RESEARCH ARTICLE

Effect of ant predation and abiotic factors on the mortality of medfly larvae, *Ceratitis capitata*, in the Argan forest of Western Morocco

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(Received 7 September 2009; returned 28 October 2009; accepted 26 February 2010)

The Argan *Argania spinosa* (L.) Skeels (Ericales: Sapotaceae) is an endemic and emblematic tree growing in the centre and the southwest of Morocco. Argan fruits are frequently infested by the Mediterranean fruit fly *Ceratitis capitata* Wied (Diptera: Tephritidae). To date, no control program has been undertaken in the Argan forest. This research is the first investigation of natural mortality factors of *C. capitata* larvae in the Argan forest. The study was conducted at two localities near the city of Essaouira with different climatic conditions. Observations were conducted using 260 late instar larvae which were individually deposited on the ground, under fruiting host trees, where they naturally fall to find a suitable pupation site. Overall, 42% of the larvae died before being able to burrow into the ground, irrespectively of the location. Larval survival and their likelihood of burrowing decreased with increasing ground temperature, as 53% of all the larvae deaths occurred at temperatures over 48°C. However, at lower ground temperature, predation by ants and spiders accounted for 47% of all mortality. Four species of ants carried out 94% of the captures. *Monomorium subopacum* Mayr (Hymenoptera: Formicidae), which frequently forages under Argan trees, was by far the most efficient predator, due to a powerful sting that rapidly immobilizes the prey. Our results suggest that the burrowing performance of larvae is constrained by high thermal conditions and the presence of ant predators at lower temperatures.

**Keywords:** *Ceratitis capitata*; *Argania spinosa*; ants; predation; biological control

Introduction

In economic terms, the Mediterranean fruit fly or medfly, *Ceratitis capitata* (Wiedemann 1824), is probably the most important fruit pest among the Tephritidae (Aluja and Mangan 2008). In the Argan forest, *C. capitata* is the sole representative species of the Tephritidae (Naamani 2004). Its destructive capacity is favored by its wide geographical distribution (EPPO 2004), rapid dispersion (Papadopoulos, Carey, Katsoyannos, and Kouloussis 1996; Papadopoulos, Katsoyannos, and Nestle 2003) and adaptation to various climates (Putruelle 1998). This very polyphagous and
cosmopolitan fly attacks over 300 plant species, of which many are fruit crops (Liquido, Shinoda, and Cunningham 1991). Medfly larvae feed on fruit pulp, which they exit at the last instar to find a suitable pupation site in the ground. This stage, during which they are no longer protected inside the fruit, is possibly the most risky for flies which are subject to high mortality due to abiotic and biotic factors.

Ants constitute an important component of forest ecosystems (Wilson 1990; Folgarait 1998). Due to their wide distribution, abundance and predominance in many terrestrial biotopes, ants have a substantial ecological impact on the evolution and population dynamics of other sympatric species (Carroll and Janzen 1973; Finnegan 1974; Gotwald 1986; Hölldobler and Wilson 1990). They are a major cause of mortality of many arthropods, including medflies (Carroll and Risch 1990; Way and Khoo 1992; Perfecto and Castineiras 1998; Van Mele, Vayssieres, Van Tellingen, and Vrolijk 2007). Pemberton and Willard (1918) reported that the ant *Pheidole megacephala* (Hymenoptera: Formicidae) was responsible for more than 80% of the attacks on immature tephritids in Hawaii. More contemporary authors have also shown that ants are a common predator causing substantial reduction of fruit fly populations (Bateman 1976; Wong, McInnis, Nishimoto, Ota, and Chang 1984; Eskafi and Kolbe 1990; Thomas 1993, 1995; Hodgson, Sivinski, Quintero, and Aluja, 1998; Aluja, Sivinski, Rull and Hodgson 2005). Nevertheless, in spite of their importance as a potential biological control agent (Yang 1982), ants remain relatively underestimated in biological control programs, and many aspects of their impact on fruit pests are still unclear. This is partly due to the fact that too few studies have analyzed their impact on regulating phytophagous populations.

The Argan, *Argania spinosa* L. (Skeels 1911) of the Sapotacae family is an endemic and emblematic tree of central and southwest Morocco. It covers an area estimated at more than 800,000 ha (Ayad 1989). The Argan is a tree of great ecological and socioeconomic importance, constituting the last barrier against the open desert, which poses a serious threat to Southern Morocco. In the Souss region, especially, the Argan forest is surrounded by large citrus orchards. The medfly frequently infests Argan fruits as a support for larval development (Sacantanis 1957). Therefore, the Argan forest may represent an enormous potential reservoir for the proliferation and dissemination of this species to other fruiting plants (Debouzie and Mazih 1999). No study has yet been undertaken to evaluate the success of the *C. capitata* during its biological cycle in the Argan forest biotope and to highlight the potential causes of natural mortality, including ants, which can affect the population dynamics of this species. Our goal is to estimate the success of *C. capitata* larvae in finding a pupation site and quantifying their mortality rate caused by both biotic and abiotic factors. The contribution of the Argan forest myrmecofauna to medfly larval mortality was quantified and behavioral interactions between larvae prey and their predator ants were described.

**Material and methods**

**Field site**

Our study was carried out in the Argan forest of Essaouira in Western Morocco (Figure 1), in May, 2006, at the beginning of the Argan maturation season, when the highest number of *C. capitata* can be observed on the fruits in the Arganeraie. This
The region has a pronounced Mediterranean, arid climate with dry, hot summers and relatively cool winters. Precipitations average 300 mm/year, concentrated in the winter.

The study was conducted at two localities about 50 km apart, which differed in terms of their vegetation and distance from the coast. These populations were chosen because they are representative of the Argan forest distribution range. The Boutazarte site, is located 20 km south of Essaouira city on the littoral band and is directly exposed to oceanic influences that reduce year-round variations in temperature. The Argan forest at this locality is relatively dense with 4–8 m high trees every 3–20 m. The understory is composed of sparse woody plants (Chamaerops humilis L., Ziziphus lotus L.) and cultivated cereals (Hordeum vulgare L., Triticum spp. L.).

The Lahssinate site, is located 40 km east of Essaouira city and is under semi-continenetal influence. The sparse forest is composed of 6–10 m high Argan trees separated by gaps of 5–40 m. Vegetation between Argan trees includes olive trees (Olea europaea), vines (Vitis vinifera), common fig (Ficus carica L.) and cactus (Opuntia ficus indica Mill.). At both sites litter does not exceed 3–4 cm.
Data collection
Observations were carried out in the two sites from 08:00 to 18:00 h during 2 weeks in late spring 2006, coinciding with the natural peak of emergence of medfly third instar larvae. Third larval instars of *C. capitata* are easily distinguishable (8–9 mm in length, anterior buccal carina and anterior spiracles nearly straight on dorsal of tubule row). Because the larvae used in our experiments were collected just before emergence from infested Argan fruits obtained in the respective study sites we assume their behavior is similar to that of larvae naturally searching for pupation sites. Larvae were deposited on the ground under 10 trees at each location, reproducing the normal exit of the larvae from the fruits and fall to the ground. All trees were of similar size and at least 10 m apart. During the 30 min following the release of the larvae we recorded whether they burrowed or died. Two causes of death were identified: predation by terrestrial arthropods (ants and spiders) and heat shock (when the larva rapidly died after a few convulsions). The time to either event (burrowing, apparent heat shock and predation by arthropod) was also noted, as well as the predator species attacking the medfly. Particular attention was paid to the predatory behavior of the ant *Monomorium subopacum*, this being the main source of biotic mortality. Burrowing success versus either cause of mortality was noted in relation to ground temperature, ground texture and sun exposure. Ground temperature was measured with an Electronic thermometer (with Stainless Steel Probe for High-Temp. Sensing – Effective measuring area, 40–50 mm from the tip) at the beginning of each bioassay. Ground texture (sandy, soft, with sand predominance; or argillaceous, hard, with clay predominance) and sun exposure were determined visually by each experimenter before releasing the larvae.

Data analysis
Statistics were conducted using the R software (R Development Core Team 2009). The proportion of larvae that succeeded in burrowing into the ground or that died from heat shock or from an attack by arthropods was compared between field stations by means of a Pearson Chi-square test. Larval survival time was also analyzed as a function of ground texture, sun exposure, ground temperature, field site and tree, using Cox proportional hazards regression model (Crawley 2007). Generalized linear models were then used to test the main effects of ground texture, sun exposure, ground temperature, field site and tree within field site on the probability of burrowing vs. death and on death by arthropod attack vs. death by heat shock. For proportions, the binomial error distribution and Logit link function were used. For time to burrowing, heat shock and predation by arthropod, the normal error distribution was used with the identity link function.

Results
At both localities, all larvae deposited under Argan trees either rapidly burrowed into the ground or died from heat shock or from an attack by arthropods, but none remained more than 30 min alive on the ground. The probability of either event occurring (burrowing, heat shock or attack by arthropods) was not significantly different between study sites (Table 1; Pearson Chi-square: $\chi^2 = 0.78$, df = 2,
Statistical analyses of the effect of ground temperature, sun exposure, ground texture, field station and individual Argan tree on larval survival are listed in Table 2. The Cox model first indicated that survival time decreased significantly with ground temperature and did not depend on other factors. Generalized linear models then provided additional information on factors affecting the probability of and time to death (that is, the probability of not burrowing). The probability of death did not differ between localities or trees within study field station (Table 2; GLM 1). The time to death, irrespective of the cause, differed significantly between trees within site field station, but not between localities. Ground conditions greatly affected the probability of death vs. burrowing. Thus, larvae succeeded in burrowing more frequently and more rapidly on sandy than on argillaceous ground (Probability of success: 68.79% vs. 45.87%, respectively; Time to burrowing: 3.40 ± 0.43 min vs. 8.07 ± 1.38 min (mean ± SE), respectively). Burrowing was also more frequent in shade than under direct sun exposure (77.55% vs. 36.97%, respectively), although the time until burrowing did not differ significantly according to sun exposure (4.44 ± 0.55 min vs. 5.87 ± 1.33 min (mean ± SE), respectively). Finally, the probability of death increased significantly with ground temperature (dotted line and filled diamonds in Figure 2). While larval death was recorded at all temperatures, no larvae survived when the ground temperature exceeded 48°C. The time until burrowing was not significantly affected by ground temperature.

The 42% of larvae that did not burrow within 30 min eventually died of two major causes: heat shock (22%) and predation by arthropods (20%). Among the larvae that did not survive, the probability of predation by arthropods decreased significantly with ground temperature and was higher in shade than under direct sun exposure (62.67% vs. 30.30%, respectively). All attacks except one were recorded below 48°C (open triangles in Figure 2), while over this threshold all deaths were due to heat shock. The probability of predation by arthropods did not vary significantly between the Boutazarte and the Lahssinate sites, but varied significantly between trees within each locality. Nor did the probability of predation vary significantly between soft and hard ground.

Ants captured 94% of the larvae that did not burrow into the ground or die from heat shock, whereas spiders attacked the remaining 6%. More than 70% of the attacks occurred during the first 5 min after larvae were released on the ground and, on average, when attacks occurred they were recorded after only 5.90 ± 1.09 min (mean ± SE; N = 51). The time to arthropod attack only differed significantly between trees within field stations but not according to type of ground, sun exposure, ground temperature or the field station.

Table 1. Main larval fate of *C. capitata* larvae after their experimental release under Argan trees at the Boutazarte site and the Lahssinate site.

<table>
<thead>
<tr>
<th></th>
<th>Boutazarte</th>
<th>Lahssinate</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burial</td>
<td>72 (55.38)</td>
<td>79 (61.54)</td>
<td>151 (58.46)</td>
</tr>
<tr>
<td>Death by heat shock</td>
<td>31 (23.85)</td>
<td>27 (20.00)</td>
<td>58 (21.92)</td>
</tr>
<tr>
<td>Predation by arthropods</td>
<td>27 (20.77)</td>
<td>24 (18.46)</td>
<td>51 (19.62)</td>
</tr>
</tbody>
</table>

Values are of events with percentages in parentheses.
Only four ant species were involved in all the attacks on medfly larvae: *Monomorium subopacum*, *Tapinoma simrothi*, *Cataglyphis viatica* and *Messor picturatus maura*. Among these ant species, attacks by *M. subopacum* and *T. simrothi* were by far the most frequent (more than 95% of all the ant attacks), although this differed slightly between localities. Hence, at Lahssinate, *M. subopacum* and *T. simrothi* accounted for 43 and 52% of the attacks, respectively, while at Boutazarte they were responsible for 88 and 8% of the captures, respectively (Yates corrected Chi-square: $\chi^2 = 9.50$, df = 2, $P = 0.002$).

Ant species did not react in the same manner after an encounter with a larva. Predation efficiency of *M. subopacum*, which could be defined as the probability of a worker having discovered a larva corresponding to an attack and a capture, was clearly higher than that of *T. simrothi* (Figure 3; Yates Chi-square: $\chi^2 = 12.1$, df = 1, $P = 0.005$). Indeed, *T. simrothi* workers attacked only 56% of the larvae they discovered ($N = 25$), whereas *M. subopacum* foragers attacked almost all the larvae

<table>
<thead>
<tr>
<th>Model</th>
<th>Response variable</th>
<th>Predictors</th>
<th>$\chi^2$</th>
<th>df</th>
<th>$P$</th>
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<td>Survival time</td>
<td>G</td>
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<td>1</td>
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<tr>
<td></td>
<td></td>
<td>E</td>
<td>0.00</td>
<td>1</td>
<td>0.99</td>
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<td></td>
<td></td>
<td>T</td>
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<td></td>
<td></td>
<td>S</td>
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<td>1</td>
<td>0.13</td>
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<td></td>
<td></td>
<td>A(S)</td>
<td>0.01</td>
<td>45</td>
<td>0.75</td>
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<td>14.02</td>
<td>1</td>
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<td>GLM3</td>
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<td>0.322</td>
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<td>GLM4</td>
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<td></td>
<td></td>
<td>A(S)</td>
<td>58.81</td>
<td>16</td>
<td>0.001</td>
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</table>
they encountered (97%, N = 33). Six encounters were observed between medfly larvae and other arthropods (other than *M. subopacum* and *T. simrothi*), giving rise to an attack in five cases.

Detailed behavioral observations indicated that numerous workers of *M. subopacum* and *T. simrothi* foraged under Argan trees. Workers seemed to forage haphazardly and to detect larvae by antennal contact. *M. subopacum* responded almost immediately, seizing the larva in its mandible and stinging it. Larvae sometimes got free of ants by jumping aside, but were often caught and stung again. Fights never lasted more than 4 min and always resulted in the immobilization of the larva. Thereafter, the *M. subopacum* worker temporarily released its prey and recruited up to 20 nestmates to help transport it to the nest. In the case of *T. simrothi*,

![Figure 2](image1.png)

Figure 2. The fate of *C. capitata* larvae as a function of ground temperature below Argan trees. Filled diamonds show the observed fate for all fly larvae (1 – death, top of graph; 0 survival, bottom of graph). The respective GLM predicted values (dotted line) show that the probability of death increases significantly with ground temperature. Open triangles show the observed fate of fly larvae due to predation by arthropods (1 – death, top of graph; 0 escape, bottom of graph) vs. other events (0). The GLM predicted values (plain line) indicate that the probability of predation by arthropods decreases with temperature.

![Figure 3](image2.png)

Figure 3. Number of attacks of medfly larvae after being discovered by *Monomorium subopacum*, *Tapinoma simrothi* and other arthropods.
whose workers lack a sting, they had to immobilize their prey by multiple bites. This strategy, however, was much less efficient, and *C. capitata* larvae often succeeded in escaping.

**Discussion**

The results of this study showed that the mortality of *C. capitata* larvae deposited on the ground under Argan host trees in the area of Essaouira is due to biotic and abiotic factors. Searching for a suitable site for pupation in the ground constitutes the most risky step in the development of *C. capitata* larvae. According to our observations, more than half of the larvae deposited on the ground at both sites succeeded in burrowing. However, larval success depended on environmental factors. On sandy ground, larvae gained protection more quickly than on argillaceous ground. In the latter case, larvae had to spend more time burrowing, which increased the probability of being encountered by a predator. A similar result was found by Aluja et al. (2005) in the Mexican fruit fly *Anastrepha* spp. (Diptera: Tephritidae), whose time until burrowing varies between populations according to the abundance of organic matter.

Our results also indicate that the possibility of burrowing depends on the risk of death by heat shock or predation, as suggested by Thomas (1995). According to this author, at low predation pressure, larvae spend more time (up to 1 h) searching for the best pupation site than when predation pressure is high. In our study, larvae either burrowed within 5 min or, most often, they died from heat or predation. Therefore, rapid burrowing behavior is probably a response to the risks of predation and other environmental pressures. Even after burrowing, however, medfly larvae and pupae can still be subject to other ground predators. Eskafi and Kolbe (1990) found 34 and 47% mortality in coffee and citrus orchards of *C. capitata* pupae caused by ground predators. This high predation rate was mostly due to eight species of rove beetles and other coleopterans.

In addition to ground texture, two abiotic factors increased larval death under host trees. The major convulsions shown by medfly larvae suggests ground temperature and the exposure to solar rays induced a thermal stress that caused larval dehydration. Both factors have already been reported as main causes of mortality of tephritid immature stages (Serit and Tan 1990; Hennessy 1994; Thomas 1995; Urbaneja et al. 2006). In our study, when ground temperature exceeded 48°C, larval death was in fact certain, irrespective of ground texture; in a laboratory study Gazit, Rossler, Wang, Tang, and Lurie (2004) observed that at 48°C all (300 individuals) the third instar larvae died within 15 min. Interestingly, low temperatures are also known to induce mortality, not only of the larvae, but also of the nymphs (Eskafi and Fernandez 1990; Serit and Tan 1990; Urbaneja et al. 2006). The result of our experiment adds to these studies, suggesting that extreme temperature could be a major mortality factor for exposed larvae, especially in arid climates. Once burrowed, larvae may still die from desiccation or heat shock although ground temperature probably decreases rapidly with depth from ground surface.

At lower temperatures, predation by arthropods was the main source of mortality. Overall, ants caused 20% of the total mortality of the *Ceratitis* larvae under Argan trees. Two species, *M. subopacum* and *T. simrothi* were responsible for
the majority of captures. However, the former was much more efficient than the latter. First, *M. subopacum* is one of the most abundant species under Argan trees (El Keroumi unpublished data), allowing a rapid discovery of prey. Second, this species is an important predator that systematically responds to prey detection by an attack (this study). Third, like the majority of the Myrmicinae ants, *M. subopacum* has a powerful venom that contains a complex mixture of 17-carbon alkaloids (Jones, Zottig, Robertson, and Snelling 2003) able to immobilize larvae in a few seconds. By contrast, *T. simrothi* lacks venom and often ‘loses’ the prey. In effect, this species is known mostly as an aphid-tender ant that rears Homoptera on plants to collect their honeydew. *C. viatica*, however, is an omnivorous, large-size species that is certainly capable of easily transporting *C. capitata* larvae. Its weak contribution in larval predation may be because *Cataglyphis* are mostly scavengers that rarely capture prey alive. They prefer to forage in sunny open gaps rather than in tree shade, which reduce their chances of finding the prey under Argan trees. Similarly, *Messor picturatus maura* is a granivorous species that forages in open habitats (Cagniant and Espadaler 1998), mostly among trees, which explains why it was responsible for only 4% of the predation. Overall, these results confirm previous findings in Hawaii and Guatemala orchards, where several ants (*P. megacephala*, *S. geminata*, *Linepithema humile*) were identified as serious predators of various fruit flies (Pemberton and Willard 1918; Wong et al. 1984; Eskafi and Kolbe 1990). Ants are also responsible for predation on larvae of other Tephritidae, such as *Anastrepha* spp. in Mexico (Aluja et al. 2005), the apple fruit fly *Rhogolletis pomonella* and the olive fly *Bactrocera oleae* (Allen and Hagley 1990; Bressan-Nascimento 2001; Orsini, Kent, Karen, and Erik 2007).

Biotic and abiotic factors of mortality, such as thermal stress and predation pressure, could induce adaptations of larval behavior to reduce mortality risks. However, anti-predator behaviors of phytophagous immature stages, such as tephritid fruit flies, are poorly known compared to adults (White 2000). An important means of escaping predation could be to adapt the pupation rhythm to avoid hours of maximum ground temperature, on the one hand, and maximum predator activity on the other hand. Future studies should include nocturnal patterns of larval emergence from fruit and the role of birds in predation. According to our observations, ants played an important role in predation of *C. capitata* larvae under Argan trees. The proportion of attacked larvae was different between the two study sites. While ant population structure, their specific richness and their abundance in each biotope seem to be preeminent factors explaining their contribution in larval predation under trees, *M. subopacum* appears to be the most effective ant species in predation. This characteristic can justify its interest as a potential agent in a possible biological control program. This predator species, which seems to be well adapted in the field under trees, is likely to play a key role in the regulation of *Ceratitis* populations in the Argan forest, as in the neighboring citrus orchards. The conservation of habitat favorable to *M. subopacum* and the periodic release of colonies in the Argan forest could potentially increase its contribution to predation of kmedfly larvae. In depth studies on the ecology, behavior and structure of ant populations in the Argan forest will be important to biological and integrated pest management of this fruit fly in this region of Morocco.
Acknowledgements
We thank Professor J.H. Delabie (Itabuna, Brazil) and Professor H. Cagniant (Toulouse, France) for ant identification and Dr A. Bakri (Marrakech, Morocco), and two anonymous reviewers for helpful comments on a previous version of this article. We were assisted by Mrs Jacqueline Minett for English editing and by Mr David Aragones for illustrations and figures. This work was funded by Agencia Española de Cooperacion Internacional (AECI – PCI program, Moroccan-Spanish cooperation projects A3478/05 and A/4774/06). It was conducted with the authorization of the Essaouira Directorate of Waters and Forests.

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