

Resistance of cactus pear clones (*Opuntia* spp.) to *Dactylopius opuntiae*: pomological and phenological characterization

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Abstract. *Dactylopius opuntiae* is a pest that threatens cactus pear cultivation worldwide. In Morocco, thousands of hectares have been completely destroyed since its introduction in 2014. The use of resistant ecotypes remains the most effective strategy to safeguard cactus cultivation at the national scale. The objective of the present study was to evaluate, under greenhouse conditions over a 45-day period, the resistance of 11 cactus pear ecotypes, as well as to perform pomological and phenological characterization of these clones. The results showed a very high level of resistance in ecotype 54, with 0% infestation by adult females. This ecotype prevented the development of cactus cochineal larvae into the adult stage, whereas the other ecotypes allowed the establishment of adult female colonies with infestation rates not exceeding 25%. In contrast, ecotype 149 was found to be highly susceptible. Analysis of colonization dynamics using an exponential growth model confirmed these results. However, clones 10, 11, 14, 19, 27, 28, and 34 exhibited rapid population growth of *D. opuntiae*, with multiplication factors close to those observed in ecotype 149 and the susceptible control. Pomological characterization revealed that clone 54 exhibited low pomological performance, whereas the ten other tested clones showed medium to high pomological profiles. Phenological monitoring indicated that clones 14, 18, 27, 28, 29, 34, 54 and 149 were characterized by fruit maturity occurring from late July to mid-August. In contrast, clones 10 and 11 were late-maturing, with fruit maturity beginning in mid-September.

Keywords: *Dactylopius opuntiae*, cactus pear, Morocco, resistant ecotypes, pomological characterization, phenological characterization.

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Introduction

Agriculture is one of the main economic sectors in Morocco. This is particularly reflected in its contribution to GDP (approximately 12%) and its role as a major source of employment for a large segment of the population (nearly 38% of the employed labor force) (Louali, 2019). However, in recent years, several regions of the country have been affected by declining and irregular rainfall, which has constrained agricultural development and hindered improvements in the living standards of populations in vulnerable areas (Gommes et al., 2009).

The cactus pear (*Opuntia* spp.), since its introduction by the Moriscos at the beginning of the 17th century (Schielief et al., 2000), has attracted particular interest in the arid and semi-arid zones of the country, where it has been regarded as an alternative crop capable of adapting to the most critical environmental conditions, accounting for 11.07% of the total fruit tree area (Boujghagh and Chajia, 2001). Within the framework of the Green Morocco Plan (GMP) and the National Program to Combat Desertification (PNLCD), cactus cultivation has experienced significant expansion. The cultivated area has tripled, increasing from 45,000 ha in the early 1990s to more than 150,000 ha in 2016 (Mabrouk et al., 2016). The development of this sector has enabled rural populations to generate substantial income through the valorization of cactus products and by-products, including cosmetics, therapeutic applications, and livestock feed (Sbaghi et al., 2019).

The development of cactus cultivation in Morocco was disrupted by the introduction of *Dactylopius opuntiae* in 2014. This pest is considered the most destructive insect affecting *Opuntia* species worldwide; larvae and adult females live in aggregations on the cladodes, typically at the base of the spines (Moussa et al., 2017). Once established, the female becomes sessile and feeds at the same site throughout her lifetime. Initially, infested plants exhibit discoloration and swelling around the cochineal feeding sites. Over time, as *D. opuntiae* populations increase, the affected tissues wilt, turn brown, and eventually die. Infestation of more than 75% of the cladodes results in plant death (Mann, 1969; Vanegas-Rico et al., 2010).

In Brazil, for instance, damage caused by *D. opuntiae* on *Opuntia ficus-indica* grown for fodder production led to the loss of approximately 100,000 ha, corresponding to an estimated economic loss of 25 million US dollars (Lopes et al., 2009). In Mexico, damage to fruits and nopalitos (young cladodes of edible *Opuntia* spp.) caused by this insect resulted in yields falling below production costs (Badii and Flores, 2001; Portillo and Viguera, 2006). In Morocco, since its detection in the Khémis Zemamra region, this pest has caused severe damage in several cactus-growing areas, where extensive cultivated surfaces have been completely destroyed, leading to substantial socio-economic and environmental losses.

At the global scale, research on *Dactylopius opuntiae* remains limited and is still in its early stages. Large-scale chemical control is mainly restricted to the use of organophosphate insecticides (Badii and Flores, 2001), which have adverse effects on human health (Galloway and Handy, 2003) as well as on the environment (Arias-Estévez et al., 2008). Consequently, alternative strategies such as the use of mineral oils, natural enemies, plant extracts, and mycoinsecticides have been implemented to reduce reliance on these insecticides and to limit the presence of their residues on cactus crops and fruits (Palacios-Mendoza et al., 2004; Viguera et al., 2009; Borges et al., 2013).

Moreover, varietal resistance represents a promising alternative, as it is environmentally friendly, cost-effective, and does not require any specific technical skills from farmers. Within this context, several research programs have been conducted to evaluate cactus resistance to the cochineal. Studies carried out by Brazilian researchers (Da Silva et al., 2009; Vasconcelos et al., 2009; Borges et al., 2013) have shown that, in addition to highly susceptible clones, there exist ecotypes ranging from moderately susceptible to highly resistant, as well as others that are completely immune to *D. opuntiae* infestations. In Morocco, researchers from the National Institute for Agricultural Research (INRA), in collaboration with the International Center for Agricultural Research in the Dry Areas (ICARDA),

identified eight ecotypes considered immune to this pest through field screening under both natural and artificial infestation conditions (Sbaghi et al., 2019). Collectively, these studies demonstrate the existence of substantial variation in the susceptibility of *Opuntia* genotypes to cactus cochineal and highlight the potential of varietal resistance as an effective component of integrated pest management. In this context, the present study, conducted in partnership between the National School of Agriculture of Meknes (ENAM) and Les Domaines Agricoles, aims to evaluate the resistance of 11 cactus pear ecotypes (10, 11, 14, 18, 19, 27, 28, 29, 34, 54, and 149) belonging to the Les Domaines Agricoles collection, which is characterized by high genetic diversity and therefore provides an opportunity to identify resistant clones. We also aimed to characterize the pomological and phenological traits of these clones. We hypothesized that cactus pear clones differ significantly in their ability to support *D. opuntiae* development and that their resistance may be associated with distinct pomological and phenological characteristics.

Materials and Methods

Evaluation of resistance to the cactus cochineal

The experiment was conducted under greenhouse conditions (temperature= 25 °C; relative humidity=75%) at the El Bassatine Agricultural Domain in Meknes. The tested plant material consisted of 2-year-old cactus plants grown in plastic pots (27 cm diameter × 24 cm height) filled with a substrate composed of a 1:1 (v/v) mixture of peat and sand. The 11 tested clones and the susceptible control were arranged according to a completely randomized design (CRD) with five replications, with one cactus pear plant considered as one experimental unit.

Plants were subjected to selection pressure exerted by the cactus cochineal using heavily infested cladodes from a susceptible clone collected from the hedges surrounding the El Bassatine Domain. The infestation period lasted 45 days, with re-infestation performed every 15 days to maintain uniform pest pressure.

Two parameters were evaluated. First, the percentage of infestation by adult females was estimated at the end of the experiment (45 days after infestation) following the method proposed by Azzouzi et al., (2024). For each experimental unit (plant), three randomly selected one-year-old cladodes were evaluated. The three cladodes were considered subsamples (pseudoreplicates) of the same experimental unit rather than independent biological replicates. The infestation scores obtained from the three cladodes were averaged to obtain a single mean infestation value for each plant, which was subsequently used for statistical analysis. The mean infestation percentage was scored using a rating scale from 0 to 4 (Table 1), according to Lara (1991), to determine the presumed resistance level of each clone.

Table 1. Rating scale for varietal resistance levels proposed by Lara (1991).

Evaluation scale	Percentage infestation (%)	Level of resistance
0 : Uninfested	0-1	Resistant
1 : Lightly infested	1-25	Tolerant
2 : Moderately infested	26-50	Moderately sensitive
3 : Highly infested	51-75	Sensitive
4 : Generalized infestation	76-100	Very sensitive

Second, on the same three cladodes, the number of colonies established per cladode was recorded every five days starting from the appearance of the first colonies of second-instar larvae (10 days after infestation). This parameter was used to characterize the temporal dynamics of infestation and to compare varietal resistance among the 11 tested clones. Colony development over time was analyzed using a linear mixed-effects model for repeated measures (Sileshi, 2006).

To linearize the exponential pattern of colony development, colony abundance was transformed using the formula $\log(\text{Colonies} + 1)$. Time was treated as a continuous variable and centered at the mean observation time (27.5 days). The statistical model included centered time, genotype (clone or susceptible control), and their interaction as fixed effects. Plant identity was included as a random intercept to account for biological replication and repeated measurements performed on the same experimental unit. Because successive observations obtained from the same plant were expected to exhibit temporal correlation, a first-order autoregressive [AR (1)] correlation structure was specified for the residual errors within each plant. The model was formulated as follows:

$$Y_{ijt} = \beta_0 + \beta_1 T_{ijt}^c + \alpha_j + \gamma_j T_{ijt}^c + u_{ij} + \varepsilon_{ijt} \quad [1]$$

Where $Y_{ijt} = \log(C_{ijt} + 1)$, C_{ijt} is colony abundance for plant (i), genotype (j), and observation time (t); T^c is centred time; β_0 and β_1 represent the intercept and temporal slope of the susceptible control, respectively; α_j represents the genotype effect; γ_j represents the genotype $\times$ time interaction; u_{ij} is the plant-specific random intercept; and ε_{ijt} is the residual error.

Within each plant residual correlations were modelled as $\text{Corr}(\varepsilon_{ijt} + \varepsilon_{ijs}) = \rho^{|t-s|}$, where (t) and (s) represent two measurement time points. The terms ε_{ijt} and ε_{ijs} denote the residual errors corresponding to two observations from the same plant, and ρ is the first-order autocorrelation coefficient.

Because the objective of the study was to determine whether each tested clone differed from the susceptible control, slope contrasts were assessed using multiple comparisons with Dunnett adjustment, with the susceptible control specified as the reference group. Model adequacy was evaluated using residual diagnostics, assessment of residual autocorrelation, and information criteria (AIC and BIC). In addition, a complementary model incorporating plant-specific random temporal slopes was fitted to assess the robustness of the results.

Pomological and phenological characterization

The pomological characterization of the 11 clones was carried out by measuring several traits on mature fruits. The fruits were collected from the three-year-old cactus pear collection at Les Domaines Agricoles, established under field conditions in a row planting system. Each row of the collection included seven clones, with five plants per clone, with a spacing of 1 m between plants of the same clone and 2 m between plants of different clones, with spacing maintained in the four directions. For each of the 11 clones evaluated in this study, five plants were considered as independent biological replicates. Two mature fruits were randomly harvested from each plant, resulting in 10 fruits per clone. The two fruits collected from the same plant were considered subsamples rather than independent biological replicates, and their measurements were averaged to obtain a single value for each plant

before statistical analysis. Thus, the plant was considered the biological unit of replication for the pomological evaluation ($n = 5$ plants per clone).

The evaluated parameters included fruit length and width, total fruit weight, peel weight, seed weight, and soluble solids content. To avoid redundancy in the dataset, fruit length and width were used to calculate the fruit shape index (width/length). Values closer to 0 indicate elongated fruits, whereas values closer to 1 indicate round fruits. In addition, peel and seed weights were used to calculate the percentages of pulp and seeds, respectively, relative to the total fruit weight. To avoid artificial redundancy between directly measured traits and variables mathematically derived from them, the corresponding raw measurements were not simultaneously included with their derived variables in the Principal Component Analysis (PCA). The PCA was therefore performed using: fruit shape index, pulp percentage, seed percentage, and soluble solids content. Prior to PCA, variables were centered and standardized to unit variance (mean = 0 and standard deviation = 1) to account for differences in measurement scales. PCA was performed on the standardized data, and the first two principal components were retained for graphical interpretation.

Phenological monitoring of these clones was also conducted in the same cactus pear collection at 15-day intervals over one year, from 15 June 2023 to 15 June 2024. Observations focused on the presence or absence of vegetative buds, floral buds, flowers, and fruits at different developmental stages (fruit set, enlargement, and ripening) in three-year-old plantations, with five replicates per clone. Each plant was considered an independent biological replicate for the phenological evaluation ($n = 5$ plants per clone).

The clones were morphologically identified using botanical identification keys following Britton and Rose (1963), Fournier (1954), and Scheinvar (1995). Based on their morphological characteristics, the studied ecotypes were assigned to the respective *Opuntia* species and were considered non-hybrid. However, no molecular analysis was performed to confirm their species identity or exclude hybrid ancestry.

Statistical data analysis

To analyze the infestation percentages recorded 45 days after infestation, a one-way analysis of variance (ANOVA1) was performed, followed by Tukey's post hoc test for mean comparisons. Prior to the ANOVA, the normality of the model residuals was assessed using the Shapiro-Wilk test, and the homogeneity of variances was assessed using Levene's test. The assumptions of normality and homogeneity of variance were satisfied; therefore, no data transformation was required.

In addition, a principal component analysis (PCA) was conducted on the set of pomological variables in order to classify the clones based on fruit performance. All statistical analyses, as well as the modeling of colony number dynamics over time, were carried out using R software (version 4.5.2).

Results

Varietal resistance

The analysis of variance of infestation percentages by adult female of the cactus cochineal revealed significant differences among the studied clones. Clone 54 exhibited the lowest infestation percentage (0%), indicating the highest level of resistance, conventionally classified as resistant. In contrast, clone

149 showed the lowest resistance level and was classified as highly susceptible according to the scale described by Lara (1991). The remaining clones were considered tolerant based on the same scale, with infestation percentages ranging from $9.10 \pm 0.47\%$ to $24.52 \pm 3.61\%$ (Table 2).

Table 2. Percentage of infestation by adult female cactus cochineal 45 days after infestation and resistance level of each studied clone.

Clone	Percentage of infestation (%)	Evaluation scale	Level of resistance
10	$9.10 \pm 0.47b$	1	Tolerant
11	$9.23 \pm 0.88b$	1	Tolerant
14	$15.96 \pm 1.07c$	1	Tolerant
18	$18.66 \pm 0.68d$	1	Tolerant
19	$9.73 \pm 0.32b$	1	Tolerant
27	$18.43 \pm 2.14d$	1	Tolerant
28	$24.52 \pm 3.61f$	1	Tolerant
29	$24.51 \pm 0.76f$	1	Tolerant
34	$21.32 \pm 1.93e$	1	Tolerant
54	$0.00 \pm 0.00a$	0	Resistant
149	$87.31 \pm 12.02g$	4	Very sensitive
Sensitive control	$90.40 \pm 0.98g$	4	Very sensitive

Means followed by the same letter belong to the same homogeneous group according to the Tukey test.

The repeated-measures linear mixed-effects analysis showed that the temporal rate of colony development differed significantly among the tested genotypes ($p < 0.0001$). The susceptible control exhibited a positive temporal slope ($b=0.0496$) (95% CI: 0.0387–0.0606). Dunnett-adjusted comparisons of genotype-specific slopes with that of the susceptible control identified three clones exhibiting significantly slower colony development, namely clones 18 (Dunnett-adjusted $p = 0.0113$), 29 ($p = 0.0459$), and 54. The strongest response was observed for clone 54, which exhibited a negative temporal slope ($b= -0.0410$) (95% CI: -0.0519 to -0.0300), markedly lower than that of the susceptible control ($p < 0.0001$). In contrast, the slopes of clones 10, 11, 14, 19, 27, 28, 34, and 149 did not differ significantly from that of the susceptible control after Dunnett adjustment ($p > 0.05$). Overall, these results indicate markedly slower colony establishment and development on clones 18, 29, and particularly 54 compared with the susceptible control, supporting the resistant phenotype previously observed for clone 54 (Table 3). Model diagnostics supported an adequate fit. The AR(1) structure substantially improved model fit (AIC = 188.43 vs. 284.68; $p < 0.0001$), while the low remaining residual autocorrelations ($|ACF| \leq 0.16$) indicated that temporal dependence was adequately accounted for.

Table 3. Estimated colony growth rates (b) of *Dactylopius opuntiae* on the tested *Opuntia* clones and comparisons with the susceptible control using Dunnett's test.

Clone	b	95% CI	Dunnett-adjusted p-value
Control	0.0496	[0.0387; 0.0606]	—
10	0.0427	[0.0317; 0.0536]	0.9229
11	0.0500	[0.0391; 0.0610]	1.0000
14	0.0371	[0.0262; 0.0480]	0.5453
149	0.0530	[0.0420; 0.0639]	0.9954
18	0.0239	[0.0129; 0.0348]	0.0113
19	0.0338	[0.0228; 0.0447]	0.2876
27	0.0600	[0.0491; 0.0710]	0.7217
28	0.0533	[0.0424; 0.0643]	0.9930
29	0.0275	[0.0166; 0.0385]	0.0459
34	0.0309	[0.0200; 0.0419]	0.1377
54	-0.0410	[-0.0519; -0.0300]	<0.0001

Larvae of the cactus cochineal infested all the studied ecotypes. Larval settlement on cladodes occurred in an ascending pattern, starting with primary cladodes, followed by secondary cladodes, and eventually reaching the most distal cladodes. Insects preferentially settled on the most shaded areas of the cladodes, initially colonizing the junctions between cladodes and the regions surrounding the areoles. The appearance of female colonies was observed from the 20th day after infestation on the cladodes of all studied ecotypes, except for ecotype 54, in which the insect failed to progress beyond the second larval instar. This response is consistent with an antibiosis-type resistance mechanism (Akroud *et al.*, 2021), which occurs when the plant exerts detrimental effects on insect biology, resulting in larval mortality, mortality during developmental transitions, reduced longevity, or impaired reproduction.

Pomological and phenological characterization

The first two principal components accounted for 78.34% of the total variation in pomological traits, with PC1 explaining 53.03% and PC2 explaining 25.31% (Figures 1). PC1 was mainly characterized by pulp percentage, seed percentage, and soluble solids content (Table 4). These variables contributed 35.35%, 29.34%, and 27.01% to PC1, respectively. In contrast, PC2 was predominantly associated with fruit shape index for 76.21% of the contribution to this axis (Table 4). The 11 evaluated clones were classified into three groups based on their pomological characteristics. Clone 54, which exhibited the highest level of resistance, was characterized by a very high peel proportion associated with low fruit weight, a low seed percentage, low soluble sugar content, and a round fruit shape, reflecting an overall poor pomological performance. In contrast, clones 14, 18, 19, 27, 28, 29, 34, and 149 were characterized by heavier and sweeter fruits, with a higher seed percentage, a lower peel proportion, and an elongated shape, indicating better internal fruit quality and valorization. Clones 10 and 11 occupied an intermediate position, exhibiting average pomological profiles (Figures 2).

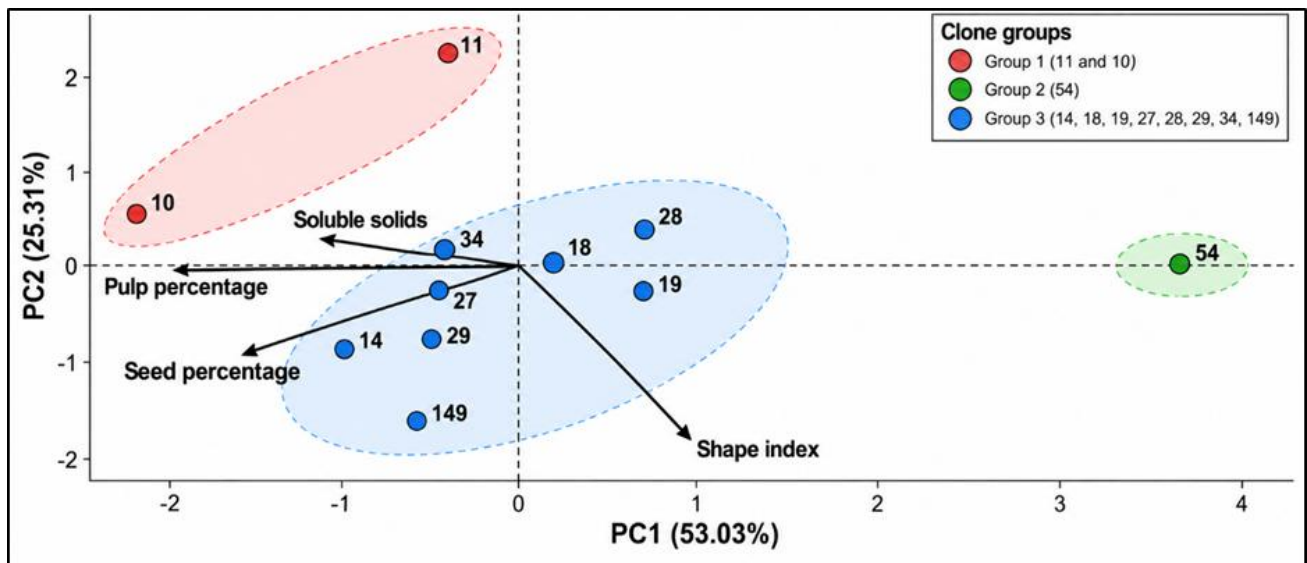


Figure 1. Distribution of variables and clones along the first two principal component axes (PC1 and PC2).

Table 4. PCA loadings and relative contributions of pomological variables to the first two principal components (PC1 and PC2).

Variable	Loading PC1	Contribution PC1	Loading PC2	Contribution PC2
Shape index	0.288	8.30 %	-0.873	76.21 %
Pulp percentage	-0.595	35.35 %	-0.032	0.10 %
Seed percentage	-0.542	29.34 %	-0.483	23.37 %
Soluble solids	-0.520	27.01 %	0.056	0.32 %
Total		100 %		100 %

Phenological monitoring allowed the classification of the 11 clones into two groups. The first group consisted of clones 14, 18, 19, 27, 28, 29, 34, 54, and 149, characterized by the appearance of vegetative buds from mid-March to mid-June. Floral buds emerged from mid-March to mid-May, flowering occurred during the second half of June, and fruit development began with the fruit set stage from early June to mid-July. Fruit enlargement took place during the second half of July, version occurred during the first half of August, and fruit maturity extended from mid-August to early September (Figure 3a). The second group consisted of clones 10 and 11, classified as late-maturing, as fruit maturity began in mid-September and could extend until early October. In these clones, bud break did not begin until mid-April (Figure 3b).

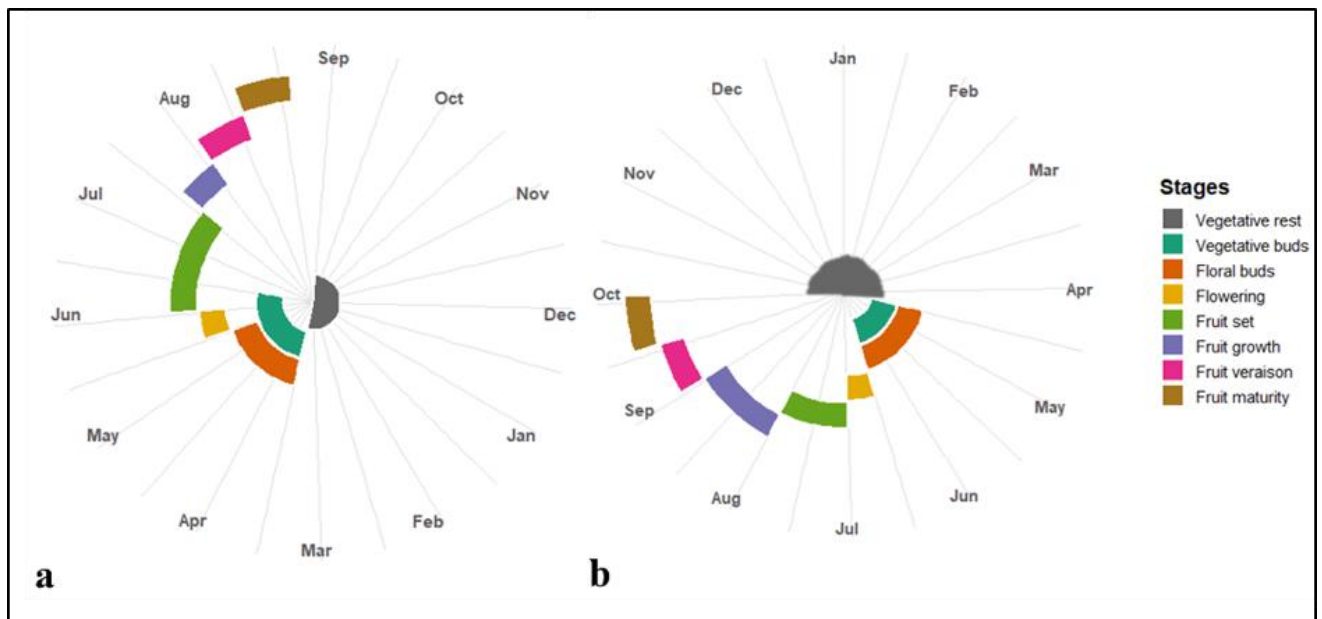


Figure 2. **a.** Phenological calendar of clones 14, 18, 19, 27, 28, 29, 34, 54, and 149. **b.** Phenological calendar of clones 10 and 11.

Morphological identification of the 11 clones revealed that clones 10, 14, 18, 19, 28, 29, 34, and 149 belonged to the species *Opuntia ficus-indica* (Figure 3), clones 11 and 27 belonged to *O. megacantha* (Figure 4), and clone 54 belonged to *O. hyptiacantha* (Figure 5).



Figure 3. General morphology of *Opuntia ficus-indica*.



Figure 4. General morphology of *Opuntia megacantha*.



Figure 5. General morphology of *Opuntia hyptiacantha*

Discussion

The evaluation of varietal resistance in 11 *Opuntia* spp. clones showed that nine clones were classified as tolerant, with infestation levels not exceeding 25% after 45 days of infestation. Analysis of cactus cochineal colonization dynamics further revealed contrasting responses among these tolerant clones. Clones 18 and 29 exhibited intermediate to slow colony development, whereas clones 10, 11, 14, 19, 27, 28, and 34 supported relatively rapid colony growth, with multiplication rates approaching those observed in clone 149, classified as highly susceptible, and in the susceptible control. These findings suggest that the apparent tolerance of these clones, as determined from infestation levels recorded at 45 days, should be interpreted with caution, because relatively rapid colony development may indicate limited stability of their response under prolonged or repeated infestation. This finding also highlights the importance of distinguishing tolerance from resistance when evaluating responses to *D. opuntiae*, as a low final infestation level does not necessarily imply strong inhibition of pest establishment or development. More broadly, these results emphasize the limitations of classification based on infestation level at a single evaluation time. Longer-term assessments, preferably under different environmental conditions, are therefore needed to determine the stability and durability of these responses.

Clone 54 exhibited the strongest resistance response, characterized by a decreasing trend in colony abundance over time. Individuals that established on the cladode surface of this clone remained arrested at the second larval stage, and no adult female colonies were observed throughout the infestation period. This developmental arrest may be consistent with an antibiosis-type resistance mechanism, whereby plant characteristics adversely affect pest survival or development. However, the present experiment was not designed to identify the underlying resistance mechanism. Further anatomical, biochemical, and behavioral investigations are therefore required to determine whether the response of clone 54 results from antibiosis, antixenosis, or a combination of resistance mechanisms.

Importantly, clone 54 also revealed a marked agronomic trade-off: the strongest resistance to *D. opuntiae* was associated with comparatively poor pomological performance, whereas the other tested clones generally exhibited more favorable fruit characteristics. This contrast is particularly relevant for breeding because pest resistance and fruit quality represent distinct selection objectives that are not necessarily combined within the same genotype. Thus, selection based exclusively on resistance could result in the retention of plant material with limited value for direct fruit production, highlighting the need to consider both resistance and agronomic performance when identifying candidate genotypes.

In this context, clone 54 represents a potentially valuable source of resistance germplasm against *D. opuntiae*. Although it was classified as resistant according to the scale described by Lara (1991), its relatively poor pomological performance may limit its direct value as a fruit-producing cultivar. In contrast, the other ten clones showed medium to high pomological potential. Nevertheless, the strong resistance expressed by clone 54 makes it particularly relevant for breeding programs aimed at combining resistance to *D. opuntiae* with desirable fruit and agronomic characteristics. If the resistance is demonstrated to be heritable and transferable, it could potentially be incorporated into genotypes with superior fruit quality and agronomic performance. Future studies should therefore investigate the

genetic basis, heritability, and stability of resistance in clone 54 and evaluate appropriate breeding strategies for combining this resistance with favorable pomological traits.

Phenological monitoring provided an additional agronomic criterion for differentiating the tested material. Clones 14, 18, 19, 27, 28, 29, 34, 54, and 149 exhibited a fruit-ripening period extending from late July to mid-August, whereas clones 10 and 11 were late-ripening, with fruit maturation beginning in mid-September. These differences in ripening period, together with resistance and pomological performance, further emphasize the need for a multi-trait approach when evaluating the agronomic value of candidate clones.

In interpreting these results, it is important to clarify the terminology used to describe the response of the tested clones. In the present study, the term “tolerant” is used according to the classification proposed by Lara (1991), in which clones are categorized on the basis of their observed infestation level. However, this terminology differs from the broader concept of tolerance commonly used in plant–insect interactions. In this context, tolerance generally refers to the ability of a plant to withstand or compensate for herbivore injury while maintaining growth, reproduction, fitness, or productivity, whereas resistance refers to plant traits that reduce herbivore establishment, survival, development, reproduction, or the resulting injury (Strauss and Agrawal, 1999; Stout, 2013; Peterson et al., 2017). Therefore, the clones classified as “tolerant” in the present study should be understood as belonging to the tolerance category defined by the Lara (1991) scale rather than as demonstrating physiological tolerance to herbivory. This distinction is particularly relevant because some clones classified as tolerant according to their infestation level nevertheless supported relatively rapid colony development, indicating that a low infestation level at a single assessment time does not necessarily imply strong inhibition of pest development.

Other studies conducted worldwide have also made it possible to identify sources of resistance to the cactus cochineal. In Brazil, research on resistant cactus pear clones began in 2002 under the initiative of the Instituto Agrônomo de Pernambuco (IPA). Several studies were carried out under field, greenhouse, and laboratory conditions. The clones F-13, F-15, F-16, ‘Miúda’, and ‘Orelha de Elefante Mexicana’ showed a high level of resistance, with no establishment of the pest being observed (Santos et al., 2006; Silva et al., 2009; Vasconcelos et al., 2009). Within the same framework, Borges et al. (2013) studied, under laboratory conditions over a 45-day period, the resistance of 11 cactus pear clones. The authors observed that the cultivars ‘IPA-Sertânia’, ‘Orelha de Elefante Mexicana’, ‘Miúda’, ‘Orelha de Onça’, and ‘Orelha de Elefante Africana’ showed no establishment of the cochineal, indicating a high level of resistance. More recently, Batista et al. (2022) evaluated the agronomic performance and resistance to *D. opuntiae* of 121 clones under semi-arid conditions. The results showed that clones 10, 110, 115, and 119 were characterized by strong developmental potential, associated with high productivity, resistance to the cochineal, and marked genetic divergence expressed through specific agronomic traits. Similarly, Almeida et al. (2022) assessed the resistance of 121 *Opuntia* spp. clones, among which 39 clones were classified as highly resistant to *D. opuntiae*.

In the same context, cultivars belonging to *O. ficus-indica*, *O. stricta*, and *O. robusta* were assessed, revealing significant differences in resistance among the three species. Clones of *O. robusta* and *O. stricta* proved to be resistant, whereas all tested lines of *O. ficus-indica* were fully susceptible (Teklu et al., 2024). In Jordan, an evaluation of the resistance of cactus pear clones originating from several

countries (Morocco, South Africa, Syria, Italy, Jordan, Mexico, Algeria, Argentina, Brazil, and Tunisia) was conducted. The results demonstrated a high level of resistance in four clones against attacks by *D. opuntiae* (Qasqas et al., 2024).

In Morocco, researchers from the National Institute for Agricultural Research evaluated the resistance of 248 ecotypes belonging to different *Opuntia* spp. species through studies conducted under laboratory, greenhouse, and open-field conditions. The results showed that only the ecotypes Aakria, Marjana, Belara, Karama, Ghalia, Angad, Cherratia, and Melk Zhar were resistant to attacks by *D. opuntiae*. These eight resistant ecotypes were registered in the national cactus catalog (Sbaghi et al., 2019). Morphological and phenological characterization of these clones revealed that the Aakria ecotype is distinguished by small-sized, bright red fruits and very reduced cladodes. The Belara ecotype exhibits large cladodes and large, yellow-green, very sweet fruits, whereas Marjana is characterized by very thick cladodes and large, highly sweet fruits. The Melk Zhar, Angad, and Cherratia ecotypes are characterized by wide, spiny cladodes bearing the longest spines, as well as by large-sized fruits. The Karama and Ghalia clones are distinguished by large cladodes and medium-sized fruits. Phenological monitoring of these cultivars showed that the periods of vegetative and floral budding, flowering, and fruit development are longer in Aakria and shorter in Marjana (El Aalaoui and Sbaghi, 2023). Moreover, among 322 clones evaluated by Akroud et al. (2021), ten showed significant resistance to *D. opuntiae* 60 days after infestation. Studies on the resistance mechanisms of these ten clones revealed the involvement of two categories of resistance: antibiosis and antixenosis.

Conclusions

Through this study, a highly resistant clone (clone 54) to the cactus cochineal was identified, which did not allow the establishment of adult female colonies, as well as nine cultivars considered tolerant, exhibiting infestation rates below 25% forty-five days after infestation. Fruit characterization of these clones revealed that clone 54, which showed the highest level of resistance, displayed low pomological performance, whereas the ten other tested clones were characterized by medium to high pomological profiles. These ecotypes should be subjected to further in-depth studies in order to assess the stability of their resistance to *D. opuntiae* attacks under different soil and climatic conditions and over an extended period of time.

ETHICS STATEMENT

Not applicable

CONSENT FOR PUBLICATION

Not applicable

COMPETING INTEREST

Not applicable

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AUTHOR CONTRIBUTION

Conceptualization, A.A. and A.H.; methodology, A.A.; software, A.A.; validation, B.J.A, L.R., A.M and T.B.; formal analysis, A.A.; investigation, A.A.; resources, A.H. and A.M; data curation, A.A.; writing—original draft preparation, A.A.; writing—review and editing, B.T.; visualization, T.B.; supervision, T.B.; project administration, B.T. and A.M; funding acquisition, A.H.

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References

- Akroud, H., Sbaghi, M., Bouharroud, R., Koussa, T., Boujghagh, M. and El Bouhssini, M. 2021. Antibiosis and antixenosis resistance to *Dactylopius opuntiae* (Hemiptera: Dactylopiidae) in Moroccan cactus germplasm. *Phytoparasitica*. 49:623-631. <https://doi.org/10.1007/s12600-021-00897-w>
- Almeida, I.V.B., Primo, L.G.S. and Pereira, E.J.G. 2022. Selection of *Opuntia* spp. accessions with resistance to false carmine cochineal (*Dactylopius opuntiae*). In: X International Congress on Cactus Pear and Cochineal: Cactus – The New Green Revolution in Drylands. Vol. 1343, pp. 7-14.
- Arias-Estévez, M., López-Periago, E., Martínez-Carballo, E., Simal-Gándara, J., Mejuto, J. C., and García-Río, L. 2008. The mobility and degradation of pesticides in soils and the pollution of groundwater resources. *Agriculture, Ecosystems & Environment* 123: 247-260.
- Azzouzi, A., Anejjar, H., Id-M'hamed, A., Ait Chitt, M., Boutaleb Joutei, A., Lahlali, R. and Benziane, T. 2024. Assessment of mineral oils, black soap, and essential oils for controlling *Dactylopius opuntiae* (Cockerell, 1929) (Hemiptera: Dactylopiidae). *International Journal of Tropical Insect Science*. 44:2803-2813. <https://doi.org/10.1007/s42690-024-01369-4>
- Badii, M.H. and Flores, A.E. 2001. Prickly pear cacti pests and their control in Mexico. *Florida Entomologist*. 84:503–505. <https://doi.org/10.2307/3496379>
- Batista, M.C., do Nascimento, R., de Almeida, I.V.B., de Medeiros, L.T.V., Souza, J.T.A., de Oliveira Santos, J.P. and Araújo, J.R.E.S. 2022. Production and selection of accessions of *Opuntia* spp. with resistance to false carmine cochineal. *Comunicata Scientiae*. 13:e3869. <https://doi.org/10.14295/cs.v13.3869>
- Borges, L.R., Santos, D.C., Cavalcanti, V.A.L.B., Gomes, E.W.F., Falcão, H.M. and da Silva, D.M.P. 2013. Selection of cactus pear clones regarding resistance to carmine cochineal *Dactylopius opuntiae* (Dactylopiidae). *Acta Horticulturae*. 995:359-366.
- Boujghagh, M., and Chajia, L. 2001. Le cactus: outil de gestion de la sécheresse dans le Sud marocain. *Terre et Vie*. 52:1-7.
- Britton, N.L. and Rose, J.N. 1963. *The Cactaceae: descriptions and illustrations of the plants of the cactus family*. Vols. I–II. Dover Publications.
- El Aalaoui, M. and Sbaghi, M. 2023. Morphological and phenological characterization of Moroccan *Opuntia* cactus varieties (Karama, Ghalia, Belara, Marjana, Cherratia, Angad, and Melk Zhar) resistant to the cactus cochineal *Dactylopius opuntiae* (Cockerell). *Journal of the Professional Association for Cactus Development*. 25. 115-135. <https://doi.org/10.56890/jpacd.v25i.519>

- Fournier, P. 1954. *Les cactées et les plantes grasses*. Encyclopédie Pratique Naturelle XXXVIII. Lechevalier.
- Gommes, R., El Hairech, T., Rosillon, D. and Balaghi, R. 2009. Impact of climate change on agricultural yields in Morocco. World Bank – Morocco Study on the Impact of Climate Change on the Agricultural Sector. Food and Agriculture Organization of the United Nations.
- Lara, F.M. 1991. *Princípios de resistência de plantas a insetos*. Ícone.
- Lopes, E.B., Brito, C.H., Albuquerque, I.C. and Batista, J.L. 2009. Desempenho do óleo de laranja no controle da cochonilha-do-carmim em palma gigante. *Engenharia Ambiental*. 6:252–258.
- Louali, A. 2019. *Le secteur agricole marocain: tendances structurelles, enjeux et perspectives de développement*. Ministry of Economy and Finance, Financial Studies and Forecasting Directorate.
- Mabrouk, A., Abbas, Y., Fakiri, M., Benchekroun, M., El Kharrassi, Y., El Antry-Tazi, S. and El Mzouri, E. 2016. Caractérisation phénologique de différents écotypes de cactus (*Opuntia* spp.) marocains sous les conditions édapho-climatiques de la région de Chaouia-Ouardigha. *Journal of Materials and Environmental Science*. 7:1396-1405.
- Mann, J. 1969. *Cactus-feeding insects and mites*. U.S. National Museum Bulletin No. 256.
- Palacios-Mendoza, C., Nieto-Hernández, R., Llanderal-Cázares, C. and González-Hernández, H. 2004. Efectividad biológica de productos biodegradables para el control de la cochinilla silvestre *Dactylopius opuntiae* (Cockerell) (Homoptera: Dactylopiidae). *Acta Zoológica Mexicana*. 20:99-106.
- Peterson, R.K.D., Varella, A.C. and Higley, L.G. 2017. Tolerance: the forgotten child of plant resistance. *PeerJ*. 5:e3934. <https://doi.org/10.7717/peerj.3934>
- Portillo, L. and Viguera, A.V. 2006. A review of the cochineal species in México, hosts and natural enemies. *Acta Horticulturae*. 728:249-256. <https://doi.org/10.17660/ActaHortic.2006.728.35>
- Qasqas, R., Katbeh-Bader, A., Frasheri, D., Al-Jboory, I. and Hassan, S. 2024. Screening cactus varieties resistant to cochineal scale, *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactylopiidae) in Jordan. *Jordan Journal of Natural History*.11: 43-50.
- Santos, D.C., Lira, M., Farias, I., Dias, F.M., Costa, A.F., Pereira, V.L.A., and Silva, D.M.P. 2006. Seleção de clones de palma forrageira resistentes à cochonilha do carmin *Dactylopius* sp. em condições de campo. In: Reunião Anual da Sociedade Brasileira de Zootecnia, João Pessoa, Paraíba, Brasil. <https://doi.org/10.1590/S1516-35982009000500007>
- Sbaghi, M., Bouharroud, R., Boujghagh, M., and El Bouhssini, M. 2019. Sources de résistance d'*Opuntia* spp. contre la cochenille à carmin, *Dactylopius opuntiae*, au Maroc. *EPPO Bulletin* 49: 585–592. <https://doi.org/10.1111/epp.12606>
- Scheinvar, L. 1995. Taxonomy of utilized *Opuntias*. In: Agroecology, cultivation and uses of cactus pear. FAO Plant Production and Protection Paper No. 132, pp. 20-27. Food and Agriculture Organization of the United Nations.
- Schielif, S., Jacob, H., and Hoffmann, W. 2000. Importance of *Opuntia ficus-indica* (L.) Mill. for arid and semi-arid regions of Morocco. In: Forage, rangeland improvement and desertification:

Proceedings of the IVth International Congress on Cactus Pear and Cochineal and the IVth General Meeting of FAO-CACTUSNET, p. 82.

- Sileshi, G. 2006. Selecting the right statistical model for analysis of insect count data using information theoretic measures. *Bulletin of Entomological Research*. 96:479-488. <https://doi.org/10.1079/BER2006449>
- Silva, D.M.P., Houllou-Kido, L.M., Santos, D.C., Ferreira, W.M., Lima, M.S., Falcão, H.M., Tabosa, F.S., Ferreira, R.G. and Arruda, G.P. 2009. Resistance of *in vitro* grown forage cactus clones to *Dactylopius opuntiae* (Hemiptera: Dactylopiidae). *Acta Horticulturae*. 811:299-302. <https://doi.org/10.17660/ActaHortic.2009.811.40>
- Strauss, S.Y. and Agrawal, A.A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution*. 14(5):179-185. [https://doi.org/10.1016/S0169-5347\(98\)01576-6](https://doi.org/10.1016/S0169-5347(98)01576-6)
- Stout, M.J. 2013. Reevaluating the conceptual framework for applied research on host-plant resistance. *Insect Science*. 20(3):263-272. <https://doi.org/10.1111/1744-7917.12011>
- Teklu, G.W., Ayimut, K.M., Abera, F.A., Gerima, Y.G.E.W., and Fitiwi, I. 2024. Evaluation of *Opuntia* species for their resistance to carmine cochineal (*Dactylopius coccus*) insect in Tigray, northern Ethiopia. *Haseltonia*. 31: 80-88. <https://doi.org/10.2985/026.031.0109>
- Vanegas-Rico, J.M., Lomeli-Flores, J.R., Rodríguez-Leyva, E., Mora-Aguilera, G. and Valdez, J.M. 2010. Natural enemies of *Dactylopius opuntiae* (Cockerell) on *Opuntia ficus-indica* (L.) Mill. in Central Mexico. *Acta Zoológica Mexicana*. 26:415-433.
- Vasconcelos, A.G.V., Lira, M.A., Cavalcanti, V.A.L.B., Santos, M.V.F. and Willadino, L. 2009. Seleção de clones de palma forrageira resistentes à cochonilha-do-carmim (*Dactylopius* sp.). *Revista Brasileira de Zootecnia*. 38:827-831. <https://doi.org/10.1590/S1516-35982009000500007>
- Vigueras, A.L., Cibrián-Tovar, J. and Pelayo-Ortiz, C. 2009. Use of botanical extracts to control wild cochineal (*Dactylopius opuntiae* Cockerell) on cactus pear. *Acta Horticulturae*. 811:229-234. <https://doi.org/10.17660/ActaHortic.2009.811.28>