# BROAD SPECTRUM ARTHROPOD RESISTANCE MEDIATED BY LEAF ACYLSUGAR CONTENTS IN TOMATOES

**GABRIEL MASCARENHAS MACIEL**

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Dissertação apresentada à Universidade Federal de Lavras como parte das exigências do Programa de Pós-Graduação em Fitotecnia, para a obtenção do título de "Mestre".

Orientador

Prof. Dr. Wilson Roberto Maluf

LAVRAS
MINAS GERAIS - BRASIL
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APROVADA em 12 de fevereiro de 2008

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| Dr. Ernani Clarete da Silva | UNIFENAS |

Prof. Dr. Wilson Roberto Maluf
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(Orientador)

LAVRAS
MINAS GERAIS - BRASIL

***DEDICO***

***Aos meus pais,***

***Antonio dos Santos Maciel e Marisa Uzêda Mascarenhas Maciel,***

***pelo carinho e atenção dedicados durante toda a minha vida.***

***A minha namorada Jaqueline por todo amor, apoio e amizade.***

***Meus irmãos, Gustavo e Guilherme por toda compreensão.***

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MACIEL, Gabriel Mascarenhas. **Amplo espectro de resistência a artrópodes praga mediada pela presença de acilaçúcar em folíolos de tomateiro.** 2008. 34p. Dissertação (Mestrado em Fitotecnia) – Universidade Federal de Lavras, Lavras, MG.*

Três linhagens de tomate geneticamente melhoradas (TOM-687, TOM-688 e TOM-689) com alto teor de acilaçúcar (AA) e duas linhagens com baixo teor de AA foram utilizadas para obtenção de híbridos de tomateiro. A partir da combinação destas linhagens foram obtidos seis híbridos entre linhagens com baixo teor de AA x alto teor de AA (Híbridos com teores intermediários de AA), um híbrido entre duas linhagens com alto teor de AA. (Híbrido com alto teor de AA) e um híbrido entre duas linhagens com baixo teor de AA (Híbrido com baixo teor de AA). Após a obtenção dos híbridos todos os genótipos foram submetidos a testes de resistência as principais pragas do tomateiro (*Tetranychus urticae, Bemisia argentifolii e Tuta absoluta)* e comparados com as testemunhas *L.pennelli* 'LA-716' (Acesso selvagem com alto teor de AA) e TEX-154 (Híbrido comercial com baixo teor de AA). Os genótipos com alto teor de AA em todos os testes apresentaram maior resistência às pragas quando comparados com os genótipos de baixo teor. Os híbridos com teores intermediários de AA apresentaram resistência a *B. argentifolii* e *T. absoluta* tanto quanto os genótipos com alto teores de AA sendo que a maioria apresentando repelência a *T. urticae.* O alto teor de AA condicionou resistência a um amplo espectro de pragas. A escassez de linhagens de tomate geneticamente melhoradas com alto teor de AA não seria fator limitante para a obtenção de híbridos comerciais com resistência a pragas. Os híbridos obtidos a partir de combinações entre linhagens com alto teor de AA x baixo teor de AA apresentaram níveis satisfatórios de resistência as principais pragas do tomateiro.



Palavras-chave: acilaçúcar; resistência a pragas; *Tuta absoluta*; *Bemisia argentifolii*; *Tetranychus urticae*; insetos; ácaros.


*Comitê Orientador: Wilson Roberto Maluf – UFLA (Orientador), Ernani Clarete da Silva – UNIFENAS.

## ABSTRACT

MACIEL, Gabriel Mascarenhas. **Broad spectrum arthropod resistance mediated by leaf acylsugar contents in tomatoes.** 2008. 34p. Dissertação (Mestrado em Fitotecnia) – Federal University of Lavras, Lavras, MG, Brasil.*

Three elite tomato breeding lines (TOM-687, TOM-688, TOM-689) with high foliar acylsugar (AS) contents were obtained, and used along with two low AS lines (TOM-690, TOM-684) in hybrid combinations, in order to obtain six hybrids between one low AS line x one high AS line (= hybrids with intermediate AS levels), one hybrid between 2 high AS lines (=high AS hybrid), and one hybrid between two low AS lines (=low AS hybrid). These genotypes were tested for resistance to three different tomato pests (spider mites *Tetranychus urticae*, silverleaf whitefly *Bemisia argentifolii* and the South American tomato pinworm *Tuta absoluta*) along with hybrid TEX-154 (low AS) and/or *L.pennelli* 'LA-716' (high AS wild accession). In all three instances, high AS genotypes showed higher levels of pest resistance than low AS genotypes. Hybrids with intermediate AS levels showed resistances that were just as high as those of high AS genotypes for *B. argentifolii* and *T. absoluta*, and nearly as good as those for *T. urticae.* Acylsugars were confirmed as being a major component of the high levels of pest resistances found in *L. pennelli* - a component that was successfully introgressed into elite tomato breeding lines. Acylsugar-mediated pest resistance is effective against a broad spectrum of tomato pests. Given the current scarcity of elite high AS tomato breeding lines, the deployment of hybrids between one high AS line x one low AS line would be a quick viable alternative to obtain commercial pest resistance hybrids.



Key words: acylsugars; sugar esters; pest resistance; *Tuta absoluta*; *Bemisia argentifolii*; *Tetranychus urticae*; insects; mites.


*Guidance Committee: Wilson Roberto Maluf – UFLA (Adviser), Ernani Clarete da Silva – UNIFENAS.

# BROAD SPECTRUM ARTHROPOD RESISTANCE MEDIATED BY LEAF ACYLSUGAR CONTENTS IN TOMATOES

(Preparado de acordo com as normas da revista "*Euphytica"*).

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## ABSTRACT

Three elite tomato breeding lines (TOM-687, TOM-688, TOM-689) with high foliar acylsugar (AS) contents were obtained, and used along with two low AS lines (TOM-690, TOM-684) in hybrid combinations, in order to obtain six hybrids between one low AS line x one high AS line (= hybrids with intermediate AS levels), one hybrid between 2 high AS lines (=high AS hybrid), and one hybrid between two low AS lines (=low AS hybrid). These genotypes were tested for resistance to three different tomato pests (spider mites *Tetranychus urticae*, silverleaf whitefly *Bemisia argentifolii* and the South American tomato pinworm *Tuta absoluta*) along with hybrid TEX-154 (low AS) and/or *L.pennelli* 'LA-716' (high AS wild accession). In all three instances, high AS genotypes showed higher levels of pest resistance than low AS genotypes. Hybrids with intermediate AS levels showed resistances that were just as high as

those of high AS genotypes for *B. argentifolii* and *T. absoluta*, and nearly as good as those for *T. urticae.* Acylsugars were confirmed as being a major component of the high levels of pest resistances found in *L. pennelli* - a component that was successfully introgressed into elite tomato breeding lines. Acylsugar-mediated pest resistance is effective against a broad spectrum of tomato pests. Given the current scarcity of elite high AS tomato breeding lines, the deployment of hybrids between one high AS line x one low AS line would be a quick viable alternative to obtain commercial pest resistance hybrids.

Key words: acylsugars; sugar esters; pest resistance; *Tuta absoluta*; *Bemisia argentifolii*; *Tetranychus urticae*; insects; mites

## INTRODUCTION

Current tomato (*Lycopersicon esculentum* Mill.) cultivars are susceptible to an ample array of insect and mite species, often demanding chemical sprays with significant environmental impact. Wild taxa of *Lycopersicon* are reported to resist many tomato pests (Gentile & Stoner 1968; Gentile et al. 1968, 1969; Rick 1973; Kennedy & Yamamoto 1979; Williams et al. 1980; França et al. 1984a,b; Ecole et al. 1999), but they do not have immediate commercial value. Introgression of their arthropod resistance into tomato cultivars is often limited by difficulty in maintaining the uniform infestations necessary to select for resistance (Stevens & Rick 1986), and direct selection for pest resistance is usually an expensive and slow process.

Indirect selection techniques based on correlated traits with high heritability could be used to speed up introgression (Juvik et al. 1982). Several allelochemicals present in wild *Lycopersicon* taxa have been associated with pest resistance: methyl-ketones such as 2-tridecanone in *L. hirsutum* var. *glabratum* (Williams et al. 1980; Fery & Kennedy 1987; Weston et al. 1989; Eigenbrode & Trumble 1993a,b; Maluf et al. 1997; Gonçalves et al. 1998), sesquiterpenes in *L. hirsutum* var. *hirsutum* (Snyder et al. 1987; Eigenbrode et al. 1994; Azevedo et al. 1999), acylsugars in *L. pennellii* (Goffreda et al. 1989). Selection for high content of these allelochemicals would therefore seem to be efficient techniques of indirect selection for pest resistance: indeed, there is strong evidence that selection for either high 2-tridecanone (2-TD), sesquiterpene (zingiberene) or acylsugar contents will increase the levels of resistance to the South American tomato pinworm (Maluf et al., 1997; Azevedo et al. 2003; Resende et al., 2006), to the silverleaf whitefly (Freitas et al. 2002;

Resende, 2003) and to spider mites (Gonçalves et al., 1998; Maluf et al., 2001; Resende, 2003; Gonçalves et al., 2006).

*Lycopersicon pennellii* accessions (particularly the widely studied accession LA-716) show a very high level of resistance to the whitefly *Bemisia tabaci/Bemisia argentifolii* complex, a major tomato pest worldwide, as well as to aphids (*Macrosiphum euphorbiae, Myzus persicae*), to spider mites *Tetranychus* spp., and to Lepidopteran pests (Gentile et al. 1968, 1969; Juvik et al. 1982; Goffreda et al. 1989) including the South American tomato pinworm *Tuta* (= *Scrobipalpula* = *Scrobipalpuloides*) *absoluta* (França et al., 1989). Multiple pest resistance of *L. pennellii* 'LA-716' is reportedly due to the presence of type IV glandular trichomes that occupy the whole surface of the plant, together with the viscous phytochemicals that they secrete (Gentile et al. 1968; Goffreda et al. 1989). These phytochemicals are glucose and sucrose esters of fatty acids (acylsugars), and can play an important role in the resistance to tomato pests. Purified acylsugars act by reducing feeding of the aphids *Macrosiphum euphorbiae* and *Myzus persicae*, by reducing feeding, larval development and survival of *Helicoverpa zea* and *Spodoptera exigua*, and by reducing oviposition and feeding of the leaf miner *Liriomyza trifolii* and of the silver leaf whitefly *Bemisia argentifolii* (Goffreda et al. 1988, 1989; Hawthorne et al. 1992; Rodriguez et al. 1993; Juvik et al. 1994; Liedl et al. 1995).

The inheritance of acylsugar contents was studied in the interspecific cross between *L. esculentum* x *L. pennellii* 'LA-716', and found to be under control of a single major locus, with incomplete dominance of the *L. esculentum* allele for low-acylsugar content over the *L. pennellii* allele for high content (Resende et al. 2002). The degree of dominance was estimated to be -0.74. Because these studies of inheritance may be distorted by deviations from Mendelian segregation in this wide cross (Sawant 1958; Zamir & Tadmor 1986), they were repeated later in a segregating ($F_2$) population from the third

backcross to *L. esculentum* after the original cross with *L. pennellii* 'LA-716' (Gonçalves et al. 2007), and the hypothesis of monogenic inheritance was further confirmed. This simple mode of inheritance favours introgression of the high acylsugar trait into the cultivated tomato, and several tomato breeding lines with high acylsugar contents and good horticultural qualities are now available in our breeding programme.

Similarly to what happens to *L. pennellii* 'LA-716' itself, high acylsugar contents in tomato lines derived from the interspecific cross with this accession have been shown to be largely responsible for resistance to a broad array of tomato pests. Acylsugars restricted nymphal development of the silverleaf whitefly *Bemisia argentifollii* (Resende 2003), drastically reduced feeding damage caused by the South American tomato pinworm *Tuta absoluta* (Resende et al. 2006), and increased repellence to spider mites *Tetranychus urticae* (Resende et al. 2002) and *Tetranychus evansi* (Gonçalves 2006). Selection of high acylsugar *L. esculentum* lines would therefore seem to be an effective way of breeding for a broad spectrum of pest resistances in tomato.

A great effort in tomato breeding in the last decades has been dedicated to the development of hybrid cultivars. Breeding of pest resistant hybrids could be impaired by the current limited availability of high acylsugar lines with good horticultural quality, associated with the essentially recessive nature of its inheritance (Resende et al. 2002; Gonçalves et al. 2007). The number of hybrids with good horticultural quality could be greatly increased if only one high acylsugar parental line should be necessary, but hybrids thus developed could have acylsugar levels only slightly higher than those of the low acylsugar parent, and may not present satisfactory levels of pest resistance. A critical assessment of the pest resistance levels in hybrids between high acylsugar lines x low acylsugar lines is therefore needed.

High acylsugar line x low acylsugar line tomato hybrids were therefore tested for resistance to three major arthropod pests __ the spider mites *Tetranychus urticae,* the silverleaf whitefly *Bemisia argentifolii* and the South American tomato pinworm *Tuta absoluta* __, and compared to the resistance levels of their parental lines and of selected commercial checks.

## MATERIALS AND METHODS

*Tomato lines and hybrids tested.* Contrasting genotypes with reference to acylsugar contents were used in this study (Table 1). The high acylsugar (AS) accession *Lycopersicon pennellii* 'LA-716', the low acylsugar *L. esculentum* line TOM-684 and the commercial hybrid TEX-154 were used as check treatments. TOM-687, TOM-688 and TOM-689 are proprietary pre-commercial large-fruited high acylsugar breeding lines from HortiAgro Sementes Ltda. (Ijaci-MG, Brazil) derived from the interspecific cross *L. esculentum* x *L. pennellii* 'LA-716', followed by 3 backcrosses do *L. esculentum.* During the course of the backcross breeding programme, plants were selected primarily for high foliar AS contents in the segregating (F2) generation of each backcross, and subsequently tested for resistance to either spider mites *Tetranychus* spp*.,* to the South American tomato pinworm *Tuta absoluta*, and/or to the silverleaf whitefly *Bemisia argentifolii* (Resende, 2003; Gonçalves, 2006). Line TOM-690 is a pre-commercial large-fruited low acylsugar breeding line that was selected in the third backcross generation for low rather than high AS contents, and shares similar genetic background to TOM-687, TOM-688 and TOM-689, except for the foliar AS levels. TOM-687, TOM-688, TOM-689, TOM-690 and TOM-684 were obtained from backcrosses in which the proprietary elite tomato line TOM-

584 was used a recurrent parent, and are similar (though not identical) in fruit size, shape and horticultural plant traits. TOM-687, TOM-688, TOM-689, TOM-690 and TOM-684 were combined in order to obtain six hybrids between one low AS line x one high AS line, one hybrid between 2 high AS lines, and one hybrid between two low AS lines (Table 1).

*Assessment of acylsugar contents in tomato genotypes.* Plants from all genotypes were grown (1 plant per 5 L plot) and sampled ca. 60 days after germination for their foliar acylsugar contents. Thirty plants were sampled per genotype. Acylsugars in tomato leaflets were quantified by the method described by Resende et al. (2002). Six leaf disks were taken from the upper third portion of each tomato plant with a 3/8" diameter cork borer (4.2 $cm^2$ total leaf area), and placed in a test tube with 1 ml dichloromethane for extraction of acylsugars. The tubes were stirred with a Vortex mixer for 30 s. Leaflets were removed, the solvent was evaporated, and 0.5 ml 0.1 N sodium hydroxide dissolved in methanol (Merck) was added. The mixture was evaporated, the residue was maintained at $100^o$ C and methanol was added three times at 2-min intervals to guarantee the completion of the saponification reaction. After evaporation of the methanol, the residue was dissolved in 0.4 ml water. Sucrose was converted into glucose and fructose by adding 0.1 ml 0.04 N hydrochloric acid, boiling for 5 min and cooling. The Sommogy-Nelson reagent (Nelson 1944) was added and the mixture was heated to boiling for 10 min and cooled to room temperature in a stream of cold water. Arsenomolibdate (0.5 ml) was added, the solution was stirred on a Vortex mixer for 15 s and the absorbance was measured at 540 nm in a spectrophotometer (Nelson 1944). A standard curve was determined using standard glucose solutions, and absorbance readings were converted to concentrations expressed in nmol/$cm^2$ of leaf area.

*Mite repellence tests (thumbtack bioassay).* Spider mites were collected from naturally infested bean *Phaseolus vulgaris* plants, confirmed as being

*Tetranychus urticae* at the Department of Entomology, Universidade Federal de Lavras, Lavras-MG-Brazil, and thereafter reared onto susceptible tomato plants cv. Santa Clara. Plants were grown in 3.5 L pots filled with artificial substrate, and reserved for the mite repellence test. The repellence of the tomato genotypes to *Tetranychus urticae* was assessed with the thumbtack bioassay developed by Weston & Snyder (1990). Fully expanded tomato leaflets of similar sizes were removed from the upper third portion of flowering plants. One leaflet of each plant was attached to a sheet of styrofoam through a metallic thumbtack (9 mm diameter) placed in the center of its adaxial surface, and leaflets from all genotypes under test were randomly placed onto the styrofoam sheet, to comprise one replication. Ten replications (plants) were used per genotype. Ten female spider mites were transferred with a fine artist's brush to the head of each thumbtack. The trial was carried out in a chamber at 16º ± 1ºC and 64 ± 4% relative humidity. The shortest distances between each mite specimen and the thumbtack edge were considered as being the distances covered the mites onto the adaxial leaf surface, and were recorded after 20, 40 and 60 minutes. Mites which stayed on the thumbtack were considered to have travelled a distance equal to zero. Shorter distances travelled by mites onto the leaf surface were taken as an indication of higher levels of mite repellence (resistance).

*Test of resistance to the silverleaf whitefly Bemisia argentifolii.Bemisia argentifolii* was reared in tomato plants cv. Santa Clara kept in plastic houses for the necessary plant infestations. Five 80-day old plants from each of the 15 tomato genotypes (Table 1), grown in 3.5 L pots, were exposed to insect infestation for 48 hours, and subsequently removed for oviposition counts. Four leaflets of the upper third portion of each plant were sampled for oviposition counts. The number of eggs per 2 $cm^2$ leaf area was counted with the aid of a 80X stereomicroscope, and the leaflets sampled were tagged for future counts of last instar nymphs. Plants were then placed in a non-infested greenhouse, and the

number of last instar nymphs per 2 $cm^2$ leaf area was counted 20 days later in tagged leaflets, also with the aid of the stereoscope. Average temperatures and relative humidities from infestation through the nymph count dates varied respectively from 18.2 to 28$^oC$ and from 82 to 100%. Lower oviposition and/or lower nymph counts were taken as indicative of higher levels of resistance to *Bemisia argentifolii.*

*Test of resistance to the South American tomato pinworm* <u>*Tuta absoluta*</u>*.* Tomato cv. Santa Clara plants infested with *Tuta absoluta* larvae and adults were continuously kept in a 50 $m^2$ screenhouse in order to secure high insect populations. Seeds of all genotypes (Table 1) except LA-716 were sown in seedling trays in a *Tuta*-free greenhouse, transplanted to 5 L pots 25 days later, and transfered to the infested screenhouse 54 days after the sowing date. Five plants of each of the genotypes were arranged in a completely randomized design in the screenhouse in order to be exposed to infestation by the insect. Throughout the infestation period, temperatures ranged from 17.5 to 28.4$^oC$, and relative humidity from 87.5 to 100%. Ten days after the infestation date, an oviposition count was taken by sampling 2 $cm^2$ areas in previously tagged leaflets from the upper third portion of each plant. Oviposition counts were repeated 3 more times at 2-day intervals. Maximum egg counts were obtained in the second sampling date (12 days after infestation), and these data were chosen to represent oviposition by *Tuta absoluta.* Plants were scored for insect feeding damage, starting 20 days after infestation, with evaluations at 2-day intervals until the 36th day after infestation. Scoring systems (Maluf et al., 1997) were used (Table 2) to rate leaflet lesion type (LLT), percent leaflets attacked (PLA) and overall plant damage (OPD). LLT will more likely reflect feeding deterrence, because it is less biased by differences in ovipositioning. PLA will likely reflect the differences in ovipositioning, whereas OPD will reflect both differences in ovipositioning and feeding deterrence. The areas under the curves of *feeding*

*damage x time* for LLT, PLA and OPD were taken as measures of the degree of resistance to *Tuta absoluta*, with lower areas representing higher levels of resistance.

*Statistical analyses.* Analyses of variances were performed for data on acylsugar contents, mite repellence, and resistance to *T. absoluta* and *B. argentifolii*, and genotype means were separated by Duncan´s multiple range test. For the pest resistance assays, selected contrasts among groups of genoypes with different acylsugar contents were calculated (Table 3), in order to characterize possible differences in pest resistance levels as a function of allelochemical content.

## RESULTS AND DISCUSSION

*Assessment of acylsugar contents in tomato genotypes.* Acylsugar (AS) levels in lines selected for high AS content (TOM-687, TOM-688 and TOM-689) were indeed significantly higher than in the low AS genotypes [TOM-690, TOM-684, TEX-154, and F1(TOM-684 x TOM-690)] (Table 4), but lower than those found in *L. pennellii* 'LA-716'. Acylsugar contents are controlled by the action of a single gene locus (Resende et al., 2002, Gonçalves et al., 2007), therefore lower levels in the high AS *L. esculentum* lines when compared to *L. pennellii* LA-716 can be accounted for by differences in the genetic backgrounds of these *Lycopersicon* species. The AS content of the sole high AS x high AS hybrid [($F_1$(TOM-687 x TOM-689)] was similar to those of the high AS *L. esculentum* lines (Table 4). AS levels in the six hybrids between low AS x high AS lines were usually intermediate between those of high AS and low AS genotypes (Table 4), and the degree of dominance estimates for the trait had a mean value of 0.1125 (Table 4) __ an indication of predominantly additive gene action. The

degrees of dominance estimated by Resende et al.(2002) and Gonçalves et al. (2007) were lower than our current results, and indicated incomplete dominance for the *L. esculentum* allele that controls low AS. A similar indication of incomplete dominance was found by Saeidi et al. (2007) in crosses with another *L.pennellii* acession ('LA 2963'). It should be noted, however, that our degree of dominance estimates varied widely among the six hybrids considered: the estimated value of 0.1125 is subject to a substantial sampling error (Table 4), and therefore cannot be taken to contradict the results by those previous authors. In any event, it is clear that AS levels in hybrids between low AS x high AS lines are expected to be intermediate between those of high AS and low AS genotypes, and this set of six hybrids will be referred to as "intermediate AS genotypes" in further discussions along this paper.

*Mite repellence tests (thumbtack bioassay).* Distances travelled by spider mites onto the tomato leaf surface after 20, 40 or 60 minutes were shorter in high AS than in low AS genotypes, whether these be lines or hybrids (Table 5, contrasts C10, C11). Mites travelled shorter distances onto high AS lines than onto either low AS lines or the commercial hybrid check TEX-154 (contrasts C1, C2, Table 5), whereas low AS lines did not differ from TEX-154 (C3). The only discrepant result was that obtained for line TOM-687, where distances travelled by the mites were significantly longer than those in the other two high AS lines (TOM-688, TOM-687), but this fact could be accounted for by sampling errors, because hybrids in which TOM-687 was used as a parent were amongst the treatments with shortest mean distances travelled (Table 5). Mite repellence in the hybrid between low AS x low AS lines was similar to that of other low AS genotypes (contrasts C7, C9), and significantly lower than that in high AS lines (contrast C6), while repellence in the high AS x high AS hybrid was higher than in low AS genotypes (contrasts C5, C8) and generally similar to that in high AS lines (contrast C4). These results confirm the conclusions by Resende et al. (2002) and

Gonçalves (2006) that acylsugars are major components of repellence to spider mites, *Tetranychus urticae* and *T. evansi,* respectively, in tomato populations derived from the interspecific cross *L. esculentum* x *L. pennellii.* Intermediate AS genotypes showed slightly lower repellence to mites than high AS lines at 20 and 40 minutes, but the differences between these genotypes were non-significant after 60 minutes (Contrast C14); they showed, however, higher repellence levels to spider mites than all low AS genotypes, for all time intervals tested (Contrasts C13, C15, C16). AS levels in low AS x high AS hybrids are therefore sufficient to promote increased levels of repellence to spider mites, and can by themselves explain the acceptable levels of resistance to *Tetranychus urticae* found in heterozygous genotypes __ a conclusion that is in contrast with that of Saeidi et al. (2007), who attributed the mite resistance found in heterozygous $F_1$ genotypes solely to other factors besides AS also present in *L. pennellii*. The fact that *L. pennellii* 'LA-716' showed higher levels of mite repellence than all other genotypes, whether high (Table 5, contrasts C18, C20), low (contrasts C19, C21) or intermediate AS genotypes (contrast C22) indicates, however, that other factors present in LA-716 may also contribute to the high levels of mite repellence in this wild accession __ a conclusion that is in only partial agreement with Saeidi et al. (2007)'s more emphatic statement.

*Test of resistance to Bemisia argentifolii.* Both whitefly oviposition and nymph survival were highly affected by acylsugar levels in tomato genotypes (Table 6). Oviposition and nymph survival were significantly lower in high AS than in low AS genotypes (Table 6, contrasts C1, C2, C5, C6, C8, C10, C11). No significant differences were found in comparisons among different low AS genotypes (Table 6, contrasts C3, C7, C9, C12) or among different high AS genotypes (Table 6, contrasts C4, and means T1,T2,T3). These results indicate a clear decrease in oviposition and nymph survival in high AS genotypes, supporting previous reports of acylsugar-mediated plant resistance to whiteflies by Liedl et

al. (1995) and Resende (2003). Hybrids between a low AS line x a high AS line had substantially lower oviposition counts and nymph survival than low AS genotypes (Table 6, contrasts C13, C15, C16), and did not differ from counts shown by homozygous high AS genotypes (Table 6, contrasts C14, C17). AS levels in intermediate AS genotypes were high enough to ensure high levels of resistance to *Bemisia argentifolii.* The fact that *L. pennellii* 'LA-716' showed higher levels of whitefly resistance than all other genotypes, whether high (Table 6, contrasts C18, C20), low (contrasts C19, C21) or intermediate AS genotypes (contrast C22) indicates, however, that other factors present in LA-716 may also contribute to the high levels of resistance in this wild accession __ a conclusion previously found valid for *T. urticae* also.

*Test of resistance to Tuta absoluta. T. absoluta* oviposition was highly affected by acylsugar levels present in tomato genotypes (Table 7). Oviposition and nymph survival were significantly lower in high AS than in low AS genotypes (Table 7, contrasts C1, C2, C5, C6, C8, C10, C11), even though one of the high AS lines (TOM-687) presented higher counts than the other two (TOM-688, TOM-689). No significant differences were usually found in comparisons among different low AS genotypes (Table 7, contrasts C3, C7, C12), but egg counts in the hybrid $F_1$(TOM-684 x TOM-690) were slighlty but significantly lower than in the commercial hybrid check TEX-154 (contrast C9). Hybrids between a low AS line x a high AS line had usually lower oviposition counts than low AS genotypes (Table 6, contrasts C13, C15), in spite of the fact that in one case (contrast C16) the difference was not high enough to be detected as significant. These intermediate AS genotypes as a group did not differ in oviposition from the set of high AS lines (contrast C14), but had lower egg counts than the sole low AS x low AS hybrid tested (contrast C16). Oviposition counts in these intermediate AS genotypes are at least comparable to those of the high AS genotypes, and lower than those of low AS genotypes. A consistent tendency of

high AS genotypes to present lower *Tuta absoluta* egg counts is clear. In a previous report (Resende et al., 2006), *Tuta absoluta* oviposition was not found to be related to AS levels. That assay included plants in the first backcross generation to *L. esculentum* after the original cross *L. esculentum* x *L. pennellii,* maintained via rooted cuttings; in the current trial, plants had two additional backcrosses towards *L. esculentum*, and were propagated via seeds, which could account for the differences in the results obtained.

Damage scores (LLT, PLA and OPD, measured through de areas under the curves *damage x time* over a period that spanned up to the 36th day after infestation, showed a similar trend relative to the AS levels (Table 8). LLT, PLA and OPD scores were significantly lower in high AS than in low AS genotypes (Table 8, contrasts C1, C2, C5, C6, C8, C10, C11). No significant differences were generally found in comparisons among different low AS genotypes (Table 8, contrasts C3, C7, C9, C12), with few exceptions (contrast C9 for PLA/OPD, Contast C7 for PLA). Non-significant differences were also the rule for comparisons among different high AS genotypes (Table 8, contrast C4), with a single exception of the contrast between the "High AS lines vs. $F_1$(high AS line x high AS line)" (contrast C4 for LLT, Table 8), which ultimately reflects the even lower damage levels presented by the $F_1$(high AS line x high AS line) over the high AS breeding lines themselves. Once again, there is evidence that high acylsugar contents are reflected in lower feeding damage caused by *Tuta absoluta* (higher levels of insect resistance), reinforcing similar results previously obtained by Resende et al. (2006) and Maciel et al.(2007). Damages in high AS genotypes are lower whether the OPD alone or its components LLT and PLA are considered (Table 8).

Hybrids between a low AS line x a high AS line showed significantly lower damage scores for LLT, PLA and OPD than low AS genotypes (Table 8, contrasts C13, C15, C16), and did not differ from scores shown by high AS lines

(Table 8, contrasts C14). These intermediate AS genotypes had only slightly higher damage scores than the hybrid $F_1$(high AS line x high AS line) [= $F_1$(TOM-687 x TOM-689)] __ the genotype with lowest damage scores. Similarly to what happened with reference to resistances to *T. urticae* and to *B. argentifolii,* AS levels in intermediate AS genotypes were high enough to ensure high levels of resistance to *Tuta absoluta.*

**CONCLUSIONS**

Our current data reinforces previous inferences (Goffreda et al. 1989; Gonçalves 2006; Hawthorne et al. 1992; Juvik et al. 1994; Liedl et al. 1995; Resende et al. 2002; Resende et al. 2006; Rodriguez et al. 1993; Saeidi et al. 2007) that acylsugars derived from *L. pennellii* are largely responsible for high levels of pest resistance: selection for high AS contents indeed led to pest resistant improved tomato lines (TOM-687, TOM-688 and TOM-689). Acylsugars may not be the sole factor involved in the high levels of pest resistance found in *L. pennellii* 'LA 716', as indicated by its higher degree of resistance to spider mites and *Bemisia argentifolii* when compared to the *L. esculentum* high AS lines. Nonetheless, acylsugars are a major component of that resistance (as our data demonstrates), are simply inherited (Resende et al., 2002; Gonçalves et al., 2007) and high AS levels can be easily introgressed into elite tomato breeding lines.

The advanced *L. esculentum* lines bred for increased foliar AS contents (TOM-687, TOM-688, TOM-689) were demonstrated to be resistant to at least three taxonomically divergent tomato pests __ the insects *Tuta absoluta* and *Bemisia argentifolii,* and the two-spotted spider mite *Tetranychus urticae.* This

indicates that acylsugars mediate resistance to a wide array of tomato pests, and that the high AS lines may also be resistant to pests such as the potato aphid *Macrosiphum euphorbiae* (Goffreda et al., 1989), the green peach aphid *Myzus persicae* (Rodriguez et al., 1993), the leafminer *Liriomyza trifolii* (Hawthorne et al., 1992), the tomato fruitworm *Helicoverpa zea,* the beet armyworm *Spodoptera exigua* (Juvik et al., 1994), among others. Whether or not AS levels in TOM-687, TOM-688 and TOM-689 would be high enough to promote acceptable degrees of resistance to these other tomato pests will remain to be determined.

Acylsugar levels in hybrid genotypes between low AS x high AS lines proved to be intermediary between those of the parental lines. Previous reports indicated that the allele from *L. pennellii* that controls high AS contents is recessive, but with an incomplete degree of dominance (Resende et al., 2002; Gonçalves, 2006). In any event, it is expected that AS levels in these hybrids should be higher than in current low-AS tomato genotypes. Our results demonstrated that these intermediate AS hybrid genotypes possess satisfactory levels of pest resistances __ similar to the resistance levels shown by homozygous high AS lines in the case of *Bemisia argentifolii* and *Tuta absoluta*, and only slightly lower than those of the high AS lines in the case of *Tetranychus urticae*. The practical implication of this fact is that hybrids resistant to a broad array of tomato pests can be developed with only one of the parents being a high AS line: should two high AS parents be necessary to obtain a pest-resistant hybrid, tomato breeding would be severely limited by the current scarcity of high AS elite breeding lines. We can now suggest that even with a scarce number of elite high AS lines, an ample number of putative pest-resistant commercial hybrids can be easily developed through a suitable choice of second parents within an array of elite low AS inbreds.

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Table 1. Genotypes tested for leaf acylsugar (AS) contents and for resistance to spider mites *Tetranychus urticae*, to the silverleaf whitefly *Bemisia argentifollii* and to the South American tomato pinworm *Tuta absoluta*[(a)]

| Treatment Number (ID) | Genotype | Description |
|---|---|---|
| T1 | TOM-687 | Pre-commercial advanced tomato breeding line with high leaf acylsugar (AS) contents |
| T2 | TOM-688 | Pre-commercial advanced tomato breeding line with high leaf acylsugar contents |
| T3 | TOM-689 | Pre-commercial advanced tomato breeding line with high leaf acylsugar contents |
| T4 | TOM-690 | Pre-commercial advanced tomato breeding line with low leaf acylsugar contents |
| T5 | TOM-684 | Commercial advanced tomato breeding line with low leaf acylsugar contents |
| T6 | F1 (TOM-684 x TOM-687) | Experimental $F_1$ hybrid (low AS line x high AS line) |
| T7 | F1 (TOM-684 x TOM-688) | Experimental $F_1$ hybrid (low AS line x high AS line) |
| T8 | F1 (TOM-684 x TOM-689) | Experimental $F_1$ hybrid (low AS line x high AS line) |
| T9 | F1 (TOM-690 x TOM-687) | Experimental $F_1$ hybrid (low AS line x high AS line) |
| T10 | F1 (TOM-690 x TOM-688) | Experimental $F_1$ hybrid (low AS line x high AS line) |
| T11 | F1 (TOM-690 x TOM-689) | Experimental $F_1$ hybrid (low AS line x high AS line) |
| T12 | F1 (TOM-687 x TOM-689) | Experimental $F_1$ hybrid (high AS line x high AS line) |
| T13 | F1 (TOM-684 x TOM-690) | Experimental $F_1$ hybrid (low AS line x low AS line) |
| T14 | TEX-154 | Commercial $F_1$ hybrid check (low AS line x low AS line) |
| T15 | LA-716 | *Lycopersicon pennellii*, high AS accession |

[(a)] T15 was not included in the *Tuta absoluta* assays.

Table 2. Scoring systems utilized for evaluation of leaflet lesion type (LLT), overall plant damage (OPD) and percent leafletls attacked (PLA) in plants infested by the South American tomato pinworm *Tuta absoluta.*

| |
|---|
| LLT (= Leaflet lesion type) Scores: |
| 0 = no lesion. |
| 1 = lesions small, rare. |
| 2 = small to medium-size lesions, usually towards the leaflet borders. |
| 3 = medium to large-size lesions, coalescent; foliar borders deformed. |
| 4 = large-size lesions, coalescent; leaflets deformed. |
| 5 = whole leaflet surface lesioned. |
| OPD ( = Overall Plant Damage) Scores: |
| 0 = no leaf damage. |
| 1 = up to 5% total leaf area damaged; small, non-coalescent lesions. |
| 2 = >5% up to 20% total leaf area damaged; small, non-coalescent lesions. |
| 3 = >20% up to 50% total leaf area damaged; medium to large-size lesions. |
| 4 = >50% up to 80% total leaf area damaged; lesions numerous, large, coalescent. |
| 5 = >80 to 100% total leaf area damaged. |
| PLA ( = Percent leaflets attacked) Scores: |
| 0 = no leaflets attacked. |
| 1 = >0% to 5% leaflets attacked. |
| 2 = >5% to 20% leaflets attacked. |
| 3 = >20% to 50% leaflets attacked. |
| 4 = >50% to 80% leaflets attacked. |
| 5 = >80% to 100% leaflets attacked. |

Table 3. Contrasts of interest used for comparisons among genotypes and/or groups of genotypes with different acylsugar (AS) contents

| Contrast ID | Contrast Estimate | Description |
|---|---|---|
| C1 | [(T1+T2+T3)/3 - (T4+T5)/2] | High AS lines vs. Low AS lines |
| C2 | [(T1+T2+T3)/3 - T14] | High AS lines vs. Commercial hybrid check |
| C3 | [(T4+T5)/2 - T14] | Low AS lines vs. Commercial hybrid check |
| C4 | [(T1+T2+T3)/3 –T12] | High AS lines vs. $F_1$(high AS line x high AS line) |
| C5 | [(T4+T5)/2 - T12] | Low AS lines vs. $F_1$(high AS line x high AS line) |
| C6 | [(T1+T2+T3)/3 –T13] | High AS lines vs. $F_1$(low AS line x low AS line) |
| C7 | [(T4+T5)/2 - T13] | Low AS lines vs. $F_1$(low AS line x low AS line) |
| C8 | [T12 - T14] | Experimental $F_1$(high AS line x high AS line) vs. Commercial hybrid check |
| C9 | [T13 - T14] | Experimental $F_1$(low AS line x low AS line) vs. Commercial hybrid check |
| C10 | [(T1+T2+T3+T12)/4 - (T4+T5+T13+T14)/4] | High AS genotypes vs. Low AS genotypes |
| C11 | [(T1+T2+T3+T12)/4 - T14] | High AS genotypes vs. Commercial hybrid check |
| C12 | [(T4+T5+T13)/3 - T14] | Low AS genotypes vs. Commercial hybrid check |
| C13 | [(T6+T7+T8+T9+T10+T11)/6 -T14] | Hybrids $F_1$(low AS line x high AS line) vs. Commercial hybrid check |
| C14 | [(T6+T7+T8+T9+T10+T11)/6 - (T1+T2+T3)/3] | Hybrids $F_1$(low AS line x high AS line) vs. High AS lines |
| C15 | [(T6+T7+T8+T9+T10+T11)/6 - (T4+T5)/2] | Hybrids $F_1$(low AS line x high AS line) vs. Low AS lines |
| C16 | [(T6+T7+T8+T9+T10+T11)/6 - T13] | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid $F_1$(low AS line x low AS line) |
| C17 | [(T6+T7+T8+T9+T10+T11)/6 - T12] | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid $F_1$(high AS line x high AS line) |
| C18 | [(T1+T2+T3)/3 –T15] | High AS lines vs. *L. pennellii* 'LA-716' |
| C19 | [(T4+T5)/2 - T15] | Low AS lines vs. *L. pennellii* 'LA-716' |
| C20 | [T12 - T15] | Hybrid $F_1$(high AS line x high AS line) vs. *L. pennellii* 'LA-716' |
| C21 | [T14 - T15] | Commercial hybrid check (low AS x low AS) vs. *L. pennellii* 'LA-716' |
| C22 | [(T6+T7+T8+T9+T10+T11)/6 - T15] | Hybrids $F_1$(low AS line x high AS line) vs. *L. pennellii* 'LA-716' |

Table 4. Acylsugar contents (nanomols per $cm^2$ leaflet area) in tomato lines and their hybrids, and estimates of the degree of dominance in hybrids between high acylsugar x low acylsugar lines.

| Treatment Number (ID) | Genotype | Acylsugar contents ($nmol.cm^{-2}$) | Estimated degree of dominance |
|---|---|---|---|
| T1 | TOM-687 | 20.45 BC | - |
| T2 | TOM-688 | 21.58 B | - |
| T3 | TOM-689 | 19.88 BC | - |
| T4 | TOM-690 | 11.97 G | - |
| T5 | TOM-684 | 15.36 EF | - |
| T6 | F1 (TOM-684 x TOM-687) | 18.19 CD | 0.1137 |
| T7 | F1 (TOM-684 x TOM-688) | 16.49 DE | -0.6366 |
| T8 | F1 (TOM-684 x TOM-689) | 15.92 DEF | -0.7522 |
| T9 | F1 (TOM-690 x TOM-687) | 19.88 BC | 0.8655 |
| T10 | F1 (TOM-690 x TOM-688) | 16.49 DE | -0.0593 |
| T11 | F1 (TOM-690 x TOM-689) | 20.45 B | 1.1441 |
| T12 | F1 (TOM-687 x TOM-689) | 21.58 B | - |
| T13 | F1 (TOM-684 x TOM-690) | 14.79 EF | - |
| T14 | TEX-154 | 13.66 FG | - |
| T15 | LA-716 | 39.10 A | - |
| | | **Mean degree of dominance=** | 0.1125 ± 0.771 |

Means followed by the same letter within the column do not differ from each other by Duncan's multiple range test (p=0.05)

Table 5. Distances travelled by spider mites *T. urticae* onto the tomato leaflet surface after 20, 40 and 60 minutes, and contrast of interest among genotypes and/or groups of genotypes.

| | | Distances travelled [(x)] by mites (mm) after: | | |
|---|---|---|---|---|
| | **Genotypes** | **20 min** | **40 min** | **60 min** |
| T1 | TOM-687 | 14.10 BCD | 14.76 ABC | 16.94 A |
| T2 | TOM-688 | 4.47 GH | 4.26 GH | 6.61 CD |
| T3 | TOM-689 | 5.54 FGH | 5.39 FGH | 6.81 CD |
| T4 | TOM-690 | 19.11 A | 16.80 AB | 17.67 A |
| T5 | TOM-684 | 16.22 ABC | 16.43 ABC | 17.40 A |
| T6 | F1 (TOM-684 x TOM-687) | 8.60 EFG | 8.13 EFG | 8.99 BCD |
| T7 | F1 (TOM-684 x TOM-688) | 12.61 CDE | 12.95 BCD | 9.76 BC |
| T8 | F1 (TOM-684 x TOM-689) | 16.70 ABC | 18.03 A | 19.88 A |
| T9 | F1 (TOM-690 x TOM-687) | 9.71 DEF | 8.90 DEFG | 8.86 BCD |
| T10 | F1 (TOM-690 x TOM-688) | 11.27 ED | 11.89 CDE | 14.15 A |
| T11 | F1 (TOM-690 x TOM-689) | 13.32 BCDE | 9.49 DEF | 8.57 BCD |
| T12 | F1 (TOM-687 x TOM-689) | 6.07 FG | 6.02 FGH | 5.93 CD |
| T13 | F1 (TOM-684 x TOM-690) | 17.53 AB | 17.90 A | 19.97 A |
| T14 | TEX-154 | 19.23 A | 18.09 A | 16.67 A |
| T15 | LA-716 | 1.06 I | 2.11 I | 2.94 D |

| | | Contrast estimates [(y)] : | | |
|---|---|---|---|---|
| | **Contrasts of interest** | **20 min** | **40 min** | **60 min** |
| C1 | High AS lines vs. Low AS lines | -9.62 ** | -8.47 ** | -7.41 ** |
| C2 | High AS lines vs. Commercial hybrid check | -11.19 ** | -9.95 ** | -6.55 ** |
| C3 | Low AS lines vs. Commercial hybrid check | -1.56 ns | -1.47 ns | 0.86 ns |
| C4 | High AS lines vs. $F_1$(high AS line x high AS line) | 1.96 ns | 2.11 ns | 4.18 ** |
| C5 | Low AS lines vs. $F_1$(high AS line x high AS line) | 11.59 ** | 10.59 ** | 11.60 ** |
| C6 | High AS lines vs. $F_1$(low AS line x low AS line) | -9.49 ** | -9.76 ** | -9.85 ** |

"...continua..."

"TABLE 5, Cont."

| | | | | |
|---|---|---|---|---|
| C7 | Low AS lines vs. $F_1$(low AS line x low AS line) | 0.13 ns | -1.28 ns | -2.43 ns |
| | Experimental $F_1$(high AS line x high AS line) vs. | -13.16 ** | -12.07** | -10.74 ** |
| C8 | Commercial hybrid check | | | |
| | Experimental $F_1$(low AS line x low AS line) vs. | -1.70 ns | -0.19 ns | 3.29 ns |
| C9 | Commercial hybrid check | | | |
| C10 | High AS genotypes vs. Low AS genotypes | -10.47 ** | -9.69 ** | -8.85 ** |
| C11 | High AS genotypes vs. Commercial hybrid check | -11.68 ** | -10.48** | -7.60 ** |
| C12 | Low AS genotypes vs. Commercial hybrid check | -1.61 ns | -1.04 ns | 1.67 ns |
| | Hybrids $F_1$(low AS line x high AS line) vs. Commercial | -7.19 ** | -6.52 ** | -4.97 ** |
| C13 | hybrid check | | | |
| C14 | Hybrids $F_1$(low AS line x high AS line) vs. High AS lines | 3.99 ** | 3.42 ** | 1.58 ns |
| C15 | Hybrids $F_1$(low AS line x high AS line) vs. Low AS lines | -5.63 ** | -5.04 ** | -5.83 ** |
| | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid $F_1$(low | -5.49 ** | -6.33 ** | -8.26 ** |
| C16 | AS line x low AS line) | | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid | 5.96 ** | 5.54 ** | 5.77 ** |
| C17 | $F_1$(high AS line x high AS line) | | | |
| C18 | High AS lines vs. *L. pennellii* 'LA-716' | 6.97 ** | 6.02 ** | 7.17 ** |
| C19 | Low AS lines vs. *L. pennellii* 'LA-716' | 16.60 ** | 14.50 ** | 14.59 ** |
| | Hybrid $F_1$(high AS line x high AS line) vs. *L. pennellii* | 5.01 ** | 3.91 ** | 2.99 ns |
| C20 | 'LA-716' | | | |
| | Commercial hybrid check (low AS x low AS) vs. *L.* | 18.17 ** | 15.98 ** | 13.73 ** |
| C21 | *pennellii* 'LA-716' | | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. *L. pennellii* | 10.97 ** | 9.45 ** | 8.76 ** |
| C22 | 'LA-716' | | | |

(x) Means followed by the same letter within the columns do not differ from each other by Duncan's multiple range test (p=0.05)
(y) **, * , ns = significant at p=0.01, at p=0.05 and non-significant, respectively, by the F test

Table 6. Oviposition (mean number of eggs per 2 $cm^2$ leaflet area, measured six days after infestation) and number of nymphs of *Bemisia argentifollii* in the upper third portion of the tomato plants (measured 20 days after infestation).

| | **Genotypes** | **No. eggs per 2 $cm^2$** [(x)] | **No. nymphs per leaflet** [(x)] |
|---|---|---|---|
| T1 | TOM-687 | 85.60 CD | 66.20 CD |
| T2 | TOM-688 | 61.40 D | 42.40 CD |
| T3 | TOM-689 | 52.60 D | 45.00 CD |
| T4 | TOM-690 | 218.40 B | 151.40 AB |
| T5 | TOM-684 | 282.20 A | 210.00 A |
| T6 | F1 (TOM-684 x TOM-687) | 63.20 D | 53.20 CD |
| T7 | F1 (TOM-684 x TOM-688) | 41.80 D | 29.40 CD |
| T8 | F1 (TOM-684 x TOM-689) | 107.40 C | 92.60 CB |
| T9 | F1 (TOM-690 x TOM-687) | 78.20 CD | 65.00 CD |
| T10 | F1 (TOM-690 x TOM-688) | 109.00 C | 100.80 CB |
| T11 | F1 (TOM-690 x TOM-689) | 65.60 CD | 55.00 CD |
| T12 | F1 (TOM-687 x TOM-689) | 57.80 D | 47.20 CD |
| T13 | F1 (TOM-684 x TOM-690) | 243.20 AB | 204.80 A |
| T14 | TEX-154 | 233.00 B | 156.20 AB |
| T15 | LA-716 | 0.60 E | 0.00 D |
| | | **Contrast estimates** [(y)] **:** | |
| | **Contrasts of interest** | **No. eggs per 2 $cm^2$** | **No. nymphs per leaflet** |
| C1 | High AS lines vs. Low AS lines | -183.7** | -129.5** |
| C2 | High AS lines vs. Commercial hybrid check | -166.4** | -105.0** |
| C3 | Low AS lines vs. Commercial hybrid check | -017.3ns | -024.5ns |
| C4 | High AS lines vs. $F_1$(high AS line x high AS line) | -008.7ns | -03.9ns |
| C5 | Low AS lines vs. $F_1$(high AS line x high AS line) | 192.5** | 133.5** |
| C6 | High AS lines vs. $F_1$(low AS line x low AS line) | -176.6** | -153.6** |

"...continua..."

"TABLE 6, Cont."

| | | | |
|---|---|---|---|
| C7 | Low AS lines vs. $F_1$(low AS line x low AS line) | -7.1ns | -24.1ns |
| | Experimental $F_1$(high AS line x high AS line) vs. | -175.2** | -109.0** |
| C8 | Commercial hybrid check | | |
| | Experimental $F_1$(low AS line x low AS line) vs. | -10.2ns | -48.6* |
| C9 | Commercial hybrid check | | |
| C10 | High AS genotypes vs. Low AS genotypes | -179.8** | -130.4** |
| C11 | High AS genotypes vs. Commercial hybrid check | -168.6** | -106.0** |
| C12 | Low AS genotypes vs. Commercial hybrid check | -14.9ns | -32.5ns |
| | Hybrids $F_1$(low AS line x high AS line) vs. | -155.4** | -90.2** |
| C13 | Commercial hybrid check | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. High | -10.9ns | -14.7ns |
| C14 | AS lines | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. Low | -172.7** | -114.7** |
| C15 | AS lines | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid | -165.6** | -138.8** |
| C16 | $F_1$(low AS line x low AS line) | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid | 19.7ns | 18.7ns |
| C17 | $F_1$(high AS line x high AS line) | | |
| C18 | High AS lines vs. *L. pennellii* 'LA-716' | -65.9** | -51.1** |
| C19 | Low AS lines vs. *L. pennellii* 'LA-716' | -249.7** | -180.7** |
| | Hybrid $F_1$(high AS line x high AS line) vs. *L.* | -57.2** | -47.2* |
| C20 | *pennellii* 'LA-716' | | |
| | Commercial hybrid check (low AS x low AS) vs. | -232.4** | -156.2** |
| C21 | *L. pennellii* 'LA-716' | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. *L.* | -76.9** | -65.9** |
| C22 | *pennellii* 'LA-716' | | |

(x) Means followed by the same letter within the columns do not differ from each other by Duncan's multiple range test (p=0.05)
(y) **, * , ns = significant at p=0.01, at p=0.05 and non-significant, respectively, by the F test.

Table 7. Egg counts (number of eggs per 2 $cm^2$ leaflet area) measured on the upper third portion of the tomato plants 10 days after infestation with the South American pinworm *Tuta absoluta*.

| | **Genotypes** | **Egg counts (No. eggs per 2 $cm^2$ leaflet area)** |
|---|---|---|
| T1 | TOM-687 | 17.60 ABC |
| T2 | TOM-688 | 9.00 DE |
| T3 | TOM-689 | 8.60 DE |
| T4 | TOM-690 | 20.20 AB |
| T5 | TOM-684 | 21.00 AB |
| T6 | F1 (TOM-684 x TOM-687) | 17.00 ABC |
| T7 | F1 (TOM-684 x TOM-688) | 17.20 ABC |
| T8 | F1 (TOM-684 x TOM-689) | 14.00 CD |
| T9 | F1 (TOM-690 x TOM-687) | 10.80 DE |
| T10 | F1 (TOM-690 x TOM-688) | 14.00 CD |
| T11 | F1 (TOM-690 x TOM-689) | 9.20 DE |
| T12 | F1 (TOM-687 x TOM-689) | 8.00 E |
| T13 | F1 (TOM-684 x TOM-690) | 16.60 BC |
| T14 | TEX-154 | 22.40 A |
| | **Contrasts of interest** | **Contrast estimates (y) : (No. eggs per 2 $cm^2$ leaflet area)** |
| C1 | High AS lines vs. Low AS lines | -8.86** |
| C2 | High AS lines vs. Commercial hybrid check | -10.66** |
| C3 | Low AS lines vs. Commercial hybrid check | -1.80 ns |
| C4 | High AS lines vs. AS line x high AS line) | -3.73 ns |
| C5 | Low AS lines vs. $F_1$(high AS line x high AS line) | 12.60** |
| C6 | High AS lines vs. $F_1$(low AS line x low AS line) | -4.86* |
| C7 | Low AS lines vs. $F_1$(low AS line x low AS line) | -4.00 ns |
| C8 | Experimental $F_1$(high $F_1$(high AS line x high AS line) vs. Commercial | -14.40** |

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"TABLE 7, Cont."

| | | |
|---|---|---|
| | hybrid check | |
| C9 | Experimental $F_1$(low AS line x low AS line) vs. Commercial hybrid check | -5.80* |
| C10 | High AS genotypes vs. Low AS genotypes | -9.25** |
| C11 | High AS genotypes vs. Commercial hybrid check | -11.60** |
| C12 | Low AS genotypes vs. Commercial hybrid check | -3.13 ns |
| C13 | Hybrids $F_1$(low AS line x high AS line) vs. Commercial hybrid check | -8.69** |
| C14 | Hybrids $F_1$(low AS line x high AS line) vs. High AS lines | -1.96 ns |
| C15 | Hybrids $F_1$(low AS line x high AS line) vs. Low AS lines | -6.89** |
| C16 | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid $F_1$(low AS line x low AS line) | -2.89 ns |
| C17 | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid $F_1$(high AS line x high AS line) | 5.70** |

(x) Means followed by the same letter within the columns do not differ from each other by Duncan's multiple range test (p=0.05)
(y) **, * , ns = significant at p=0.01, at p=0.05 and non-significant, respectively, by the F test

Table 8. Damage scores in tomato plants in response to infestation of the South American tomato pinworm *Tuta absoluta*: areas under the curves *damage x time* up to the 36th day after infestation, for leaflet lesion types (LLT), percent leaflets attacked (PLA) and overall plant damage (OPD) scores

| | | **Areas under the curves damage scores x time** | | |
|---|---|---|---|---|
| | **Genotypes** | **Leaflet Lesion Types (LLT)** | **% leaflets attacked (PLA)** | **Overall plant damage (OPD)** |
| T1 | TOM-687 | 47.6 BC | 40.0 DEF | 37.2 CDE |
| T2 | TOM-688 | 39.0 DEF | 36.4 EFG | 32.8 DEF |
| T3 | TOM-689 | 37.2 EF | 33.8 FG | 27.6 F |
| T4 | TOM-690 | 58.0 A | 52.8 AB | 50.2 A |
| T5 | TOM-684 | 56.2 A | 56.4 A | 49.0 AB |
| T6 | F1 (TOM-684 x TOM-687) | 43.6 CDE | 38.8 DEFG | 35.4 CDEF |
| T7 | F1 (TOM-684 x TOM-688) | 46.8 BCD | 45.2 ABCD | 41.2 BCD |
| T8 | F1 (TOM-684 x TOM-689) | 46.0 BCD | 43.4 CDE | 38.4 CDE |
| T9 | F1 (TOM-690 x TOM-687) | 37.6 EF | 34.0 FG | 30.8 EF |
| T10 | F1 (TOM-690 x TOM-688) | 43.8 CDE | 38.8 DEFG | 35.6 CDEF |
| T11 | F1 (TOM-690 x TOM-689) | 37.4 EF | 34.8 FG | 30.0 EF |
| T12 | F1 (TOM-687 x TOM-689) | 31.6 F | 31.6 G | 27.6 F |
| T13 | F1 (TOM-684 x TOM-690) | 53.0 AB | 48.4 BC | 43.2 ABC |
| T14 | TEX-154 | 60.2 A | 57.2 A | 51.2 A |
| | | **Contrast estimates [(y)] :** | | |
| | **Contrasts of interest** | **Leaflet Lesion Types (LLT)** | **% leaflets attacked (PLA)** | **Overall plant damage (OPD)** |
| C1 | High AS lines vs. Low AS lines | -15.83** | -17.86** | -17.06** |
| C2 | High AS lines vs. Commercial hybrid check | -18.93** | -20.46** | -18.66** |
| C3 | Low AS lines vs. Commercial hybrid check | -3.10 ns | -2.60 ns | -1.60 ns |
| C4 | High AS lines vs. $F_1$(high AS line x high AS line) | -9.66** | -5.13 ns | -4.93 ns |
| C5 | Low AS lines vs. $F_1$(high AS line x high AS line) | 25.50** | 23.00** | 22.00** |
| C6 | High AS lines vs. $F_1$(low AS line x low AS line) | -11.73** | -11.66** | -10.66** |

"…continua…"

"TABLE 8, Cont."

| | | | | |
|---|---|---|---|---|
| C7 | Low AS lines vs. $F_1$(low AS line x low AS line) | -4.10 ns | -6.20* | -6.40 ns |
| | Experimental $F_1$(high AS line x high AS line) vs. | -28.60** | -25.60** | -23.60** |
| C8 | Commercial hybrid check | | | |
| | Experimental $F_1$(low AS line x low AS line) vs. | -7.20 ns | -8.80* | -8.00* |
| C9 | Commercial hybrid check | | | |
| C10 | High AS genotypes vs. Low AS genotypes | -18.00** | -18.03** | -17.10** |
| C11 | High AS genotypes vs. Commercial hybrid check | -21.35** | -21.75** | -19.90** |
| C12 | Low AS genotypes vs. Commercial hybrid check | -4.46 ns | -4.66 ns | -3.73 ns |
| | Hybrids $F_1$(low AS line x high AS line) vs. | -17.66** | -18.03** | -15.96** |
| C13 | Commercial hybrid check | | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. High | -1.26 ns | -2.43 ns | -2.70 ns |
| C14 | AS lines | | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. Low | -14.56** | -15.43** | -14.36** |
| C15 | AS lines | | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid | -10.46** | -9.23** | -7.96** |
| C16 | $F_1$(low AS line x low AS line) | | | |
| | Hybrids $F_1$(low AS line x high AS line) vs. Hybrid | 10.93** | 7.56** | 7.63* |
| C17 | $F_1$(high AS line x high AS line) | | | |

(x) Means followed by the same letter within the columns do not differ from each other by Duncan's multiple range test (p=0.05)
(y) **, * , ns = significant at p=0.01, at p=0.05 and non-significant, respectively, by the F test

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