Mineral fertilization modulates survival, reproduction, and population growth of Cactus Cochineal *Dactylopius opuntiae* (Cockerell)

El-Aalaoui Mohamed and Sbaghi Mohamed

mohamed.elaalaoui@inra.ma

Institut National de la Recherche Agronomique, Avenue Ennasr, BP 415 Rabat principale, 10090 Rabat, Maroc

Abstract

Opuntiae cactus cochineal *Dactylopius opuntiae* (Cockerell) is a specific scale pest that causes enormous economic losses on cactus pear worldwide. In this study, the effects of synthetic fertilizer N-P-K applications on the development, biology and reproduction of cactus cochineal were investigated. The experiments were carried out under greenhouses at 28°C/17°C (day/night). Synthetic fertilizer N-P-K tested treatments were T1: 0–0–0; T2: 30–40–40; T3:60–80 –80; T4: 60–0–0; T5: 0–80–0; T6: 0–0–80; and T7: 40–100-80 kg ha^{-1}. Cactus cochineal feeding on Cactus *opuntia ficus-indica* [L.] Mill. plants receiving the highest nitrogen level fertilizer (T4) had the shortest total time of development (79.1 and 27.2 days for female and male, respectively), the highest pre-adult survival rate (80%), the highest proportions of females (40%), the shortest pre-oviposition period (34.4 days), and the longest oviposition period (22.4 days), as well as the greatest fecundity (406.7 egg/female) and fertility (90%) compared to the other treatments. The net reproductive rate (R_0) (163.84 females/female/generation), the intrinsic rate of natural increase (r_m) (0.12 females/female/day) and the finite rate of increase (l) (1.13 $days^{-1}$) were significantly the highest at T4 and the lowest at T7 treatments. In contrast, increasing concentration of potassium and phosphorus from T5 to T7 treatments decreased the host suitability for the cactus cochineal and negatively affected its biology, reproduction and population incidence (population incidence = 1.2 at T7 treatment). This means that, compared to potassium and phosphorus, higher nitrogen fertilization improves the suitability of cactus *O. ficus-indica* for cactus cochineal *D. opuntiae*, whose performance and reproduction are then increased.

Key words: *Dactylopius opuntiae*, O*puntia ficus-indica,* synthetic fertilizer N-P-K, population incidence, net reproductive rate, intrinsic rate of natural increase.

La fertilisation minérale module la survie, la reproduction et la croissance de la population de la cochenille du cactus *Dactylopius opuntiae* (Cockerell)

Résumé

La cochenille de cactus *Dactylopius opuntiae* (Cockerell) est un ravageur spécifique qui a causé d'énormes pertes économiques sur le cactus dans le monde entier. Dans cette étude, les effets de l'application d'engrais synthétiques N-P-K sur le développement, la biologie et la reproduction de *la cochenille* ont été étudiés. Les expériences ont été réalisées sous serres à 28°C/17°C (jour/nuit). Les traitements d'engrais synthétiques N-P-K testés étaient T1: 0-0-0; T2: 30-40-40; T3: 60-80-80; T4: 60-0-0; T5: 0-80-0; T6: 0-0-80; et T7: 40-100-80 kg ha^{-1}. Les cochenilles se nourrissant de plantes du Cactus O*puntia ficus-indica* [L.] Mill. ayant reçu une fertilisation azotée plus élevée (T4) avaient une durée totale de développement plus courte (79,1 et 27,2 jours pour les femelles et les mâles, respectivement), un taux de survie pré-adulte plus élevé (80 %), de grandes proportions de femelles (40 %), une période de pré-oviposition plus courte (34,4 jours), une période de ponte plus longue (22,4 jours), ainsi qu'une fécondité plus élevée (406,7 œufs/femelle). Le taux de reproduction net (R_0) (163,84 femelle/femelle/génération), le taux intrinsèque d'accroissement naturel (r_m) (0,12 femelle/femelle/jour) et le taux d'accroissement fini (λ) (1,13 jours-1) étaient significativement plus élevés au traitement T4 et plus faibles au traitement T7. En revanche, l'augmentation de la concentration du potassium et du phosphore entre les traitements T5 et T7 a diminué l'adéquation du Cactus pour *la cochenille* et a affecté négativement sa biologie, sa reproduction et l'incidence de sa population (incidence de la population = 1,2 au traitement T7). Cela signifie que, par rapport au potassium et au phosphore, une fertilisation azotée plus élevée améliore l'aptitude du Cactus *O. ficus-indica* pour la cochenille *D. opuntiae*, et par conséquent augmente sa performance et sa reproduction.

Mots clés : *Dactylopius opuntiae, Opuntia ficus-indica*, engrais synthétique N-P-K, incidence sur la population, taux de reproduction net, taux intrinsèque d'accroissement naturel.

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التسميد المعدني للصبار يعدل التطور البيولوجي, وتكاثر ونمو الحشرة القرمزية *Dactylopius opuntiae* (Cockerell)

العلاوي محمد والسباغي محمد

ملخص

الحشرة القرمزية *Dactylopius opuntiae* (Cockerell) هي حشرة خاصة تعيش فقط على بعض اصناف نبات الصبار وقد تسببت في خسائر اقتصادية هائلة للصبار في جميع أنحاء العالم. في هدا البحث، تمت دراسة تأثير استخدام الأسمدة الاصطناعية N-P-Kعلى التطور البيولوجي و تكاثر الحشرة القرمزية. أجريت التجارب في صوبات زراعية تحت 28 درجة مئوية / 17 درجة مئوية (نهاراً / ليلاً). كانت معاملات الأسمدة الاصطناعية N-P-K التي تم اختبارها كالتالي : T1: 0-0-0؛ T2: 30-40-40؛ T3: 60-80-80؛ T4: 60-0-0؛ T5: 0-80-0؛ T6: 0-0-80؛ T7: 40-100-80 كيلوغرام في الهكتار. الحشرات القرمزية التي تغذت على نباتات الصبار *opuntia ficus-indica* [L.] Mill. التي تلقت الكمية العالية من النيتروجين (T4) كان لها وقت نمو إجمالي أقصر (79.1 و 27.2 يومًا للإناث والذكور، على التوالي)، ومعدل بقاء أعلى قبل البلوغ (80٪)، ونسبة عالية من الإناث (40٪)، وفترة أقصر قبل وضع البيض (34.4 يوم)، و فترة وضع أطول (22.4 يوم)، وخصوبة أعلى (406.7 بيضة/أنثى). كان معدل التكاثر الصافي (163,84 femelle/femelle /génération) (R_0)، والمعدل الجوهري للزيادة الطبيعية (r_m) (0,12 femelle/femelle/jour) ومعدل الزيادة المحدودة (l) (1.13 يوم$^{-1}$) أعلى بشكل كبير في المعاملة T4وأقل في المعاملة T7. في المقابل، أدت زيادة تركيز البوتاسيوم والفوسفور بين المعاملات T5و T7إلى انخفاض ملائمة الصبار ل *D. opuntiae* وهذا يعني أنه بالمقارنة مع البوتاسيوم والفوسفات، فإن التسميد العالي بالنيتروجين يحسن ملائمة الصبار *O. ficus-indicae* للحشرة القرمزية *D. opuntiae* ، ويزيد من أدائها وتكاثرها.

الكلمات المفتاحية: *Dactylopius opuntiae*، *Opuntia ficus-indica* ، سماد اصطناعي N-P-K، التأثير العددي، معدل التكاثر الصافي، المعدل للزيادة الطبيعية.الجوهري.

Introduction

In the arid and semi-arid regions where agriculture suffers from several constraints due to the scarcity of rainfall and repeated periods of drought, the Opuntia cactus (*Opuntia ficus-indica*[L.] Mill.) plays a primary role in the food security of the populations living in these difficult conditions (Nefzaoui et al., 2014). It is considered a perennial drought-tolerant crop of high nutritional, cosmetic, and medicinal value with important integration in the production and diversification processes of agriculture and as well as in the development of new typical agricultural products (Ramos et al., 2015).

Like other crops, cactus pear suffer from several abiotic and biotic diseases. Gastropods, cryptogamic diseases, and specific cactus scale pests such as *Diaspis echinocacti* (Hemiptera: Sternorrhyncha: Diaspididae), and Dactylopius species which are the main enemies of this crop (Walali Loudyi, 1998). Cactus cochineal, *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactylopiidae) appears to be the most serious pest of this crop (Sheehan and Potter, 2017). Cactus cochineal, affects about 16 species of Opuntia cactus in different geographical regions around the world (Mazzeo et al., 2019). It causes economic losses of several million dollars per year, either through loss of production or pest control costs (Mazzeo et al., 2019; Portillo and Vigueras, 2006; Badii and Flores, 2001). In Morocco, attacks by this serious scale pest were rapid and uncontrollable in some cases, and resulted in thousands of hectares of different cactus ecotypes, totally destroyed causing enormous socio-economic and environmental losses (Sbaghi et al., 2019). The severe damage caused by cactus cochineal *D. opuntiae* in several countries of the world requires an integrated control approach that also takes into account the importance of environmental protection and biodiversity (Santos et al., 2006). This approach should include several methods that are cultural, genetic, biological (natural enemies), chemical, mechanical, physical and other methods (Lopes et al., 2007; Santos et al., 2006; Cavalcanti et al., 2001) and that can be combined in various ways to obtain the best results in controlling this serious pest.

Fertilizers are some of the main factors for increasing crop vegetation and yield, but they can also influence pest populations by reducing or stimulating plant resistance to insects (Perrenoud, 1990; Way et al., 2006). Several experiments have been carried out to compile evidence on nitrogen (N), potassium (K) and phosphorus (P)-disease interactions from a large number of greenhouse and field trials. The prevailing view is that high K and P status reduces the incidence of many pests or diseases (Fuchs and Grossmann, 1972; Facknath and Lalljee, 2005; Prabhu et al., 2007), while for some crops, increased application of nitrogen (N), would lead to the abundance and attraction of severe herbivorous pests (Bi et al., 2001; Ge et al., 2003).

Dactylopius opuntiae feeds directly on cactus pear and exclusively on phloem sap causing chlorosis and premature fall of cladodes and fruits and in case of severe infestation (greater than 50% of the cladode surface) can cause death of the host plant (Vanegas-Rico et al., 2016). K and P nutrients profoundly affect the profile and distribution of primary and secondary metabolites in plant tissues, which in turn could affect negatively the attractiveness of the plants to insects and pathogens and their growth and subsequent development on and in the plant (Facknath and Lalljee 2005; Amtmann et al. 2008).

Therefore, the objective of the present study is to examine the fertilization effect at different combinations and doses of N-P-k on the biology, life cycle and density of *D. opuntiae* on *O. ficus-indica* under greenhouse conditions.

Materials and methods

The experimental site and plant material used in the study

The trials were carried out at the experimental station of the National Institute of Agricultural Research (CRRA SETTAT-INRA Morocco) in the locality of Zemamra (casablanca-settat region) (33°15' N, 8°30' W) during two consecutive seasons; 2019/2020 (Season I) and 2020/2021 (Season II). The experimental site is characterized by an average monthly temperatures ranging from about 1°C in January to 33°C in July, with a daily maximum temperature reaching 45°C in June-August.

The experiments were carried out in three greenhouses (11 m long×7 m wide×3 m high) with an average temperature of 28°C/17°C (day/night) containing cactus pear plants (*O. ficus-indica* (L.) Mill.) very sensitive to *D.opuntiae* (Sbaghi et al., 2019) and planted in plastic pots (33 cm diameter by 12 cm height), filled with 15 Kg of the experimental site soil. Each greenhouse contained 150 two years old plants, arranged in six rows (0.5 m spacing between rows, 5 cm between plants, and each row had 25 plants) (Fig. 1). The plants were irrigated as needed. The cactus ecotype used in this study is a thornless ecotype of *O. ficus-indica* with yellow-orange fruits at maturity. The temperature data of the greenhouses were recorded from 6 thermometer measurements taken at 2 h intervals. The night temperature was determined from the 3 lowest daily values (Vinogradova et al., 2013).

Concerning the experimental site soil, it is of two types: i) Vertisol with an angular structure in the first 15 cm, deep to 1.5 m, difficult to work in dry conditions than with a high water content, and ii) Light soil with a hydromorphic sandy-clay structure with an alkaline pH. The chemical composition of the soil before fertilizer application was as follows: N (200 mg/kg), P_2O_5 (46 mg/kg), K_2O (203 mg/kg), Mo% (1.5 mg/kg), Ec (0.35) and pH (8.6).

Figure 1. General view of cactus after two days after plantation under greenhouse conditions.

The cactus cochineal colony establishment

Prior to the establishment of *D. opuntiae* colony, subsamples of females and nymphs were collected from infested cactus pear fields, placed in tubes containing 75% ethanol and taken to the laboratory for species confirmation by morphological characteristics. A strain colony of *D. opuntiae* was started in entomological cages (80×80×80 cm) with infested cladodes of *O. ficus-indica* collected from fields of Zemamra locality (32°37'48'' N, 8°42'0'' W) in the Sidi-Benour region in Morocco and maintained under laboratory conditions (26±2 ºC, 60±10% RH, and 12 h of photophase), using the method described by Aldama-Aguilera and Llanderal-Cazares (2003). In order to increase the number of insects and to check their age, the first instar nymphs of *D. opuntiae* (24 h old) were transferred to another cage with the same characteristics as described above to complete their development.

Treatments and experimental design

The following combinations of nitrogen (ammonia-N), phosphorus f (P_2O_5) and potassium (K_2O) fertilizer were applied (in kg ha^{-1}): T1: 0–0–0; T2: 30–40–40; T3 :60–80 –80; T4: 60–0–0; T5: 0–80–0; T6: 0–0–80; and T7: 40–100-80 or (T1: 0–0–0; T2: 0.26–0.34–0.34; T3 :0.51–0.68 –0.68; T4: 0.51–0–0; T5: 0–0.68–0; T6: 0–0–0.68; T7: 0.26–0.85-0.68 (g/pot)). The recommended N-P-K level suitable for planting opuntia cactus is 60–80–80 kg ha^{-1} in Morocco (Arba et al., 2017). The seven treatments were evaluated in a completely randomized design (plants are the experimental units).

Each greenhouse contained the seven doses corresponding to the fertilization treatments, where twenty plants were used per greenhouse for each treatment. Thus 60 plants were used for each treatment (three greenhouses). All experiments were repeated twice over different time (realized 2019/2020, and repeated 2020/2021) to ensure reproducibility of the results using the plastic pots of the same size, same cactus ecotype, same experimental design and treatments, and soil analysis was conducted only during the first year of the study. The water-soluble fertilizer doses were spread ten cm from the center line around the plants. They were applied once every five weeks during the plant growth period (before infestation) when all experimental pots were irrigated. The plants received the fertilizer doses three times before being infested by cactus cochineal *D. opuntiae*.

Measuring the biological parameters

Thirty one-day-old first instar nymphs of *D. opuntiae* (obtained from adult eggs of the colony of the strain maintained in the laboratory) were carefully transferred to the trial plants using a fine camel hair brush (No. 000, CAMLIN, USA) (30 nymphs/plant). To determine pre-imaginal development, duration of pre-oviposition, oviposition and post-oviposition periods, adult longevity times and cumulative survival rates, we observed individuals from the first instar nymph to the adult death twice a day (08:00 h and 17:00 h). The sex of each nymph was determined at the second nymphal stage, after which the developmental cycle and morphology differed for males and females (El Aalaoui et al., 2020). Sex determination was carried out according to the morphological characteristics quoted by El Aalaoui et al. (2020) and Flores-Hernández et al. (2006).

Measuring the reproduction parameters

To evaluate the adults reproductive parameters, the gravid females (n=20) (stage before oviposition) were carefully and individually removed from the treated plants using a needle, and placed on treated *O. ficus-indica* cladodes inside separate entomological cages with the same characteristics described above (80×80×80 cm) in the laboratory at 26±2 ºC, 60±10% RH, and 12 h of photophase. The treated cladodes used in laboratory conditions were obtained from plants treated at the same time as those in greenhouses. Each female was observed daily in order to be able to record longevity, and fecundity (number of eggs laid per female). The pre-adult survival rate and sex ratio (proportion of females) were also determined. All experiment was repeated thrice over different time.

Measuring the population growth parameters

The following population growth parameters were estimated for each tested dose of fertilizer: the net reproductive rate ($R_0=\Sigma l_x m_x$), the mean generation time (T), the intrinsic rate of natural increase r_m (= $\ln R_0/T$), the finite rate of increase ($l= e^r$) and the doubling time (DT= $\ln 2/r_m$). The l_x corresponds to age-specific survival of females and the m_x to age-specific fertility (= nymphe born/female) (Southwood & Henderson, 2000; Vasicek et al., 2004; Kontodimas & Stathas, 2005).

Incidence of the cactus cochineal

Incidence of *D.opuntiae* was recorded from 20 randomly selected plants in all three greenhouses for each treatment, in the scale of zero to five according to Silva (1991): 0: No damage; 1: Up to 10 colonies per cladode; 2: 11 to 40 colonies per cladode; 3: 41 to 80 colonies per cladode; 4: 81 to 120 colonies per cladode; 5: more than 120 colonies per cladode. The number of colonies per cladode was measured with the help of a needle. The experiment was repeated during two seasons of the study.

Plant morphology and productivity

To investigate the effect of different fertilizer treatments on plant morphology and production under the same greenhouse conditions described above, 20 plants were randomly selected in all three greenhouses for each treatment one day before the infestation. The evaluation of plant morphology and productivity was based on: plant height (cm) (PH), plant diameter in the east-west direction (cm) (PD), number of cladodes per plant (Nc), cladode length (cm) (CL), cladode width (cm) (CW), cladode thickness (cm) (CT). The experiment was repeated during two seasons of the study.

Statistical analysis

The data recorded during the two years of the study from the three greenhouses on the development time of different stages of the cactus cochineal and the production periods of pre-oviposition, oviposition and post-oviposition, as well as plants morphology and production were transformed by log (x), and the fecundity and fertility data by log (x + 1) prior to analysis of variance (ANOVA), in order to correct the effects of heteroscedasticity (Hill and Hill, 2002). Mean statistical differences that existed among the data sets ($P < 0.05$), were separated by Tukey's Least Significant Difference (LSD) tests. Cumulative survival rates (egg to adult) were analyzed by the multiple comparison test for proportions (Zar, 1996). All analyses were performed using the

2004 SPSS program, ver. 18 for Windows. The presented values are regular means and standard errors.

Results

Biological parameters

Development times of the cochineal under different fertilizer treatments are presented in Table 1. The longest time of development was recorded for T7 (40–100-80) treatment (99.5 and 51.0 days for female and male, respectively) and the shortest under T4 (60-0-0) (79.1 and 27.2 days for female and male, respectively) (female life cycle duration $p < 0.0001$; male life cycle duration $p < 0.0001$). Adult female and male mean longevities were significantly the highest at T4 and the lowest at T7 treatments (female longevity $p < 0.0001$; male longevity $p < 0.0001$).

Table 1. Average Development times (days ± SE) of *D. opuntiae* under the tested fertilizer treatments.

D.opuntiae life stages	Fertilizer treatments						
	T1 N = 124	T2 N = 124	T3 N = 124	T4 N = 124	T5 N = 124	T6 N = 124	T7 N = 124
N1	11.3±0.6^{c}	8.3±0.9^{e}	10.5±0.8^{d}	5.4±0.9^{f}	12.8±0.6^{b}	13.2±0.7^{b}	14.4±0.7^{a}
N2 Female	14.5±0.9^{c}	13.0±0.6^{d}	14.9±0.7^{c}	11.7±1.1^{e}	20.3±1.3^{b}	20.6±1.2^{b}	24.4±0.7^{a}
N2 Male	7.5±0.8^{d}	7.8±0.6^{d}	10.4±0.8^{c}	6.1±0.6^{e}	11.5±0.9^{b}	11.9±1.3^{b}	14.5±1.0^{a}
Young female	19.5±0.9^{e}	20.42±0.8^{d}	21.3±1.2^{c}	16.2±0.7^{f}	23.1±0.9^{b}	23.7±1.1^{b}	26.1±0.9^{a}
Male pupal duration (Pupa+Cocoon)	7.4±0.7^{e}	8.4±0.8^{d}	10.4±0.9^{c}	6.4±0.6^{f}	13.3±0.8^{b}	13.7±0.9^{b}	15.7±1.0^{a}
Total pre-adult female	46.2±1.5^{e}	42.8±1.7^{f}	47.6±1.6^{d}	34.3±1.7^{j}	57.2±1.7^{c}	58.5±2.0^{b}	65.9±1.4^{a}
Total pre-adult male	27.1±1.2^{e}	25.4±1.4^{f}	32.3±1.5^{d}	18.8±1.4^{j}	38.7±1.4^{c}	39.7±1.9^{b}	45.6±1.6^{a}
Female longevity	43.5±0.9^{b}	41.5±1.2^{c}	40.0±0.9^{d}	44.8±1.5^{a}	37.4±0.8^{f}	38.2±1.2 ^{e}	33.6±1.0^{j}
Male longevity	8.2±0.7^{a}	7.4±0.7^{b}	6.5±0.7^{c}	8.4±0.8^{a}	6.2±1.4^{cd}	5.9±1.0^{e}	5.4±0.7^{f}
Female life cycle	89.7±1.7^{d}	84.3±1.9^{f}	87.6±1.9^{e}	79.1±2.0^{j}	94.6±2.0^{c}	96.7±2.4^{b}	99.5±1.7^{a}
Male life cycle	35.3±1.3^{d}	32.8±1.5^{e}	38.8±1.7^{c}	27.2±1.5^{f}	44.8±1.6^{b}	45.6±2.0^{b}	51.0±1.8^{a}

N1 and N2 = first, and second nymphal stages, respectively. N = size of the cohort

Within lines values followed by the same letters are not statistically different according to Tukey's LSD test at α = 0.05.

The pre-adult survival rate was the highest at fertilizer treatment T4 (60–0–0) (0.80) in comparison with the other treatments (Table 2). It was also noticed that a large proportions of females were found on cladodes fertilized only with a high nitrogen concentration (T4: 60-0-0) (0.40) (Table 2). Cumulative survival rate was not affected by treatments (all $P > 0.05$) (Fig. 2).

Table 2. Sex ratio (proportion of females) and nymphs mortality rates of *D.opuntiae* population under the tested fertilizer treatments N = size of the cohort

Fertilizer treatments	N	Sex ratio **	The pre-adult survival rate*
T1	124	0.35	0.71
T2	124	0.37	0.74
T3	124	0.38	0.77
T4	124	0.40	0.80
T5	124	0.31	0.64
T6	124	0.24	0.61
T7	124	0.26	0.53

***calculated using all individuals (males and females) in the population.*

** calculated using all the immature stage in the population.*

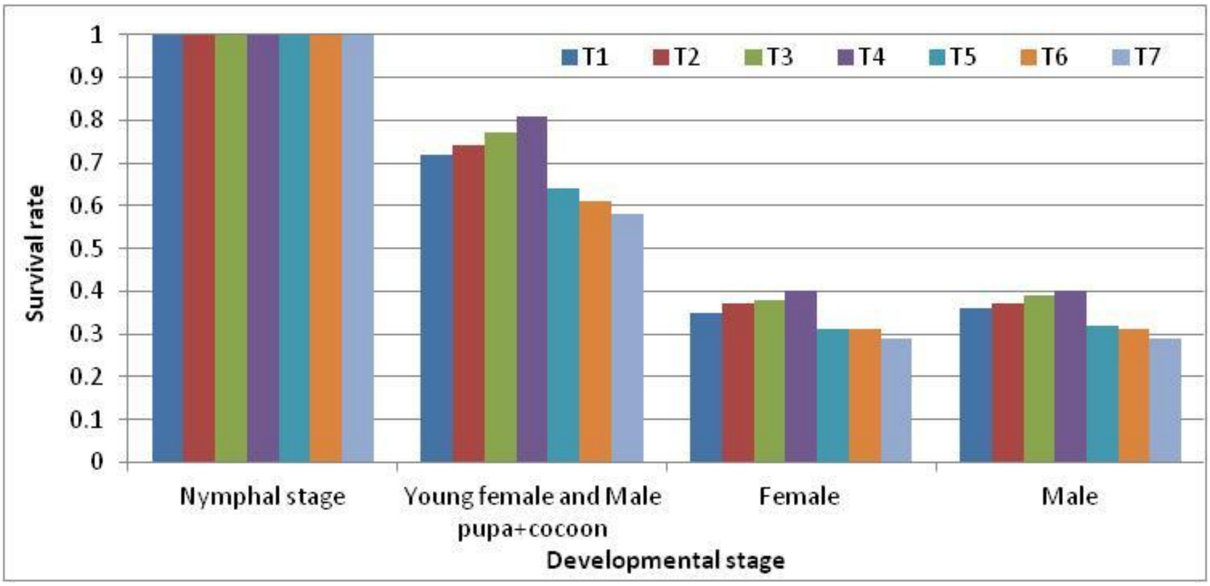

Figure 2. Survival rates of *D. opuntiae* developmental stages under the tested fertilizer treatments. No significant differences were observed among treatments according to tukey's LSD (5%) test (all P > 0.05).

For all fertilizer treatments and ages, the age-specific survival curve of females (lx) shows a consistent mortality rate with a typical type II hypothetical survival curve (Fig. 3). Mortality of last individual of the cochineal on each of the seven treatments occurred respectively on the 93rd, 90th, 91st, 83rd, 100th, 103rd, and 102nd days of the experiment.

These results showed, overall, that increasing nitrogen concentration from T1 to T4 treatments has positive effects on the development, survival, and performance of *D. opuntiae*. In contrast, increasing concentration of potassium and phosphorus from T5 to T7 treatments decreased the host suitability for *D. opuntiae* and negatively affected the development and survival of the scale insect.

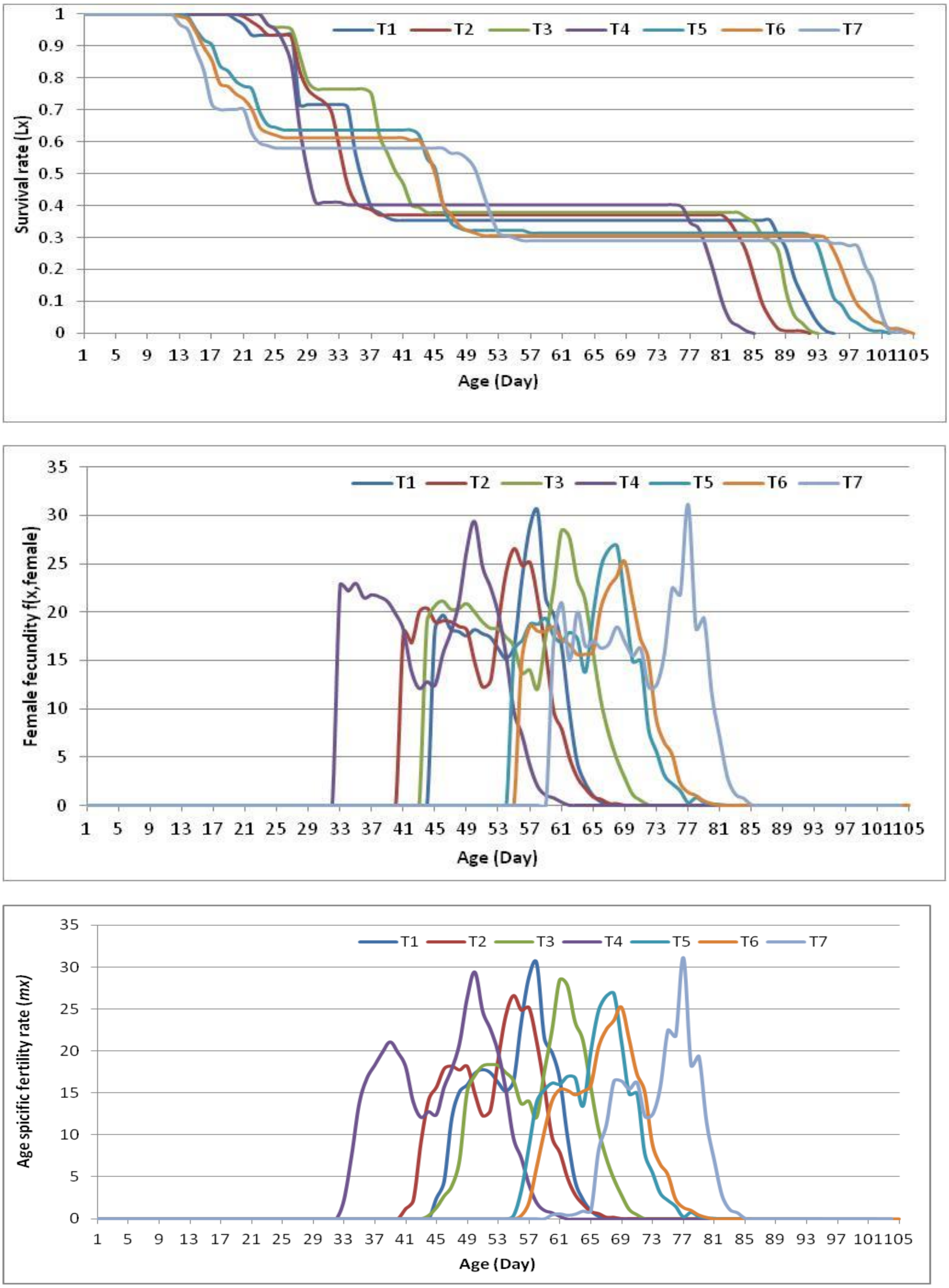

Figure 3. Age-specific survival rate (l_x), female age-stage fecundity (f_x) (eggs/ female), and age-specific fecundity (m_x) of *D. opuntiae* fed on *O. ficus-indica* (L.) at the seven tested fertilizer treatments

Reproduction parameters

The pre-oviposition period was significantly the longest for T7 treatment (65.8 days) followed by T6 (58.4 days), and T5 (57.0 days). The shortest pre-oviposition period was observed at T4 treatment (34.4 days) ($p < 0.0001$), while oviposition period was significantly the highest at T4 (22.4 days) than at the other fertilizer treatments ($p < 0.0001$). Similarly, the total lifetime fecundity was significantly the longest at T4 treatment (406.7 egg/female), and the shortest at T7 treatment (264.5 egg/female) ($p < 0.0001$) (Table 3).

Overall, the results showed that phosphorus and potassium treatments (T7, T6, and T5) had a positive effect on the pre-oviposition period of the cochineal. However, the nitrogen treatments (T2-T4) had minimal impact on pre- and post-oviposition periods compared to the control treatment, while inducing high fecundity compared to the other tested treatments. The curves for age-stage specific fecundity (f_x, female), and age-specific fecundity (m_x) showed several peaks, with the highest one observed at T7 treatment. Two peaks were identified at T1, T2, T3, T5, and T6 treatments, three at T4 treatment and five peaks were identified at T7 treatment (Fig. 3).

Table 3. Average Reproduction parameters of *D.opuntiae* under the tested fertilizer treatments N = size of the cohort

Reproduction parameters	Fertilizer treatments						
	T1 N = 44	T2 N = 46	T3 N = 47	T4 N = 50	T5 N = 39	T6 N = 38	T7 N = 36
Total pre-oviposition period (days)	46.3 ±1.5^{e*}	43.0 ±1.8^{f}	47.7 ±1.8^{d}	34.4 ±1.7^{j}	57.0 ±2.0^{c}	58.4 ±1.9^{b}	65.8 ±1.7^{a}
Oviposition period (days)	16.7 ±0.6^{d}	19.2 ±0.8^{c}	20.6 ±1.0^{b}	22.4 ±1.1^{a}	15.7 ±1.2^{e}	15.7 ±1.2^{e}	15.7 ±1.2^{e}
Post-oviposition period (days)	26.8 ±1.1^{a}	22.3 ±1.3^{b}	19.4 ±1.5^{c}	22.4 ±1.8^{b}	21.7 ±1.7^{b}	22.7 ±1.7^{b}	18.0 ±1.5^{d}
Total fecundity	309.2 ±12.9^{d}	339.9 ±14.9^{c}	360.4 ±17.4^{b}	406.7 ±18.4^{a}	291.4 ±21.0^{e}	281.4 ±21.5^{e}	264.5 ±21.2^{f}
Daily reproduction (eggs/female)	18.1 ±0.8^{a}	17.8 ±0.9^{ab}	17.6 ±1.0^{ba}	18.2±0.8^{ab}	18.6±1.8^{a}	18.0 ±1.9^{ab}	17.0 ±1.7^{c}

**Within lines values followed by the same letters are not statistically different according to the Tukey's LSD test at α = 0.05.*

Population growth parameters

Dactylopius opuntiae population growth parameters in the different tested fertilizer treatments are presented in Table 4. The net reproductive rate (R_0) ($p < 0.0001$), the intrinsic rate of natural increase (r_m) ($p < 0.0001$) and the finite rate of increase (l) ($p < 0.0001$) were significantly the highest at T4 and the lowest at T7 treatments, while the doubling time (DT) ($p < 0.0001$) and the mean generation time (T) ($p < 0.0001$) were significantly the highest at T7 and the lowest at T4 treatments.

Table 4. Average Population growth parameters of *D.opuntiae* under the tested fertilizer treatments

Fertilizer treatments	Population growth parameters				
	R_0	T	r_m	l	DT
T1	109.60±0.38[d*]	54.0±0.05[e]	0.09±0.00[d]	1.10±0.00[d]	7.97±0.01[d]
T2	126.06±0.20[c]	51.16±0.03[f]	0.10±0.00[b]	1.10±0.00[b]	7.33±0.01[f]
T3	136.55±0.26[b]	56.39±0.04[d]	0.09±0.00[c]	1.09±0.00[c]	7.95±0.01[e]
T4	163.84±0.68[a]	43.10±0.08[j]	0.12±0.00[a]	1.13±0.00[a]	5.86±0.02[j]
T5	91.64±0.16[e]	64.44±0.02[c]	0.10±0.00[e]	1.07±0.00[e]	9.89±0.01[c]
T6	86.25±0.02[f]	65.90±0.00[b]	0.07±0.00[f]	1.07±0.00[f]	10.20±0.00[b]
T7	76.78±0.02[j]	73.30±0.03[a]	0.06±0.00[j]	1.06±0.00[j]	11.70±0.00[a]

**Within columns values followed by the same letters are not statistically different according to the Tukey's LSD test at α = 0.05.*

Incidence of *D.opuntiae*

The population incidence of *D.opuntiae* on *O. ficus-indica* plants treated with different fertilizer treatments are presented in figure 4. Statistical analysis showed that the number of the cochineal colonies was significantly the highest on cactus plants treated with T4 treatment (population incidence= 4.8) (p < 0.0001). The lowest number of *D.opuntiae* colonies was found on plants treated with T7 treatment (population incidence = 1.2). Generally, the results show that the number of *D.opuntiae* colonies increased significantly with increasing nitrogen concentration and decreased significantly with increasing phosphorus and potassium concentration.

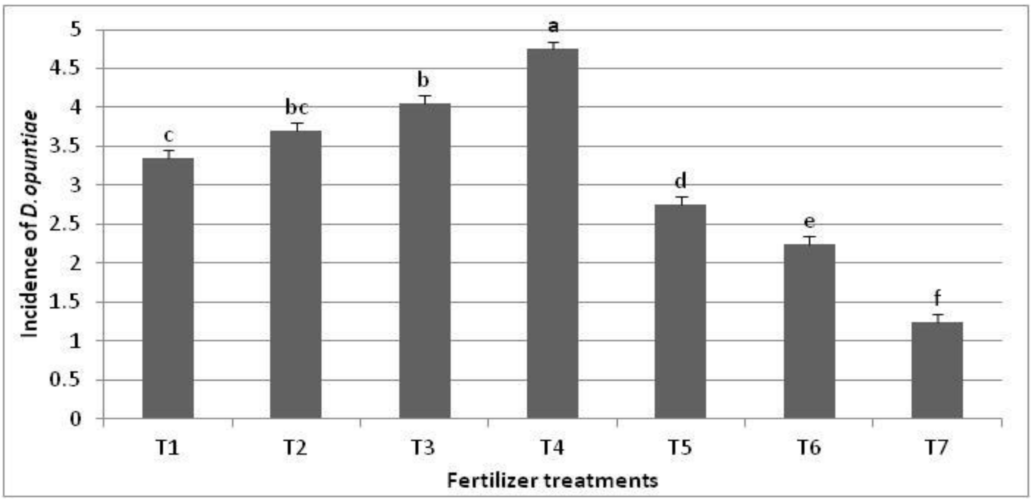

Figure 4. Incidence of *D.opuntiae* on *O. ficus-indica* plants treated with the different fertilizer treatments

Plant morphology and productivity

Morphological parameters and productivity of *O. ficus-indica* plants grown under different fertilizer treatments for the two seasons of the trial are presented in Table 5. The result showed that plants treated with T3 (60-80-80) treatment have the greatest height (p < 0.0001), diameter (p < 0.0001), number of cladodes per plant (p < 0.0001), cladode length (cm) (p < 0.0001), cladode width (cm) (p < 0.0001), and cladode thickness (p < 0.0001) compared to the other treatments.

Table 5. Average plant height (cm) (PH), plant diameter in the east-west direction (cm) (PD), number of cladodes per plant (Nc), cladode length (cm) (CL), cladode width (cm) (CW), and cladode thickness (cm) (CT) of *O. ficus-indica* under different synthetic fertilizer N-P-K treatments over two seasons [2019/2020 and 2020/2021]

Fertilizer treatments	Plant morphology and productivity parameters					
	PH	PD	NC	CL	CW	CT
T1	26.3±0.6^{j*}	30.7±1.5^{j}	4.3±0.7^{j}	23.1±0.7^{j}	16.3±0.6^{j}	1.4±0.2^{e}
T2	36.5±0.8^{d}	50.9±1.4^{d}	12.6±1.0^{d}	26.3±0.7^{d}	20.7±1.0^{d}	1.9±0.3^{c}
T3	65.2±1.8^{a}	57.5±0.7^{a}	18.7±1.5^{a}	38.7±0.9^{a}	28.2±0.5^{a}	2.6±0.2^{a}
T4	43.7±1.0^{c}	53.0±0.9^{c}	14.5±0.9^{c}	30.4±1.0^{c}	23.2±0.8^{c}	1.9±0.3^{c}
T5	34.4±0.9^{e}	45.2±0.7^{e}	10.0±0.7^{e}	25.6±1.0^{e}	19.6±0.7^{e}	1.6±0.3^{d}
T6	32.4±0.7^{f}	39.5±1.1^{f}	6.0±0.5^{f}	23.4±0.7^{f}	19.0±0.5^{f}	1.5±0.2^{d}
T7	55.6±1.0^{b}	54.5±0.6^{b}	16.3±0.7^{b}	37.5±0.7^{b}	25.0±0.6^{b}	2.5±0.2^{b}

**Within columns values followed by the same letters are not statistically different according to the Tukey's LSD test at α = 0.05.*

Discussion

Plant vigor is mainly enhanced by fertilization in order to maximize agricultural production. However, the use of fertilizers can impact insect development in two ways: i) by changing the nutritional status of the plant and ii) by influencing the plant's defense compounds (Awmack and Leather, 2002). Insects receive an optimal level of macronutrients from the plant tissues, which would justify that a change in the ratio of macronutrients in the plant could affect the feeding and performance of phytophagous insects (Sterner and Elser, 2002) and therefore their numbers (Awmack and Leather, 2002; Zehnder and Hunter, 2009). Estimation of the performance of *D. opuntiae*, including development time, cumulative survival rate, reproduction and population growth parameters under different fertilizer treatments can contribute to the identification of the most appropriate fertilizer doses to be used under different environmental conditions in order to control this serious pest that has caused significant economic losses to Opuntia cactus worldwide.

Our results showed that the total development time of *D. opuntiae* decreased significantly by increasing the nitrogen level compared to potassium and phosphorus. These results confirm that sap-sucking insects such as cochineals are positively influenced by increased levels of nitrogen in plant sap (Awmack and Leather, 2002; Behmer, 2009) and that high doses of potassium and phosphorus decreases nitrogen uptake and therefore negatively affect insect biology, reproduction, and behavior (Facknath and Lalljee, 2005). In addition, excessive potassium and phosphorus caused quantitative changes in nutrients and allelic chemicals and strongly influenced the chemical environment of the plant and therefore played an important role in suppressing insect population (Bala et al., 2018).

Accumulated survival rates of *D. opuntiae* pre-adult stages were the highest at T4 (60–0–0), T1 (0–0–0), T2 (30–40–40), T3 (60–80 –80) treatments and lowest at T5 (0–80–0), T6 (0–0–80) and T7 (60–100-80) treatments. Some scientists even refer to the fact that in the diet of phytophagous insects, nitrogen level is the most important factor affecting their performance (Awmack and Leather, 2002). Reproductive performance of *Myzus persicae* (Sulzer, 1776), for example, is correlated with the concentration of

soluble protein in the leaves of the host plant (Van Emden, 1966, Van Emden and Bashford, 1971). Increased nitrogen levels in host plants favor survival, fecundity and development of several phytophagous insects including scale pest (Thomas and Hodkinson, 1991). The results obtained suggest that addition of nitrogen fertilization would cause an increase in the scale pest population since the highest survival rate was observed at T4 treatment (80%).

The longest and shortest oviposition periods (22.4 and 15.7 days, respectively), female and male longevity (44.8; 8.4 and 33.6; 5.4 days, respectively), and fecundity (406.7 and 264.5 eggs per female, respectively) were recorded in T4 and T7 treatments, respectively. Similar results were obtained by Alasvand Zarasvand et al. (2013) who recorded that increased nitrogen level caused an increase in fecundity of the green bug, *Schizaphis graminum* (Rondani , 1852). Similarly, increased nitrogen level caused an increase in fecundity of *M. persicae* and *Brevicoryne brassicae* (Linnaeus, 1758) (Van Emden and Bashford, 1969). The pre-oviposition period of *D. opuntiae* at T7 treatment was much longer than at other fertilizer treatments. A possible explanation for this fact may be related to the negative effect of high K and P concentration on egg maturation, suggesting that reproduction of *D. opuntiae* may be negatively affected at concentrations above 60-100-80 Kg ha^{-1}.

The net reproductive rate (R_0), the intrinsic rate of natural increase (r_m) and the finite rate of increase (l) were the highest at T4 and the lowest at T7 treatments. Doubling time (DT) and the mean generation time (T) were the highest at T7 and much lower at T4 treatments. This divergence can be explained by the positive effect of nitrogen and the negative effect of potassium and phosphorus on the development, survival rate and reproduction of the cochineal. High nitrogen concentrations promote insect growth and reproduction (Douglas, 1993; Slosser et al., 1998) and would decrease their susceptibility to some insecticides (McKenzie et al., 1995).

In the present study, fertilizer treatment with high nitrogen concentration, compared to phosphorus and potassium, (T4 treatment) caused a significant increase in the population incidence of *D. opuntiae* (Fig.3). Plant nutritional status influences the occurrence of pests and diseases in crops (Amtmann et al., 2008). A high level of K in the plant reduces the incidence of many pests and diseases (Fuchs & Grossmann, 1972). Therefore, farmers are generally advised to apply K fertilizers to improve crop vigor (Amtmann et al., 2008). A publication by the International Potash Institute (Perrenoud, 1990) reviewed many studies that have shown the negative effect of potassium on the performance and survival of insects. Phosphorus also decreases host suitability to various insect pests, and secondary macronutrients and micronutrients such as calcium, zinc, sulfur and silicon also reduce pest populations (Bala et al., 2018).

Conclusion

Most phytophagous insects satisfy their macronutrient requirements from the plant tissues. This would justify the fact that a change in the ratio of macronutrients in the plant could affect directly or indirectly their feeding and performance. Fertilization increases the nitrate and amino acid levels in the plants (Mengel and Kirkby, 2001), and therefore increases their nutritional quality and attractiveness to phytophagous insects (Bentz et al., 1995). The present study demonstrated that nitrogen has positive effects on the performance of *D. opuntiae* infesting *O. ficus-indica*. The scale insects feeding on plants receiving higher nitrogen fertilizer T4 (60-0-0 kg ha^{-1}) had shorter total development time, shorter total pre-oviposition period, longer reproductive period, higher fecundity, and higher R_0, r_m, and I than those developed on the other treatments. Treatment with high levels of potassium and phosphorus T7 (40-100-80 kg ha^{-1}) adversely affected the biology, reproduction and population incidence of the scale insect. Our work showed also that the T3 treatment (60-80-80 kg ha^{-1}) favored a significant increase in growth and cladode production compared to the other treatments. More research is however still needed to further support this hypothesis and to further clarify mechanisms by which K and P affect negatively *D. opuntaie* development and reproduction.

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