

Resistance of grapevine to the erineum strain of *Colomerus vitis* (Acari: Eriophyidae) in western Iran and its correlation with plant features

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Abstract The interaction of grape erineum mite (GEM), *Colomerus vitis* Pagenstecher (Acari: Eriophyidae), with grape was investigated in the laboratory. We studied some plant morphological biochemical features potentially related to vine resistance/tolerance of eight native grapevine cultivars, extensively cultivated in western Iran, and two non-native cultivars. Free-choice experiments indicated that the cultivars Shahani, Flame seedless and Yaghuti were colonized by lower levels of GEM, whereas Muscat Gordo, Gazne and White Thompson seedless hosted denser populations. These differences between cultivars may be due to differential attractiveness to GEM, possibly associated with plant biochemical and morphological traits. In no-choice assays with six grapevine cultivars, mite population development and some cultivar features were assessed. Mite populations grew fastest on Gazne and Muscat Gordo, and slowest on Yaghuti and Shahani. The degree of mite infestation was associated with reduction of leaf area, increase of leaf weight, shortening of shoots and more numerous erineae: these features were larger on the most infested Gazne, whereas morphological features of Shahani and Yaghuti were scarcely affected by GEM infestation. Also trichome type and density of the assayed cultivars appeared to be related to mite density: the most infested cultivars (Gazne and Muscat Gordo) displayed higher ranks of blade and vein hairs and lower ranks of blade and vein bristles and domatia. No correlation was found between mite density and leaf thickness of mature leaves. The amount of leaf waxes was highest in Shahani and Yaghuti, which displayed the lowest mite density, the fewest erineae and the largest leaves. Carbohydrate amount of uninfested leaves was lowest on the least infested Shahani and highest on the most infested Gazne; phenols

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increased in leaves of Shahani and decreased in those of Gazne after mite infestation. Finally, cultivars also appeared to influence some morphological traits of the mites: larger specimens were detected on White Thompson seedless, Flame seedless and Gazne, whereas smaller mites were found on leaves of the less infested Yaghuti and Shahani. These results indicate that leaf hairiness, leaf wax and carbohydrate contents may be useful tools for a preliminary screening among vine cultivars and help predict resistance/tolerance to GEM. Shahani and Yaghuti seem quite promising for developing grape resistance programs against GEM in western Iran.

Keywords Grape · Resistance · Antixenosis · Antibiosis · Tolerance · Erineum mite · Plant morphology · Plant physiology

Introduction

Various phytophagous arthropods feed on grapevine, *Vitis vinifera* L., but a few can actually threaten its production in commercial vineyards. Among these pests, *Colomerus vitis* (Pagenstecher) (Acari: Eriophyidae) is fairly common and its harmfulness appears to be quite variable within the grape-growing regions of the world (e.g., Duso and de Lillo 1996; Avgin and Bahadiroğlu 2004; Bernard et al. 2005; Linder et al. 2006; Walton et al. 2007; Luchian et al. 2008; Tomoioaga and Comsa 2010; Craemer and Saccaggi 2013). Based on the feeding symptoms induced, *C. vitis* comprises three strains with different lifestyle but apparently identical morphology: a bud strain, a leaf gall-inducing erineum strain (here indicated as grape erineum mite, GEM), and a leaf curl strain (Smith and Stafford 1948; Duso and de Lillo 1996). GEM is much more frequently and widely recorded than the other strains; it causes conspicuous white, later brown, felt patches (erinea) on the lower leaf surface, which appear blister-like on the upper surface, and it affects grape production (Avgin and Bahadiroğlu 2004). The bud strain can induce malformation of leaves, abnormal shoot growth, premature falling of flower clusters and bud death. It has been suggested to be a closely related but separate species from GEM based on Internal Transcribed Spacer 1 (ITS1) sequences (Carew et al. 2004); this species status has not been supported by morphological and reproductive evidence. Finally, the leaf curl strain is associated with leaf abnormalities and stunted and scarred shoots (Smith and Stafford 1948; Duso and de Lillo 1996). GEM is a real threat to the vine plantations in Iran (Khanjani and Hadad Irani-Nejad 2009) and its population dynamics were studied only in the western part of the country (Gholami et al. 2005b). However, the relevance of the grapevine cultivation for grape and leaf production, and the severity of GEM infestations recorded also in other parts of Iran (Tafazoli et al. 1992) make their control necessary.

In general, the adverse effects of pesticide use and the increased restrictions for pesticide applications have stimulated the exploration of eco-friendly pest control tactics. Plant genotypes strongly influence density, distribution and fitness of pests, and the degree of injury caused by them (Peterson and Higley 2001; Hochwender et al. 2005). Accordingly, the survey and selection of genotypes provided with antixenosis, antibiosis and tolerance properties can contribute to integrated pest management (IPM) tactics (Smith 2005; Hoy 2011). Antixenosis influences the plant feeders' behavior and makes the plant less attractive for feeding, sheltering and egg-laying (non-preference effect). Antibiosis affects the pest's biology and often reduces its survivorship, fecundity, longevity and developmental rate, so that its impact is reduced compared to that expected on a susceptible host. Tolerance is the plant's ability to withstand pest attack and to recover from damage without loss in fitness or

yield. Plant morphology (e.g., leaf trichomes, thickened plant epidermal layers, waxy deposits on plant surfaces) and plant physiology (e.g., primary and secondary plant metabolites) are involved in these defense reactions (Johnson 1975; Beck and Maxwell 1976; Gibson and Valencia 1978; Dhaliwal and Dilawari 1993; Panda and Khush 1995; Commenil et al. 1997; Walling 2000; Khanjani and Khalghani 2008). Plant defensive factors are also implied in the interaction between eriophyoid mites and their host plants, but they have been investigated in detail in only few cases (Duso et al. 2010), even though host specificity and plant susceptibility have been studied at species and cultivar level for weeds and few other plants of economic interest (e.g., Herr 1991; Smith et al. 2009).

Bergh and Weiss (1993) identified antibiosis effects on the oviposition and development rate of the pear rust mite, *Epitrimerus pyri* (Nalepa), infesting pear cultivars and other *Pyrus* species under laboratory conditions, but relationships with plant features were not described. Similarly, effects on fecundity and survival of the apple rust mite, *Aculus schlechtendali* (Nalepa), were detected in laboratory experiments on differently resistant apple varieties (Kozłowski 1995). A differential increase of proteins, phenols and other chemicals in infested leaf tissues seemed to be quite common and it was hypothesized to be an adaptive response of the plant's physiology towards stress factors and/or to be involved with antibiosis (Balasubramanian and Purushothamam 1972; Tandon and Arya 1980; Tandon 1984; Bronner et al. 1991; Ning et al. 1996; Goncalves et al. 1998; Tomczyk and Boczek 2006; Petanović and Kielkiewicz 2010; Kielkiewicz et al. 2011).

When looking at morphology alone, coconut varieties producing large fruits appeared to be less susceptible to the coconut mite, *Aceria guerreronis* Keifer, than varieties producing small fruits (Mariau 1977). Yet, leaf morphology, trichome types and trichome density on tomato (*Solanum lycopersicum* L. [= *Lycopersicon esculentum* Mill.] and *Solanum habrochaites* S. Knapp & D.M. Spooner [= *Lycopersicon hirsutum* f. *glabratum* C.H. Muell.]) appeared to be largely responsible for its resistance to the tomato russet mite, *Aculops lycopersici* (Tryon) (Leite et al. 1999). Similarly, morphological features of the leaves of tea varieties resistant to the tea pink mite, *Acaphylla theae* (Watt), were related to feeding inhibition of the mite (Ning et al. 1996). Further examples of cultivar resistance to eriophyoid mites can be found for black currant (Herr 1991), olive (Mohiseni et al. 2011), wheat (Li et al. 2007) and a few other crops.

The interactions between plants and eriophyoids could also concern (phenotypic) variation of the mites, which may be the result of adaptation to micro-environmental conditions created by the host and last throughout mite ontogeny (Dres and Mallet 2002). In particular, Kozłowski (1998) ascertained differences in body size and ventral seta length of protogyne females in apple rust mite collected from different apple tree cultivars. Skoracka et al. (2002) pointed out differences in some phenotypic traits of the grass rust mite complex, *Abacarus hystrix* (Nalepa), living on different host plants which were later, in part, demonstrated to discriminate cryptic species (Skoracka 2009).

Interactions between GEM and grapevine cultivars have been investigated poorly (Dellei and Szendrey 1991; Gholami et al. 2005a; Luchian et al. 2008), whereas knowledge of factors influencing plant responses to this mite can surely assist in implementing IPM by using resistant cultivars. The present study was aimed at developing an experimental method for evaluating the resistance/sensitiveness of Iranian-native and non-native grapevine germplasm to the grape erineum (GEM) strain of *C. vitis* under controlled laboratory conditions. Based on previous field observations (Gholami et al. 2005a) eight native grapevine cultivars, extensively cultivated in western Iran, were selected for this study, as well as two non-native cultivars, originally from largely cultivated Australian and North American germplasm, but crossed with oriental cultivars that are widely used in Iran. In addition, plant

morphological and biochemical features potentially related to the host plant's resistance were identified and could also be useful for provisional resistance screening.

Materials and methods

Plant material

The selected native cultivars, from amongst the most common in vineyards of western Iran, were: Fakhri, Yaghuti, Asgari and Khalili (used for fresh consumption), White Thompson seedless and Red Thompson seedless (cultivated for both fresh and dried—raisin—markets), and Gazne and Shahani (used for juice production). The non-native Flame seedless is used for fresh usage, whereas the non-native Muscat Gordo is cultivated for fresh and dried consumption, and wine making. The native cultivars were obtained from the Vine Research Institute of Malayer (Iran), whilst the non-native ones were provided by the Vine Collection of Bu-Ali Sina University, Hamedan (Iran).

The cuttings (40–50 per cultivar) were treated with the fungicide Benomyl (Agrocit[®], Bayer CropScience) and stored in the field to stimulate their rooting. Once rooted (in January–February 2010), they were planted singly in 2.5-kg pots containing sand and sheep manure, and kept in a garden at the Faculty of Agriculture, Bu-Ali Sina University, Hamedan (Iran) until September 20, 2010.

Before beginning the experiments, the new plants were treated by Tebuconazole (Folicur[®], Bayer CropScience) against powdery mildew and by Abamectin (Vertimec[®], Syngenta Crop Protection) against possible mite infestation. After the treatments, all plants were kept in a garden at the Faculty of Agriculture, Bu-Ali Sina University, Hamedan (Iran). About 5 plants per cultivar were randomly selected and checked at the beginning of the assays (bud break) by means of a washing and sieving procedure (de Lillo 2001; Monfreda et al. 2008) in order to ensure the lack of GEM infestation and other mites, including predators. The assays on these plants started 6 months after the miticide spray and no fertilizers or pesticides were further applied.

Mite population source

Two days before each assay, leaves infested by *C. vitis* were collected from white Sahebi vineyard cultivated in the area of Heydarh village (Hamadan, Iran; 34°48'N, 48°28'E, 1,830 m asl). Leaf samples were stored in plastic bags within a cooler and transported to the laboratory (about 2 km from the collection site) for being used as infesting source; organisms different from GEM were carefully removed from these leaves. A few erinea were detached from leaves randomly selected within the samples. The mites were extracted through the above-mentioned washing and sieving method and the mite density (i.e., mite number per unit area) was calculated.

The Sahebi cultivar was excluded among the assayed genotypes in favor of other cultivars, in order to preclude effects of rearing history on the biological parameters of GEM.

Free-choice assay (antixenosis)

A free-choice assay was carried out to assess the cultivar preferences of GEM. The assay was set up in a white cylindrical plastic cage (1 m diameter, 15 cm high), with 10 round

holes (5 cm diameter, 1.5 cm in between) in a circular arrangement in the bottom plate (see Fig. 1). Ten potted plants (one per cultivar) with similar vegetative growth (mean size of new canes ca. 40 cm) were randomly selected. One apical leaf of each plant was introduced through a hole in the bottom plate, allowing the simultaneous comparison of all cultivars (Fig. 1).

For each replicate, 20 erineae from Sahebi leaves were placed in the center of the ring of test leaves (Fig. 1). Each erineum had a surface of $2 \pm 0.03 \text{ cm}^2$ and a mean density of 180 ± 7.4 mites. Polypropylene film covered the bottom plate and the empty spaces in each of the ten holes, thus preventing the escape of mites onto other leaves of the assayed plants. During an assay, the cage was covered by a thin plastic lid to keep the air still, so that mites could not move on air currents. An assay lasted 48 h and was carried out at 16L:8D photoperiod, 300 lux light intensity on the leaf surface, and $25 \pm 1 \text{ }^\circ\text{C}$. Then, the apical leaves of the potted plants were examined under a dissecting microscope and all mites (juveniles and adults) were counted. Assays were replicated 10 times, following a completely randomized design, each plant representing a replicate.

No-choice assay (antibiosis)

A no-choice bioassay was carried out to assess cultivar effects on GEM biology. Six cultivars (Shahani, Yaghtuti, Flame seedless, Muscat Gordo, White Thompson seedless and

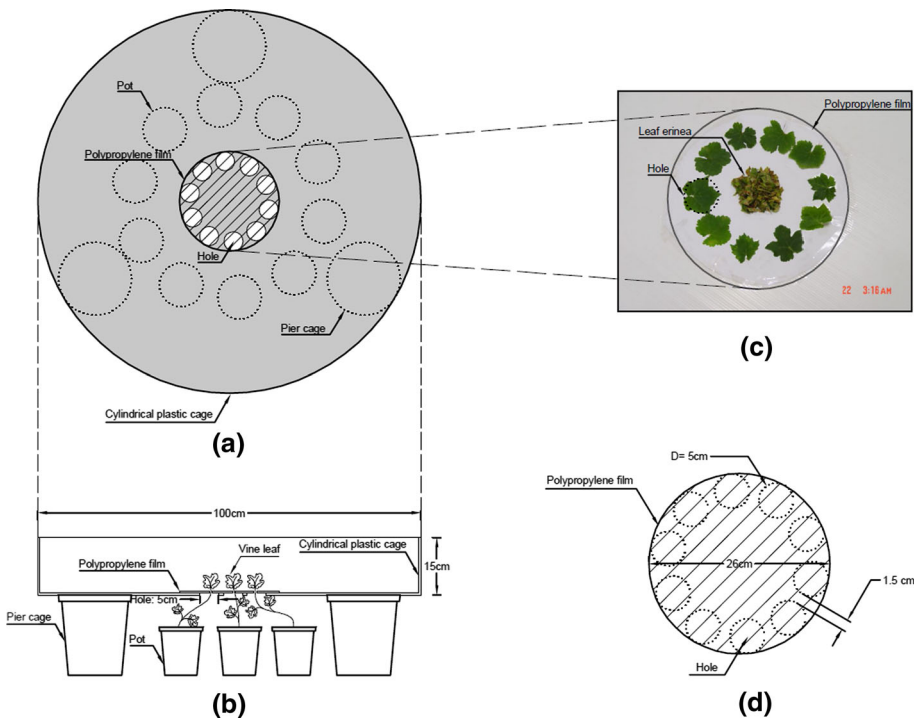


Fig. 1 Free-choice assay: **a** top view of the *cylindrical* plastic device showing the arrangement of the holes in the *bottom* plate and the position of pots and poles underneath (*dotted circles*); **b** side view of apical leaves passing through the holes in the *bottom* plate; **c** detail of the assayed cultivars and infesting erineae; **d** detail of the central part of the device

Gazne) were selected among the original pool based on the results of the free-choice assay; the four cultivars displaying intermediate mite preferences were discarded.

Ten potted plants with similar vegetative growth (mean size of new canes ca. 30 cm) were selected per cultivar. Each plant was artificially infested by two ‘eriocards’ (i.e., an ‘eriocard’ is a carton card of about 4 cm² with a piece of leaf glued to it, with a leaf erineum surface of 4 ± 0.12 cm² and a mean density of 800 ± 8.42 mites) which were tied to the plant’s stem, near the tenth node counting from the bottom of the plant. Each separate plant was fully surrounded by a net (mesh size ≤ 50 μ m) during the assay to avoid mites moving between plants. Plants were kept in a growth room under controlled conditions (25 ± 1 °C, 65 ± 5 % RH and 16L: 8D photoperiod) during the whole period of the assay. The assay was carried out on 10 groups of 6 plants (one for each cultivar) which were mixed randomly and each plant represented a replicate.

Two months after the assay starting, all leaves, buds and the entire branches were used to extract all mite stages, eggs included, according to the above-mentioned washing and sieving procedure. All mites were counted and 50 individuals per cultivar were mounted onto slides, following Amrine and Manson (1996). Individual measurements of adult females were taken under an Olympus BX 51 phase contrast microscope: body width (at widest size) and length of body (from the gnathosoma tip to the anal lobe end), idiosoma (from the gnathosoma base to the anal lobe end), gnathosoma (from the gnathosoma base to the tip of the palps) and chelicerae.

Symptoms and grape growth evaluation

This assay was performed with the same six cultivars selected for the no-choice assay. Twenty potted plants (mean size of canes was ca. 40 cm) per cultivar were transferred to a growth room under controlled conditions (25 ± 1 °C, 65 ± 5 % RH and 16L: 8D photoperiod). Ten out of 20 plants were infested by two ‘eriocards’ each (see no-choice assay), the other 10 stayed uninfested (i.e., control). All plants were singly surrounded by a thin net (mesh size ≤ 50 μ m) and mixed randomly. Two weeks later, the net was removed to avoid that plant growth would be affected by the modified microenvironment and infested plants were kept apart from the uninfested one. Four months after starting the infestation, individual measurements were taken from all plants: area and weight of a sub-sample of leaves (nodes 1 [basal node], 5, 9, 15, 19, and 25 along the cane), number of infested leaves per plant, and internode and shoot length. The leaves were detached and their area was measured using a planimeter (Koizumi AJP Model). Leaf blade weight (without the stalk) was measured with a precision balance (readability of 0.001 g). After measuring leaf area and weight, the infested and non-infested plants were transferred to outdoor natural conditions until leaf fall, in order to allow mites to move into overwintering sites. After bud break at early growth (April 2011), the total shoot length and the internode distance of the previous season’s growth were measured. Internode distances were measured from nodes 1–2 up to 24–25 (hence, 25 distances per shoot). Each plant represented a replicate.

Leaf trichomes and thickness

Density and types of trichomes of uninfested grapevine leaves were assessed according to Loughner et al. (2008) from the cultivars previously used in the no-choice assay. Trichomes were classified on the basis of length and position (bristles < 250 μ m and upright;

hairs $>250\ \mu\text{m}$ and prostrate). Pubescence was evaluated on three distal-shoot leaves per plant. Per each leaf, trichomes were measured on four vein sections (each section 5 mm long, selected randomly) (Fig. 2b) and on four circular areas between veins on the blade (each 10 mm diameter, selected randomly) (Fig. 2c). Hair and bristle density ranks of either vein or blade were assessed under $25\times$ magnifications. Bristle density was assessed also on four vein axils (selected randomly) per leaf (Fig. 2a) and their mean density generated a domatium rank (cf. Loughner et al. 2008). Measurements were taken on 10 plants per cultivar in June 2011 and each plant represented a replicate.

Leaf thickness of uninfested leaves was assessed by a digital micrometer on four mid-shoot and four distal-shoot leaves per cultivar previously used in the no-choice assay. Four segments of each leaf were measured and the mean of these values generated the thickness of each leaf. Measurements were taken on 10 grapes per cultivar in June 2011 and each plant represented a replicate.

Leaf epicuticular waxes

About 100 g of fresh vine leaf material was randomly selected from mid- and terminal-shoot leaves of each uninfested plant previously used in the no-choice assay. This plant material was washed in distilled water and dried on filter paper. The cuticular waxes were extracted by chopping the leaves, immersing the pieces in pure chloroform for 60 s (100 g leaf in 100 ml chloroform). After removing the leaf material, the organic solvent was left to evaporate at room temperature under a fume hood and the wax residues were measured with a precision balance (readability of 0.001 g) according to Casado and Heredia (1999). Amounts of epicuticular wax were expressed in mg/100 g leaf fresh weight. The measurements were replicated on five grapes per cultivar in June 2011 and each plant represented a replicate.

Total soluble carbohydrates in leaves

Fresh vine leaves were randomly selected from mid- and terminal-shoot leaves of each uninfested plant previously used in the no-choice assay. A colorimetric method was applied to determine the total soluble carbohydrates according to Irigoyen et al. (1992). About 0.5 g of leaves was treated with 15 ml of ethanol (83 %). Then, 0.1 ml of alcoholic

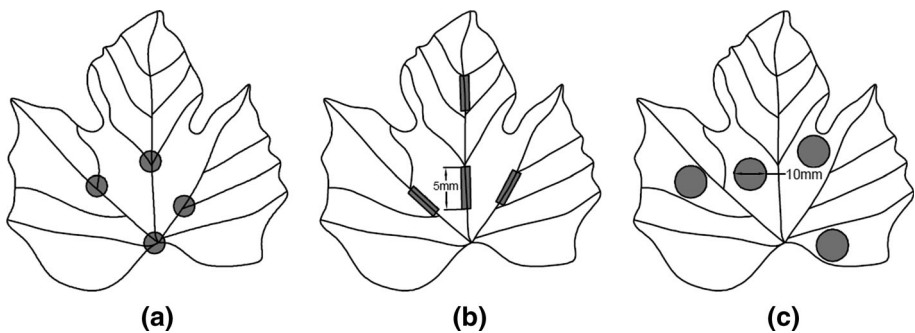


Fig. 2 Location of the various vine leaf parts for measuring (a) domatium size and rank, b leaf vein bristles and hairs, and c leaf blade bristles and hairs (modified from Loughner et al. 2008)

extract was added to 3 ml of a fresh anthron solution (150 mg anthron + 100 ml sulfuric acid at 72 %) and placed in a boiling water bath for 10 min. After cooling, the absorbance was measured at 625 nm by a UV–visible spectrophotometer (Cary model 100, Bio UV–Visible, USA). A calibration curve was obtained measuring the absorbance of a series of standard solutions at 20, 40, 60, 80, 100 and 120 mg of glucose/l. Soluble carbohydrate amount was expressed in mg/g leaf fresh weight based on the following formula:

$$\begin{aligned}\text{Soluble carbohydrate (mg/g)} &= [\text{distillate (15 ml)/leaf (0.5 g)}] \times [\text{Absorbance}/1000] \\ &= \text{Absorbance}/30000\end{aligned}$$

The measurements were replicated on five grapes per cultivar in June 2011 and each plant represented a replicate.

Total phenols in leaves

A colorimetric method was applied to determine the total phenolic content according to Singleton and Rossi (1965). Fresh grape leaves were randomly selected from mid- and terminal-shoot leaves of infested and control plants previously used in the no-choice assay. About 0.5 g of leaf lamina was powdered with methanol 85 % on a pounder. The suspension was filtered on a filter paper, and 300 μ l was taken and mixed with 1,500 μ l of diluted Folin Ciocalteu reagent (1:10 with distilled water). After 8 min at room temperature, 1,200 μ l of Na₂CO₃ 7 % was added and the solution was placed on a Burrell shaker and treated for 90 min at room temperature in darkness. Sample absorbance was measured at 765 nm by a UV–visible spectrophotometer (Cary 100). A calibration curve was obtained measuring the absorbance of a series of standards solutions at 0, 4, 8, 16, 24 and 48 mg of gallic acid/100 ml. Amount of total phenols was expressed as mg of gallic acid equivalents per 100 g of leaf fresh weight. Measurements were replicated on five grapes per cultivar in June 2011 and each plant represented a replicate.

Statistical analysis

All experiments were carried out according to a complete random design. All results, except the plant growth features, were subjected to one-way analysis of variance (ANOVA) using Proc GLM (SAS 2003), after checking normal distribution and equal variance of data. Plant growth features were analyzed with t-tests using SPSS 13.0 (2004). Percentages of infested leaves were arcsine transformed before analysis. After ANOVA indicated significant differences between treatments, mean values were separated using Tukey's test for post hoc comparison ($\alpha = 0.05$).

Pearson's correlation coefficient was determined to assess the relationship between mite population density and GEM impact on grape growth features (leaf area and weight, shoot and internode length, percentage of leaves with erineae), between mite population density and cultivar features (leaf trichome density, leaf thickness, amount of waxes, total carbohydrates and total phenols), and between mite impact on grape growth features and morphological as well as biochemical cultivar features, using SPSS 13.0 (2004).

Based on the *C. vitis* morphological measurements after the no-choice assays, cluster analysis was performed among the various vine cultivars, following Ward's (1963) method using SPSS 13.0 (2004).

All graphs were produced by Sigma Plot version 11.0 (Systat Software 2008).

Results

Free-choice assay (antixenosis)

The mean density of juveniles and adults of GEM was unevenly distributed over the apical leaves of the various vine cultivars and it was significantly different among cultivars ($F_{9,90} = 99.32$, $P < 0.0001$) (Fig. 3). The lowest densities were detected on Shahani (mean = 20.0 mites per leaf), Flame seedless (24.2) and Yaghuti (24.7). The highest densities were found on leaves of Muscat Gordo (100.4), Gazne (95.5) and White Thompson seedless (87.4) (Fig. 3).

No-choice assay (antibiosis)

When feeding of GEM was limited to leaves of one of six vine cultivars, mite density after two months was highly different among cultivars ($F_{5,54} = 23852.9$, $P < 0.0001$) (Fig. 4). The lowest number of eggs, juveniles + adults was recorded on Shahani (mean = 44.7 specimens per plant), the most severe mite infestation was detected on Gazne (822.7) (Fig. 4).

The body size analysis of female mites on each of the six vine cultivars indicated that the largest mites were found on White Thompson seedless and Flame seedless, whereas the

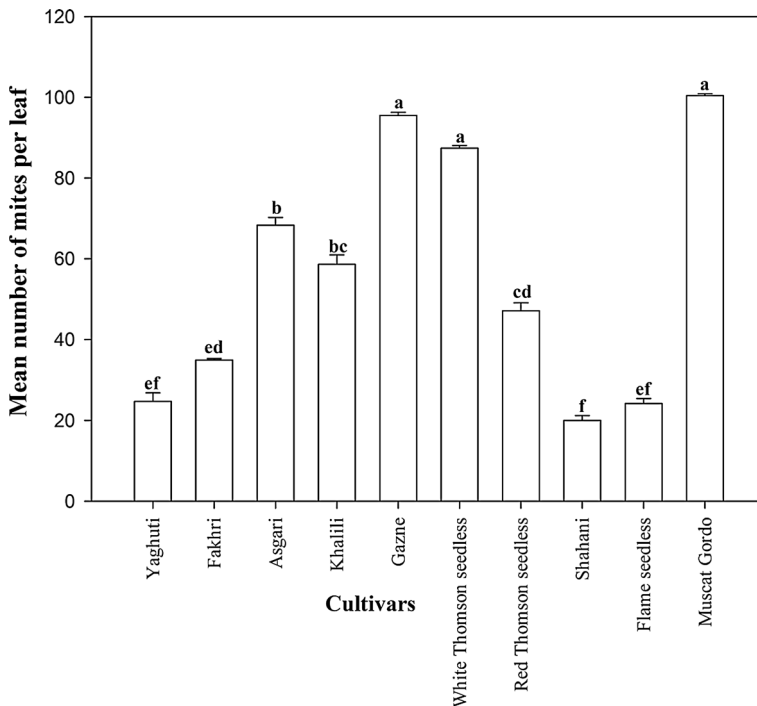


Fig. 3 Free-choice assay: *Colomerus vitis* density (mean + SE number of mites per leaf; $n = 10$) after 48 h on each of ten vine cultivars, when offered simultaneously (see Fig. 1 for test set-up). Means capped by different letters are significantly different ($P < 0.05$, Tukey's test)

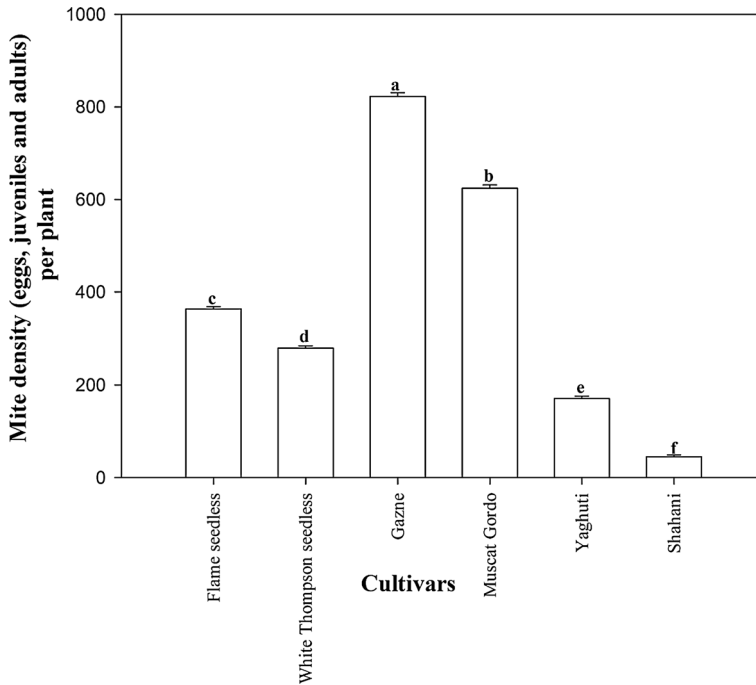


Fig. 4 No-choice assay: *Colomerus vitis* density (mean + SE number of eggs, juveniles + adults per plant; $n = 10$) after 2 months of population development on the six vine cultivars. Means capped by different letters are significantly different ($P < 0.05$, Tukey's test)

smallest mites were found on Shahani and Yaghuti (Table 1). Significant differences among cultivars were found for all body size parameters: body length ($F_{5,294} = 352.87$), idiosoma length ($F_{5,294} = 357.23$), body width ($F_{5,294} = 301.29$), chelicera length ($F_{5,294} = 121.98$) and gnathosoma length ($F_{5,294} = 75.84$; all $P < 0.0001$).

Cluster analysis based on the mite body measurements clearly pointed out the existence of two groups of cultivars: White Thompson seedless, Flame seedless and Gazne vs Shahani, Yaghuti and Muscat Gordo (Fig. 5).

Table 1 No-choice assay: mean (\pm SE; $n = 50$) size (μm) of five morphological traits of female *Colomerus vitis* collected from populations developing for 2 months on the various vine cultivars

Cultivars	Length of body	Width of body	Length of idiosoma	Length of gnathosoma	Length of chelicerae
White Thompson seedless	213.9 \pm 0.40a	73.9 \pm 0.5a	188.7 \pm 0.56a	25.2 \pm 0.41a	26.8 \pm 0.44a
Flame seedless	210.9 \pm 0.83a	64.3 \pm 0.67b	189.6 \pm 0.66a	21.6 \pm 0.90b	24.2 \pm 0.53b
Gazne	200.1 \pm 0.46b	63.5 \pm 0.83b	178.5 \pm 0.41b	21.6 \pm 0.49b	23.6 \pm 0.32b
Muscat Gordo	167.1 \pm 0.93c	52.9 \pm 0.60c	148.1 \pm 0.79c	19.0 \pm 0.64c	18.2 \pm 0.99c
Yaghuti	151.8 \pm 1.01d	43.8 \pm 0.93d	136.7 \pm 0.95d	15.1 \pm 0.84e	17.5 \pm 0.72c
Shahani	161.3 \pm 0.85cd	38.9 \pm 0.79e	144.5 \pm 0.88c	16.8 \pm 0.51d	15.8 \pm 0.78d

Means within columns followed by different letters are significantly different (Tukey's test: $P < 0.05$)

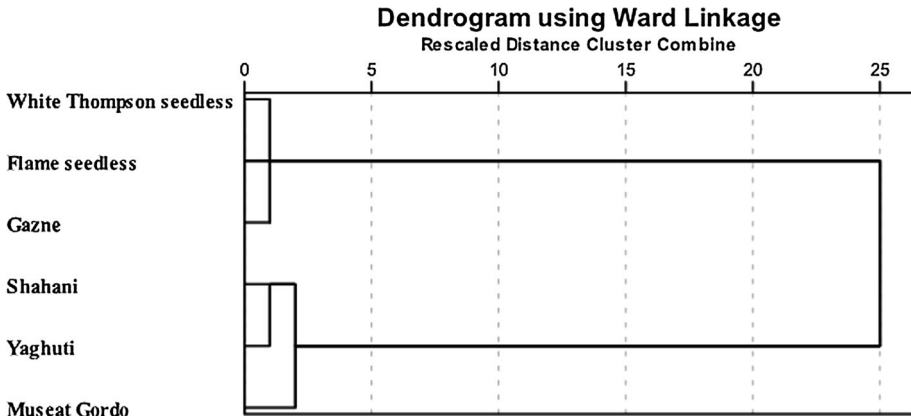


Fig. 5 No-choice assay: cultivars dendrogram generated from the selected body morphological details assessed on GEM populations developed on the assayed cultivars

Symptoms and grape growth evaluation

The occurrence of erineum leaf patches after direct mite infestation (tolerance assay) differed among the six selected cultivars ($F_{5,54} = 1462.98, P < 0.0001$). The highest percentage of affected leaves was found on Gazne, whereas no erineum were recorded on Shahani (Table 2).

The mite population that developed after the artificial infestation affected various vegetative growth features in most of the six vine cultivars, in comparison with those of uninfested plants (Table 3). Overall, the mites had a pronounced effect on leaf area and weight, whereas their influence on shoot growth was quite weak. Infested leaves were significantly smaller than uninfested ones in all cultivars, except Shahani where no difference was found ($F_{1,18} = 1.35, P = 0.26$) (Table 3). Similarly, infested leaves were always heavier than those collected from control plants and these differences were significant on White Thompson seedless, Flame seedless and Gazne. Shoot and/or internode lengths were slightly longer on uninfested than on infested plants and these differences were significant on Gazne and Muscat Gordo (Table 3).

Correlation analysis indicated that mite density (number of eggs, juveniles + adults) was negatively related with infested leaf area (Pearson’s coefficient = -0.86), shoot length (-0.87 ; both $P < 0.01$) and internode length ($-0.28, P < 0.05$), and it was positively related with leaf weight (0.57) and percentage of affected leaves (0.81 ; both $P < 0.01$).

Table 2 Mean (\pm SE) percentage of leaves with erineum by *Colomerus vitis* on the assayed cultivars

Cultivars	Leaves with erineum (%)
Gazne	89.30 \pm 0.34a
Flame seedless	75.08 \pm 0.40b
White Thompson seedless	71.02 \pm 0.38bc
Muscat Gordo	66.10 \pm 0.45d
Yaghuti	17.94 \pm 0.59e
Shahani	0.00 \pm 0.00f

Means followed by different letters are significantly different (Tukey’s test: $P < 0.05$)

Table 3 Differences in mean (\pm SE) size of selected vegetative growth features in infested vs uninfested plants of six vine cultivars

Cultivars		Leaf area (cm ²)	Leaf weight (g)	Shoot length (cm)	Internode length (cm)
Gazne	Infested	35.57 \pm 0.97b	0.55 \pm 0.012a	31.41 \pm 0.74b	1.71 \pm 0.052a
	Uninfested	68.75 \pm 1.56a	0.30 \pm 0.011b	48.42 \pm 0.63a	2.38 \pm 0.047a
Flame seedless	Infested	32.32 \pm 0.83b	0.38 \pm 0.013a	36.17 \pm 0.89a	2.40 \pm 0.013a
	Uninfested	47.35 \pm 0.49a	0.24 \pm 0.015b	40.63 \pm 0.94a	2.80 \pm 0.017a
White Thompson seedless	Infested	40.33 \pm 1.10b	0.61 \pm 0.021a	29.13 \pm 1.29a	2.14 \pm 0.066a
	Uninfested	63.62 \pm 0.86a	0.42 \pm 0.031b	33.39 \pm 1.25a	2.17 \pm 0.081a
Muscat Gordo	Infested	33.40 \pm 0.93b	0.71 \pm 0.016a	43.80 \pm 0.81b	2.09 \pm 0.023a
	Uninfested	55.98 \pm 1.09a	0.56 \pm 0.013a	56.07 \pm 0.96a	2.86 \pm 0.056b
Yaghuti	Infested	30.98 \pm 1.8b	0.38 \pm 0.012a	45.53 \pm 1.01a	1.34 \pm 0.072a
	Uninfested	39.06 \pm 0.82a	0.31 \pm .021a	51.48 \pm 0.93a	1.37 \pm 0.092a
Shahani	Infested	29.45 \pm 1.29a	0.41 \pm 0.013a	26.25 \pm 1.05a	1.91 \pm 0.064a
	Uninfested	31.43 \pm 1.16a	0.39 \pm 0.015a	25.63 \pm 0.81a	1.93 \pm 0.110a

Means within cultivars and within columns followed by different letters are significantly different (*t* test: $P < 0.05$)

Cluster analysis based on the vegetative growth features pointed out the existence of three groups of cultivars: (1) White Thompson seedless and Flame seedless, (2) Yaghuti and Shahani, and (3) Muscat Gordo and Gazne (Fig. 6).

Leaf trichomes and leaf thickness

Rank density of the five plant trichome types differed significantly among grape cultivars (Table 4): blade bristle ($F_{5,54} = 259.04$), blade hair ($F_{5,54} = 72.27$), vein bristle ($F_{5,54} = 1778.69$), vein hair ($F_{5,54} = 1449.30$) and domatia ($F_{5,54} = 469.90$; all $P < 0.0001$). Blade bristle rank ranged from (mean \pm SE) 4.6 \pm 0.2 (Shahani) to

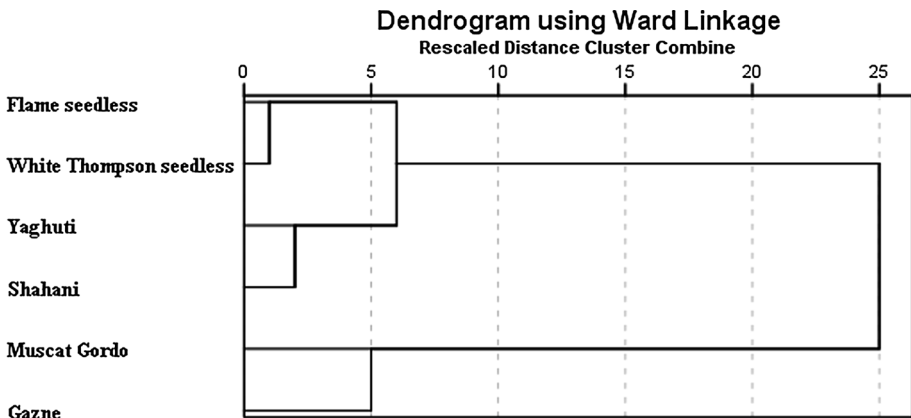


Fig. 6 Cultivars dendrogram based on selected vegetative growth features of GEM infested versus uninfested vine cultivars

0.05 ± 0.02 bristles per mm^2 (Flame seedless, Gazne); blade hair rank ranged from 2.7 ± 0.1 (Muscat Gordo) to 0.01 ± 0.01 hairs per mm^2 (Shahani); vein bristle rank ranged from 13.5 ± 0.2 (Yaghuti) to 0.06 ± 0.04 bristles per mm^2 (Flame seedless); vein hair rank ranged from 14.7 ± 0.2 (Muscat Gordo) to 0.03 ± 0.03 hairs per mm^2 (Shahani); and domatia rank ranged from 37.4 ± 0.5 (Yaghuti) to 16.7 ± 0.3 trichomes per mm^2 (Gazne) (Table 4). Leaf thickness differed among cultivars ($F_{5,54} = 25.75$, $P < 0.0001$); uninfested leaves of Shahani, Yaghuti and Gazne were thickest (Table 5).

Correlation analysis of mite population density (number of eggs, juveniles + adults) and leave thickness and trichome features, assessed on leaves of uninfested plants of the same grapevine cultivars, indicated that mite density was negatively related with blade bristle rank (Pearson's coefficient = -0.73), vein bristle rank (-0.65), and domatium rank (-0.81), and it was positively related with blade hair rank (0.76) and vein hair rank (0.56 ; all $P < 0.01$). No significant correlation was found between mite density and leaf thickness (-0.05 , $P > 0.05$).

Biochemical features

Significant differences among vine cultivars were found in the amount of leaf epicuticular waxes ($F_{5,24} = 8.33$, $P = 0.0001$) and total carbohydrate content ($F_{5,24} = 215.42$, $P < 0.0001$). The amount of leaf epicuticular waxes ranged from 0.17 (Shahani) to 0.11 mg/100 g (White Thompson seedless, Flame seedless), total carbohydrate content ranged from 295.4 (Gazne) to 187.0 mg/g (Shahani) (Table 6).

The amount of phenolic compounds in uninfested leaves did not differ among the six vine cultivars ($F_{5,24} = 1.26$, $P = 0.31$) (Table 6). When infested by GEM, the differences

Table 4 Mean (\pm SE) trichome rank density (number of trichomes per mm^2) on leaves of six grapevine cultivars, separated by trichome type

Cultivars	Blade bristle rank	Blade hair rank	Vein bristle rank	Vein hair rank	Domatium rank
Shahani	$4.55 \pm 0.20a$	$0.01 \pm 0.01c$	$7.89 \pm 0.21b$	$0.03 \pm 0.03e$	$33.75 \pm 0.53b$
Yaghuti	$3.16 \pm 0.19b$	$0.11 \pm 0.03c$	$13.53 \pm 0.16a$	$0.29 \pm 0.03de$	$37.38 \pm 0.48a$
White Thompson seedless	$0.10 \pm 0.04c$	$0.31 \pm 0.02c$	$0.30 \pm 0.09dc$	$5.25 \pm 0.25b$	$24.30 \pm 0.35c$
Flame seedless	$0.05 \pm 0.02c$	$0.30 \pm 0.06c$	$0.06 \pm 0.04d$	$0.84 \pm 0.10d$	$19.15 \pm 0.30e$
Muscat Gordo	$0.22 \pm 0.09c$	$2.65 \pm 0.10a$	$0.65 \pm 0.15c$	$14.66 \pm 0.15a$	$20.82 \pm 0.27d$
Gazne	$0.05 \pm 0.02c$	$1.42 \pm 0.18b$	$0.10 \pm 0.05dc$	$4.10 \pm 0.16c$	$16.73 \pm 0.26f$

Means within columns followed by different letters are significantly different (Tukey's test: $P < 0.05$)

Table 5 Mean (\pm SE) thickness (mm) of leaves of six grapevine cultivars

Cultivars	Leaf thickness (mm)
Shahani	$0.18 \pm 0.02a$
Yaghuti	$0.18 \pm 0.03a$
Gazne	$0.18 \pm 0.03a$
White Thompson seedless	$0.16 \pm 0.01b$
Muscat Gordo	$0.15 \pm 0.03bc$
Flame seedless	$0.14 \pm 0.03c$

Means followed by different letters are significantly different (Tukey's test: $P < 0.05$)

Table 6 Mean (\pm SE) content of selected biochemical compounds in leaves of six grapevine cultivars

Cultivars	Epicuticular waxes (mg/100 g)	Carbohydrates (mg/g)	Phenols (mg/100 g gallic acid)	
			In uninfested vines	In infested vines
Shahani	0.17 \pm 0.009a	187.02 \pm 1.59e	0.12 \pm 0.01a	0.13 \pm 0.04a
Yaghuti	0.15 \pm 0.03ab	193.70 \pm 2.80ed	0.12 \pm 0.006a	0.12 \pm 0.04a
White Thompson seedless	0.11 \pm 0.01c	220.30 \pm 2.73c	0.12 \pm 0.02a	0.12 \pm 0.01a
Flame seedless	0.11 \pm 0.04c	201.31 \pm 1.88d	0.12 \pm 0.02a	0.12 \pm 0.02a
Muscat Gordo	0.13 \pm 0.03bc	243.97 \pm 1.89b	0.12 \pm 0.03a	0.12 \pm 0.02a
Gazne	0.13 \pm 0.01bc	295.42 \pm 4.60a	0.12 \pm 0.02a	0.10 \pm 0.02b

Means within columns followed by different letters are significantly different (Tukey's test: $P < 0.05$)

in phenol content among cultivars were still small (range: 0.10 \pm 0.02–0.13 \pm 0.04 mg/100 g gallic acid), but significant ($F_{5,24} = 15.83$, $P < 0.0001$) (Table 6).

Correlation analysis indicated that mite density (number of eggs, juveniles + adults) was negatively related with leaf wax contents (Pearson's coefficient = -0.42) and phenol concentration in infested leaves (-0.97), and it was positively related with carbohydrate concentration of uninfested leaves (0.93; all $P < 0.01$). The correlation between mite density and phenol concentration in uninfested leaves was not significant (-0.25 ; $P > 0.05$).

Correlation of vegetative growth vs leaf biochemical and trichome features

Correlation analysis indicated negative relations between leaf area and shoot length vs carbohydrate content, and between leaf weight and % leaves with erinea vs phenol content in infested leaves and amount of epicuticular waxes (Table 7). Significant positive relations were found between leaf weight and % leaves with erinea vs carbohydrate content, between leaf area and shoot length vs phenol content in infested leaves, and between leaf area, shoot length and internode length vs epicuticular wax amount; phenol content of uninfested leaves were not significantly related to any vegetative growth feature (Table 7).

Correlation analysis indicated strong positive relations between leaf area and shoot length vs blade bristle, vein bristle and domatium ranks, and between leaf weight and % leaves with erinea vs blade hair and vein hair ranks (Table 8). Strong negative relations were found between leaf weight and % leaves with erinea vs blade bristle, vein bristle and

Table 7 Correlation coefficient (Pearson's coefficient) between vegetative growth features and biochemical characters of six grapevine cultivars

Vegetative growth features	Carbohydrates (mg/g)	Phenols (mg/100 g of gallic acid) in uninfested vines	Phenols (mg/100 g of gallic acid) in infested vines	Epicuticular waxes (mg/100 g)
Leaf area	-0.87^{**}	0.12ns	0.73**	0.52**
Leaf weight	0.57**	0.05ns	-0.27^*	-0.31^*
Shoot length	-0.87^{**}	0.13ns	0.71**	0.26*
Internode length	-0.19 ns	0.23ns	0.14ns	0.26*
% Leaves with erinea	0.72**	-0.23 ns	-0.68^{**}	-0.71^{**}

** $P < 0.01$; * $P < 0.05$; ns, $P > 0.05$

Table 8 Correlation coefficient (Pearson's coefficient) between vegetative growth features and leaf trichome rank densities of six grapevine cultivars

Vegetative growth features	Blade bristle rank	Blade hair rank	Vein bristle rank	Vein hair rank	Domatium rank
Leaf area	0.79**	-0.58**	0.71**	-0.51**	0.78**
Leaf weight	-0.54**	0.74**	-0.55**	0.89**	-0.48**
Shoot length	0.53**	-0.67**	0.38**	-0.49**	0.56**
Internode length	0.25ns	-0.41**	0.29*	-0.40**	0.31*
% leaves with erinea	-0.95**	0.48**	-0.86**	0.43**	-0.92**

** $P < 0.01$; * $P < 0.05$; ns, $P > 0.05$

domatium ranks, and between leaf area, shoot length and internode length vs to blade hair and vein hair ranks (Table 8).

Discussion

Host selection by eriophyoid mites is probably the combined result of differential attractiveness of a plant (in this case, grapevine cultivars towards GEM) and its biochemical and morphological features opposing mite infestation. Strategies and mechanisms applied by eriophyoids in selecting their host plants are still mostly vague and unexplained, but it appears likely that the few known chemosensilla on legs and mouthparts of these tiny mites (de Lillo and Aldini 2001; de Lillo et al. 2002, 2005) are involved in perceiving and discriminating plant chemical cues (short distance volatiles and contact compounds) among thousands of compounds on plant surfaces, mostly with unknown roles (Michalska et al. 2010). Considering the homogeneity of the environmental conditions during the experiments described in this study, the differences in mite size and population density observed on the various grapevine cultivars might be consequences of mite adaptation to the biochemical and morphological features of the hosts, which are involved in mite nourishment and/or plant defense mechanisms.

Intraspecific variation in morphology has rarely been investigated in eriophyoids. Some studies concerned the morphological variability in natural populations inhabiting closely related host plant species, e.g., of *Aculus fockeui* (Nalepa & Trouessart) protogyne females on *Prunus* species (Boczek et al. 1984) and *Aceria tosichella* Keifer on grass species (Skoracka and Kuczyński 2006), or in geographically separated populations, e.g., of *A. guerreronis* females on *Cocos nucifera* L. (Navia et al. 2006). Discontinuous morphological variation allowed the discrimination of cryptic entities, already genetically and biologically separated, within the generalist *A. hystrix* complex (Skoracka 2009) or *Cirsium*-associated *Aceria* spp. (Vidović et al. 2010) and *Ribes-Cecidophyopsis* species (Amrine et al. 1994). In addition, effects of plant cultivars on mite morphology have been reported in the free-living *Aculus schlechtendali*, pointing out differences in body size and length of the ventral setae within protogyne females (Kozłowski 1998).

Interestingly, GEM population density on Flame seedless in the no-choice assay was higher than expected based on the free-choice assays. Relative attractiveness, repellence and physical features of Flame seedless plants will have played a role during free-choice assay. But when the mite was forced to feed on less-preferred plants, no negative effect on the mite physiology became apparent, as indicated by the large size of the mite. In other

words, the intrinsic features of Flame seedless appear not detrimental to the development of the mite population. Similar apparently contradictory results of free-choice *vs* no-choice assays have been found for *Aceria salsolae* de Lillo and Sobhian (Smith et al. 2009) and *Aceria solstitialis* de Lillo et al. (Stoeva et al. 2012) in host specificity trials in the laboratory.

Reduction of leaf surface, leaf weight increase, shoot shortening and erineum formation were related to mite density and were greatest on Gazne, while Shahani and Yaghuti were scarcely affected by GEM infestation. Plant feeding effects (distortive and non-distortive) are largely the result of eriophyoid piercing and injecting of salivary compounds, which redirect the plant's physiology and cell development, the details of which are far from clear (Oldfield 1996; de Lillo and Monfreda 2004; Monfreda and Spagnuolo 2004; Monfreda and de Lillo 2006; Petanović and Kielkiewicz 2010). Leaf erineum mites, such as GEM, are known to induce cell re-differentiation, which alters the size and the chemical content of infested organs (Petanović and Kielkiewicz 2010).

Mite density appeared to be largely related to the leaf physical structures (trichome types and density) of the assayed cultivars. Ning et al. (1996) found that some tea varieties resistant to *A. theae* had denser pubescent leaves than susceptible varieties. GEM can induce erineum leaf patches on very young leaves, which are smaller and have denser hairs (i.e., more trichomes per unit area) than mature leaves which were submitted during the current experiments. Perhaps these young leaves form favorable microhabitats that allow GEM to hide away from predators during the initial colonization of leaves and can offer a more suitable microclimatic and nutritional environment. Also long leaf hairs can favor escaping or hiding of free-living eriophyoids: the mites may climb into the hairs and stay unnoticed by predators wandering on the leaf surface (Michalska 2003; Michalska et al. 2010; Simoni and Sabelis 2010).

No significant correlation was found between mite density and leaf thickness of mature leaves; leaves of the least infested cultivars (Shahani and Yaghuti) were the thickest, along with Gazne which was largely infested. Measurements should be extended to the blade thickness of the youngest leaves, i.e. the most preferred by the mites and the most susceptible to the induction of erineum at the initial phase of the leaf infestation (Petanović and Kielkiewicz 2010).

Interactions between mite density and (non-glandular) trichome arrangement of grapevine leaves were previously observed in the field for GEM and grape rust mite, *Calepitrimerus vitis* (Nalepa), along with other phytophagous and predatory mites, on strongly haired leaves of Canaiolo in comparison to the weakly haired leaves of Sangiovese (Castagnoli et al. 1997). Similar results were obtained, still in the field, by Dellei and Szendrey (1991) on Hungarian and international cultivars. The complexity of the investigated microenvironments, the simultaneous presence of mites with different feeding behaviors and the various aims of the studies did not allow determining correlations of leaf physical structures *vs* eriophyoid population development. In addition, erinose species seem to take advantage of the leaf domatia stimulating the further development of dense hair-like structures inside them (O'Dowd and Willson 1997). Our observations in the current study regard unfested leaves.

The amount of leaf waxes was the highest in Shahani and Yaghuti, which hosted the lowest mite density and showed the least erineum on infested leaves. Higher wax content corresponded to lower leaf erineum induction and larger leaf area. It is well known that epicuticular waxes of the plant surfaces could affect the feeding behavior of herbivores and physically prevent their movement across the leaf surface (Howe and Schaller 2008). Wax compounds could interfere with mite feeding and, consequently, affect survival rates,

developmental duration, egg production and other biological parameters. Thus, wax may be a valuable indicator for screening cultivar resistance. A potential correlation exists between the leaf wax layer and the thickness of leaf cuticle and epidermal cell walls. Eriophyoids pierce the cuticle and the epidermal cell walls by means of their short stylets, while injecting saliva into the cells, or, as some researchers believe, stylet piercing follows the digestion of epidermal cell wall components by means of mite salivary secretion (Schmeits and Sassen 1978; Thomsen 1988; Hoy 2011). The interference of the wax layer with cell piercing and the actual thickness of the leaf cuticle has already been related to resistance of pigeon pea, *Cajanus cajan* (L.) Millsp., to *Aceria cajani* Channabasavanna (Reddy et al. 1995).

Mite impact on the assayed cultivars proved to be strongly correlated with total soluble carbohydrates and phenols: mites appeared to thrive better on cultivars with higher leaf carbohydrate content, and infestation was lower on cultivars which do not increase leaf phenol content. Carbohydrate amount in uninfested leaves was lowest on the least mite-infested Shahani and highest on the heavily infested Gazne, whereas phenols increased in leaves of Shahani and decreased in leaves of Gazne after mite infestation. Similarly, lower contents of reducing and water-soluble sugars were found in shoots of tea varieties resistant to *A. theae* and this was supposed to have an antibiotic effect (Ning et al. 1996). Carbohydrates and proteins are known to (1) be required as nutrients by herbivorous arthropods (Bernays and Chapman 1994), (2) act as cues that affect plant susceptibility (Sadasivam and Macickam 1992; Dhaliwal and Dilawari 1993), and (3) affect the success of phytophagous organisms (Shi and Tomczyk 2001). Plant phenols are well known to interact with plant pests/pathogens and they play a role as antioxidants and modulators of the activity of other phytochemicals (Martin-Tanguy 1997). How eriophyoids may induce modifications in a plant's phenol profile is still unclear and studies on other biochemical responses of host plants to eriophyoid feeding are scarce (Royalty and Perring 1996; Shi and Tomczyk 2001; Petanović and Kielkiewicz 2010). An increase of phenols after mite infestation has been recorded in olives fruits infested by *Aculus olearius* Castagnoli and *Aceria oleae* (Nalepa) (Cetin et al. 2011), in lemon buds infested by *Aceria sheldoni* (Ewing) (Ishaaya and Sternlicht 1969), in leaves of blackberry cultivars infested by *Epirimerus gibbosus* (Nalepa) (Shi and Tomczyk 2001), but its detailed relationship with plant resistance to the mites was not always investigated. Some previous research pointed out that eriophyoid infestations (*E. gibbosus* on the evergreen blackberry cultivar Thornless, *A. schlehtendali* on a susceptible apple cultivar) can increase the ratio between total phenol compounds to carbohydrates in infested leaves (Kozłowski 1998; Shi and Tomczyk 2001); this higher ratio can depend both on the increase of phenols and the reduction of sugars (Kozłowski and Kozłowska 1996; Tomczyk and Boczek 2006).

In conclusion, the grapevines can be divided in (relatively) resistant, sensitive and intermediate cultivars. Shahani and Yaghuti can be considered resistant, because few mites were attracted by them, mite population development was poor and few or no erineum leaf patches were induced. In addition, infested and non-infested vines appeared to tolerate mite occurrence well. Muscat Gordo and Gazne were the most sensitive cultivars, as they sustained high populations of GEM and their leaves and shoots were affected considerably by the feeding mites. The seedless cultivars Flame and White Thompson showed intermediate responses concerning mite attraction and mite-plant interaction.

Leaf hairiness, leaf surface waxes and leaf carbohydrate contents could be used as tools to predict resistance/tolerance to GEM in preliminary screenings among vine cultivars.

Further experiments should be conducted, on these selected cultivars and also others with a larger distribution in the world, to investigate whether GEM affects gas exchange,

photosynthesis, stomatal conductance, transpiration and other parameters more closely related to vine physiology and grape yield (carbohydrate reserves of grapes and harvest quality), such as carried out in part on Muscat in Swiss vineyards (Linder et al. 2006). The effects of cultivars on the reproductive fitness of the mites should be compared along with morphological details of the mite populations. Finally, the search for genes responsible for resistance may offer a potential tool in the IPM of these mites.

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