purchase or to become immortalized on the leaf and subsequently die (Mckinney, 1938 and Johnson, 1956). The primary components of exudates from glandular trichomes *viz.*, the acylsugars and 2-tridecanone secreted by type IV trichomes of *Lycopersicon pennellii* and type VI trichomes of *L. hirsutum*, respectively mediate the insect resistance.

#### Acylsugars:

The leaves, stem and fruit of most accessions of *L. pennellii* are covered with type IV glandular hairs, which exude a sticky exudate composed of acylsugars in *L. pennellii* LA716 (Burke *et al.*, 1987; Goffreda *et al.*, 1989; Steffens and Walter, 1991). Acylsugars have been found to act as feeding deterrents for *Myzus euphorbiae* (Goffreda *et al.*, 1989) and the green peach aphid (*M. persicae*) or oviposition deterrent for leaf minor species (*Lyriomyza trifolii*) and white flies (Liedl *et al.*, 1995) and reduces growth and development in larvae of *Helicoverpa zea* and *Spodoptera exigua* (Hawthorne *et al.*, 1992; Rodriguez *et al.*, 1993; Juvick *et al.*, 1994). Potato aphid resistance in *L. pennellii* is related to the presence of glucose esters in type IV trichome exudates (Goffreda *et al.*, 1988; Goffreda *et al.*, 1989). Sugar ester content was significantly correlated with type IV trichome density ( $r=0.575$ ,  $P<0.0002$ ;  $n=40$ ) and droplet size ( $r=0.589$ ,  $P<0.0001$ ;  $n=40$ ) but there was no significant relationship between sugar ester content and type VI densities ( $r=0.015$ ,  $P>0.9$ ;  $n=40$ ) (Burke *et al.*, 1987). The cultivated tomato does not possess type IV trichomes and does not accumulate these epicuticular lipids on its surface (Fobes *et al.*, 1985). The development of tomato cultivars with the ability to synthesize sugar esters could substantially increase the level of insect resistance in this species.

#### 2-tridecanone:

The major volatile and sole acutely toxic chemical potent fumigant and neurotoxic properties identified as 2-tridecanone was found to be located in the lobular tetra cellular tips of (presumably) type VI trichomes of wild tomato *L. hirsutum f. glabratum* (PI134417). This compound is 72 times more abundant in this species than in *L. esculentum* (Williams *et al.*, 1980). The 2-tridecanone content of excised leaf lets has been reported to be related to the numbers of the type VI trichomes present (Dimock, 1981). However, Kennedy *et al.* (1981) concluded that the level of horn worm resistance observed in *L. hirsutum f. glabratum* was related more to total quantity of the compound present in the foliage than to the density of the glandular trichomes. This compound is lethal to several species of larval moths and aphids (Kennedy and Yamamoto, 1979), tobacco horn worm (*Manduca sexta*), tomato fruit worm (*Heliothis zea*), aphid (*Aphis gossypii*) and Colorado potato beetle (*Leptinotarsa decimlineata*) (Dimock and Kennedy, 1983, Dimock *et al.*, 1982, Kennedy and Dimock, 1983 and Williams *et al.*, 1980).

#### Inheritance of resistance :

##### Inheritance of trichomes:

The presence of type IV trichomes reported to be simply inherited in *L. esculentum* x *L. pennellii*, controlled by 2 unlinked genes in a duplicate dominant epistasis model (Lemke and Mutschler, 1984). Broad sense heritability estimates for type IV trichome density indicated a high heritability for this trait. Due to simple inheritance and high heritability, it should be possible to select successfully for the presence of type IV trichomes in the segregating populations. However, In another report by Blauth *et al.* (1998), 3 loci were found to be associated with trichome density without any effect on acylsugar levels indicating that increasing trichome density may not be an effective strategy for raising acylsugar level in breeding populations.

Determining the genetic control of the type VI trichome density is more complicated than type IV density because both *L. pennellii* and *L. esculentum* are contributing genes for type VI trichomes. Low to moderate broad sense heritability estimates for type VI trichome density trait indicate considerable environmental effects on the expression of a trait. Hence, selection for this trait will be difficult. However, in cereals like in sorghum crop inheritance of trichome densities is under the control of major loci and highly heritable and hence selection may not be difficult (Sajjanar, 2002).

*Inheritance of accumulation of Acylsugars:*

The genetic control of synthesis and accumulation of sugar esters appears to be more complex with the hybrids synthesizing both glucose and sucrose esters that also have a different fatty acid composition than the glucose esters of *L. pennellii* (Unpublished). A high percentage of acylsugars produced by *L. pennellii* LA716 are acylglucoses as opposed to acylsucroses. The bimodal distribution in F<sub>2</sub> population indicated the action of a single locus in which the LA716 allele conferring high percentage acylglucose is dominant (Blauth *et al.*, 1998). This suggests an epistatic interaction between genes controlling percentage acylglucoses over levels of acylsugar accumulation.

*Genetic analysis of 2-tridecanone concentration and insect resistance:*

The study on genetic nature of 2-tridecanone concentration and on the relationship between 2-tridecanone concentration, tobacco horn worm resistance and type VI glandular trichomes within *L. hirsutum f. glabratum* revealed the following results (Fery and Kennedy, 1987):

- At least three recessive condition high 2-tridecanone concentration
- The genetic system that condition high 2-tridecanone concentration is the same genetic system responsible for the high level of *M. sexta* resistance.
- The segregation for trichome density did not have a large impact on the expression of 2-tridecanone mediated resistance.
- The genes controlling type VI trichome density, 2-tridecanone and tobacco horn worm resistance are not linked. Morphological characteristics of the type VI trichomes would probably not be useful selection indices for high 2-tridecanone concentration.

However, Zamir *et al.* (1984) observed continuous variation for 2-tridecanone that is characteristic of quantitative trait.

*Sesquiterpenes*

A study on spidermite resistance and its causal mechanisms evaluated in *Lycopersicon hirsutum* LA2329 and hybrids with *L. esculentum*, Zaofen 2 revealed that resistance is likely dominant and controlled by one or a few genes. The chemical analysis of trichome secretions by LA2329 indicated that some components of the secretions are more repellent than others. Predominant components trichome secretions were oxygenated derivatives of sesquiterpenes. Additional characterization of the trichome secretions is underway

(Snyder and Min, 2006).

*Qtl. analysis and marker assisted selection (MAS) :*

Breeding for insect resistance in tomato is hampered by apparent quantitative inheritance. Due to complexity of genetics of characters related to insect resistance *viz.*, trichome density, acylsugar content and 2-tridecanone content, attempts have been made to identify the genomic regions associated with the characters related to resistance and marker assisted transfer to cultivated tomato. The studies related to this are presented in following headings.

*QTL analysis for trichome density:*

A study was made by Maaliepaard *et al.* (1995) to map QTLs involved in white fly resistance and trichome densities using a set of RFLP markers with known map positions (Tanksley *et al.*, 1992). QTL mapping analysis reveals that the two QTLs for type IV trichome density, TriIV-1 and TriIV-2 mapped to chromosome 5 and 9, respectively, where as the two QTLs affecting white fly oviposition rate mapped to chr. 1 and 12. So the white fly resistance mapped in the experiment was clearly independent of the presence of type IV trichomes. This opens the possibility of incorporating white fly resistance from *L. hirsutum f. glabratum* into cultivated tomato without undesirable type IV trichomes which is of major importance for the growers.

An interspecific F<sub>2</sub> population derived from tomato crossed with *Lycopersicon hirsutum* LA1777 was assayed for resistance based on egg counts and type IV trichome counts. Resistant and susceptible groups were screened with over 400 molecular markers that span the tomato genome at 10cM intervals. So far, markers in 5 regions on 4 different chromosomes appear clearly associated with resistance and markers in 4 other regions might be associated with resistance. Crosses have been made between RILs to combine the target resistance regions in plants that will be bioassayed to determine if resistance is obtained (Momotaz *et al.*, 2006).

*QTL analysis for acylsugar level and composition:**QTL analysis using interspecific population:*

An interspecific cross F<sub>2</sub> population created by the cross *L. esculentum* X *L. pennellii* LA716 was surveyed for accumulation of acylglucoses, acylsugars and total acylsugars as well as with acylglucoses as a percentage of total acylsugars (mole per cent acylglucoses). QTL analysis revealed that five genomic regions two on chr.2 and one each on chr.3,4 and chr.11 were detected as being associated with one or more aspects of acylsugar

production (Mutschler *et al.*, 1996).

#### *QTL analysis using intraspecific populations:*

QTL analysis using Intraspecific F<sub>2</sub> populations between *L. pennellii* LA716 and *L. pennellii* LA 1912, the latter an accession that assort for low level of acylsugar accumulation, revealed that twelve putative QTLs were found to be associated with type IV trichome density, acylsugar level and percentage acylglucose. The 2 QTLs on chr.3 and 10, respectively are primarily associated with percentage acylglucoses and acylsugar levels, respectively (Blauth *et al.*, 1998).

Five QTLs identified in the study by Blauth *et al.*, (1998) were also reported in one or more of the prior studies. QTL (2B) associated with acylsugar accumulation levels was also detected by Mutschler *et al.* (1996) and Bonierbale *et al.* (1994). Mutschler was also found this QTL to be associated with percentage acylglucoses. QTL 3A associated with acylsugar accumulation levels was detected by Mutschler *et al.* (1996) and was also found to be associated with percentage acylglucoses. QTL 4A associated with acylsugar accumulation level was also detected by Mutschler *et al.* (1996) and Bonierbale *et al.* (1994). In addition this QTL was found to be linked to type IV trichome density and acylsugar accumulation levels was found to be associated with both traits by Bonierbale *et al.* (1994) and associated with type IV trichome density by Maaliepaard *et al.* (1995). QTL 11 A affecting type IV trichome density was also detected by Bonier bale *et al.* (1994).

The results of QTL analysis furthers understanding of acylsugar accumulation and aids in the transfer of acylsugar mediated resistance to cultivated tomato.

#### **MAS for insect resistance:**

A marker-assisted selection breeding program was used to attempt the transfer of the ability to accumulate acylsugars to cultivated tomato by Lawson *et al.* (1997). RFLP and PCR-based markers were used through three backcross generations to select plants containing 5 target regions associated by QTL analysis with acylsugar accumulation done by Mutschler *et al.* (1996). The BC<sub>1</sub>F<sub>1</sub> plant selected possessed all 5 target regions and accumulated acylsugars at a moderate level similar to that of the interspecific F<sub>1</sub> control. The BC<sub>2</sub>F<sub>1</sub> and BC<sub>3</sub>F<sub>1</sub> selections contained complementary subsets of the 5 target regions and did not accumulate acylsugars. BC<sub>3</sub>F<sub>1</sub> plants with complementary subsets of the 5 target regions were intermated to produce populations segregating for the 5 target regions. From 1000 BC<sub>3</sub>F<sub>1</sub>-intermated plants, three plants were found which accumulated acylsugars

at low levels and contained 3 to 5 of the target regions. The recovery of acylsugar accumulation in progeny of the intermated BC<sub>3</sub>F<sub>1</sub> plants supports the involvement of at least some of the 5 target regions in acylsugar biosynthesis. However, since the levels of acylsugars accumulated by these plants were lower than that of the interspecific F<sub>1</sub>, it was thought that another, as of yet unidentified, region is necessary for accumulation of higher levels of acylsugars.

In a recent report by Mutschler and Ortiz (2006), the initial transfer of acylsugar production to tomato produced 97FL, a line producing moderately high levels of acylsucroses, and demonstrable pest resistance. 97FL possesses nine *S. pennellii* introgressions, representing 27 per cent of its nuclear genomes. Using this information, a series of hybrids created and selected ones showed sharply reduced infection by a greenhouse whitefly transmitted virus. As 97FL is not directly useful horticulturally due to larger *S. pennellii* introgressions, a series of PCR based markers were created to allow efficient screening of segregating populations for modifications of introgressions through recombination. The integration of the direct acylsugar assay and the molecular markers allowed the rapid creation of acylsugar lines possessing fewer and/or smaller introgressions, accompanied by improvements in horticultural type. Work in 2002-2003 resulted in the second generation of 5 acylsugar lines, with 4 to 9 introgressions for 77 to 90 per cent of their genomes derived from tomato. Work in 2004-2005 resulted in the third generation of 21 acylsugar lines with 4 to 8 introgressions for 85 to 90 per cent of their genomes derived from tomato. These lines are to be tested in advanced trials. Similarly, the molecular mapping for trichome densities in sorghum has been detected QTLs and marker assisted back cross breeding has been initiated to introgress these regions in the genetic background of shoot fly susceptible elite lines (Unpublished).

Acylsugar producing hybrids would be of use to reduce crop loss or damage directly caused by insect pests when used alone. Additionally, the addition of acylsugar mediated pest resistance in hybrids transgenic for Bt could provide greater breadth or levels of control and reduce the likelihood of creating Bt resistant insects. Acylsugar producing hybrids might also be of use to reduce crop loss or damage indirectly caused by insect pests that vector virus (Mutschler and Ortiz, 2006).

#### **Conclusion:**

In conclusion, the development of tomato cultivars with the ability to synthesize sugar esters and increased 2-tridecanone content may substantially increase the level

of insect resistance in cultivated tomato. Marker assisted breeding will enable introgression of multiple QTLs of inheritance of insect resistance in tomato *via* gene pyramiding.

## REFERENCES

- Blauth S.L., Churchhill, G.A. and Mutschler, M.A. (1998).** Identification of quantitative trait loci associated with acylsugar accumulation using intraspecific populations of the wild tomato, *Lycopersicon pennellii*. *Theor. Appl. Genet.*, **96**: 458-467.
- Bonierbale, M., Plaisted, R.L., Pinedo, O and Tanksley, S.D. (1994).** QTL analysis of trichome mediated insect resistance in potato. *Theor. Appl. Genet.*, **87**: 973-987.
- Burke, B.A., Goldsby, G., Mudd, J.B. (1987).** Polar epicuticular lipids of *Lycopersicon pennellii*. *Phytochem.*, **26**: 2567-2571.
- De ponti, O.M., Pet, G and Hogenboom, N.G. (1975).** Resistance to the glasshouse white fly (*Trialeurodes vaporariorum* Westw.) in tomato (*Lycopersicon esculentum* Mill.) and related species. *Euphytica*, **24**: 645-649.
- Dimock, M.B. (1981).** Chemical and physiological studies of antibiosis in the wild tomato *Lycopersicon hirsutum* f. *glabratum* to the tomato fruit worm, *Heliothis zea*. M.Sc. Thesis, North Carolina State University, Raleigh.
- Dimock, M.B. and Kennedy, G.G. (1983).** The role of glandular trichomes in the resistance of *Lycopersicon hirsutum* f. *glabratum* to *Heliothis zea*. *Ent. Expt. & Applications*, **33**: 263-268.
- Dimock, M.B., Kennedy, G.G. and Williams, W.G. (1982).** Toxicity studies of analogs of 2-tridecanone a naturally occurring toxicant from a wild tomato. *J. Chem. Ecol.*, **8**: 837-842.
- Fery, R.L. and Curth bert, J.R. (1975).** Antibiosis in *Lycopersicon* to the tomato fruit worm (*Heliothis zea*). *J. American. Soc. Hort. Sci.*, **100**: 276-278.
- Fery, R.L. and Kennedy, G.G. (1987).** Genetic analysis of 2-tridecanone concentration, leaf trichome characteristics and tobacco horn worm resistance in tomato. *J. American Soc. Hort. Sci.*, **112**: 886-891.
- Fobes, J.F., Mudd, J.B., Marsden, M.P.F. (1985).** Epicuticular lipid accumulation on the leaves of *Lycopersicon pennellii* (Corr.) D'Arcy and *Lycopersicon esculentum* Mill. *Plant Physiol.*, **77**: 567-570.
- Gentile, A.G. and Stoner, A.K. (1968).** Resistance to *Lycopersicon* and *Solanum* species to the potato aphid. *J. Econ. Entomol.*, **61**: 1152-1154.
- Gentile, A.G., Webb, R.E. and Stoner, A.K. (1969).** *Lycopersicon* and *Solanum* spp. resistant to the carmine and two apterous spider mite. *J. Econ. Entomol.*, **62**: 834-836.
- Goffreda, J.C., Mutschler, M.A. and Tingey, W.M. (1988).** Feeding behaviour of potato aphid affected by glandular trichomes of wild tomato. *Entomol. Exp. Appl.*, **48**: 101-107.
- Goffreda, J.C., Mutschler, M.A., Ave, D., Tingey W.M. and Steffens, J.C. (1989).** Aphid deterrence by glucose esters in glandular trichome exudates of the wild tomato, *Lycopersicon pennellii*. *J. Chem. Ecol.*, **15**: 2135-2147.
- Goffreda, J.C., Steffens, J.C. and Mutschler, M.A. (1990a).** Association of epicuticular sugars with aphid resistance in hybrids with wild tomato. *J. American Soc. Hort. Sci.*, **115**: 161-165.
- Goffreda, J.C., Szymkowiak, E.J., Sussex, I.M. and Mutschler, M.A. (1990b).** Chimeric tomato plants show that aphid resistance and triaculglucose production are epidermal autonomous characters. *Pl. Cell*, **2**: 643-649.
- Hawthorne, D.M., Shapiro, J.A., Tingey, W.M. and Mutschler, M.A. (1992).** Trichome borne and artificially applied acylsugars of wild tomato deter feeding and oviposition of the leaf miner, *Liriomyza trifolii*. *Entomol Exp Appl.*, **65**: 65-73.
- Johnson, B. (1956).** The influence on aphids of the glandular hairs of tomato plants. *Plant Pathol.*, **54**: 130-2
- Juvick, J.A., Berlinger, M.J., Ben-David and Rudich, J. (1982).** Resistance among accessions of the genera *Lycopersicon* and *Solanum* to four of the main insect pests of tomato in Israel. *Phytoparasitica*, **10**: 145-156.
- Juvick, J.A., Shapiro, J.A., Young, T.E. and Mutschler, M.A. (1994).** Acylglucosides from tomatoes alter behavior and reduce growth and survival of *Helicoverpa zea* and *Spodoptera exigua* (Lepidoptera : Noctuidae ). *J. Econ. Entomol.*, **87**: 482-492.
- Kennedy, G.G. and Henderson, W.R. (1978).** A laboratory assay for resistance to the tobacco hornworm in *Lycopersicon* and *Solanum* spp. *J. American Soc. Hort. Sci.*, **103**: 334-336.
- Kennedy, G.G. and Dimock, M.B. (1983).** 2-tridecanone: a natural toxicant in a wild tomato responsible for insect resistance, p. 123-128. In: *IUPAC Pesticide chemistry: Human welfare and the environment* (Ed. J. Miyamoto), Pergamon, New York.
- Kennedy, G.G. and Sorenson, C.E. (1985).** The role of glandular trichomes in the resistance of *Lycopersicon hirsutum* f. *glabratum* to Colorado potato beetle. *J. Econ. Entomol.*, **78**: 547-551.
- Kennedy, G.G. and Yamamoto, R.T. (1979).** A toxic factor causing resistance in a wild tomato to the tobacco hornworm and some other insects. *Ent. Expt. & Applications*, **26**: 121-126.
- Kennedy, G.G., Yamamoto, R.T., Dimock, M.B., Williams, W.G. and Bordner, J. (1981).** Effect of day length and light intensity on 2-tridecanone levels and resistance in *Lycopersicon hirsutum* f. *glabratum* to *Manduca sexta*. *J. Chem. Ecol.*, **7**: 707-716.
- Lawson, D.M., Lunde, C.F. and Mutschler, M.A. (1997).** Marker-assisted transfer of acylsugar mediated pest resistance from the wild tomato, *Lycopersicon pennellii*, to the cultivated tomato, *Lycopersicon esculentum*. *Molecular Breeding*, **3**: 307-317.

- Lemke, C.A. and Mutschler, M.A. (1984).** Inheritance of glandular trichomes in crosses between *Lycopersicon esculentum* and *Lycopersicon pennellii*. *J. American Soc. Hort. Sci.*, **109**: 592-596.
- Levin, D.A. (1973).** The role of trichomes in plant defense. *Quart. Rev. Biol.*, **48**: 3-15.
- Liedl, B.E., Lawson, D.M., White, K.K., Shapiro, J.A., Cohen, D.E., Carson, W.G., Trumble, J.T. and Mutschler, M.A. (1995).** Acylglucosides of the wild tomato *Lycopersicon pennellii* (Corr.) D'Arcy alters settling and reduces oviposition of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *J. Econ. Entomol.*, **88**: 742-748.
- Luck Will, L.C. (1943).** The genus *Lycopersicon*: an historical, biological, and taxonomic survey of the wild and cultivated tomatoes. Aberdeen University Studies No.120. Scotland, Aberdeen University Press, Aberdeen.
- Mckinney, K.B. (1938).** Physical characteristics on the foliage of beans and tomatoes that tend to control some small insect pests. *J. Econ. Entomol.*, **31**: 630-631.
- Maalipaard, C., Bas, N., Heusden, S.V., Kos, J., Pet, G., Verkerk, R., Vrielink, R., Zabel, P. and Lindhout, P. (1995).** Mapping QTLs for glandular trichome densities and *Trialeurodes vaporariorum* (greenhouse white fly) resistance in an F<sub>2</sub> from *Lycopersicon esculentum* x *lycopersicon hirsutum* f. *glabratum*. *Heredity*, **75**(4): 425-433.
- Momotaz, A., Scott J.W and Schuster, D.J. (2006).** Identification of *Bemisia argentifolii* resistance loci in *Lycopersicon hirsutum* accession LA1777. Presented in Tomato Breeders Roundtable and Tomato Quality Workshop, Tampa, Florida, from May 7-11, 2006.
- Mutschler, M.A. and Lobato, R. (2006).** Rapid generation and characterization of tomato lines with acylsugar mediated broad spectrum insect resistance. In proceedings of *Tomato Breeders Roundtable and Tomato Quality Workshop*, 7-11 May, 2006, Tampa, Florida.
- Mutschler, M.A., Doerge, R.W., Liu, S.C., Kuai, J.P., Liedl, B.E. and Shapiro, J.A. (1996).** QTL analysis of pest resistance in the wild tomato *Lycopersicon pennellii*: QTLs controlling acylsugar level and composition. *Theor. Appl. Genet.*, **92**: 709-718.
- Rodriguez, A.E., Tingey, W.M. and Mutschler, M.A. (1993).** Acylsugars produced by type IV trichomes of *Lycopersicon pennellii* deter settling of green peach aphid, *Myzus persicae*. *J. Econ. Entomol.*, **86**: 34-39.
- Sajjanar, G. M. (2002).** Genetic analysis and molecular mapping of components of resistance to shoot fly (*Atherigona soccata* Rond.) in sorghum [*Sorghum bicolor* (L.) Moench]. Ph. D. Thesis, University of Agricultural Sciences, Dharwad (India).
- Schuster, D.J. (1977).** Resistance in tomato accessions to the tomato pinworm, *J. Econ. Entomol.*, **70**: 434-436.
- Schwartz, P.H. and Klassen, A. (1981).** Estimate of losses caused by insects and mites to agricultural crops, pp. 15-77. In: *CRC Hand book of Pest Management in Agriculture*, Vol. I. D. (Ed. David Pimentel), CRC, Boca Raton, FL.
- Snyder, J.C. and Carter, C.D. (1984).** Leaf trichomes and resistance of *Lycopersicon hirsutum* and *L. esculentum* to spider mites. *J. American Soc. Hort. Sci.*, **109**: 837-843.
- Snyder, J. and Min, C. (2006).** Spidermite resistance and trichome secretions in *Lycopersicon hirsutum* LA2329 and hybrids with *L. esculentum*. In: *Proceedings of Tomato Breeders Roundtable and Tomato Quality Workshop*, 7-11 May, 2006, Tampa, Florida.
- Stefens, J.C. and Walters, D.S. (1991)** Biochemical aspects of glandular trichome mediated insect resistance in the Solanaceae. In: *Naturally occurring Pest Bioregulators* (Ed. Hedin, P.A), ACS Symp, Ser. 449. American Chemical Society, Washington, DC, pp. 136-149.
- Tanksley, S.D. (1993).** Mapping polygenes. *Annu. Rev. Genet.*, **27**: 205-233.
- Tanksley, S.D., Ganal, M.W., Prince, J.P., deVicente, M.C., Bonierbale, M.W., Broun, P., Fulton, T.M., Giovannani, J.J., Grandillo, S., Martin, G.B., Messeguer, R., Miller, J.C., Miller, L., Patterson, A.A.H., Pineda, O., Roder, M., Wing, R.A., Wu, W., and Young, N.D. (1992).** High density linkage molecular maps of the tomato and potato genomes. *Genet.s*, **132**: 1141-1160.
- Webb, R.E., Stoner, A.K. and Gentile, A.G. (1971).** Resistance to leaf miners in *Lycopersicon* accessions. *J. American Soc. Hort. Sci.*, **96**: 65-67.
- Weston, P.A., Johnson, D.A., Burton, H.T. and Snyder, J.C. (1989).** Trichome secretion composition, trichome densities and spider mite resistance of ten accessions of *Lycopersicon hirsutum*. *J. American Soc. Hort. Sci.*, **114**: 492-498.
- Williams, W.G., Kennedy, G.G., Yamamoto, R.T., Thacker, J.D. and Bordner, J. (1980).** 2-tridecanone: A naturally occurring insecticide from wild tomato *Lycopersicon hirsutum* f. *glabratum*. *Science*, **207**: 888-889.
- Zamir, D., Selila, Ben David, T., Rudich, J. and Juvick, J.A. (1984).** Frequency distributions and linkage relationships of 2-tridecanone in interspecific segregating generations of tomato. *Euphytica*, **33**: 481-488.

---

Received : December, 2007; Accepted : August, 2008