

PORCELLIO LAEVIS (CRUSTACEA, ISOPODA) FROM SOIL DETRITIVORE TO VEGETABLE CROP PEST: CASE STUDY OF THE MELON (*CUCUMIS MELO* L., CUCURBITACEAE)

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ABSTRACT. – Terrestrial isopods play a particularly important ecosystem function in mineralizing organic matter but, according to the species and the cultivated agroecosystem, their status of pest is yet to be confirmed. In this context, *Porcellio laevis* Latreille, 1804 is considered as a serious pest for some varieties of melon (*Cucumis melo* L.) in Tunisia. Monthly samples (March 2013 to December 2015) showed that the important variation in density of *P. laevis* depended both on season and melon variety: afamia, canary, cantaloupe and tziri. Furthermore, this density was positively correlated with maturity stage of melon (immature, ripe and overripe). In melon, analysis of total phenolic contents and hydrophilic antioxidant activity exhibited a significant difference between varieties and maturity stages ($P < 0.01$). Our results showed that the most damaged varieties afamia and cantaloupe, characterized by (i) thinner cortex, (ii) higher total phenolic contents, (iii) high concentration of internal ethylene and (iv) liberation of aromatic odor during mature and post mature stages, offered favorable conditions for fast growth, longer survival and higher fertility of *P. laevis* leading to an increase in population and turning it into a crop pest.

INTRODUCTION

Terrestrial isopods, based on an updated world list of species containing 3,710 species belonging to 527 genera and 37 families (Sfenthourakis & Taiti 2015), are fundamental representatives of soil fauna. They play an important role in decomposing leaf litter and in mineralizing organic matter (Hassall & Sutton 1978, Sutton 1980, Paoletti & Hassall 1999, Souty-Grosset *et al.* 2005). Traditionally, terrestrial isopods are considered as beneficial organisms in most terrestrial ecosystems (Zimmer & Topp 1997). However, investigations were performed on their relationships and impacts within the agroecosystems (Souty-Grosset *et al.* 2005, Faberi *et al.* 2011, 2014, Alfaress 2012). In this context, woodlice richness and abundance were reported to be influenced by agricultural practices such as tillage, drainage, fertilizer and pesticide applications (Paoletti & Hassall 1999, Fraj *et al.* 2010). Although they were mainly beneficial in the garden or landscape, terrestrial isopods have been shown to damage a number of agriculturally important crops, including alfalfa, sunflower, cereals, and soybean (Paris 1963, Byers & Bierlein 1984, Saska 2008, Honek *et al.* 2009,

Tulli *et al.* 2009, Faberi *et al.* 2014). Recent observations in Argentina agroecosystems revealed that *Armadillidium vulgare* was turning into a crop pest (Faberi *et al.* 2011, 2014).

The melon (*Cucumis melo* L., Cucurbitaceae) is native to Africa and it is cultivated worldwide. The domestication of the melon is old and dates back to 2500-3000 BC in Egypt, Mesopotamia and China. *Cucumis melo* L. is among the most consumed fruit in summer because of its high water content (90 %) (Kaçar *et al.* 2012). Currently, China and Turkey are the largest producers of melon (FAO 2009). This species, highly diversified under ecological, morphological and genetic aspects (Kikbride 1993), exhibited several intraspecific classifications (Nuñez-Palenius *et al.* 2008, Szamosi *et al.* 2010, Kaçar *et al.* 2012). Consumer preference for this fruit is largely determined by its sweetness (i.e, sugar, content), flavour or aroma, texture and more recently by being a rich source of phytonutrients (Lester 2008).

In Tunisia, the melon (*Cucumis melo* L.) is mainly cultivated in open fields with 104,482 tons of production and 10,447 ha of harvested area in 2011 (Henane *et al.* 2013). The main cultivated areas are in the regions of Beja, Jandouba, Kairouan, Sidi Bouzid and the Sahel. The most locally commercialized and consumed varieties of melon are the introduced afamia, cantaloupe, canary and

tziri. They have replaced the most known landraces such as abdellaoui, beji, bouricha, chefli, stambouli and the ancient introduced varieties (Maazoun & Galaoui), which risk genetic erosion (Jebbari *et al.* 2004, Elbekkay *et al.* 2008, Trimech *et al.* 2015). Currently, for farmers, afamia, canary, cantaloupe and tziri, are the most economically significant melons grown, because they are well-appreciated by the consumers and exhibit high yields.

Porcellio laevis Latreille was found to become a dreadful pest for some melon varieties (*Cucumis*). In ripe fruits, *P. laevis* nibbles small holes in the skin and eats the fruit flesh. According to the number of attackers, these holes increase and become galleries in the flesh which damage the fruit. This damage can result in considerable losses depending on variety and thus affects the yield. Consequently, the need for sound ecological information about pests and crop environment is essential for efficient Integrated Pest Management (IPM) program implementation.

The present study aims to investigate the relationship between four commercial melon varieties and the *Porcellio laevis* population dynamic in the crop fields of the low Mejerda valley agroecosystems.

MATERIAL AND METHODS

Study area: In Tunisia, Medjerda is the most important river (Fig. 1) and in its valley, agriculture is among the oldest practice in the country (Abbes *et al.* 2005). In fact, 51 % of the population in this area is composed of farmers and most of them use irrigated agriculture (21,317 ha among 29,761 ha of cultivated area are irrigated) (Report of Wadi project 2009).

Sampling methodology

Plant Material: In the present study, we focused on four varieties of melon afamia, canary, cantaloupe and tziri that were subjected to different damage degrees by *P. laevis* (Fig. 2). In fact, field monitoring was conducted in the second half of April, in separate plots of 1 ha each, and separated by dikes of drainage to ensure the isolation of different populations of *P. laevis*.

Chemical fertilizers were applied throughout the crop cycle since transplantation (145 kg N ha^{-1} , $140 \text{ kg P}_2\text{O}_5 \text{ ha}^{-1}$, $210 \text{ kg K}_2\text{O ha}^{-1}$). Furthermore, Imidacloprid (Promochimie, Tunis, Tunisia) (200 g l^{-1}) was used to fight against aphids, Acetamiprid (SEPCM Tunis, Tunisia) (200 g l^{-1}) was spread in the fight against thrips and Abamectin (Bioprotection Tunis, Tunisia) (18 g l^{-1}) was used to fight against the mites.

Phenolic and antioxidant activity analysis: Total phenols were extracted according to the Folin-Ciocalteu colorimetric method modified by Singleton *et al.* (1999) and Eberhardt *et al.* (2000). Measurement of hydrophilic antioxidant activity was determined by the bleaching method of ABTS (Pellegrini *et al.* 2007). Ethylene production during ripening was measured using the protocol of Chillet *et al.* (2008). Measured ethylene production can be compared among different melon varieties or among fruit produced in different pedo-climatic conditions (Chillet *et al.* 2008).

Plant data analysis: Differences, between the mean wide of the cortex and the commercial weight of mature fruit between varieties, were tested by one-way analysis of variance (ANOVA), after verifying normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene test).

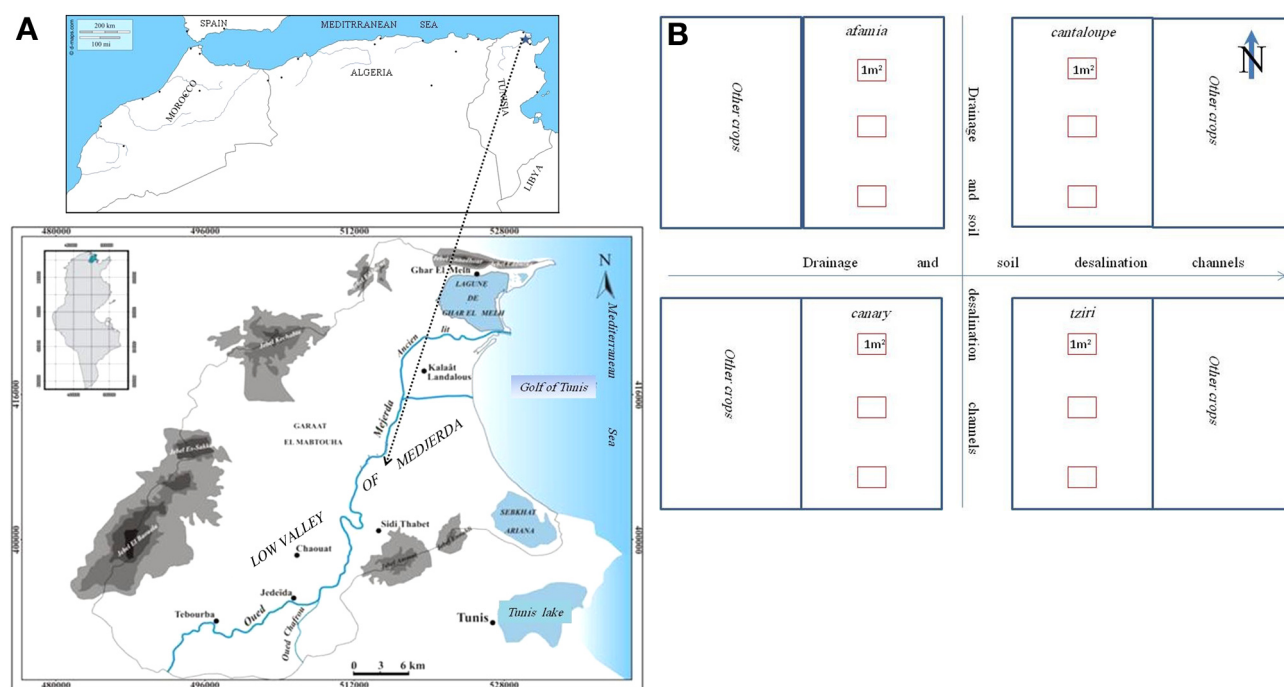


Fig. 1. – Sampling site and methods. **A:** Geographical position of the low Valley of Medjerda in Tunisia; **B:** Plots separated by channels, and the quadrats method which was used to estimate density (ten replicates in each plot).



Fig. 2. – The varieties of melon (*Cucumis melo* L. 1753) grown in the Medjerda low plain. A: Afamia, in contact with the soil, many individuals (2-19) (a) nibble the bark to reach the flesh of the fruit; B: Cantaloupe, specimens eat the bark (a) and reach the flesh through holes (b) and galleries (c); C: Canary; D: Tziri, during the ripeness of the fruit, some individuals (1-5) are observed digging near the peduncle (a) or on its opposite side, near the remaining flower parts (b).

Isopod material: To estimate the mean density (individuals.m⁻²) of *Porcellio laevis*, monthly samplings were carried out from March 2013 to December 2015, using a metal quadrat of 1 m² with 10 replicates, randomly distributed in each plot. Moreover, during the fruition (from May to September), 100 fruits were taken at random during each stage of maturity and examined in each variety. Isopods, under and in the fruits, were counted and preserved in 70 % ethanol.

Porcellio laevis Latreille, called “Boushikh” in the Medjerda low plain, reach the fields through cattle manure which is mainly used by farmers to fertilize the soil (Fraj *et al.* 2010).

During the breeding period (from April/May to September/October), various isopod life history descriptors were estimated through a weekly sampling in each plot. These descriptors include body size and mass, developmental rate, lifespan, fecundity, parental investment, reproductive allocation (RA), and mean densities (individuals.m⁻²).

Reproductive females detected in these samples were separated, placed in individual plastic boxes and weighed daily until parturition. Released manca were counted and weighed together in an electronic analytical balance (± 0.001 g). To quantify reproductive allocation, the following traits were measured: mean fecundity (eggs per female); manca mass (MM) = individ-

ual offspring dry mass in mg; brood mass (BM) = (MM × fecundity); female dry mass in mg (FM). The MM/FM ratio gave a gravimetric index of maternal investment (Warburg 1994). The BM/FM ratio was calculated for each ovigerous female, then, female states were compared via ANOVA. Reproductive allocation (RA) was calculated as the percentage of weight lost by the female during the process of producing a brood of young:

$$RA = \frac{W_0 - W_1}{W_0} \times 100$$

Where W_0 is the initial female weight before the mancae release and W_1 is the female weight immediately following mancae release (Warburg 1994). The weight of individual manca can be calculated by dividing the body mass lost by the female (on the parturition day) by the total number of mancae it reproduced (Warburg 2011).

Isopod data analysis: The expected and observed values of the sex ratio, calculated as NM/NF (number of males/number of females), were compared using a χ^2 test. Moreover, χ^2 test was used to test variety effect on and its maturity stage in the number of isopods found under the fruit. Possible differences in densities and in various isopod life history descriptors between populations in different plots were tested by one-way analysis of variance (ANOVA). The relationship between fecundity and female body size was tested by one-way ANCOVA, after testing the normality of data using Shapiro-Wilk test (W) for all varieties. Post-hoc comparisons of the treatment populations were implemented. Tukey-Kramer test was used to find if the means of life history traits significantly different from each other. The link between mean body size of the breeding females and mean fecundity was tested by ANOVA test. XLSTAT V 7.5.2 software was used these data analysis.

In order to estimate growth, field growth data were fitted to the von Bertalanffy growth function (VBGF) as followed:

a. Nonlinear modelling of growth curves: Variation of length (L) (mm) of *P. laevis* with time (t) (days) was mathematically analyzed using von Bertalanffy model (Ratkowsky 1986, Ricker 1975, Phillips & Campbell 1968, Allen 1966):

$$(1) L = L_{max} (1 - B \times e^{-kt})$$

with: L : length at time t ; L_{max} : asymptotic length reached at the end of growth; B : a parameter without unit, associated to initial state (theoretical birth) of length; k : a constant rate (time^{-1}) associated to a regulatory implicit decreasing phase.

Parameters of nonlinear model were estimated by the maximum method using JMP statistical software. The nonlinear model was separately applied in four datasets of *P. laevis* sizes from four plots (afamia, cantaloupe, canary, tziri).

Alternative linear modelling of growth: Complementary to the nonlinear von Bertalanffy model, reparameterization of (1) was applied for alternative estimation of L_{max} (Allen 1976):

$$(2) L = L_{max} - C \times e^{-kt}$$

with: $C = L_{max} \cdot B$

This alternative model allowed to estimate L_{max} as intercept using linear regression model in e^{-kt} values which was initially calculated using the parameter k given by (1).

Estimation of growth rate: Growth rates were estimated as the slopes of linear regressions between logarithmic values of lengths (e -basis) and time (Ricker 1975). Logarithm transformations of lengths showed two increasing phases: a rapid initial phase and a slow final phase. Growth rates (GR) were estimated during the rapid initial phase (Schnute & Fournier 1980).

RESULTS

Melon results

Fruit characteristics of the studied varieties

Table I summarizes the characteristics of the fruit varieties. The canary cortex was 0.91 cm wide, twice that of afamia and cantaloupe, 0.42 and 0.45 cm, respectively ($F = 8.197$, $p = 0.028$).

Change of total phenolic contents according to the stage of maturity

Total phenolic contents showed their lowest values during the immature stages in all the studied varieties (Fig. 3), then it increased steadily until it reached high levels of around 1403.12 mg GAE kg^{-1} FW in afamia at ripe stage. Total phenolic contents during the three maturity stages were significantly different ($P < 0.05$). Furthermore, they increased with the advancement of the ripening process stage. During the mature stage, the afamia variety exhibited the highest total phenolic content (1168.59 mg GAE kg^{-1} FW) followed by cantaloupe (879.56 mg GAE kg^{-1} FW), canary (721.78 mg GAE kg^{-1} FW) and tziri (619.17 mg GAE kg^{-1} FW) ($F = 49.77$, $p = 0.0004$), while the lowest ones were recorded in the immature stages (116.64 mg GAE kg^{-1} FW and 117.12 mg GAE kg^{-1} FW).

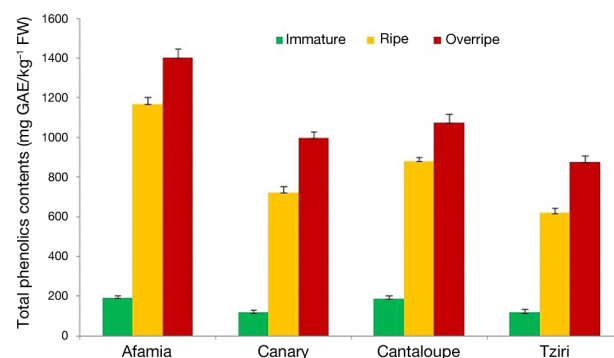


Fig. 3. – Levels of total phenols in the melon varieties cultivated in the low Medjerda low plain (mean $\pm$ SE), harvested during three different maturity stages. Levels of significance (t-test) (** = $P < 0.01$, *** = $P < 0.001$).

Table I. – Evaluations throughout the harvest of four varieties during two maturity stages.

	afamia	cantaloupe	tziri	canary
Fruit characteristics	* Globular to slightly elongated, wrinkled * At physiological maturity: - pale yellow flesh, - bark color changes from dark green to yellow, - large release of aromatic odor.	* Round to oval shape, warty skin, * At physiological maturity: - orange flesh and juicy, - bark color changes from dark green to yellow, - large release of aromatic odor.	* Round extending shape, green skin with dark green or yellowish tasks. * At physiological maturity: - the color of the bark turns from dark green to yellowish green, - flesh white, greenish, slightly sweet, - low release of aromatic odor.	* Oval shape, smooth skin. * At physiological maturity: - sweet white flesh, - bark color changes from dark green to yellow, - low release of aromatic odor.
Mature fruit (commercial weight (kg))	$0.750 \leq W \leq 3.836$	$0.500 \leq W \leq 1.273$	$0.750 \leq W \leq 2.621$	$0.750 \leq W \leq 3.735$
mean width of the cortex of mature fruit (cm) (40 fruits)	0.422 ± 0.064	0.451 ± 0.026	0.71 ± 0.024	0.908 ± 0.019
Number of isopod / fruit				
immature	1-2	1-2	0	0
ripe	1-12	1-7	1-3	1-2
overripe	2-19	1-10	1-5	1-3
Percentage of damaged fruits (%)				
immature	0	0	0	0
ripe	17	7	0	1
overripe	49	23	5	2

Table II. – Total Antioxidant activity of extracts obtained from four varieties of melon harvested during three different maturity stages (μM Trolok 100 g^{-1} FW).

Stages	Afamia	Cantaloupe	Canary	Tziri
Immature	152.37 ± 1.3	98.45 ± 1.8	103.79 ± 4.7	37.02 ± 0.3
Ripe (mature)	295.74 ± 2.6	271.93 ± 1.3	259.17 ± 1.8	163.27 ± 0.8
Overripe (post-mature)	273.68 ± 0.7	235.86 ± 0.7	233.72 ± 1.5	125.47 ± 1.9

Table III. – Concentration of internal ethylene in four varieties of melon harvested during different ripening stages (ppm).

Stages	Afamia	Cantaloupe	Canary	Tziri
Immature	0.3	0.4	0.2	0.2
Ripe	29.7	25.9	13.8	7.6
Overripe	36.8	31.7	27.1	26.5

FW) in both canary and tziri, respectively ($F = 50.72$, $p = 0.00038$).

Change in antioxidant activity and concentration of internal ethylene

Significant intra-varietal variations and inter-varietal differences of antioxidant activity were detected during maturation stage. The highest activity was recorded in the mature stage in all varieties (Table II). It ranged from $163.27 \mu\text{M}$ Trolok 100 g^{-1} FW (tziri variety) to $295.74 \mu\text{M}$ Trolok 100 g^{-1} FW (afamia variety). In fact, a significant increase in antioxidant activity was detected during the transition from immature to mature stage ($F = 16.27$, $p = 0.0068$). Then, in the overripe stage, this activity began a long decline leading to a low level around $125.47 \mu\text{M}$ Trolok 100 g^{-1} FW in the tziri variety. Never-

theless, the concentration of internal ethylene did not stop its increase in mature stage, and it rose steadily until reaching a high level around 36.7 ppm in the overripe stage in afamia. During the immature stage, the concentration of internal ethylene remained fairly flat ($0.2\text{--}0.4 \text{ ppm}$), then it began to rise with the advancement towards a fully ripe stage. The internal ethylene increased in a consistent pattern up to the mature stage and during the last ripening stages of the four melon varieties. In tziri, the internal ethylene during the overripe stage (26.2 ppm) increased by more than three times over the mature stage (7.6 ppm). In canary it increased two times (13.8 to 27.1 ppm) (Table III) ($F = 11.8$, $p = 0.0013$).

Isopod results

Densities of Porcellio laevis

Low densities were observed from November to February. However, in March, the beginning of spring, which was characterized by a rise in temperature and the start of land preparation for crops, there was an increase in *P. laevis* density in the different plots. In fact, the highest values (889 ind.m^{-2}) were recorded in July in the cantaloupe plot and (1316 ind.m^{-2}) in October in the afamia

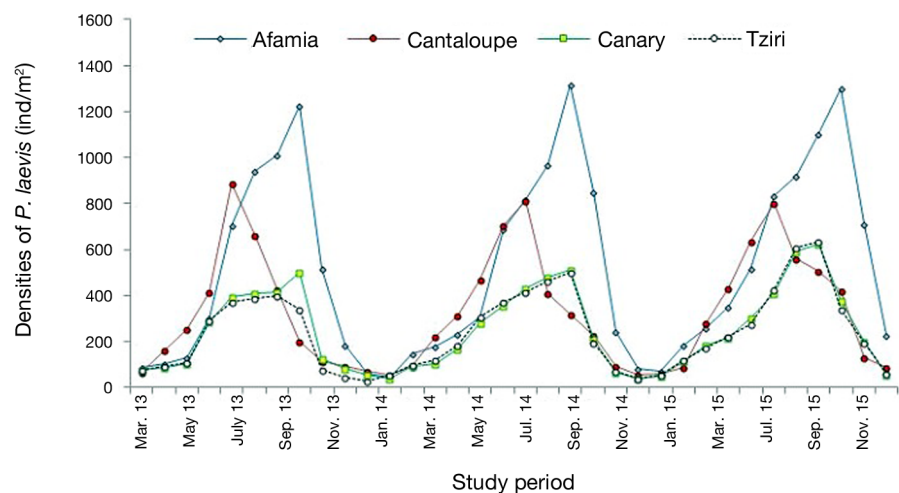


Fig. 4. – Variation of density of field populations of *P. laevis* in four melon variety plots.

plot. These periods corresponded to the maturation of these varieties, respectively, and coincided with the breeding of *P. laevis*. Since October, density decreased gradually to reach the lowest values in January (41 ind.m^{-2}) (Fig. 4). An ANOVA indicated significant differences in densities of *P. laevis* between plots ($F = 7.817$; $p = 7.66E-05$). The number of individuals per fruit varied according to both the stage of fruit maturity and the melon variety. Thus, the highest number of individuals per fruit was recorded in the overripe stage of all varieties. Whatever the stage of maturity, the highest numbers of *P. laevis*, were collected under the afamia fruits (2-19 individuals/fruit), followed by the cantaloupe fruits (1-10 individuals/fruit) whereas the lowest ones were found under the canary fruits (1-3 individuals/fruit). In fact as more of the fruit skin contacted the ground, more specimens were found underneath it ($p < 0.001$).

Chi-2 test (χ^2) concerning associative effect of melon variety and maturation degree on isopod abundance (under fruits) gave a highly significant result ($\chi^2 = 16.67$; $p\text{-value} = 0.01$). This significant χ^2 -value was mainly due to strong variation in isopod numbers between the four melon varieties during immature stage. Afamia was found to be the most favorable for isopod existence in the three maturation degrees compared to the three other varieties. However, the relative importance of favorable conditions varied through maturation periods: afamia was relatively more favorable for isopod existence than the three other varieties during immature and ripe stages. This was indicated by positive differences between observed and expected numbers combined with high χ^2 -value for the cell (afamia, immature state). A positive correlation between these two variables strongly decreased for afamia ($r = 0.70$, $p < 0.001$ in overripe period).

Population structure and breeding activity of *P. laevis*

In the initial sampling implemented in March 2013, all collected individuals were adults, with body size ranging

between 8.3 mm and 13.2 mm. The appearance of reproductive females in April/May indicated the start of breeding activity which would be interrupted during July and August then resumed in September. From the second half of October 2013 until March 2014, reproductive females could not be collected. Thus, *P. laevis* showed a seasonal reproduction activity with two distinct breeding waves. While the first wave was characterized by large reproductive females ($9.87 \pm 0.39 \text{ mm}$) in all plots in spring, the second one contained both large and small females ($7.78 \pm 0.62 \text{ mm}$) in the afamia and cantaloupe plots in autumn.

The overall sex ratio of males to females was $1 \sigma:1.08 \phi$. A χ^2 test showed no significant difference in the numbers of individuals of each sex ($\chi^2 = 10.22$, $df = 11$, $p = 0.51$). Seasonal analysis of the sex ratio revealed that it was bimodal with a predominance of males in early spring and autumn followed by a predominance of females in summer and winter.

Life history traits of *Porcellio laevis*

Body size of ovigerous females and length of the brooding period

During the period of investigation, samples collected from all plots showed that egg production began in April/May. There was no difference in the onset of reproduction between studied populations. At the onset of reproduction, the body size of examined ovigerous females ranged between 8.2 and 13.2 mm. However, ovigerous females living in both afamia and cantaloupe plots showed a brooding period shorter than those associated with canary and tziri plots ($F = 54.34$, $p = 0.00$) (Table IV).

Fecundity

The number of marsupial eggs per female in *P. laevis* species ranged from 4 to 117 eggs in females with sizes ranging from 5.4 mm to 13.2 mm, respectively (Table IV). The fecundity showed a seasonal intra-population variation: the mean fecundity was 32.16 ± 26.49 eggs for the

Table IV. – Life history traits of *Porcellio laevis* in different plots.

Life history traits (measured by)	(afamia)	(cantaloupe)	(tziri)	(canary)	F value	p value
Onset of reproduction	April/May	April/May	April/May	April/May		
Mean brooding period (days)	20.25 ± 1.83	24.95 ± 3.69	30.27 ± 1.64	35.9 ± 1.62	64.49	19.92 E-05
Size of the smallest female (mm) (n = number of manca)	5.5 (n = 6)	5.4 (n = 4)	8.2 (n = 28)	8.3 (n = 29)		
Size of the largest female (mm) (n = number of manca)	13.2 (n = 117)	12.8 (n = 82)	12.3 (n = 67)	12.5 (n = 63)	19.67	8.19E-05
Offspring dry mass (mg) (M ± SE)	0.26 ± 0.18	0.37 ± 0.29	0.43 ± 0.51	0.39 ± 0.23	14.14	0.009394
Juvenile mortality (after 15-30 days from hatching) (%)	12.93 ± 1.96	14.15 ± 2.71	17.28 ± 3.02	16.45 ± 2.47	1.515	0.003245
Mean fecundity [eggs/embryos (100♀)] (Mean ± SE)						
In spring (April/May)	79 ± 32.51	62 ± 12.83	46.73 ± 13.33	44.39 ± 14.21	24.3	0.002713
In autumn (September/October)	37.44 ± 10.4	32.16 ± 26.49	39.39 ± 14.35	38.38 ± 13.37	39.17	1.08E-06
Eggs losses (%)	3.1	3.8	4.2	4.5	3.856	0.09
Reproductive allocation RA [Brood mass/female mass (50 ♀)] (%)						
In spring (Mean ± SE)	33.2 ± 1.8	28.3 ± 0.9	17.1 ± 1.2	18.5 ± 1.62	33.5	0.001159
In autumn (Mean ± SE)	27.4 ± 0.79	26.1 ± 1.65	21.1 ± 0.93	19.7 ± 0.48	22.6	0.002147
[Manca mass/female mass (50 ♀)] (Mean ± SE)	1.24 ± 0.56	1.38 ± 0.87	1.49 ± 0.31	1.63 ± 0.26	2.678	0.152 > 0.05
Longevity (months)	22	20	17	17.5	15.65	1.59E-05

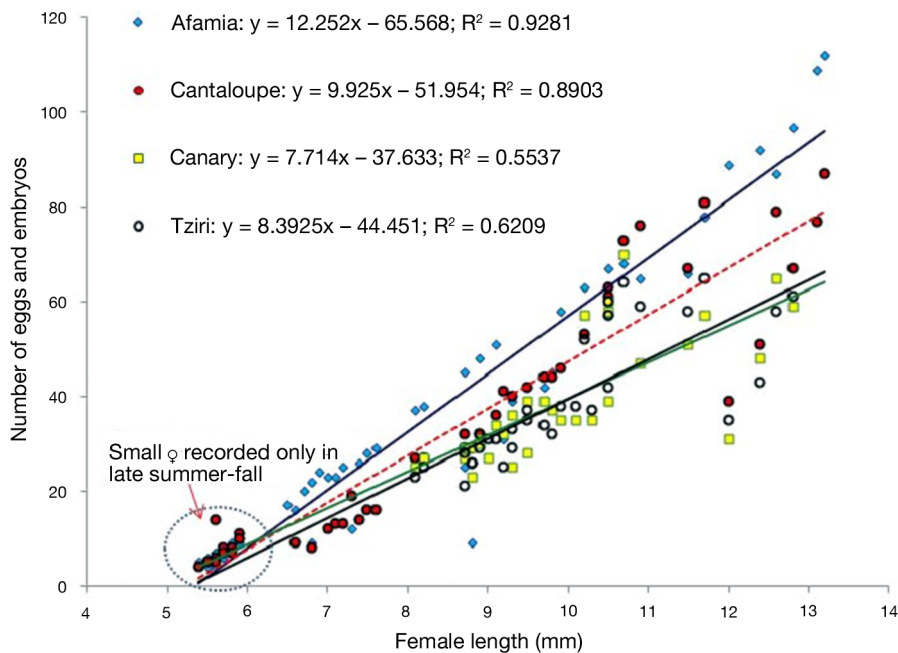


Fig. 5. – Fecundity among field populations collected in four melon variety plots.

females caught in the cantaloupe plot in autumn and 79 ± 32.5 eggs for those collected in the afamia plot in spring (Table IV). After testing the normality of data using Shapiro-Wilk test (W) for both groups ($W = 0.897$, $p < 0.05$ for afamia and cantaloupe and $W = 0.865$, $p < 0.05$ for canary and tziri) and using one-way ANCOVA, a positive correlation between body size of females and fecundity was reported for all populations. Moreover, significant differences in body size/fecundity relationships were recorded between females collected in autumn and those collected in spring ($F = 24$, $p = 0.002$) (Fig. 5).

Reproductive allocation (RA) and maternal investment (MI)

In spring (April/May), large females in all varieties of melon, constituting the first breeding wave and exhibiting high fecundity and reproductive effort, invested more in brood size than in individual offspring. However, in autumn (September/October), in the afamia and cantaloupe plots, the second breeding wave formed by both large and small females invested more in individual offspring than in a brood size because fecundity was much lower (Table IV). Indeed, the mean size of the oviger-

ous females varied significantly between the spring and the autumn samples ($t = 12.092$, $p < 0.0001$). Thus, for the first wave, reproductive effort (RA) ranged from $(17.1 \pm 1.2) \%$ to $(33.2 \pm 1.8) \%$ in the tziri and afamia plots respectively ($F = 33.55$, $p = 0.001$). Nevertheless, in autumn the mean reproductive effort decreased in both the afamia and cantaloupe plots $(27.4 \pm 0.79) \%$ to $(26.1 \pm 1.65) \%$, respectively and increased in the canary and tziri plots $(19.7 \pm 0.48) \%$ and $(21.1 \pm 0.93) \%$, respectively ($F = 22.6$, $p = 0.002$). The mean maternal investment ranged between $(1.24 \pm 0.56) \%$ in the afamia plot and $(1.63 \pm 0.26) \%$ in the canary plot ($F = 2.678$, $p = 0.152$).

Longevity of *Porcellio laevis*

From December to February, when barley was cultivated in all plots in, there were no significant differences between maximum sizes of adults ($p \geq 0.05$). However, the maximum size of isopods reached in the afamia and cantaloupe plots was higher than that reached in the canary and tziri plots ($F = 19.67$, $p = 8.19E-05$) (Table IV).

The longevity was estimated at 22 months for population living in afamia, 20 months for those living in the cantaloupe plot, and around 17 months for those living

in both canary and tziri plots ($F = 156.5$, $p = 1.59E-05$) (Table IV).

Growth analysis

Von Bertalanffy models suggested that *P. laevis* populations living in the afamia and cantaloupe plots had higher maximal lengths (12.95 and 13.3 mm, respectively) than those living in the canary and tziri plots (12.51 and 11.75 mm, respectively) (Fig. 6A). These values generally conserved the same ranks when they were estimated based on the intercept of linear models (Fig. 6B): 13.3 mm (cantaloupe), 12.31 mm (afamia), 11.75 mm (tziri) and 11.74 mm (canary). Despite the inversion between the afamia and cantaloupe ranks, comparative models' results tended to confirm the advantage of cantaloupe followed by afamia as nutritive sources for growing *P. laevis*. This could be linked to the fruit contents of these two melon varieties relative to the alimentary needs of isopod growth.

Apart from the maximal length (L_{max}) and growth rate constant GR , rate constant k of von Bertalanffy models varied in inverse way to that of L_{max} (Galucci & Quinn II 1979). Thus, minimal k value was obtained for cantaloupe model (0.0032 d^{-1}) while L_{max} was the greatest (13.3 mm) (Fig. 6A, E). However, maximal k -value (0.0045) con-

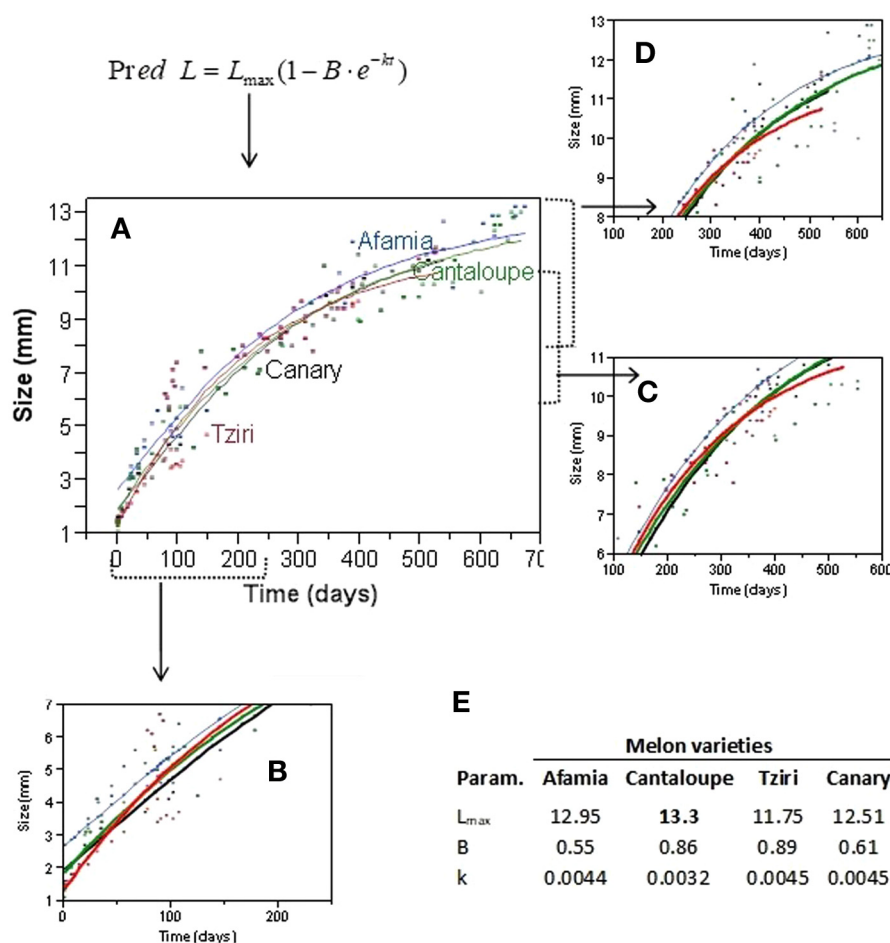


Fig. 6. – **A**: Bertalanffy models fitting the growth of field populations of *P. laevis* collected from four melon variety plots (*afamia*, *cantaloupe*, *canary*, *tziri*); **B**, **C**, **D**: Zooms of fitted growth curves associated with different age phases; **E**: Table of estimated parameters by von Bertalanffy model.

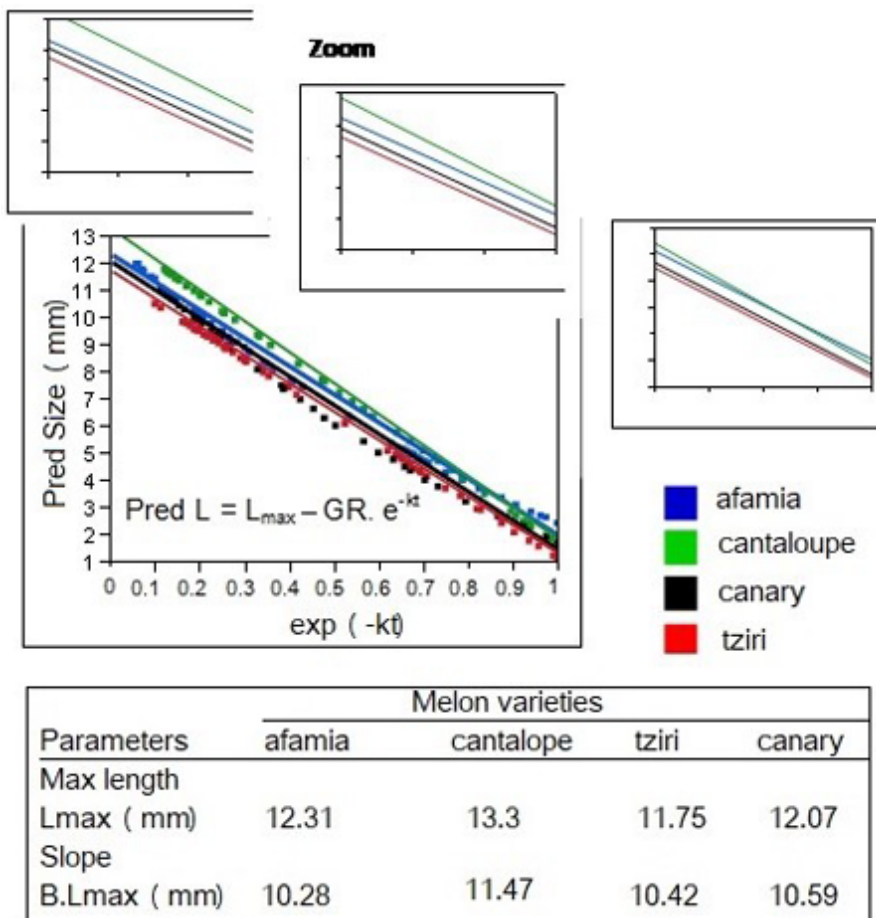


Fig. 7. – Linear regression plots issued from the linearization of von-Bertalanffy models applied to isopod growth linked to four melon varieties: afamia (blue), cantaloupe (green), canary (black), tziri (red).

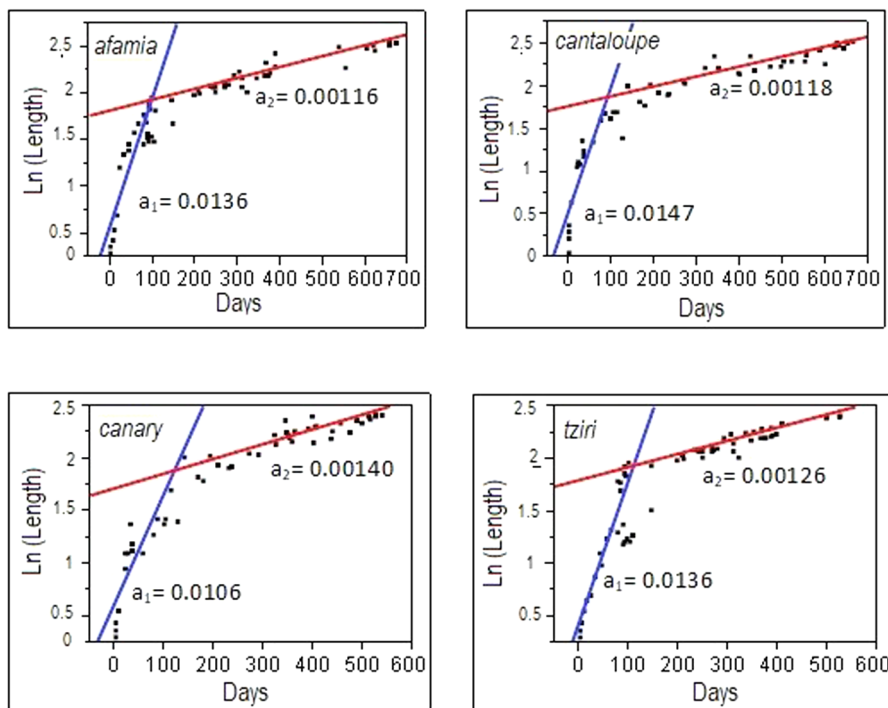


Fig. 8. – Log-linear models of length vs days used for the calculation of growth rate constant as the slope (a_1) of first phase (blue line); (a_2) slope of slow growth phase corresponding to post sexual maturation (red line).

cerned *tziri*-model which gave the minimal value of L_{max} (11.75 mm) (confirmed by linear model) (Fig. 6A, E). Finally, the afamia model exhibited the highest size values of both initial and final growth phases of isopod (Fig. 6A-D).

Linear regression analysis of predicted sizes on $\exp(-kt)$ gave four linear models with different intercepts and slopes (Fig. 7): Cantaloupe exhibited the maximal intercept value ($L_{max} = 13.3$ mm) followed by afamia (12.31 mm), canary (12.1 mm) and *tziri* (10.3 mm). This confirmed the growth condition order of isopods given by von-Bertalanffy models where cantaloupe and afamia appeared to be more favorable than canary and *tziri*.

Concerning slopes, the highest value concerned cantaloupe (11.47 mm) followed by canary (10.58 mm), *tziri* (10.42 mm) and afamia (10.28 mm). These results indicated that cantaloupe-based growth occurred with maximal overcoming of metabolism maintenance (i.e., in favor of growth). This confirmed the potential benefit of cantaloupe for isopod growth, and was compatible with calculated maximal growth rate in initial phase. Moreover, isopod growth seemed to be subject to constraints hindering growth in the canary and *tziri* plots. This changed as a compensatory increase of growth rates occurred in the second phase (Fig. 7).

The advantage of cantaloupe consumption for the growth of *P. laevis* was further indicated by higher growth rate constant (GR) estimated by the slope of log-linear model, $\ln(\text{lengths})$ vs days (Fig. 8). The estimation of this parameter as the slope of the first (rapid) linear growth phase gave $GR = 0.0147 \text{ day}^{-1}$ for cantaloupe followed by 0.0136 day^{-1} for afamia and *tziri*, with a minimum of 0.0106 day^{-1} for canary. Confirmed benefit of cantaloupe could be indicative of synchronicity between the growth needs of isopods and fruit maturation due to its appropriate contents. However, in the second (slow) phase, low constant rates showed maximal value for canary (0.0014 day^{-1}) followed by *tziri* (0.0013 day^{-1}) then cantaloupe and afamia (0.0012 day^{-1}). The slight delayed improvement of canary-dependent growth of *P. laevis* could be indicative of asynchronous processes where temporal change of fruit content of canary (during maturation) could have occurred at a period where the growth needs of isopods decreased significantly.

DISCUSSION

In the Medjerda low plain, the terrestrial isopod community was found to be dominated by *Porcellio laevis* (Fraj *et al.* 2010). During the study period, fluctuations in the density of this species were governed by both intrinsic and extrinsic factors. Intrinsic factors include birth rate, growth rate of the young, duration of the sexual rest and death of the post reproductive adults. Extrinsic factors include environmental factors and melon variety in

the present study. The highest density was recorded from July to October in the afamia and cantaloupe plots. During this period, *P. laevis* densities averaged three times higher in the aforementioned plots. Moreover, the difference between *P. laevis* densities recorded in the four plots, which represented the study area, was also significant during the same period ($P < 0.001$).

Thus, the high abundance of isopods in the afamia and cantaloupe plots compared to the canary and *tziri* plots could be related to the fruit components (i.e., phenolic and nitrogen contents). In fact, many authors have used different leaf species and diets to examine the influence of leaf litter attributes on isopods (Rushton & Hassall 1983, Zimmer & Topp 1997, 2000, Kautz *et al.* 2000, Lavy *et al.* 2001, Lardies *et al.* 2004).

The breeding activity of *P. laevis*, in the Medjerda low plain, occurred from April to June and from the latter half of August to the end of September in two distinct waves. Terrestrial isopod species exhibited a seasonal reproduction with more or less variations concerning the onset and the duration of this reproduction; this is the case of *P. laevis* populations studied in Tunisia, in their natural habitats in Chambi Park (Central of Tunisia) (Achouri 2012) and in Wadi Joumin in Bizerte (Northern Tunisia) (Ghemari *et al.* 2016). In the Delhi region, Nair (1984) reported that egg production began in February/March and continued until October with a cessation during the hot summer months of May and June. Besides, the genus *Porcellio* was studied through several species including *P. albinus*, *P. buddelundi*, *P. variabilis* (Medini-Bouaziz *et al.* 2017), and *P. lamellatus* (Khemaissia *et al.* 2016). However, for *Armadillidium pelagicum* and *A. sulcatum* the breeding season was relatively shorter (from March/April to August) (Hamaïed & Charfi-Cheikhrouha 2016). In the xeric species adapted to arid environment, *Hemilepistus reaumurii*, reproduction is even more limited, not exceeding 3 months (May-June-July) (Achouri 2012). Our study indicated that the breeding activity of *P. laevis* coincided with the growing season of the four varieties of melon, afamia, cantaloupe, canary and *tziri* and with other species of Cucurbitaceae, widely grown in the low valley of Majerda. Moreover, life history traits of *P. laevis* were significantly influenced by some synchronicity with the life cycle of the melon variety.

Indeed, populations sampled in the afamia and cantaloupe varieties showed that individuals reached sexual maturity earlier than those recorded in the canary and *tziri* varieties. While larger gravid females were found during the entire reproductive period in all plots, gravidity in smaller females was restricted to the second breeding wave in the afamia and cantaloupe plots. Moreover, another factor was noteworthy: a remarkable increase in the offspring number released from females living in the afamia and cantaloupe plots. As mentioned by many reports about most terrestrial isopods from different parts of the world (Quadros *et al.* 2008, Kashani *et al.* 2011,

Khemaissia *et al.* 2016), a positive correlation between fecundity and female body-mass has been established in *P. laevis*. Fecundity increased with the size of *P. laevis* female, for that reason bigger females released more juveniles in all plots. However, the fecundity varied between breeding seasons with a large number in spring and a small number in autumn.

In the afamia and cantaloupe plots, females showed a higher reproductive allocation while in canary and tziri, females invested more in individual offspring rather than in brood size because individual offspring was relatively heavy and fecundity is much lower. Another aspect was related to the ability to inflict damage on crops. Bigger individuals were able to inflict more damages on afamia and cantaloupe fruits. Our results showed that afamia and cantaloupe fruits had finer cortex (0.42-0.45 cm), higher total phenolic content and antioxidant activity (295.74-271.93 μM Trolox 100 g^{-1} FW) and higher concentration of internal ethylene (31.7-36.8 ppm) which might have allowed *P. laevis* to grow faster exposing crops to a more abundant and potentially more harmful population of this species. In the afamia and cantaloupe plots, the growth rate was around 0.0136 and 0.0139, respectively, but it was lower in canary (0.0106 mm day^{-1}). In this context, several other variables were recognized as responsible for food quality. Zimmer & Topp (2000) found that *Porcellio scaber* and *Oniscus asellus* performed better, in terms of growth, reproduction and mortality, on litter with low C/N ratio, relatively high pH levels, and low phenolic contents. In *A. vulgare*, females fed with dicotyledonous species were able to produce more juveniles (Rushton & Hassall 1983). In other isopods, differences were observed in fecundity per female under different N content diets (Kautz *et al.* 2000, Lardies *et al.* 2004, Hassall *et al.* 2005, Faberi *et al.* 2011). Fox & Czesak (2000) reported that maternal diet influenced young size in many arthropods. Brody & Lawlor (1984) observed that females produce larger progeny on low food concentration in terrestrial isopods. Lardies *et al.* (2004) found that the smallest offspring were obtained from females fed with high protein diets. Thus, the ability to reduce or to increase fecundity and the duration of brooding appeared to be an adaptive response to changing environmental conditions including, but not necessarily limited to physical stress (Kighti & Nevo 2004) or availability of resources.

Longevity seems to be related to melon variety. In fact it was relatively longer for animals living in the afamia (22 months) and cantaloupe (20 months) plots compared to those living in canary (17 months) and tziri (17.5 months) plots ($F = 15.65$, $p = 1.59\text{E-}05$). A previous study found that food availability was also known to affect generation lifespan of isopods, where high levels of food availability are associated with outbreak populations of isopods (Caseiro *et al.* 2000), and changes in pest status (Wallner 1987). In another terrestrial isopod, *A. vulgare*, Rushton & Hassall (1983) demonstrated that food quality

could significantly change growth rate, directly affecting the age during the first reproduction.

The history of harmful isopod populations is not specific to *P. laevis*. *Armadillidium nasatum* has been reported to feed on cucumber plants (Goats 1985). Other studies showed that *A. vulgare* was found to cause damage to tomato, radish, lettuce, mustard, pea, and bean crops (Garthwaite *et al.* 1995). This species was also found to cause damage to the green leaves of plants such as *Picris echioides* and *Silybum marianum* in the grasslands of California (Paris 1963). This same species has been shown to damage a number of agriculturally important crops in fields where the population can switch between dead and live plants: leaves, stems, flowers, and seeds (Paris & Sikora 1965, Byers & Bierlein 1984, Sasaka 2008, Faberi *et al.* 2014). Recent observations in soybean under no-tillage management in central Kansas, revealed that *A. vulgare* feeds on succulent stem tissues beneath the cotyledons of seedlings, causing significant stand reductions (Alfaress 2012). Similar results were observed in Argentina in sunflower and soybean (Faberi *et al.* 2011, 2014). Moreover, *P. laevis*, like *A. vulgare* and other terrestrial isopods, is mainly a detritivore that feeds on dead plants, however, changes in production practices from consumer (Saska 2008) to pest, may be enabling a shift from a minor or opportunistic pest status to a greater impact pest especially that there are many studies mentioning *A. vulgare* as “granivory” seed or seedling feeder of different plants (Honek *et al.* 2009) such as Alfalfa (Byers & Bierlein, 1984), sunflower, and soybean (Tulli *et al.* 2009, Faberi *et al.* 2011, 2014, Alfaress 2012).

In the Medjerda low plain, the effect of insecticides on *P. laevis* was limited due to the vertical migration of these animals into the soil during the spray application. Similar vertical migrations were reported in other populations of this species by Nair (1984) in the Delhi region, by Paris & Pitelka (1962) in *A. vulgare* populations and by Sutton (1968) for *Trichoniscus pusillus*.

Considering the damage that could reach 23 % of the cantaloupe variety fruits and around 49 % of the afamia variety fruits, farmers therefore avoided cultivating these varieties and replace them with other varieties that were imported and requested by the market and the consumer. This caused crop reduction or disappearance of varieties such as afamia, maazoun and galaoui for the benefit of others such as canary. Therefore genetic erosion affected Tunisian melons by the disappearance or the substitution of agrarian or old cultivars by elite ones (Trimech *et al.* 2015).

CONCLUSION

Studies of *P. laevis* as pest are currently rare. There is information regarding the biology of isopods under different food conditions, basically leaf litter from forests

and natural land species. The present study represents a source of information on *P. laevis* biology in different varieties of melon (*Cucumis melo* L.), concluding that the biology of this species differ according to these varieties.

However, it is difficult to define which dietary features determine food quality. To precisely establish which specific characteristics of the variety affect the biological performance of *P. laevis* requires further study. Even if traits that determine food quality are still unknown, some general agricultural suggestions could be taken into account to establish the basis for an Integrated Pest Management (IPM) program implementation of this species as pest. In the afamia and cantaloupe plots, *P. laevis* found the best conditions for faster growth, longer survival and relatively higher fecundity. Consequently, in the afamia and cantaloupe fields, a more abundant population of *P. laevis* that also contained larger individuals was found. Both of these aspects, abundance and size, could have caused more damage to the crop. Nevertheless, further studies under natural conditions are still necessary to provide the best resource for the Integrated Management of *P. laevis*.

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