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Heritability of 2-tridecanone-mediated arthropod resistance in an interspecific segregating generation of tomato

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ABSTRACT

The methyl-ketone, 2-tridecanone (2-TD), present in the tips of glandular trichomes abundant in *Lycopersicon hirsutum* var. *glabratum* is the major toxic factor involved in the high levels of anthropod resistance found in this taxon. The introgression of high 2-TD content into the cultivated tomato species *Lycopersicon esculentum* could lead to improved insect tolerance of tomato cultivars. In this study, 2-TD content was measured colorimetrically in the foliage of *L. esculentum* line TSWV-547 (P_1), *L. hirsutum* var. *glabratum* PI 134417 (P_2), as well as in the F_1 ($P_1 \times P_2$) and F_2 generations. Mean 2-TD concentrations (in 10^{-12} mol/100 mm^2 leaf area) were 34.5, 224.1, 83.5 and 88.3, respectively for P_1, P_2, F_1 and F_2. Generation mean analysis indicated that a simple additive-dominance model does not fit the data. Broad-sense heritability of 2-TD concentration was estimated as 0.61 ± 0.18, indicating that 2-TD-based selection should be effective as an indirect selection criterion for arthropod resistance.

INTRODUCTION

The wild tomato species *Lycopersicon hirsutum* var. *glabratum* has been reported as highly resistant to a number of arthropod pests, including spider mites (Aina *et al.*, 1972; Weston and Snyder, 1990), glasshouse whitefly *Trialeurodes vaporariorum* (De Ponti *et al.*, 1975), tomato fruitworm *Heliothis zea* (Fery and Cuthbert Jr., 1975), Colorado potato beetle *Leptinotarsa decimlineata* (Schalk and Stoner, 1976), tomato pinworm *Keiferia lycopersicela* (Schuster *et al.*, 1979), vegetable leafminer *Lyriomiza sativae* (Schuster *et al.*, 1979), and the South American tomato pinworm *Scrobipalpuloides absoluta* (Gilardón and Benavent, 1981; França *et al.*, 1984). Williams *et al.* (1980) indicated that 2-tridecanone (2-TD), a methyl-ketone, was the major toxic factor involved in the defense against insects in that wild tomato taxon. 2-TD is present in the tips of the glandular (type VI) trichomes which are abundant in the foliage of *L. hirsutum* var. *glabratum*; in the arthropod-susceptible cultivated tomato *L. esculentum*, glandular trichomes are substantially less abundant, and 2-TD content is therefore considerably lower.

Because *L. hirsutum* var. *glabratum* can be easily hybridized with the cultivated tomato and presents a broad spectrum of arthropod resistance, it is ideally suited to breeding programs aimed at improving insect tolerance of tomato cultivars (Williams *et al.*, 1980; Zamir *et al.*, 1984; Fery and Kennedy, 1987).

An understanding of the mode of inheritance of either insect resistance *per se* or its putatively associated 2-TD concentration in tomato leaves would greatly contribute to increased efficiency in these programs. Fery and Kennedy (1987) reported a strong association between *Manduca sexta* resistance and 2-TD concentration in segregating populations of crosses between the susceptible *L. esculentum* cultivar Walter and the resistant *L. hirsutum* var. *glabratum* 'PI 134417'.

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They also indicated that three recessive genes govern both *M. sexta* resistance and 2-TD biosynthesis. Zamir *et al.* (1984), in segregating populations of *L. esculentum* 'M82-1-8' x *L. hirsutum* var. *glabratum* 'LA 407', also reported dominance for low 2-TD levels, and found two morphological markers and three isozyme loci associated with the expression of 2-TD. Nienhuis *et al.* (1987) found restriction fragment length polymorphism (RFLP) marker loci on three different linkage groups to be correlated with 2-TD content in a similar interspecific cross.

Indirect selection for 2-TD content may prove to be less expensive and more practical than direct selection for arthropod resistance. A standard procedure for 2-TD determination is gas chromatography (Williams *et al.*, 1980; Zamir *et al.*, 1984; Fery and Kennedy, 1987), but a highly correlated less expensive colorimetric technique has also been developed (Nienhuis *et al.*, 1985; Barbosa, 1994).

The rate of gain from indirect selection in a population is a function of the magnitude of the phenotypic variance of the desired trait, the selection differential, the heritability of the indirect criteria and the genetic correlation between the direct and indirect criteria (Falconer, 1981; Nienhuis *et al.*, 1987). Therefore indirect selection for 2-TD content cannot be expected to be superior to direct selection unless 2-TD has a substantially higher heritability than arthropod resistance itself, and the genetic correlation between the two criteria is high; or unless a substantially higher intensity of selection can be applied to 2-TD content than to direct arthropod resistance (Falconer, 1981), which is presumably true, since 2-TD determination (particularly with the colorimetric technique) is quick and non-destructive.

An estimate of the heritability of the colorimetrically measured 2-TD content would therefore allow for a more precise assessment of the worth of this indirect criterion for arthropod resistance. The principal objective of this study was to obtain an estimate of heritability of 2-TD content in an F_2 population derived from the interspecific cross *L. esculentum* x *L. hirsutum* var. *glabratum* and appraise the potential of the colorimetric technique for selection of high 2-TD genotypes.

MATERIAL AND METHODS

Plant materials

The lines used as parents in the crosses were *Lycopersicon esculentum* line TSWV-547 and *L. hirsutum* var. *glabratum* 'PI 134417'. TSWV-547 (P_1) is a breeding line with indeterminate plant habit and resistance to tomato spotted wilt, but is susceptible to the major tomato insect pest in Brazil, *Scrobipalpuloides absoluta*. PI 134417 (P_2) is an accession with high 2-tridecanone content (Fery and Kennedy, 1987) and high level of resistance to *Scrobipalpuloides absoluta* (Gilardon and Benavent, 1981; França *et al.*, 1984). Seeds of the parental (P_1, P_2), F_1 (P_1 x P_2) and F_2 populations were produced in the greenhouse using standard crossing and selfing procedures.

Colorimetric analysis of 2-tridecanone content

The levels of 2-tridecanone associated with the foliage were determined by the colorimetric method of Nienhuis *et al.* (1985), modified and described by Barbosa (1994). Plants of populations P_1, P_2, F_1 and F_2 were grown (1 per pot) in 10-cm pots filled with a standard potting mix (Plantimax®); 3/8 inch leaf disks were taken with a cork borer from tomato leaflets in the upper third of the plants. Four disks taken from each plant sampled were placed in test tubes with 1 ml methyl-chloride for 2-tridecanone extraction, and shaken in a mechanical vortex for 30 sec. The extract was treated with 4 ml of a 2,4-dinitrophenylhydrazine in ethanol (previously distilled in the presence of sodium boron-hydride). The reaction was stopped with the addition of 0.5 ml of 5 N sodium hydroxide, following which the absorbance was measured in a spectrophotometer at 540 nm. A standard calibration curve was used to convert the absorbance readings into number of 10^{-12} mol 2-TD per 100 mm^2 leaf area.

Statistical design and analyses

The plants used for 2-TD determination were grown in 10-cm pots as previously described. Thirty plants were grown for each of the populations P_1 (TSWV-547), P_2 (PI 134417) and F_1 (P_1 x P_2), while 295 plants were grown for the F_2 population. Pots were placed on a greenhouse bench in accordance with a completely randomized design. Means and variances of 2-TD content were calculated for each of the populations, and an estimate of broad-sense heritability (h_a^2) was obtained as described by Ramalho *et al.* (1994): the geometric mean of the variances of P_1, P_2 and F_1 was taken as an estimate of the environmental variance (V_E); the estimate of the genetic variance was obtained by subtracting V_E from the variance of F_2. A generation mean analysis was performed on the P_1, P_2, F_1 and F_2 generation data (Rowe and Alexander, 1980) through a weighted least squares procedure where the weights

were taken as the inverse of the respective population variances.

RESULTS AND DISCUSSION

Concentrations of 2-TD were 6.5 times higher in *Lycopersicon hirsutum* var. *globratum* than in the *Lycopersicon esculentum* line (Table I). In F_1 and F_2, 2-TD was between two and three times higher than in TSWV-547, but much lower than in PI 134417, indicating that the genes involved with the control of high 2-TD levels are predominantly recessive - a conclusion similar to that of Fery and Kennedy (1987). These authors, however, found a 150-fold difference in 2-TD concentration between PI 134417 and the low 2-TD lines. A 72-fold difference was found by Williams *et al.* (1980), and a 50-fold difference by Zamir *et al.* (1984). Because 2-TD is significantly less abundant in plants grown under short day lengths (as was the case in our trial), these discrepancies could be explained by differences in day length among the various trials. It is also possible that our colorimetric method of 2-TD determination may be less precise than the standard gas chromatographic procedure employed by the other authors, especially in the lower 2-TD ranges.

Table I - Concentration of 2-tridecanone (2-TD) in leaf disks of *Lycopersicon esculentum* 'TSWV-547' (P_1), *L. hirsutum* var. *glabratum* 'PI 134417' (P_2) and their F_1 (P_1 x P_2) and F_2 populations: generation means.

Genotypes	Number of plants sampled	2-TD (x 10^{12} mol/100 mm^2)	
		Means	Range
TSWV-547 (P_1)	30	34.5	0.0 - 76.0
PI 134417 (P_2)	30	224.1	61.6 - 371.9
F_1 (P_1 x P_2)	30	83.5	9.6 - 134.2
F_2	295	88.3	0.0 - 347.9

Segregation in the F_2 generation (Figure 1) was similar to that found by Zamir *et al.* (1984) and Fery and Kennedy (1987), i.e., skewed towards lower 2-TD levels. The generation mean analysis (Table II), while showing partial dominance for 2-TD levels, indicates that a simple additive-dominance model may not be adequate to explain the data. The lack of fit of the model may be due to epistatic gene action, as found by Nienhuis *et al.* (1987), or to deviations from expected Mendelian segregation in the interspecific cross due to gametic selection, as found by Zamir *et al.* (1982).

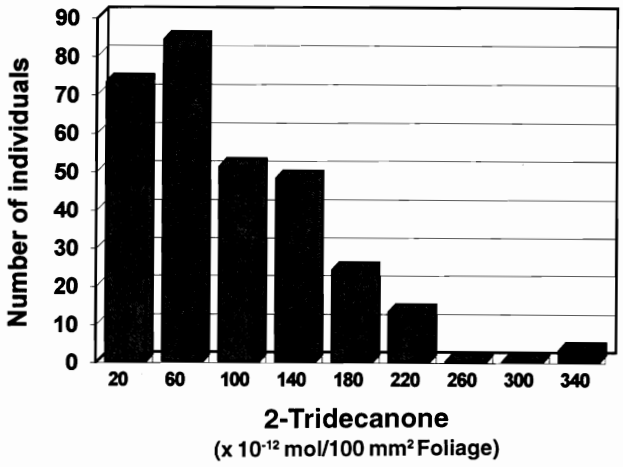

Figure 1 - Frequency distribution of 2-TD concentration in leaf disks of the F_2 generation of the interspecific cross *Lycopersicon esculentum* 'TSWV-547' x *L. hirsutum* var. *glabratum* 'PI 134417'.

Table II - Generation mean analysis and estimates of broad-sense heritability in the interspecific cross *Lycopersicon esculentum* 'TSWV-547' x *L. hirsutum* var. *glabratum* 'PI 134417'.

Model parameter	Estimate ± SD
[m]	112.1 ± 10.4
[d]	80.0 ± 11.4
[h]	-34.4 ± 15.0
Average degree of dominance - [h]/[d]	-0.43
	(χ^2 = 8.44*)
Variances	
Genetic (V_G)	2397.9
Environmental (V_E)	1556.6
Broad-sense heritability (h_a^2)	0.606 ± 0.180

*P < 0.01.

The estimates obtained for the genetic variance and broad-sense heritability indicate that a substantial portion of the total variance in F_2 is heritable. Broad-sense heritability on a plant-to-plant basis h_a^2 was high (0.606), indicating that selection of high 2-TD plants via colorimetric technique should be effective in promoting genetic gains. The magnitude of h_a^2 was similar to the correlation (r = 0.62) between RFLP-predicted and colorimetrically measured 2-TD levels obtained by Nienhuis *et al.* (1987). Since the "heritability" of the RFLP is 1.0 (Nienhuis *et al.*, 1987), one can conclude that direct selection for 2-TD is just as efficient as RFLP-based selection (Falconer, 1981). Choice between the two techniques would therefore depend essentially on costs involved, and would appear to favor the colorimetric technique over the more costly RFLP-based selection. Accordingly, given

the high correlation found (Nienhuis *et al.*, 1985) between the gas chromatographic and the colorimetric techniques, the latter again appears to be favored.

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RESUMO

A metil-cetona 2-tridecanona (2-TD) presente nas pontas dos tricomas glandulares abundantes em *Lycopersicon hirsutum* var. *glabratum* é o mais importante fator tóxico envolvido nos altos níveis de resistência aos artrópodes encontrados neste grupo taxonômico. A introgressão de alto conteúdo de 2-TD para a espécie cultivada de tomate *Lycopersicon esculentum* poderia levar a maior tolerância a insetos das cultivares de tomate. No presente estudo, o conteúdo de 2-TD foi medido colorimetricamente na folhagem da linhagem TSWV-547 (P_1) de *L. esculentum*, *L. hirsutum* var. *glabratum* PI 134417 (P_2), assim como nas gerações F_1 (P_1 x P_2) e F_2. As concentrações médias de 2-TD (em 10^{-12} mol/100 mm^2 de área da folha) foram 34,5, 224,1, 83,5 e 88,3, respectivamente para P_1, P_2, F_1 e F_2. A análise das médias das gerações indicou que um modelo simples aditivo-dominante não se ajusta aos dados. A herdabilidade em sentido amplo da concentração de 2-TD foi estimada em 0,61 ± 0,18, indicando que a seleção baseada em 2-TD deve ser eficaz como um critério indireto de seleção para resistência a artrópodes.

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