

ORIGINAL ARTICLE OPEN ACCESS

Drought Stress Promotes *Aphis gossypii* Growth but Decreases Host Attractiveness in Melon

G. Clemente-Orta^{1,2} | M. Guirao¹ | P. Madolell¹ | A. Moreno¹ | A. Fereres¹

¹Consejo Superior de Investigaciones Científicas (ICA-CSIC), Instituto de Ciencias Agrarias, Madrid, España | ²Departament de Producció Vegetal i Ciència Forestal, AGROTECNIO Center, Universitat de Lleida, Lleida, España

Correspondence: G. Clemente-Orta (gemma.clemente@udl.cat) | A. Fereres (a.fereres@csic.es)

Received: 29 September 2025 | **Revised:** 28 January 2026 | **Accepted:** 11 February 2026

Keywords: aphid behaviour | *Aphis gossypii* | climate change | *Cucumis melo* | drought stress | integrated pest management (IPM)

ABSTRACT

Drought stress is a significant environmental factor that affects plant physiology and growth, leading to considerable detrimental effects on crop productivity. *Cucumis melo*, which is widely cultivated for its economic value, is particularly susceptible to water scarcity. *Aphis gossypii* is the major pest impacting melon crops due to both the direct damage it causes and its ability to transmit several plant viruses. We investigated whether water-deficit (WD) and well-watered (WW) regimes affect aphid fitness, host preference, alighting behaviour and responses to plant volatiles. In antibiosis assays, the pre-reproductive period (PRP) was longer in aphids reared on WW regime (7.47 ± 0.13 days) than on WD (6.53 ± 0.19 days; $p < 0.001$). Similarly, mean generation time (Td) was longer under WW regime (10.12 ± 0.18 days) than under WD (8.85 ± 0.26 days, $p < 0.001$). In contrast, aphids exhibited higher intrinsic rates on WD regime ($r_m = 0.463 \pm 0.013$) than on WW (0.409 ± 0.008 ; $p < 0.001$). Mean relative growth rate (RGR) showed the same pattern, being higher under WD regime (0.539 ± 0.015) compared with WW (0.475 ± 0.009 , $p < 0.001$). In dual choice, higher numbers of alate aphids and nymphs were recorded on WW regime. In free-choice settlement assays, adult aphid preference differed between watering regimes and across time, with greater alate settlement and nymph production—particularly after 48 h—on WW regime. Olfactometry assays showed no aphid response to plant water status. Overall, our results indicate that aphid alighting on melon plants is driven primarily by visual rather than olfactory cues, with WW regime being more attractive than WD. However, once aphids settle on WD regime, population growth is enhanced relative to WW. Thus, when both plant types co-occur, aphids preferentially colonise WW regime, although higher population growth may occur on water-stressed hosts.

1 | Introduction

Drought stress is one of the most important abiotic constraints affecting crop production worldwide and is expected to intensify under ongoing climate change. Beyond its direct effects on plant growth and yield, water limitation can strongly modify plant-herbivore interactions by altering plant physiology, resource allocation and host quality for insect pests (Marček et al. 2019; Ramírez et al. 2023; Sadras et al. 2025).

Aphids (Hemiptera: Aphididae) are among the most economically important insect pests in agricultural systems due to their rapid population growth, phloem-feeding behaviour and ability to transmit numerous plant viruses (Blackman and Eastop 1994; van Emden and Harrington 2017). Aphid population dynamics are particularly sensitive to changes in host plant quality, as even subtle shifts in phloem composition, turgor pressure, or defence expression can influence aphid development, fecundity, survival and dispersal behaviour (Dixon 1998; Hales et al. 2013).

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *Journal of Applied Entomology* published by Wiley-VCH GmbH.

Drought stress can affect aphid performance through several mechanisms. Water limitation may reduce plant vigour and turgor pressure, increase phloem viscosity and constrain aphid feeding efficiency, thereby negatively affecting aphid growth and reproduction (Ferreles et al. 1988; Liu et al. 2018; Xie et al. 2022). In contrast, moderate drought may increase the concentration of soluble sugars and amino acids in phloem sap or weaken plant defences, potentially enhancing aphid performance (White 1984; Tariq et al. 2012; Cui et al. 2021; Rahman et al. 2024). These contrasting outcomes are commonly framed within the plant vigour hypothesis (Price 1991), the plant stress hypothesis (White 1984) and the pulsed stress hypothesis (Huberty and Denno 2004). These hypotheses predict different herbivore responses depending on the intensity, timing and duration of water stress (Kennedy et al. 1958; Mattson and Haack 1987; Mody et al. 2009). For example, population growth of *Aphis fabae* and *Sitobion avenae* has been shown to increase under moderate drought conditions due to improved nutritional quality or reduced plant defences (Mezgebe and Azerefege 2021; Saska et al. 2024). In contrast, prolonged or severe drought can reduce in cereal aphids such as *Sitobion avenae* and *Rhopalosiphum padi* by decreasing host suitability and plant vigour (Liu et al. 2018; Xie et al. 2022; Leybourne et al. 2022), while neutral responses have also been reported for *Sitobion avenae* feeding on wheat (Ferreles et al. 1988).

Two recent meta-analyses confirm that drought effects on aphids are highly context-dependent and shaped by plant genotype, aphid biotype, environmental conditions and stress intensity (Leybourne et al. 2021; Sadras et al. 2025). Moreover, drought may interact with other factors influencing aphid population dynamics, including aphid-associated microbiota (Díaz-Hernández et al. 2025), temperature (Beetge and Krüger 2019; Sadras et al. 2021), atmospheric CO₂ (Xie et al. 2022) and virus transmission efficiency (Sadras et al. 2024). In addition to post-settlement performance, drought may influence aphid host selection and colonisation behaviour. Changes in plant morphology, colour and volatile emissions under water stress can alter aphid alighting and settling decisions, potentially decoupling host preference from host suitability (Leybourne et al. 2021; Luo and Gilbert 2022). However, the relative importance of visual versus olfactory cues in aphid responses to drought-stressed plants remains poorly understood.

Aphis gossypii, the melon aphid, is a highly polyphagous species and is a major pest in cucurbit crops worldwide, not only because of its feeding damage but more importantly because it transmits several plant viruses such as cucumber mosaic virus (CMV) and cucurbit aphid-borne yellows virus (CABYV) (Moya-Ruiz et al. 2023). In this study, we investigated the effects of two water regimes—well-watered (WW) and water-deficit (WD)—on the performance, alighting behaviour, host preference and olfactory responses of *A. gossypii* on melon plants. Using a combination of life-table (antibiosis), alighting and settling preference (antixenosis) and olfactometry bioassays we tested whether (1) aphid life-history traits differ according to host plant water regime, (2) alate aphids preferentially settle on WW plants and (3) aphids respond to volatile cues associated with drought. By integrating physiological and behavioural measurements, this study aims to contribute

to a better understanding of how drought conditions may influence aphid–plant interactions, with direct implications for integrated pest management (IPM) under climate change scenarios.

2 | Materials and Methods

2.1 | Water Regimes, Plant Material and Growth Conditions

The field capacity (FC) concept, defined as the amount of water the soil can retain after being fully saturated and then drained by gravity (water saturation), was used to establish the two water regimes. Field capacity depends on the soil's characteristics, such as its texture, structure and organic matter content. The pots measured 11 × 11 × 12 cm and contained a 1:2 mixture of vermiculite (No. 3, Asfaltex S.A., Barcelona, Spain) and soil substrate (GoV4, Jiffy International, A.S., Norway).

We established two different water regime conditions in the pots used for the experiments: the well-watered (WW) regime, where pots were adjusted to 70%–80% of FC, and the water-deficit (WD) regime, where pots were maintained at 10%–20% of FC. The soil water content of WW and WD regimes was constantly maintained by weighing the pots daily. Water was added to each pot when necessary, using a 100 mL graduated cylinder to maintain each water regime. Water regimes were applied to all pots soon after transplanting the plants.

Melon plants (*Cucumis melo* cv. Bazán) were grown in each pot, and the phenological BBCH scale was used to score plant development weekly throughout the study (Lancashire et al. 1991). Seeds were transplanted into pots before establishing both water regime conditions. A minimum of 10 mL of water was added to each pot in both treatments to ensure seedling survival. Thereafter, plants were subjected to the two established water regimes for 2 weeks prior to the start of the experiments. All plants were kept in a plant growth chamber at 24:20°C light:dark (L:D) temperature, 60%:80% (L:D) relative humidity (RH) and a 16:8 h (L:D) photoperiod. In addition, plants were sprayed to run-off once a week with a foliar fertiliser at a dose of 1 g/L (Miller Chemical and Fertiliser Corp., Pennsylvania, USA). The water content of WW and WD treatments was maintained consistently; pots were weighed daily and watered using a 100 mL graduated cylinder. Finally, 2 weeks after transplanting (growth stage 14–15), the smallest plants were discarded and only uniform plants were used for the experiments.

2.2 | Aphid Colonies and Production of Alate Morphs

We used *A. gossypii* adults from a colony originally derived from a single virginoparous female from a population collected in Almería (Spain) in 1998 to initiate a synchronised colony, aphids of the same age. For the fitness assay, a new aphid colony was established and synchronised on melon plants to produce wingless adults of uniform age. For the alighting, settlement and olfactometry assays, we produced alate morphs by confining wingless aphids on melon plants for three complete generations

(approximately 21 days). Newly emerged alate aphids resting on the top of the cage were used for these experiments. We assumed that alate aphids located at the top of the cage were in their migratory flight phase, just prior to initiating their flight behaviour (Moericke 1955). All aphid colonies were maintained in a climate-controlled growth chamber under the following conditions: temperature 25:21°C (day: night), photoperiod 16:8 h (L:D) and 75%–80% RH.

2.3 | Life-History Traits of Wingless Aphids

To investigate the effect of plant water regime on the reproduction of *A. gossypii*, three wingless adult aphids (8–10 days old) from the synchronised colony described above were confined inside a clip cage (3 cm in diameter) on plants subjected to the two water regimes (WW and WD). The clip cages were placed on the adaxial side of the youngest fully expanded leaf of each plant. After 24 h, the adults and any newly born nymphs were removed using a damp paintbrush, leaving three nymphs per plant. These nymphs were monitored daily until they reached adults. When the first nymph reached the adult stage, the remaining ones were removed, leaving this single adult per clip cage. The progeny of each adult was then recorded daily by counting and removing newly born nymphs during a period equivalent to the pre-reproductive period (i.e., the number of days from birth to the onset of reproduction). To evaluate aphid performance under the two water regimes, a series of life-history traits, including the intrinsic rate of natural increase, were calculated. The following formulas derived from Wyatt and White (1977) were used:

Intrinsic Rate of Natural Increase (r_m): This measures the rate at which a population increases under ideal conditions.

$$r_m = \frac{0.738 \cdot \ln(Md)}{d}$$

where 0.738 is a correction factor; Md is the effective fecundity, the number of offspring produced during a period equal to the pre-reproductive period; d is the duration of the pre-reproductive period in days.

Mean generation time (T_d): The average time between the birth of parents and the birth of their offspring.

$$T_d = \frac{d}{0.738}$$

Mean relative growth rate (RGR): This indicates the growth rate of the aphid population relative to its size (Leather and Dixon 1984).

$$RGR = \frac{r_m}{0.86}$$

Finally, the adult weight of each individual aphid was weighed using a high precision scale once they reached the reproductive stage using 15 aphids by treatment, resulting in a total of 30 aphids. The number of replicates for this experiment consisted of 15 plants per water regime treatment, resulting in a total of 30 plants.

2.4 | Alighting and Settling Behaviour Assays of Alate Aphids

Two different semi-field experimental setups were carried out in greenhouse facilities at ica-csic during may and june 2023 to assess the alighting and settlement preferences of *A. gossypii* alates for melon plants grown under ww and wd regimes. Alate aphids present on each test plant were counted at different time intervals. Temperature, rh and shading were remotely controlled in the greenhouse via a central computer to maintain the following environmental conditions: temperature 25:20°C (day:night), photoperiod 16:8 h (l:d) and 75%–80% rh. In both assays, newly emerged alates (24–72 h after emergence) were collected from the top of the rearing cage with an aspirator on the same day and time when the experiments began.

A dual-choice alighting behaviour assay was performed using two melon plants (one under ww and the other one under wd regime) placed 20 cm apart, opposite to each other, inside an aphid-proof cage (93×47.5×47.5 cm). The cage structure was made of plastic with transparent mesh sides. Lighting within the greenhouse was uniform across the cage area, and the positions of the plants and cages were rotated between replicates to minimise positional bias. The assay was designed to measure the propensity of aphids to migrate from one plant to another. *A. gossypii* alates were collected with an aspirator from the rearing cages, placed in 50 mL plastic tubes 30 min and chilled for 5 min to temporarily reduce their activity prior to the start of the experiments. Then 30 alates were then released onto the oldest fully expanded leaf of each melon test plant, which had been maintained under either water regime using a brush. For each replicate (cage), the number of alates remaining on the plant onto which they had been introduced, and the number that had moved and successfully settled on the opposite plant in the cage were recorded visually. The number of alates and newborn nymphs settled on plants subjected to either ww or wd regimes was counted at the following time intervals: 0.5, 1, 3, 6, 24 and 48 h. Each dual-choice assay was replicated 15 times per treatment. A total of 450 aphids were used. The settling rate for each treatment and time point was calculated as the mean percentage of aphids settled on the receptor plant, defined as the plant where aphids alighted after migrating from the one on which they were initially released.

A free-choice settlement behaviour assay was conducted using *A. gossypii* alates, following a methodology similar to that described by Carmo-Sousa et al. (2014, 2016). A total of 12 receptor melon plants (six grown under ww and six under wd regimes) were alternated in a circular pattern inside a 1×1×1 m cage equipped with aphid-proof mesh. 120 newly emerged alate aphids were collected with an aspirator from the rearing cages and placed in 50 mL plastic tubes 30 min prior to the start of the experiments. The alates were then released from a flight platform located at the top of the cage, 0.5 m above the plant canopy, allowing them to alight and settle freely on the test plants. The number of alate aphids and new born nymphs settled on each test plant was recorded at 0.5, 2, 4 and 48 h after aphid release. Each mean value was calculated from the total of 12 plants per cage (six per treatment), with the same setup replicated across three different cages.

2.5 | Response of Alate Aphids to Olfactory Cues Based on Plant Water Regime

The bioassays were conducted using a two-way olfactometer consisting of a y-tube made of vidrafoc glass with an internal diameter of 18 mm, a 90 mm stem, and two 100 mm arms positioned at a 120° angle (vidrafoc, s.a., barcelona, spain). Each arm was connected to a closed volatile collection chamber (vcc) of 5 L vidrafoc glass, containing a plant (subjected to either the ww or wd regime) as the odour source. The y-tube was connected by three male glass adapters, two of which were connected to teflon tubing (tub-1/4-tfe-ex) leading to an air flow system controlled by a flow meter (olfm-2c-ads+b model 2510a2a29bnn, brooks instrument, hatfield, pa, usa). The air delivery system included a three-stage filtration unit. Airflow was maintained at 0.8 L/min through each arm of the olfactometer (this rate was previously determined to be optimal for eliciting aphid responses). Flow meters at the end of each teflon tube confirmed the air flux entering the y-tube.

Assays were performed on a laboratory under ambient conditions (24°C ± 2°C, 40% ± 10% rh) between 09:30 and 14:30 h. All behavioural trials were conducted in a room illuminated with daylight led lamps. The treatments were: (1) ww melon plant vs. Clean air, (2) wd melon plant vs. Clean air, and (3) ww vs. Wd melon plants. For each treatment, the odour sources (plant or clean air) were placed in the vcc chambers for 30 min without airflow, followed by 30 min with airflow before starting the assay. This assay was conducted using *A. gossypii* alates collected with an aspirator from the rearing cages and placed in 50 mL plastic tubes 30 min prior to the start of the experiments with the same age (1 week old). Each alate aphid was given 5 min to make a choice between the two arms. A choice was recorded when an aphid remained positioned 70 mm beyond the bifurcation point for at least 1 min. The choices were registered in two stages: first, when the aphid reached 70 mm above the y-junction; and second, when it reached the end of one of the olfactometer arms. 10 aphids were tested for each replicate by treatment. A total of 17 repetitions were performance using 170 aphids to ensure a minimum of aphid choice. Aphids that did not make a choice within the allocated time were recorded as non-choices and excluded from the dual-choice statistical analysis. Each melon plant was used only once. The positions of the odour sources were swapped after every five aphids to avoid positional bias. The y-tube was replaced with a clean one after testing 10 aphids.

All glassware was cleaned thoroughly using 2% soapy water, purified water, 90% ethanol and 99% acetone, then dried in a fume hood for at least 24 h before reuse.

2.6 | Statistical Analysis

Differences in aphid fitness data between plants grown under the two water treatments were analysed using Student's *t*-test for Gaussian distributions and the Mann–Whitney *U*-test for non-Gaussian distributions ($p < 0.05$).

To detect differences between treatments over time in the dual-choice and free-choice experiments, we applied a generalised linear mixed model (GLMM) with a negative binomial distribution, using the `glmer.nb` function from 'lme4' package (Bates et al. 2015). The significance of fixed effects was assessed using Wald χ^2 tests ($p < 0.05$) using 'car' package (Fox and Weisberg 2019). The dependent variables were the number of adults and nymphs, while the fixed effects were time, treatment, and their interaction. Plant position was included as a random factor. Additionally, hourly tests as a post hoc comparisons were compared at each time point (dual-choice alighting: 0.5, 1, 3, 6, 24 and 48 h; free-choice settling: 0.5, 2, 4 and 48 h) using Student's *t*-test for Gaussian distributions and the Mann–Whitney *U*-test for non-Gaussian distributions ($p < 0.05$). Post hoc tests were performed to facilitate biological interpretation of significant interactions. This approach allowed us to assess the temporal dynamics and identify specific time intervals in which significant differences between treatments occurred.

Data from the Y-tube olfactometer assays were analysed using a χ^2 test ($p < 0.05$) to determine the influence of volatiles emitted by plants grown under both water regimes compared to clean air. All statistical analyses were performed using R software, version 4.2.2.

3 | Results

3.1 | Life-History Traits of Wingless Aphids

Antibiosis (fitness) assays revealed significant effects of plant water regime on aphid performance (Table 1). The PRP was significantly longer in aphids reared on WW (7.47 ± 0.13 days)

TABLE 1 | Life-table parameters of *Aphis gossypii* reared on melon plants under two water regimes. Data were using Student's *t*-test (T) for Gaussian distributions and the Mann–Whitney *U*-test (U) for non-Gaussian distributions ($p < 0.05$).

Variables	WW	WD	Statistic test	<i>p</i>
Pre-reproductive period (<i>d</i>)	7.47 ± 0.133a	6.53 ± 0.192b	<i>U</i> = 3.24	< 0.001
Number of nymphs (Md)	62.27 ± 2.377a	58.73 ± 2.439a	<i>T</i> = 1.037	0.239
Adult weight (<i>W</i>)	0.512 ± 0.034a	0.480 ± 0.029a	<i>T</i> = 0.718	0.239
Intrinsic rate of natural increase (<i>r_m</i>)	0.409 ± 0.008a	0.463 ± 0.013b	<i>T</i> = 3.45	< 0.001
Mean generation time (Td)	10.120 ± 0.180a	8.854 ± 0.260b	<i>U</i> = 3.24	< 0.001
Mean relative growth rate (RGR)	0.475 ± 0.009a	0.539 ± 0.015b	<i>T</i> = 3.45	< 0.001

Note: Values are mean ± SE. Different letters within each row indicate significant differences between treatments ($p < 0.05$).

than on WD regime (6.53 ± 0.19 days, $p < 0.001$). Similarly, Td was longer under WW (10.12 ± 0.18 days) than under WD regime (8.85 ± 0.26 days, $p < 0.001$). In contrast, aphids developing on WD regime exhibited higher intrinsic rates of natural increase ($r_m = 0.463 \pm 0.013$) compared with those on WW (0.409 ± 0.008 , $p < 0.001$), as well as higher RGR (0.539 ± 0.015 vs. 0.475 ± 0.009 , $p < 0.001$). No significant differences were detected between water regimes in the number of nymphs produced (62.27 ± 2.38 vs. 58.73 ± 2.44 , $p = 0.239$) or in adult weight (0.512 ± 0.034 vs. 0.480 ± 0.029 , $p = 0.239$).

3.2 | Alighting and Settling Behaviour Assays of Alate Aphids

Aphid preference (antixenosis) for plants under different water regimes was analysed using two types of assays at multiple time points post-release: a dual-choice alighting assay and a free-choice settlement assay. In the alighting assay (Figure 1), significantly more adults landed on the WW regime (GLMM, Wald $\chi^2_{(df)} = 25.34$, $p < 0.001$), and differences among time points were also significant (Wald $\chi^2_{(df)} = 109.47$, $p < 0.001$). However, no significant interaction was found between treatment and time (Wald $\chi^2_{(df)} = 1.66$, $p = 0.89$) (Figure 1a). For the total number of nymphs per plant, significant differences were detected over time, with consistently higher counts on the WW regime (Wald $\chi^2_{(df)} = 56.60$, $p < 0.001$) (Figure 1b).

A similar trend was observed in the free-choice antixenosis (settlement behaviour) assay (Figure 2). A significantly greater number of adults settled on the WW regime (GLMM, Wald $\chi^2_{(df)} = 85.54$, $p < 0.001$), with statistical differences also detected among observation times (Wald $\chi^2_{(df)} = 23.66$, $p < 0.001$), but no significant interaction between treatment and time (Wald $\chi^2_{(df)} = 0.0004$, $p = 0.98$) (Figure 2a). Nymphs were recorded only 48 h after adult release, and their numbers were significantly higher on the WW compared to the WD regime (Mann-Whitney $U = 77.5$, $p = 0.006$) (Figure 2b).

3.3 | Response of Alate Aphids to Olfactory Cues Based on Plant Water Status

In the olfactometry assay, no significant preference of aphids was detected when comparing clean air vs. WD ($\chi^2_{(df)} = 0.22$, $p = 0.64$), clean air vs. WW ($\chi^2_{(df)} = 0.10$, $p = 0.76$), or WD vs. WW regime odours ($\chi^2_{(df)} = 0.40$, $p = 0.53$) (Figure 3).

4 | Discussion

Climate change has increased the frequency and severity of drought events worldwide, representing a major abiotic constraint in agricultural systems and strongly influencing plant-insect interactions. In this study, we examined the effects of water-deficit versus well-watered conditions in melon plants on the performance and behaviour of *A. gossypii*, with the aim of better understanding the consequences of drought stress on aphid biology and settlement dynamics. Here we address our three initial hypotheses formulated:

4.1 | Drought Benefits the Life-History Traits of Aphids on Melon Plants

Our results showed that drought-stressed melon plants significantly altered the life-history traits of *A. gossypii*. Specifically, aphids on the WD regime had shorter pre-reproductive periods and higher intrinsic and relative growth rates than those on the WW regime. This indicates that under the water-deficit conditions tested, melon plants provided a physiological environment that favoured faster aphid development and population growth. These findings are consistent with the plant stress hypothesis (White 1984; Tariq et al. 2012), which suggests that abiotic stress can reduce plant defence responses or modify phloem composition in ways that benefit herbivorous insects.

Although no significant differences in fecundity or adult weight were detected, the shorter developmental time on WD regime

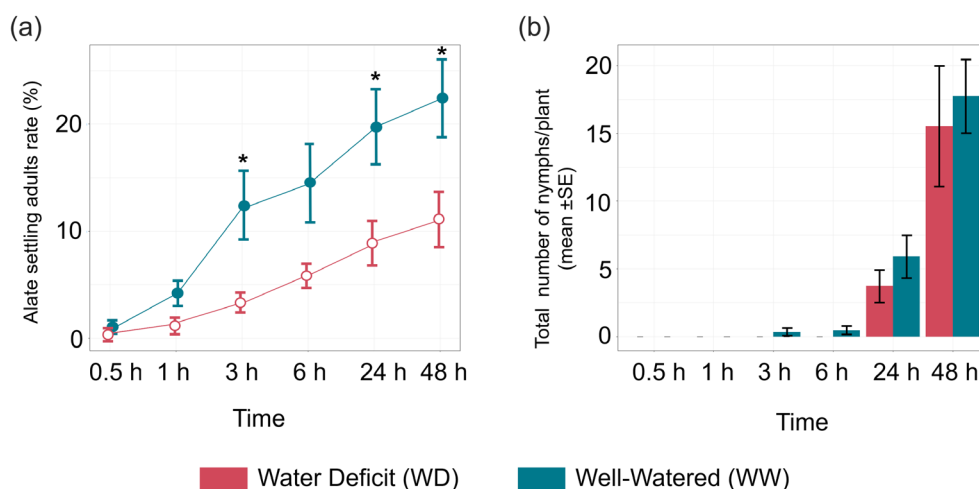


FIGURE 1 | Effects of two water regimes on the dual-choice alighting of *Aphis gossypii* adults and nymphs under dual-choice test. (a) Settling adult rate: Adults (mean $\pm$ SE) of *A. gossypii* on a WW when migrating from WD plant and vice versa at 0.5, 1, 3, 6, 24, 48 h after aphids released by plant. (b) Total nymphs: Number of nymphs (mean $\pm$ SE) present in WW and WD regimens counted at different time points at 0.5, 1, 3, 6, 24, 48 h after adults released by plant. Data were analysed using a GLMM with a negative binomial distribution; significance of treatment, time and their interaction was assessed using Wald χ^2 tests ($p < 0.05$) (*). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jen.20076)]

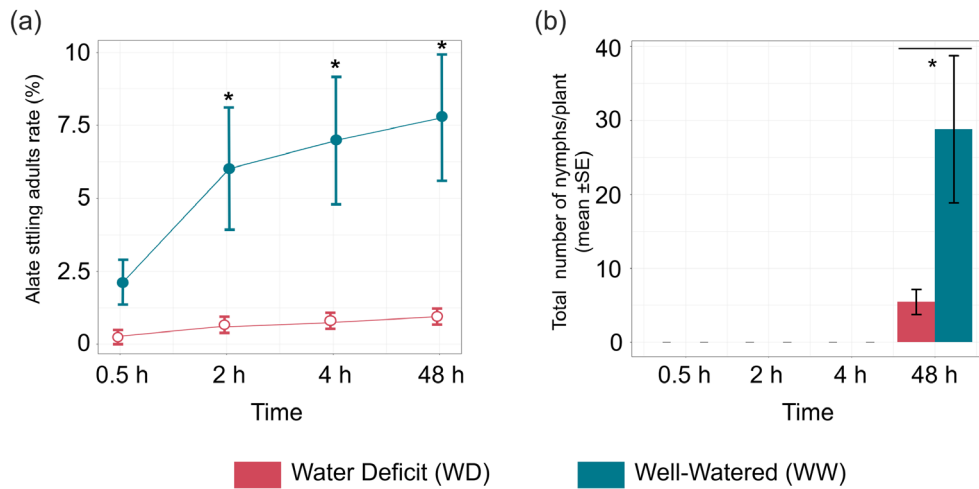


FIGURE 2 | Effects of two water regimes on the free-choice settling of *Aphis gossypii* adults and nymphs under dual-choice test. (a) Settling (mean % $\pm$ SE) of *A. gossypii* on a WW when migrating from WD plant and vice versa at 0.5, 2, 4, 48 h after aphids released by plant. (b) Total nymphs: Number of nymphs (mean % $\pm$ SE) present in WW and WD regimens counted at different time points at 0.5, 2, 4, 48 h after adults released by plant. Data were analysed using a GLMM with a negative binomial distribution; significance of treatment, time and their interaction was assessed using Wald χ^2 tests ($p < 0.05$) (*). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

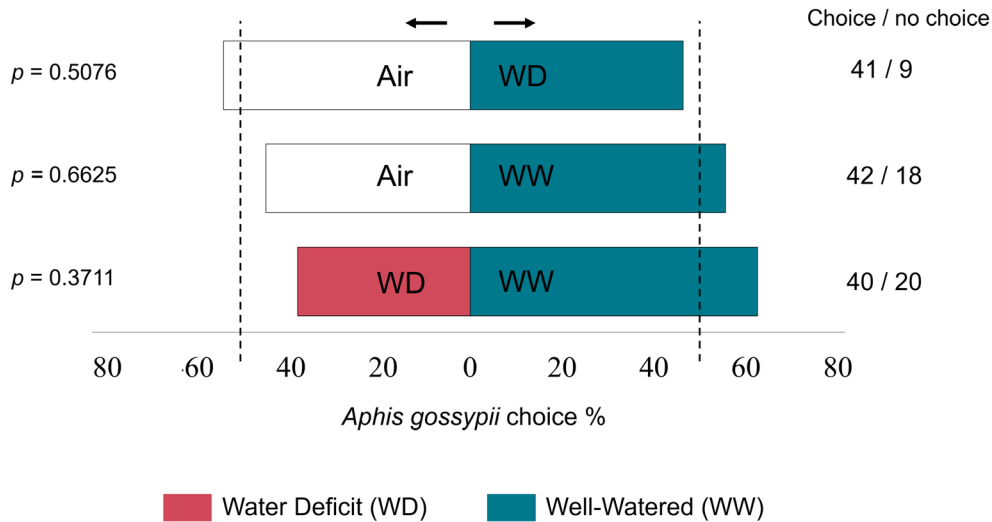


FIGURE 3 | Olfactory response of *Aphis gossypii* to two water regimes. The results are summarised in the bar graphs, with bars indicating the choices made by the aphids in the two treatments based on Chi-squared (χ^2) tests ($p < 0.05$). The 'no choice' column represents individuals that did not make a choice within the stabilised time. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

implies a clear reproductive advantage, potentially due to changes in plant nutritional quality or secondary metabolite profiles (Cui et al. 2021; Rahman et al. 2024). Previous studies have shown that mild to moderate drought can increase sugar and amino acid concentrations in the phloem, which may enhance aphid performance (Leybourne et al. 2021). In our case, the level of water stress applied (10%–20% field capacity) may have induced changes, allowing aphids to benefit from a favourable balance between reduced plant resistance and adequate nutritional availability.

4.2 | Aphids Prefer to Alight and Settle on Well-Watered Plants

Despite performing better on plants under WD regime, alate aphids consistently preferred to alight and settle on plants under

WW regime in both dual-choice and free-choice conditions. This preference remained stable across all observation periods, and a greater number of nymphs was recorded on WW regime after 48 h. These findings align with the plant vigour hypothesis (Price 1991), which postulates that herbivores tend to colonise more vigorous, healthy hosts. The greater visual appeal of WW (characterised by larger size, higher leaf number and greener foliage) likely enhanced their attractiveness to flying aphids. WW regime is generally more visually conspicuous and vigorous, which may enhance their attractiveness to flying aphids. Visual cues such as plant architecture, size and leaf area are known to play a critical role in aphid host-location and landing behaviour. Kansman et al. (2020) demonstrated that *Aphis glycines* alates preferentially alight on soybean plants with greater canopy volume and leaf surface area, independent of plant chemistry or nutritional regime. Their results emphasised that structural traits alone can strongly drive

aphid orientation and colonisation patterns. In a follow-up study, Kansman et al. (2022) further explored how plant visual traits interact with environmental cues, showing that increased plant height and leaf number significantly enhanced visual attractiveness to alate aphids, even under variable light and background conditions.

Interestingly, the avoidance of WD regime in free-choice conditions, despite their superior suitability for aphid development under no-choice (fitness) assays, reveals a marked mismatch between host preference and performance. Under confined conditions, aphids developed faster on WD regime, but when offered a choice, they selected host under WW regime and produced fewer nymphs on stressed plants. This mismatch between preference and performance highlights

that host selection does not necessarily reflect host suitability. Together, these results highlight the ecological complexity of aphid-host interactions under variable water regimes. They underscore the importance of considering both plant visual traits and physiological quality when predicting pest dynamics, especially in the context of climate-induced changes in water availability.

4.3 | Aphids Cannot Differentiate Odours Based on Plant Water Regime

Contrary to our third hypothesis, aphids did not show a preference for the odours emitted by plants grown under either WW or WD regimes in our olfactometry assays. Although a slight trend

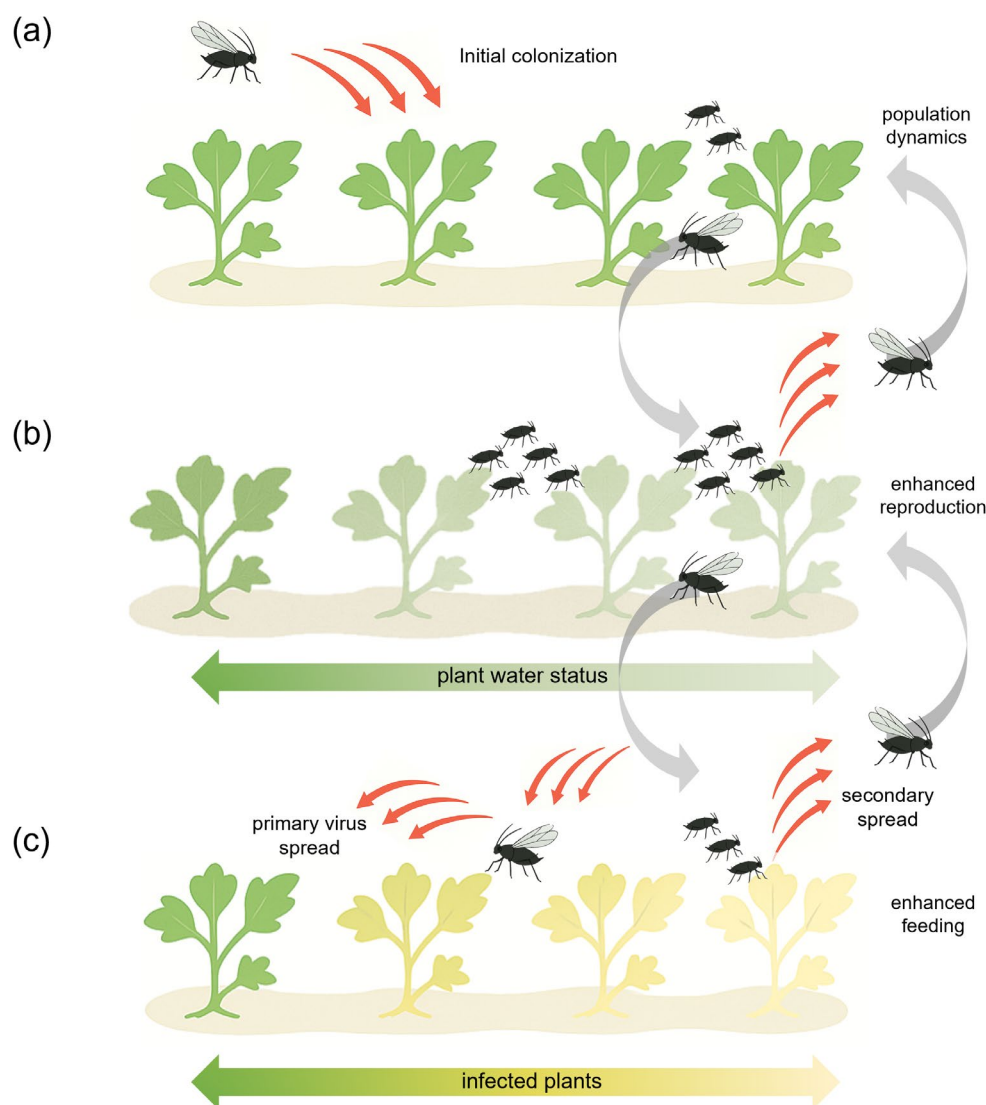


FIGURE 4 | Conceptual hypothesis illustrating potential aphid population dynamics in heterogeneous water conditions and in the presence of plant viruses. (a) In fields with interspersed WW and WD plants, alate *Aphis gossypii* are expected to initially colonise WW plants due to their greater visual attractiveness and vigour, followed by dispersal to WD plants as aphid density and competition increase. (b) Once on WD plants, aphids may develop and reproduce more rapidly, leading to a synergistic dynamic where initial attraction to WW plants and enhanced reproduction on WD plants result in accelerated population build-up compared to homogeneous WW or WD conditions. (c) Under these conditions, viruses such as CMV and CABYV, which manipulate aphid behaviour to optimise transmission, may further exacerbate this dynamic by interacting with drought-induced changes in plant physiology and vector performance, increasing viral spread. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jen.20076)]

favouring plants under WW regime was observed, it was not strong enough to be considered a reliable driver of host selection. This suggests that *A. gossypii* may rely more heavily on visual and structural cues than on VOCs when selecting hosts under water stress conditions aligning again with the plant vigour hypothesis (Price 1991). This result contrasts with some studies showing that VOC emissions can vary with drought and influence insect behaviour (Liu et al. 2023; Feng, Jian, et al. 2022; Feng, Liu, et al. 2022; Zhou and Jander 2022; Reinecke et al. 2024), but agrees with others that found olfactory responses to be species or context-dependent (Peng et al. 2022). Additionally, the relatively short time aphids had to choose and the use of whole-plant VOCs, rather than isolated compounds, might have limited our ability to detect finer olfactory distinctions. Plants integrate signals from both biotic and abiotic stresses to develop effective defence responses, highlighting the importance of cross-tolerance in resistance to aphid infestation (Foyer et al. 2016). A very important fact that must be highlighted in this study is that the aphid species used in these assays, is the main pest that affects melon crops due to its direct damage and its ability to transmit several viruses (Moya-Ruiz et al. 2023). Our findings may have implications for virus epidemiology mediated by aphid vectors. The higher rate of population increase observed on plants subjected to water stress could potentially influence virus spread under certain conditions.

5 | Ecological Implications for Sustainable Pest Management

Aphis gossypii is both a direct pest and an efficient vector of multiple viruses affecting cucurbits. Our study shows that water stress influences aphid behaviour and physiology with important implications in IPM under climate change scenarios. Based on our results, we propose conceptual scenarios (Figure 4) to guide future research: (a) In fields with mixed water conditions, alate aphids will initially colonise well-watered plants due to their greater visual attractiveness and vigour, then disperse to drought-stressed plants as population density increases. (b) On drought-stressed plants, aphids develop faster and reproduce more rapidly, potentially leading to a synergistic effect. Initial attraction to well-watered plants combined with enhanced reproduction on drought-stressed plants could accelerate overall population growth compared to uniform water conditions. This dynamic is especially relevant as irregular irrigation and drought become more common. (c) In the presence of viruses like CMV and CABYV that manipulate aphid behaviour to enhance transmission (Carmo-Sousa et al. 2014, 2016), drought may further modify these interactions by altering plant physiology and vector efficiency, increasing viral spread. Together, these findings reveal a mismatch between aphid host preference and performance, suggesting that water availability can differentially shape aphid settlement behaviour and population growth.

Author Contributions

Conceptualization, A.F., A.M. and G.C.-O.; methodology, G.C.-O. M.G. and P.M.; formal analysis, G.C.-O.; writing-original draft preparation, G.C.-O.; writing-review and editing, A.F. and A.M.; funding acquisition, A.F. and A.M. All authors have read and agreed to the published version of the manuscript.

Acknowledgements

The authors would like to thank Semillas Fito S.A. for providing the melon seeds cv. Bazán. Special thanks to Alba Tejada for her assistance during dual and free-choice assays.

Funding

Funding for this work was provided by a grant from the Spanish Ministry of Science and Innovation 'Multitrophic Interactions Between Plants, Viruses, Aphids and Natural Enemies in a Changing Climate (INTERVIRAPHID)' (PID2020-117074RB-I00) and by the Margarita Salas fellowship awarded to G. Clemente-Orta, funded by the EU—NextGenerationEU.

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study have been deposited on Figshare: <https://doi.org/10.6084/m9.figshare.31164097>.

References

- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.
- Beetge, L., and K. Krüger. 2019. "Drought and Heat Waves Associated With Climate Change Affect Performance of the Potato Aphid *Macrosiphum euphorbiae*." *Scientific Reports* 9: 3645. <https://doi.org/10.1038/s41598-019-40182-3>.
- Blackman, R. L., and V. F. Eastop. 1994. *Aphids on the World's Trees: An Identification and Information Guide*. Taylor and Francis.
- Carmo-Sousa, M., A. Moreno, E. Garzo, and A. Fereres. 2014. "A Non-Persistently Transmitted Virus Induces a Pull-Push Strategy in Its Aphid Vector to Optimize Transmission and Spread." *Virus Research* 186: 38–46. <https://doi.org/10.1016/j.virusres.2013.12.018>.
- Carmo-Sousa, M., A. Moreno, M. Plaza, E. Garzo, and A. Fereres. 2016. "Cucurbit Aphid-Borne Yellow Virus (CABYV) Modifies the Alighting, Settling and Probing Behaviour of Its Vector *Aphis gossypii* Favouring Its Own Spread." *Annals of Applied Biology* 169, no. 2: 284–297. <https://doi.org/10.1111/aab.12299>.
- Cui, H., L. Wang, G. V. Reddy, and Z. Zhao. 2021. "Mild Drought Facilitates the Increase in Wheat Aphid Abundance by Changing Host Metabolism." *Annals of the Entomological Society of America* 114, no. 1: 79–83. <https://doi.org/10.1093/aesa/saaa042>.
- Díaz-Hernández, A. M., D. A. Sepúlveda, A. González-González, L. M. Briones, M. C. Correa, and C. C. Figueroa. 2025. "Water Deficit and Aphid Resilience on Wheat: Examining *Sitobion avenae* F. And Their Bacterial Symbionts Interplay Under Controlled Laboratory Conditions." *Pest Management Science* 81, no. 1: 255–265. <https://doi.org/10.1002/ps.7631>.
- Dixon, A. F. G. 1998. *Aphid Ecology: An Optimization Approach*. Springer.
- Feng, D., H. Jian, H. Zhang, et al. 2022. "Comparison of Volatile Compounds Between Wild and Cultivated Roses." *HortScience* 57, no. 5: 657–663. <https://doi.org/10.21273/HORTSCI16036-21>.
- Feng, J., S. Liu, Q. Hu, Z. Shi, and H. Guo. 2022. "Plant Volatile-Mediated Interactions Between Drought-Stressed Plants and Insect Herbivores." *Environmental and Experimental Botany* 201: 104986. <https://doi.org/10.1016/j.envexpbot.2022.104986>.

- Fereres, A., C. Gutierrez, P. Del Estal, and P. Castanera. 1988. "Impact of the English Grain Aphid, *Sitobion avenae* (F.) (Homoptera: Aphididae), on the Yield of Wheat Plants Subjected to Water Deficits." *Environmental Entomology* 17, no. 3: 596–602. <https://doi.org/10.1093/ee/17.3.596>.
- Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*. 3rd ed. SAGE Publications.
- Foyer, C. H., B. Rasool, J. W. Davey, and R. D. Hancock. 2016. "Cross-Tolerance to Biotic and Abiotic Stresses in Plants: A Focus on Resistance to Aphid Infestation." *Journal of Experimental Botany* 67, no. 7: 2025–2037. <https://doi.org/10.1093/jxb/erw079>.
- Hales, D. F., J. Tomiuk, K. Wöhrmann, and P. Sunnucks. 2013. "Evolutionary and Genetic Aspects of Aphid Biology: A Review." *European Journal of Entomology* 94, no. 1: 1–55. <https://doi.org/10.14411/eje.1997.001>.
- Huberty, A. F., and R. F. Denno. 2004. "Plant Water Stress and Its Consequences for Herbivorous Insects: A New Synthesis." *Ecology* 85, no. 5: 1383–1398. <https://doi.org/10.1890/03-0352>.
- Kansman, J., V. Nalam, P. Nachappa, and D. Finke. 2020. "Plant Water Stress Intensity Mediates Aphid Host Choice and Feeding Behaviour." *Ecological Entomology* 45, no. 6: 1437–1444. <https://doi.org/10.1111/een.12930>.
- Kansman, J. T., S. Basu, C. L. Casteel, et al. 2022. "Plant Water Stress Reduces Aphid Performance: Exploring Mechanisms Driven by Water Stress Intensity." *Frontiers in Ecology and Evolution* 10: 846908. <https://doi.org/10.3389/fevo.2022.846908>.
- Kennedy, J. S., K. P. Lamb, and C. O. Booth. 1958. "Responses of *Aphis fabae* scop. To Water Shortage in Host Plants in Pots." *Entomologia Experimentalis et Applicata* 1, no. 4: 274–290. <https://doi.org/10.1111/j.1570-7458.1958.tb00075.x>.
- Lancashire, P. D., H. Bleiholder, T. van den Boom, et al. 1991. "A Uniform Decimal Code for Growth Stages of Crops and Weeds." *Annals of Applied Biology* 119, no. 3: 561–601. <https://doi.org/10.1111/j.1744-7348.1991.tb04895.x>.
- Leather, S. R., and A. F. G. Dixon. 1984. "Aphid Growth and Reproductive Rates." *Entomologia Experimentalis et Applicata* 35: 137–140. <https://doi.org/10.1111/j.1570-7458.1984.tb03373.x>.
- Leybourne, D. J., K. F. Preedy, T. A. Valentine, J. I. B. Bos, and A. J. Karley. 2021. "Drought Has Negative Consequences on Aphid Fitness and Plant Vigour: Insights From a Meta-Analysis." *Ecology and Evolution* 11, no. 16: 11915–11929. <https://doi.org/10.1002/ece3.7939>.
- Leybourne, D. J., T. A. Valentine, K. Binnie, A. Taylor, A. J. Karley, and J. I. Bos. 2022. "Drought Stress Increases the Expression of Barley Defence Genes With Negative Consequences for Infesting Cereal Aphids." *Journal of Experimental Botany* 73, no. 7: 2238–2250. <https://doi.org/10.1093/jxb/erac013>.
- Liu, D., P. Dai, S. Li, et al. 2018. "Life-History Responses of Insects to Water-Deficit Stress: A Case Study With the Aphid *Sitobion avenae*." *BMC Ecology* 18: 17. <https://doi.org/10.1186/s12898-018-0172-8>.
- Liu, J., C. Wang, H. Li, Y. Gao, Y. Yang, and Y. Lu. 2023. "Bottom-Up Effects of Drought-Stressed Cotton Plants on Performance and Feeding Behavior of *Aphis gossypii*." *Plants* 12, no. 14: 2886. <https://doi.org/10.3390/plants12142886>.
- Luo, R., and B. Gilbert. 2022. "Timing of Short-Term Drought Structures Plant–Herbivore Dynamics." *Oikos* 2022, no. 1: e08728. <https://doi.org/10.1111/oik.08728>.
- Marček, T., K. Hamow, B. Végh, T. Janda, and E. Darko. 2019. "Metabolic Response to Drought in Six Winter Wheat Genotypes." *PLoS One* 14, no. 3: e0212411. <https://doi.org/10.1371/journal.pone.0212411>.
- Mattson, W. J., and R. A. Haack. 1987. "The Role of Drought in Outbreaks of Plant-Eating Insects." *Bioscience* 37, no. 2: 110–118. <https://doi.org/10.2307/1310365>.
- Mezgebe, A., and F. Azerefege. 2021. "Effect of Water Stress on Glucosinolate Content of *Brassica carinata* and Performance of *brassicorhynae brassicae* and *myzus persicae*." *International Journal of Tropical Insect Science* 41, no. 2: 953–960. <https://doi.org/10.1007/s42690-020-00358-1>.
- Mody, K., D. Eichenberger, and S. Dorn. 2009. "Stress Magnitude Matters: Different Intensities of Pulsed Water Stress Produce Non-Monotonic Resistance Responses of Host Plants to Insect Herbivores." *Ecological Entomology* 34, no. 1: 133–143. <https://doi.org/10.1111/j.1365-2311.2008.01056.x>.
- Moericke, V. 1955. "Über die Lebensgewohnheiten der geflügelten Blattläuse (Aphidina) unter besonderer Berücksichtigung des Verhaltens beim Landen." *Zeitschrift für Angewandte Entomologie* 37, no. 1: 29–91. <https://doi.org/10.1111/j.1439-0418.1955.tb00775.x>.
- Moya-Ruiz, C. D., P. Gómez, and M. Juárez. 2023. "Occurrence, Distribution, and Management of Aphid-Transmitted Viruses in Cucurbits in Spain." *Pathogens* 12, no. 3: 422. <https://doi.org/10.3390/pathogens12030422>.
- Peng, W., P. Li, R. Ling, et al. 2022. "Diversity of Volatile Compounds in Ten Varieties of Zingiberaceae." *Molecules* 27, no. 2: 565. <https://doi.org/10.3390/molecules27020>.
- Price, P. W. 1991. "The Plant Vigour Hypothesis and the Attack of Herbivores." *Oikos* 62, no. 2: 244–251. <https://doi.org/10.2307/3545270>.
- Rahman, S., M. Rostás, and I. Vosteen. 2024. "Drought Aggravates Plant Stress by Favouring Aphids and Weakening Indirect Defense in a Sugar Beet Tritrophic System." *Journal of Pest Science* 97, no. 4: 1–16. <https://doi.org/10.1007/s10340-023-01690-w>.
- Ramírez, C. C., P. E. Gundel, A. J. Karley, and D. J. Leybourne. 2023. "To Tolerate Drought or Resist Aphids? A New Challenge to Plant Science Is on the Horizon." *Journal of Experimental Botany* 74, no. 6: 1745–1750. <https://doi.org/10.1093/jxb/erad032>.
- Reinecke, A., I. C. Flaig, Y. M. Lozano, M. C. Rillig, and M. Hilker. 2024. "Drought Induces Moderate, Diverse Changes in the Odour of Grassland Species." *Phytochemistry* 221: 114040.
- Sadras, V., M. Guirao, A. Moreno, and A. Fereres. 2024. "Inter-Virus Relationships in Mixed Infections and Virus-Drought Relationships in Plants: A Quantitative Review." *Plant Journal* 117, no. 6: 1786–1799. <https://doi.org/10.1111/tpj.16387>.
- Sadras, V., J. Jiménez, M. L. Juncay, A. Moreno, and A. Fereres. 2025. "Biotic and Abiotic Modulation of Drought Effects on Aphids and Plants." *Annals of Applied Biology* 187, no. 2: 142–156. <https://doi.org/10.1111/aab.12967>.
- Sadras, V., C. Vazquez, E. Garzo, et al. 2021. "The Role of Plant Labile Carbohydrates and Nitrogen on Wheat–Aphid Relations." *Scientific Reports* 11: 12529. <https://doi.org/10.1038/s41598-021-91926-3>.
- Saska, P., J. Skuhrovec, H. Platková, K. Kosová, S. J. Tuan, and P. Vítámvás. 2024. "Population-Level Responses of Aphids to Pulsed Drought Stress." *Journal of Pest Science* 97, no. 4: 1943–1956. <https://doi.org/10.1007/s10340-023-01692-8>.
- Tariq, M., D. J. Wright, J. T. Rossiter, and J. T. Staley. 2012. "Aphids in a Changing World: Testing the Plant Stress, Plant Vigour and Pulsed Stress Hypotheses." *Agricultural and Forest Entomology* 14, no. 3: 177–185. <https://doi.org/10.1111/j.1461-9563.2011.00557.x>.
- van Emden, H. F., and R. Harrington. 2017. *Aphids as Crop Pests*. 2nd ed. CABI Publishing.

- White, T. C. R. 1984. "The Abundance of Invertebrate Herbivores in Relation to the Availability of Nitrogen in Stressed Food Plants." *Oecologia* 63, no. 1: 90–105. <https://doi.org/10.1007/BF00379790>.
- Wyatt, I. J., and P. F. White. 1977. "Simple Estimation of Intrinsic Increase Rates for Aphids and Tetranychid Mites." *Journal of Applied Ecology* 14, no. 3: 757–766.
- Xie, H., F. Shi, J. Li, et al. 2022. "The Reciprocal Effect of Elevated CO₂ and Drought on Wheat–Aphid Interaction System." *Frontiers in Plant Science* 13: 853220. <https://doi.org/10.3389/fpls.2022.853220>.
- Zhou, S., and G. Jander. 2022. "Molecular Ecology of Plant Volatiles in Interactions With Insect Herbivores." *Journal of Experimental Botany* 73, no. 2: 449–462.