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Additional Information

Accepted Article

Title: Association between ants (Hymenoptera: Formicidae) and the vine mealybug (Hemiptera: Pseudococcidae) in table-grape vineyards in Eastern Spain

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Abstract

BACKGROUND

The vine mealybug, *Planococcus ficus* (Signoret) (Hemiptera: Pseudococcidae) is a key pest of grapevine in the Mediterranean Basin. Some honeydew collecting ant species are known to increase mealybug populations in other grape-growing regions. However, there is scarce information on either the ant species present in Mediterranean vineyards or their impact on mealybugs. We conducted a study in four commercial vineyards in Eastern Spain in order to i) identify the ant species foraging on the vine canopies, ii) study the association among ant

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activity, vine mealybug abundance and fruit damage, and iii) test a novel method for ant management, distracting ants from guarding vine mealybugs by providing artificial sugars.

RESULTS

We recorded three ant species native to the Mediterranean foraging on the vine canopies: *Lasius grandis* (Forel), *Pheidole pallidula* (Nylander) and *Plagiolepis schmitzii* (Forel). The mean percentage of damaged fruits per vine was positively correlated with the number of vine mealybugs captured in traps placed at the trunk. We detected a positive but weak relationship between ant activity, vine mealybug abundance and fruit damage. The provisioning of artificial sugars reduced the number of ants foraging on the vines by 23.4% although this reduction was not statistically significant. Vine mealybug abundance was significantly reduced (72%) after sugar provisioning.

CONCLUSION

Our results suggest that the ant species native to vineyards in eastern Spain induce population increases of the vine mealybug. Moreover, the provisioning of artificial sugars can be a valuable tool for ant management.

Key words: Ant community, trophic interactions, Planococcus ficus, Lasius grandis, Pheidole pallidula, Plagiolepis schmitzii, integrated pest management, grapevine.

1. INTRODUCTION

The vine mealybug, *Planococcus ficus* (Signoret) (Hemiptera: Pseudococcidae), is a key, devastating insect pest of grapevine worldwide ^(1,2). It is present in 35 countries, including the grape-growing regions of the Mediterranean Basin, Middle East, Pakistan, India, South Africa, South America, Mexico and California ⁽³⁾. The vine mealybug feeds on the sap of the vines and migrates to different areas of the plant following the distribution of carbohydrates ⁽⁴⁾. It hibernates as adult female on the roots and beneath the vine trunk bark ^(1,2). In spring it moves to the green parts of the vine and in summer it clusters on the fruits ^(5–8). The vine mealybug is a key pest of table grapes because the presence of wax, honeydew and sooty-mold fungi on the fruits can greatly reduce their market value. Furthermore, *P. ficus* can transmit leafroll-associated viruses (GLRaVs) resulting in substantial yield losses ^(9,10). In recent years, the vine mealybug has emerged as a key pest of table-grapes in Eastern Spain coinciding with the reduction of use of broad-spectrum insecticides. Therefore, there is growing interest in developing Integrated Pest Management (IPM) programs against this pest ⁽¹¹⁾.

Mealybugs, as honeydew-excreting hemipterans, establish mutualistic relationships with ants (Hymenoptera: Formicidae) ⁽¹²⁻¹⁵⁾. Ants eagerly collect the sugar-rich honeydew excretion, and in exchange, protect mealybugs from natural enemies, provide better hygiene conditions due to honeydew removal and shelter ⁽¹⁴⁻¹⁸⁾. The degree of protection depends on several factors such as ant species, abundance and quality of honeydew, and availability of alternative food for the ants ⁽¹⁹⁻²¹⁾. Some species, such as *Linepitema humile* (Mayr) and *Crematogaster peringueyi* Emery, reduced the efficacy of natural enemies in vineyards, including those of the vine mealybug ^(18,22,23). More recently, it was shown that the ant *Tapinoma nigerrimum* (Nylander) significantly disrupted either the parasitism potential or This article is protected by copyright. All rights reserved.

the predatory activity of main vine mealybug's natural enemies occurring in Mediterranean vineyards ⁽²⁴⁾. On the other hand, the ant species *Anoplolepis steingroeveri* (Forel) and *Iridomyrmex* spp. did not show a significant impact on entomophagous insects in vineyards ^(22,25). Crucially, depending on the sugar and protein availability and the nutritional requirements of the ant colony, ants may also prey on the mealybugs ⁽²⁶⁾.

In vineyards, ant control is usually advocated as part of IPM programs to enhance the activity of mealybug natural enemies ^(4,27). The most commonly used strategies for ant management are based on chemical control by means of spray applications, or the use of liquid toxic baits ^(28–33). Physical exclusion methods have been developed as well, banding the stem of the vines with sticky tape ⁽³⁴⁾. In other systems, alternative strategies have been developed to alter the mutualistic association between ants and honeydew producers. Some of these methodologies involve the provisioning of alternative sugar sources, such as nectar from cover crops ^(35,36) or artificial sugar ^(26,37).

Understanding the relationships between ants and the vine mealybug is crucial to improve the management of this pest in the Mediterranean Basin. With the exception of some previous studies by Mansour et al. ^(24,39), there is very little information available about the ant species present in Mediterranean vineyards and their impact on the vine mealybug. To tackle this problem we studied: i) the ant species complex foraging on the vine canopies in Eastern Spain table-grape vineyards, ii) the seasonal activity of the ant species, iii) the impact of ants on both the mealybug populations and fruit damage and iv) the impact of supplying artificial sugars on both ant activity and mealybug populations.

2. MATERIALS AND METHODS

2.1 Sampling sites

The study was carried out in four commercial table-grape vineyards in Vinalopó Valley, an extensive vineyard region in Eastern Spain. All sampling sites had a history of *P. ficus* infestations and economic damage. Vineyards were between five and 10 years old; had different grape cultivars, pruning and irrigation systems and their surface area ranged from 0.35 to 0.80 ha (Table 1). They were maintained free of weeds by ploughing and/or applying herbicides locally. No insecticides were applied during the study, but fungicides were used regularly in all sampling sites.

2.2 Ant species and activity

Ant activity observations were conducted in 2013 and 2014. In the second year, vineyards 3 and 4 were not included in the study because of the low ant population density recorded during the first year. Samplings were conducted monthly from April to October in 30 vines (3 replicates of 10 contiguous vines) per vineyard in 2013 and biweekly from May to September in 24 vines (4 replicates of 6 adjacent vines) per vineyard in 2014. Observations were conducted from 10 a.m to 4 p.m. On each sampling date we quantified ant activity as the number of ants crossing (either up or down) an imaginary horizontal line on the vine trunk during a 1-minute period ⁽³⁹⁾. Individual ants were collected and placed into 70% ethanol before being taken to the laboratory for identification. Ant species were identified according to Seifert ⁽⁴⁰⁾ and Bolton ⁽⁴¹⁾.

2.3 Mealybug abundance and fruit damage

Vine mealybug populations were monitored on the same date and vines on which ant activity was recorded, using a non-destructive methodology from May to October in 2013 (no vines with sugar dispensers were included in this assessments; see below). A cylindrical

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20 cm length piece of the outer bark was removed from the upper trunk of the sampled vines and was replaced by an equal sized piece of corrugated cardboard that was wrapped around the trunk with an adjustable plastic cable (DeBach, 1949). The number of vine mealybugs (from second instar nymphs to adults) present in the cardboard was counted biweekly. One week before harvest, fruit damage was estimated by counting the number of unmarketable clusters in these vines. Fruits were considered unmarketable when they had more than ten mealybugs, sooty mold or abundant honeydew.

2.4 Impact of artificial sugars on ant activity

The impact of artificial sugars on ant activity was studied in 2013. Sugar dispensers were placed on ten vines per vineyard (below the imaginary line used for ant activity assessments) distributed in two plots consisting of five contiguous vines in the same row. The dispensers consisted of 250 ml plastic bottles sealed with a perforated lid with a diameter of 28 mm. A round piece of filter paper was adjusted in the interior side of the lid to slow down the dripping of the sugar. These dispensers were filled with a solution containing one part of Biogluc[®] (Belgosuc, Belgium), a sugar solution (71.5% w/w) containing fructose (37.5%), glucose (34.5%), sucrose (25%), maltose (2%) and oligosaccharides (1%) and one part of water.(1:1 ratio). One sugar dispenser per vine was tied upside down on the lower trunk with an adjustable plastic cable. The bottles were covered with a plastic mesh (openings size 15x15 mm) to exclude bees, wasps and bumblebees. Ant activity and mealybug population density were recorded using the same methodology described above. The 30 vines sampled for ant activity (section 2.2) were used as untreated controls.

2.5 Statistical analyses

To study the relationship between ant activity and the population density of the mealybugs we used analysis of covariance (ANCOVA) with the vineyard included as a covariable. Generalized linear models (GLMs) were used to study the impact of ants and mealybugs on the percentage of damaged fruits. We assumed binomial error variance and if overdispersion or underdispersion was detected, the significance of the explanatory variables was re-evaluated using an F-test after re-scaling the statistical model by a Pearson's χ^2 divided by the residual degrees of freedom ⁽⁴²⁾. Finally, we applied a two-way ANOVA to evaluate the effect of artificial sugars on ant activity and mealybug populations among vineyards. For all the analyses we used the yearly average of mealybug and ant abundance in each vine. When necessary, logarithmic transformations were applied to stabilize the variance.

3. RESULTS

3.1 Ant species and activity

Three ant species were found foraging on the vines: *Lasius grandis* Forel, *Pheidole pallidula* (Nylander) and *Plagiolepis schmitzii* Forel. In vineyard 1, mean (\pm SE) ant activity was 1.28 \pm 0.29 and 1.12 \pm 0.22 ants per minute in 2013 and 2014, respectively (Fig. 1). The most abundant species in this vineyard was *L. grandis* representing 98% and 83% of the ant individuals counted in 2013 and 2014, respectively. In vineyard 2, the number of foraging ants per minute on the vines averaged 1.00 \pm 0.21 in 2013 and 1.66 \pm 0.30 in 2014. Here, *P. schmitzii* was the most abundant species representing 53% and 49% of the foraging ants, in 2013 and 2014, respectively, followed by *P. pallidula* with 29% and 51% in 2013 and 2014, respectively. Ant activity was lower in vineyards 3 and 4 averaging 0.20 \pm 0.06 (in 2013) and 0.32 \pm 0.08 ants per minute (in 2014).

Regarding the spatial distribution pattern of the ants, 50.0% of the vines were occupied by one ant species only, 29.8% of the vines were occupied by two ant species, whereas three ant species were found on 2.4% of the vines (Table 2). On the vines with two ant species, *P. schmitzii* was found together with *L. grandis* or *P. pallidula* on 11.3% and 18.5% of the vines, respectively. *L. grandis* and *P. pallidula* where never observed associated on the same vine except on the 2.4% of the vines where all three species were present. The seasonal activity pattern was similar for *L. grandis* and *P. schmitzii*; activity started increasing in late May and peaked in June. A second smaller increase was observed at the end of summer. In 2013, the activity of *P. pallidula* increased in July and was maintained high during the summer months, whereas in 2014 the peak of activity was observed in September (Fig. 2).

3.2 Mealybug abundance and fruit damage

Mealybug abundance in the traps placed on the trunk was positively correlated with the density of ants foraging on the vines (F = 36.88; df = 1, 118; P < 0.0001; $R^2 = 23.81$) (Fig. 3). Neither the effect of the sampling site (F = 1.95; df = 3, 115; P = 0.12) nor the interaction between mealybug abundance and sampling site were significant (F = 0.28; df = 3, 112; P = 0.83).

The mean percentage of damaged fruits per vine increased significantly with the number of mealybugs captured in the trunk traps (F = 36.02; df = 1, 116; P < 0.0001; $D^2 = 14.25$) (Fig. 4). Fruit damage differed significantly among vineyards (F = 35.09; df = 3, 113; P < 0.0001; $D^2 = 41.63$), but there was not a significant effect of the interaction between both factors (F = 1.07; df = 3, 110; P = 0.36).

Fruit damage also significantly increased with ant activity (F = 28.87; df = 1, 116; P < 0.0001; $D^2 = 10.25$) (Fig. 5). Significant differences in fruit damage were found among vineyards (F = This article is protected by copyright. All rights reserved. 44.10; df = 3, 113; P < 0.0001; $D^2 = 47.09$), whereas, the interaction between ant activity and vineyard was not significant (F = 0.73; df = 3, 110; P = 0.53).

3.3 Impact of artificial sugars on ant activity

Pooling the data from all vineyards, the application of artificial sugars reduced the number of ants foraging on the vines from 0.64 \pm 0.07 ants per minute in the control treatment to 0.49 \pm 0.12 ants per minute in the vines with sugar dispensers (23.4% reduction). However, this difference was not statistically significant (*F* = 0.54; df = 1,155; *P* = 0.46). Ant activity was different among vineyards (*F* = 13.54; df = 3,155; *P* < 0.0001), however, the interaction between treatment (artificial sugar provisioning) and vineyards was not significant (*F* = 0.36; df = 3,152; *P* = 0.78).

Among ant species, the highest reduction on ant activity was found for *L. grandis* (50% reduction) when artificial sugars were available, however, this reduction was not statistically significant (F = 1.67; df = 1,155; P = 0.20). The activity of *P. schmitzii* did not show any variation due to the provision of sugar dispensers (F = 0.01; df = 1,155; P = 0.97). Also, the activity of *P. pallidula* was not significantly different between control and sugar treatments (F = 0.18; df = 1,155; P = 0.67).

When examining separately the vineyards with the highest ant activity, we observed that in vineyard 1, the number of *L. grandis* foraging on the vines did not decrease significantly in the presence of sugar dispensers (F = 1.46; df = 1,38; P = 0.23) (Fig. 6). On the other hand, the foraging populations of *P. schmitzii* increased significantly from 0.02 ± 0.01 to 0.11 ± 0.04 (increase of 450%) (F = 9.18; df = 1,38; P = 0.005). In vineyard 2, the presence of sugar dispensers had no significant effect on the activity of both *P. schmitzii* (F = 0.28; df = 1,38; P = 0.59) and *P. pallidula* (F = 1.02; df = 1,38; P = 0.32) on the vines.

Pooling data from all vineyards, sugar provisioning (F = 14.94; df = 1,155; P = 0.0002) and vineyard (F = 10.02; df = 3,155; P < 0.0001) had a highly significant effect on the mealybug abundance, without an interaction between the two factors (F = 1.44; df = 3,152; P = 0.23). The mean number of mealybugs captured in cardboard traps was significantly lower in the vines with sugar dispensers (1.67 ± 0.39 mealybugs per trap) than in the control treatment (0.47 ± 0.29 mealybugs per trap) (72% reduction) (F = 14.94; df = 1,155; P = 0.0002). When examining vineyards separately, the effect of sugars in reducing mealybug populations was significant in vineyards 1 (F = 4.75; df = 1,39; P = 0.03) and 2 (F = 7.17; df = 1,39; P = 0.01) but not in vineyards 3 (F = 1.29; df = 1,39; P = 0.26) and 4 (F = 2.09; df = 1,39; P = 0.16) (Fig. 7).

4. DISCUSSION

The ant species complex recorded foraging in vineyards was composed by three species that had been recorded in previous studies in other open field agroecosystems in Eastern Spain (39,43–47). In these studies, the most abundant species foraging on the plant canopies or on the soil were *L. grandis*, or its sibling species *Lasius niger* L., and *P. pallidula*. This limited number of species recorded in the present study is not exceptional for monoculture systems that are characterized by a reduced biodiversity ⁽⁴⁶⁾. Crucially, the Argentine ant *L. humile*, which is invasive in the Mediterranean Basin ⁽⁴⁸⁾, was not found in our study. This species has only been recorded in orchards with specific climatic conditions and in eastern Spain ^(45–47,49). From studies in other agroecosystems this species is known to be present in orchards with relatively high humidity ^(48,50). Apparently, the low humidity (320 mm rainfall per year) might explain the absence of this species in the vineyards studied herein. We neither recorded *Tapinoma nigerrimum* (Nylander), which is the primary ant tending the vine mealybug and disrupting the action of its main natural enemies in Tunisian vineyards ^(24,38), but this species

has only been sporadically reported in Spanish agroecosystems (other than vineyards) (46,47,51)

Interestingly, the ant activity levels in our study were very low compared to those reported for other ant species in other grape producing regions (see ^{18,25} for ant species and regions). The differences in the biology of the ant species occurring in various agroecosystems and the low number of honeydew-producing hemiptera reported in our study might explain these results. The seasonal foraging patterns of *L. grandis* and *P. schmitzii* were similar due to their dependence on hemipteran honeydew ^(43,47). Ant activity increased in May, when aphids (e.g. *Aphis gossypii* Glover) were abundant on the vines and peaked in June. On the other hand, the activity of *P. pallidula*, which is less dependent on hemipteran honeydew ^(47,52) and has a higher heat tolerance, peaked in July as it has been found in studies in other agroecosystems

In absence of the sugar feeders, there was a positive but weak relationship between mealybug abundance in the trunk traps and fruit damage. This result could be due to the methodology used. Cardboard traps may be an appropriate method to estimate properly the mealybug populations on the trunk but apparently is not necessarily a good predictor of fruit damage. Other methods, for example, a simple count of grape mealybugs on three spurs per vine at midseason has been reported as the best predictor of economic damage in California vineyards ⁽⁵⁴⁾.

The relationship between ant activity and fruit damage in the control vines was significant but less important than the relationship between the mealybug-abundance and fruit damage. These results suggest that the impact of ants on fruit damage is indirect via their mutualistic association with the vine mealybug. Indeed, when no sugar feeders were provided, ant activity was positively correlated with mealybug abundance per vine. This article is protected by copyright. All rights reserved. However, this association seems to be less significant than that reported in previous studies in vineyards ^(18,22). In our study, only 16% of the mealybug colonies present in the grapes were tended by ants in 2014 (Beltrà A. unpublished). These results are in contrast with those reported in citrus orchards in Eastern Spain where the sibling species *Planococcus citri* (Risso) is heavily attended by the same ant species complex ⁽⁴³⁾. The weak relationship between "north Mediterranean ant species" and *P. ficus* recorded in our study may have practical implications for biological control given that ant interference with natural enemies is expected to be less critical than in Tunisian ("south Mediterranean") ⁽²⁴⁾, Californian ^(18,32) and South African vineyards ^(22,23). Therefore, for IPM purposes in Eastern Spain, we suggest to consider ant control only in those vineyards with high levels of ant activity and/or with the presence of aggressive and with efficient recruitment mechanisms species such as the Argentine ant. In this context, Mansour et al. ⁽¹⁾ suggested to deploy research efforts for achieving effective control of mealybug-tending ants *T. nigerrimum* before implementing biological control programs using natural enemies of *P. ficus* and *P. citri* in Tunisian vineyards and citrus orchards.

Overall, the provision of artificial sugars reduced ant activity higher up in the vine, although this reduction was not statistically significant. This result is likely due to ants visiting the sugar feeder subsequently turning back to their nests, rather than continuing to move up the vines. The response to the artificial sugars depended on the ant species. In vineyard 1, *L. grandis* showed a decreased activity up the vine, while we recorded an increase in numbers of *P. schmitzii*. Behavioral differences and the dominance status of these species might explain this result (Table 2). *P. schmitzii* is a subordinate species and its foraging activity at local food resources is limited by dominant species ⁽⁵⁵⁾. Therefore, *P. schmitzii* may increase its activity for honeydew collection when the dominant *L. grandis* is not foraging on the This article is protected by copyright. All rights reserved. canopy. On the other hand, the omnivorous behavior of *P. pallidula* could explain its lower attraction to the sugar dispensers observed in vineyard 2 $^{(53)}$.

The significant reduction in mealybug populations found in the vines provided with sugar feeders is likely attributable to the effect of sugars on ant activity. Reduced ant-attendance on the mealybugs can enhance the action of certain natural enemy species, e.g. the parasitoid species *Coccidoxenoides perminutus* Girault and *Anagyrus* sp. near *pseudococci* (Girault) (both Hymenoptera: Encyrtidae) ^(23,56,57) and accumulating honeydew may further reduce mealybug population growth. Another additional mechanism could be the increment of ant predation on the mealybugs when their needs for sugar were satisfied. Feeding with sucrose reduced the attendance of the predaceous fire ant *Solenopsis geminata* (Fabricius) on the pineapple mealybug, *Dysmicoccus brevipes* (Cockerell) ⁽²⁶⁾. Similarly, other studies have shown that predation by ants on aphids increases when excess alternative sugar sources are available ^(58,59).

All in all, we found a simple ant assemblage, composed of only three native species, foraging on the vines of eastern Mediterranean table-grape vineyards. The level of ant activity was low, especially when compared with other ant species in vineyards worldwide. In absence of sugar supplements, ant activity showed a slight positive correlation with mealybug populations and fruit damage. Thus, Mediterranean ant species likely interfere with the biological control agents in table-grape vineyards, even though this effect appears to be less disruptive than in other grape-growing regions such as California or South Africa ^(18,22). Our results suggest that ant control should be considered only in those vineyards with high levels of ant activity. The provisioning of artificial sugars impacted ant activity, depending on the ant species, and eventually the mealybug population density. These results in combination This article is protected by copyright. All rights reserved. with those of other studies by Carabalí-Banguero et al ⁽²⁶⁾, Nagy et al. ⁽³⁷⁾ and Wäckers et al.

⁽⁶⁰⁾ indicate that this method can be a simple, sustainable and effective alternative for

managing ants and associated honeydew-producing pests.

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Figure legends

Figure 1. Average foraging activity (number of ants during 1 minute) of *Lasius grandis, Pheidole pallidula* and *Plagiolepis schmitzii*. Samples from 168 vines of four table-grape vineyards sampled from May to October in 2013 and 2014. Bars represent the standard errors for the overall ant activity.

Figure 2. Seasonal foraging activity (number of ants during 1 minute) of *Lasius grandis, Pheidole pallidula* and *Plagiolepis schmitzii.* Samples from 168 vines of four table-grape vineyards sampled from April to October in 2013 and from May to September in 2014. Bars represent the standard errors.

Figure 3. Relationship between ant activity (number of ants during 1 minute) and abundance of *Planococcus ficus* on cardboard traps per vine [Log (Mealybugs + 1) = $0.76 \times \text{Log} (\text{Ants} + 1) + 0.24$; R^2 = 23.81]. Samples from 120 vines of four table grape vineyards monitored in 2013.

Figure 4. Relationship between *Planococcus ficus* abundance and fruit damage [Log(Fruit damage/1-Fruit Damage)=0.82*Log(Mealybug+1)- 2.66*V2 - 2.36*V3 + 0.67*V4 - 1.21; D² = 55.88]. V1 = Vineyard 1, V2 = Vineyard 2, V3 = Vineyard 3, V4 = Vineyard 4. Samples from 120 vines from four table-grape vineyards monitored in 2013.

Figure 5. Relationship between ant activity (number of ants during 1 minute) and fruit damage per vine. [Log(Fruit damage/1-Fruit Damage)=1.48*Log(Ants+1)- 2.54*V2 - 2.09*V3 + 1.14*V4 - 1.59; D^2 = 57.34]. V1 = Vineyard 1, V2 = Vineyard 2, V3 = Vineyard 3, V4 = Vineyard 4. Samples from 120 vines of four table grape vineyards monitored in 2013.

Figure 6. Ant activity (number of ants during 1 minute) in vines with or without sugar dispensers. Samples from 160 vines from four table grape vineyards monitored in 2013. Asterisks indicate significant differences between treatments.

Figure 7. *Planococcus ficus* abundance on cardboard traps on vines with or without sugar dispensers. Samples from 160 vines of four table grape vineyards monitored in 2013. Asterisks indicate significant differences between treatments.

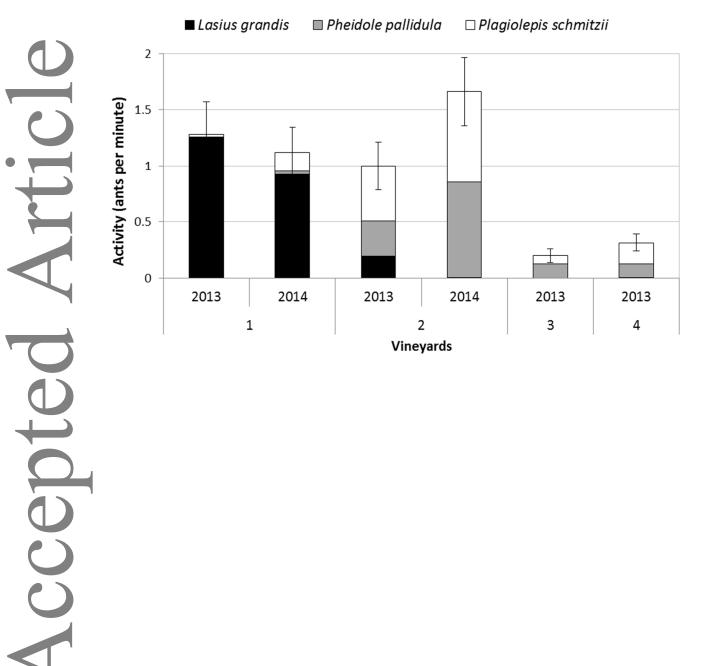
Vineyard	Locality	Geographic coordinates	Surface (ha)	Cultivar	Pruning system	Drip irrigation	Grape harvest time
1	La Romana	38º 21' 32" N, 0º 53' 29" W	0.71	Dominga	Spur-pruning	Sub- surface	November
2	Novelda	38º 22' 46" N, 0º 49' 20" W	0.63	Red globe	Spur-pruning	Surface	September
3	Novelda	38º 22' 48" N, 0º 47' 4" W	0.51	Aledo	Cane-pruning	Surface	October
4	La Romana	38º 21' 32" N, 0º 54' 4" W	0.35	Aledo	Cane-pruning	Surface	October

Table 1. Description of the vineyards sampled in the study.

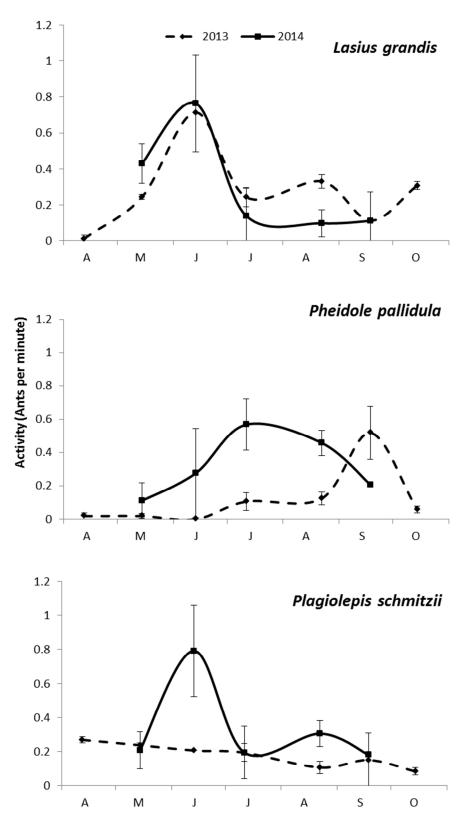
Table 2. Percentage of vines with one, two, three or without foraging ant species in each vineyard and year. Samples from 168 vines from four table grape vineyards sampled from April to October in 2013 and from May to September in 2014. Ant species: *Lasius grandis, Pheidole pallidula, Plagiolepis schmitzii*.

					1 ant species			2 ant species			
Vin	Vineyard	Year	Vines	Without ants	L. grandis	P. schmitzii	P. pallidula	L. grandis P. schmitzii	L. grandis P. pallidula	P. schmitzii P. pallidula	3 ant species
	V1	2013	30	3.3%	70.0%	6.7%	0.0%	20.0%	0.0%	0.0%	0.0%
		2014	24	8.3%	41.7%	8.3%	0.0%	33.3%	0.0%	0.0%	8.3%
	V2	2013	30	26.7%	0.0%	30.0%	10.0%	10.0%	0.0%	16.7%	6.7%
		2014	24	4.2%	0.0%	16.7%	4.2%	4.2%	0.0%	70.8%	0.0%
	V3	2013	30	40.0%	0.0%	16.7%	26.7%	0.0%	0.0%	16.7%	0.0%
\geq	V4	2013	30	20.0%	0.0%	40.0%	23.3%	3.3%	0.0%	13.3%	0.0%
Ì	Total	2013 - 2014	168	17.9%	18.5%	20.2%	11.3%	11.3%	0.0%	18.5%	2.4%

Accepted A







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Fig. 3

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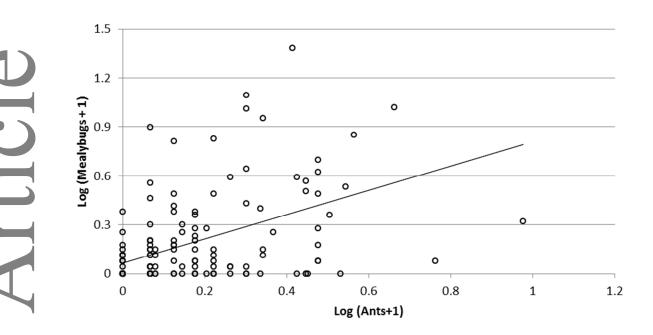
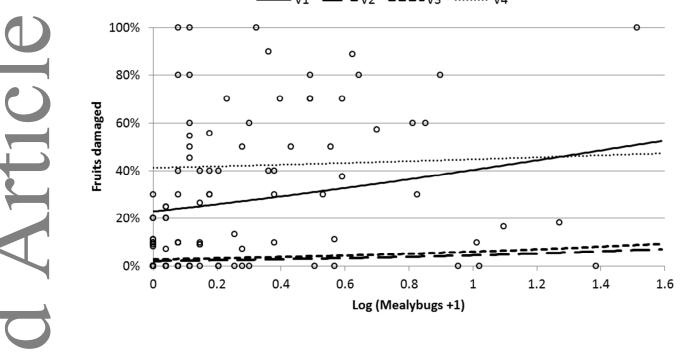


Fig. 4



— V1 — -V2 ----V3 ······· V4

Fig. 5

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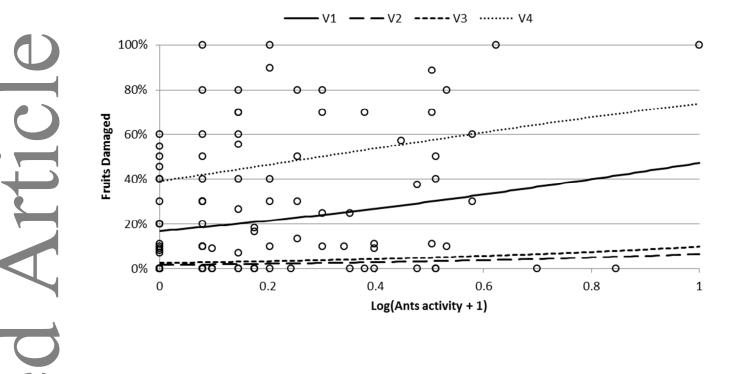
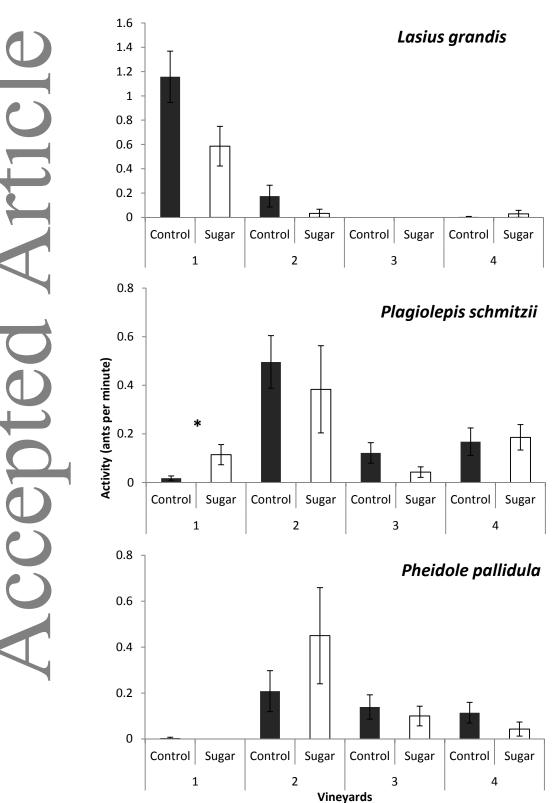


Fig. 6



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Fig. 7

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