



Population-level responses of aphids to pulsed drought stress

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Abstract

The first aim of this study was to test the pulsed stress hypothesis on a system consisting of young spring wheat (*Triticum aestivum* L.) and the rose-grain aphid *Metopolophium dirhodum* (Walker) by following the age-stage, two-sex life table theory. This hypothesis predicts that fluid-feeding insects benefit from feeding on plants intermittently stressed by drought due to the increased nutrient availability and restored cell turgor. Our second aim was to illustrate the risk of drawing different conclusions if based on a single or a small subset of parameters or if the entire lifespan of a generation is not covered compared to if the study was conducted at the population level. We applied periods of drought stress (soil water capacity, SWC = 40%) on four occasions relative to the population development of the aphids and compared those treatments with well-watered (SWC = 70%) and continuous stress conditions (SWC = 40%). The timing of the stresses appeared to be important in determining the effect on aphid performance. Although we found some improvement in fecundity when the stress occurred before the aphids were placed on the plants, the overall effect of the early-timed pulsed stress treatments on the rate of increase was negative compared to the well-watered control, which was mainly due to prolonged nymph development. The drought pulse that was timed late (the second week of aphid reproduction) did not show any effect relative to the well-watered control. This study therefore provides no clear support for the validity of the pulsed stress hypothesis.

Keywords Intermittent stress · Plant stress hypothesis · Plant vigour hypothesis · Fecundity · Population growth

Key message

- The pulsed stress hypothesis predicts that pulses of drought favour fluid-feeding insects.
- Continuous drought and an early-timed pulsed stress had negative effects on the rose-grain aphid.
- A late-timed pulse of stress had no effect on aphids compared to the well-watered control.
- This study provides no support for the pulsed stress hypothesis at the population level.

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Introduction

Insect–plant interactions have triggered research attention for centuries because the outcomes of these interactions largely affect crop yield. Plant condition is the key bottom-up driver of these interactions (Han et al. 2022). Several hypotheses have been formulated regarding the response of insects to plant conditions. The *plant vigour hypothesis* predicts that herbivores perform better on high-quality plants (measured, e.g. by water saturation of plant cells, nutritional composition, or speed of growth) (Price 1991). In contrast, the *plant stress hypothesis* asserts that herbivores perform better on stressed plants, as these plants can allocate fewer resources to producing defensive secondary metabolites or make their nutrients more easily accessible (White 1984; Tariq et al. 2012). Finally, the *pulsed stress hypothesis* was formulated for fluid-feeding insects by Huberty and Denno (2004) to explain the historical outbreaks of fluid-feeding insect pests on drought-stressed plants. This hypothesis predicts that fluid-feeding insects, such as aphids, perform better when feeding on plants that are intermittently stressed by drought compared to well-watered or continuously stressed

plants, as is sometimes observed in the field (e.g. Flint et al. 1996; Sconiers and Eubanks 2017). Huberty and Denno (2004) presumed that the mechanism behind this effect was related to increased levels of available nitrogen in the plants and to cell turgor recovery after the water supply had been replenished (e.g. Kennedy et al. 1958; Mattson and Haack 1987; Mody et al. 2009).

The sample sizes based on which Huberty and Denno (2004) formulated the *pulsed stress hypothesis* were, however, very low. They used only six studies, which is distinctly below the average for meta-analyses in this field (Philibert et al. 2012). Since it was established, the *pulsed stress hypothesis* has been subjected to only a few attempts at corroboration. Table 1 summarizes the results of a review of the available literature data. The strongest support was found in a series of studies conducted by Banfield-Zanin and Leather (2014, 2015a, b, c). They found that the parameters related to the individual growth and fecundity of *Elatobium abietinum* on *Picea sitchensis* were favoured under conditions of moderate pulsed drought (Banfield-Zanin and Leather 2015a, c), which resulted in an extended period of peak population size compared to other treatments (Banfield-Zanin and Leather 2014). The data from most other studies, however, do not show these patterns (e.g. Tariq et al. 2012; Pons et al. 2020; Luo and Gilbert 2022; Stallmann et al. 2022; Table 1). It has become clear that the level of drought severity is also important in determining its effect on herbivores (Tariq et al. 2012; Banfield-Zanin and Leather 2015a, c). The very large variations in the regimes and magnitudes of drought stresses used hamper meaningful comparisons across studies; in fact, conditions that are presented as pulsed stress regimes in one study may be considered controls or represented as continuous stress regimes in other publications (Table 1).

This study has two main aims. The first aim is to test the validity of the *pulsed stress hypothesis* by using spring wheat (*Triticum aestivum* L.)—rose-grain aphid (*Metopolophium dirhodum* (Walker)) as the model study system. The aphid model species, *M. dirhodum*, is one of the main aphid pests on cereals in Europe (van Emden and Harrington 2017). In central Europe, it is a holocyclic heteroecious species, overwintering on roses, and summer generations reproduce parthenogenetically on various *Poaceae*, including cereals (van Emden and Harrington 2017). We included four regimes of a single pulse (1 week) stress that differed in the timing of the drought period relative to the aphid development phase (e.g. before infestation, during nymphal development, and during the first or second week of reproduction) and two control regimes (e.g. well-watered and continuous stress). We expected that such timing of the stresses would affect aphid population growth to

different degrees, which would in turn be manifested specifically in the rate of population growth, and that the underlying mechanisms of the effect would be different. We particularly expected that the stresses applied early on during aphid development and during the early phase of reproduction would have greater effects than if the stress pulse occurred during the later phases of aphid life. This is because reduced survival and prolonged duration of development have a negative effect on population growth (Saska et al. 2021b, 2023). The reproductive value of a population is highest early on after the onset of reproduction (Lewontin 1965; Saska et al. 2021b), so any stress exerted on the host plant or aphids themselves during this period may reduce fecundity and thus population growth to a greater degree compared to the later phases of reproduction when the reproductive values are declining (Saska et al. 2021b). That the timing of the intermittent stress may have an effect on aphid performance was recently documented by Luo and Gilbert (2022), who found that the greatest (but negative!) effect of this drought stress occurred during the exponential phase of population growth. According to our approach, the *pulsed stress hypothesis* would hold for the study system if aphid populations would grow faster in any of the pulsed stress treatments compared to continuously stressed or well-watered plants.

The few studies that have (or have not) provided evidence for the *pulsed stress hypothesis* were based on a subset of parameters or on a selected part of the life cycle of an insect (Table 1). This is far from ideal since each parameter may be affected differently by stress (Saska et al. 2021b; see also Table 1), and the overall effect of stress on population growth cannot be established based on such data. The second aim of this study is therefore to show how using selected fitness parameters can lead to contrasting results. This study is based on the age-stage, two-sex life table approach (reviewed by Chi et al. 2020), which accurately describes the development, survival, and reproduction of insect populations and considers stage differentiation and variable developmental rates among individuals (Chi et al. 2020). In this way, the biases introduced by other approaches that result in inaccurate life table parameter estimates (e.g. overestimating the intrinsic rate of increase by 27.6%; Saska et al. 2021a) are avoided. It has been shown that this approach is also suitable for parthenogenetic populations consisting of females only (Tuan et al. 2016) and has been widely used for aphids (e.g. Akca et al. 2015; Günçan and Gümüş 2017; Saska et al. 2021a, b; 2023). The age-stage, two-sex life table makes it possible to predict aphid population growth under the given conditions, thus testing the *pulsed stress hypothesis* at the population level and eliminating the risk of drawing conclusions based on selected parameters that may provide contradicting results.

Table 1 Overview of the available studies using pulsed drought stress on fluid-feeding insects

References	Insect species	Plant species	Drought stress treatments ¹⁾	Parameter	Stress effects
Kennedy et al. (1958)	<i>Aphis fabae</i>	<i>Vicia faba</i>	C: continuously watered; MPS : rewatered after 5 days	2-d fecundity	C > MPS [before rewatering] C ≈ MPS [after rewatering]
	<i>Aphis fabae</i>	<i>Vicia faba</i>	C: daily watering to field SWC; MPS : watered when wilting occurred (40% of C); SCS : minimum watering to ensure survival (20% of C)	3-d fecundity Survival % alate offspring	C ≈ MPS ≈ SCS (C ≈ MPS) > SCS C > (MPS ≈ SCS)
Major (1990)	<i>Elatobium abietinum</i>	<i>Picea sitchensis</i>	C: SWC at field level; SCS : 10–13% of C; SPS : dried to 10–13% of C and rewatered to C	Growth curve Fecundity Adult weight Nymph weight Embryo count Development time Number of aphids after 14 days	SPS > C > SCS SPS > C > SCS C ≈ SPS ≈ SCS C ≈ SPS ≈ SCS C ≈ SPS ≈ SCS C ≈ SPS ≈ SCS C > (LPS ≈ MPS)
Mody et al. (2009)	<i>Aphis pomi</i>	<i>Malus domestica</i>	C: constantly moist soil; LPS : watered every 3 days (40% less in total than C); MPS : watered every 6 days (23% less in total than C)		
Tariq et al. (2012)	<i>Brevicoryne brassicae</i>	<i>Brassica oleracea</i>	C: 200 mL every 7 days; LCS : 150 mL every 7 days; MCS : 100 mL every 7 days; SCS : 50 mL every 7 days; MPS : 200 mL every 15 days	<i>Md</i> ²⁾ <i>r_m</i> ²⁾	MCS > LCS > MPS > (C ≈ SCS) (MCS ≈ LCS) > MPS > (C ≈ SCS)
	<i>Myzus persicae</i>	<i>Brassica oleracea</i>	Same as above	<i>Md</i> ²⁾ <i>r_m</i> ²⁾	(MCS ≈ LCS) > (MPS ≈ C ≈ SCS) (MCS ≈ LCS) > ((MPS ≈ SCS) & (SCS ≈ C)) C > MPS C > MPS MPS > (C ≈ MCS ≈ SCS ≈ SPS)
Simpson et al. (2012)	<i>Myzus persicae</i>	<i>Brassica oleracea</i>	C: 125 mL every 3–4 days; MPS : up to 500 mL every 7 days	<i>Md</i> ²⁾ <i>r_m</i> ²⁾	
Banfield-Zanin and Leather (2014)	<i>Elatobium abietinum</i>	<i>Picea sitchensis</i>	C: SWC at field level; MCS : 60% of C; SCS : 20% of C; MPS : dried to 30% of C and rewatered to 70%; SPS : dried to 20 of C and rewatered to 100%	Length of peak in <i>EN</i> ³⁾	
Banfield-Zanin and Leather (2015b)	<i>Elatobium abietinum</i>	<i>Picea sitchensis</i>	Same as in Banfield-Zanin & Leather (2014)	7-d survival Lifespan <i>T</i>	C > SPS [in 1 out of 6 exp] ⁴⁾ C > MCS [in 2 out of 6 exp] ⁴⁾ MPS > C [in 1 out of 6 exp] ⁴⁾ (SCS & SPS) > C ⁴⁾ C > MPS [in 2 out of 3 exp. in spring] ⁴⁾ MPS > C [in 1 out of 3 exp. in autumn] ⁴⁾

Table 1 (continued)

References	Insect species	Plant species	Drought stress treatments ¹⁾	Parameter	Stress effects
Banfield-Zanin and Leather (2015c)	<i>Elatobium abietinum</i>	<i>Picea sitchensis</i>	Same as in Banfield-Zanin & Leather (2014)	Reproductive days 7-d fecundity r_m ²⁾	MPS > C [in 1 out of 6 exp] ⁴⁾ C > SCS [in 3 out of 6 exp] ⁴⁾ C > SPS [in 3 out of 6 exp] ⁴⁾ MPS > C ⁴⁾ C > SCS [in 2 out of 6 exp] ⁴⁾ C > SPS [in 2 out of 6 exp] ⁴⁾ MPS > C [in 3 out of 6 exp] ⁴⁾ C > SCS [in 2 out of 6 exp] ⁴⁾ C > SPS [in 4 out of 6 exp] ⁴⁾ MPS > C [in 4 out of 6 exp] ⁴⁾ C > SCS [in 1 out of 3 exp. in spring] ⁴⁾ SCS > C [in autumn] ⁴⁾ C > SPS [in 3 out of 6 exp] ⁴⁾ SPS > C [in 1 out of 6 exp] ⁴⁾ MPS > C ⁴⁾ SCS > C [in spring] ⁴⁾ SPS > C [in 2 out of 3 exp. in spring] ⁴⁾ C > SCS [in autumn] ⁴⁾ C > SPS [in autumn] ⁴⁾ C > MCS [in 2 out of 3 exp. in autumn] ⁴⁾ MPS > C [in 5 out of 6 exp] ⁴⁾ C > SPS ⁴⁾ C > MCS [in 5 out of 6 exp] ⁴⁾ C > SCS ⁴⁾ C \approx SCS > (SCS \approx SPS) [without mycorrhiza] C \approx SCS > (SCS \approx SPS) [with mycorrhiza]
Pons et al. (2020)	<i>Sitobion avenae</i>	<i>Triticum aestivum</i>	C : near field level SWC, maintained every 48 h; SCS : 40% reduction of irrigation; SPS : watered every 8 days with cumulative amount of SCS	Number of aphids after 16 days	
Luo and Gilbert (2022)	<i>Aphis nerii</i>	<i>Asclepias syriaca</i>	C : 100 mL twice a week; MPS-2 : water withheld for 7 d starting on day 2; MPS-12 : water withheld for 7 d starting on day 12; MPS-21 : water withheld for 7 d starting on day 21; MPS-30 : water withheld for 7 d starting on day 30	Peak density Time to reach the peak density Proportion of winged aphids	C \approx MPS-2 \approx MPS-12 \approx MPS-30 > MPS-21 C \approx MPS-2 \approx MPS-12 \approx MPS-30 > MPS-21 C \approx MPS-2 \approx MPS-12 \approx MPS-21 \approx MPS-30

Table 1 (continued)

References	Insect species	Plant species	Drought stress treatments ¹⁾	Parameter	Stress effects
Stallmann et al. (2022)	<i>Sitobion avenae</i>	<i>Triticum aestivum</i>	C: near field level SWC, maintained every 48 h; SCS: 40% reduction of irrigation; SPS: watered every 8 days with cumulative amount of SCS	Number of aphids after 13 days Survival	$(C \approx SCS) > (SCS \approx SPS)$ $C > (SCS \approx SPS)$ [in 1 out of 2 exp]

Legend for drought treatments: C—control, LCS—low-level continuous stress, MCS—moderate continuous stress, SCS—severe continuous stress, LPS—low-level pulsed stress, MPS—moderate pulsed stress, and SPS—severe pulsed stress. The signs indicate the stress effects as follows: a > b—treatment a significantly outperformed treatment b; a ≈ b—performance of treatments a and b not significantly different

- Note that the notations for the treatments in the original studies differ from what is used here. This is because the magnitude of drought stress is not consistent across the studies; therefore, what was considered to be severe stress in one study may have been regarded as mild stress in comparison with other studies. SWC in this column stands for the soil water capacity
- $r_m = 0.738 \ln(Md)/d$, where d is the length of the pre-reproductive period and Md is the number of offspring produced during the period equal in length to d , starting from the onset of reproduction (Wyatt and White 1977). This method, however, overestimates the true intrinsic rate of increase, r , by ca. 28% (Saska et al. 2021a)
- $EN = 100 \left(\frac{E_s}{2N_s} \right)$, which expresses the number of aphids per 100 needles (Timms 2004). E_s equals the weekly total number of aphids per tree, and N_s equals the number of needles along one side of the stem
- Tests were conducted to contrast the drought treatments with the well-watered control. The experiment was repeated three times in spring and three times in autumn

Materials and methods

Study system

Spring wheat (*Triticum aestivum* Linnaeus cv. ‘Quintus’) was used as the study plant. This cultivar is intolerant to drought and has a low level of antibiosis against aphids (Saska et al. 2021b). Seeds were sown in field soil after pre-germination in the dark at 20 °C for 2 days. Ten seeds per pot (0.25 L) were sown in fully saturated soil and grown in a growth chamber (Tyler T-16/4, Budapest, Hungary) at 18 °C with a 16-h/8-h (light/dark) long-day photoperiod and irradiance of 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and watered accordingly (see below).

Aphid material was obtained from the long-term (> 20 years) laboratory culture that is maintained in the Crop Research Institute (Prague) (natural photoperiod, temperature 20 ± 1 °C) on young (stages 12–13 according to the BBCH scale; Meier 1997) winter wheat plants.

Drought stress regimes

Six water supply regimes were used based on specific soil water capacity (SWC) and timing of the drought stress relative to the timing of aphid introduction. The SWC levels used were 70% (well-watered state) and 40% (severe level of drought) and were derived from 100% SWC calculated as the weight of water contained in 1 g of dried soil after saturation with water and drained freely for 48 h. These stress levels were chosen according to our previous study (Saska et al. 2023) and represented the optimum and maximum levels of plant drought stress tolerated by the aphids. The level of SWC was maintained for each pot daily by adding water, the amount of which was determined by weighing and which was equal to the difference between the actual and known weight for each pot (including soil and plants).

The following treatments were established: well-watered control (denoted 70C), continuous drought control (40C), and four pulsed stress treatments. A pulse of stress was applied once by discontinuing the water supply for two days so that the SWCs gradually declined from 70 to 40%, and the SWCs were then maintained gravimetrically at this level. One week after the onset of water discontinuation, the water level was replenished to 70% SWC and maintained at this level until the end of the experiment. Pulsed stress treatments differed in the timing of when the pulse of stress was applied relative to the start of the life table study. Namely, before aphids were placed on the plants (40-0), during the first week of the life table study (40-1; equates to nymph development), and during

the second (40-2) and third (40-3) weeks of the life table study, which roughly equates to the first and second weeks of aphid reproduction.

The morphophysiological responses to drought were measured on subsamples of plants randomly selected from the 10 plants that grew in each pot. The fresh biomass, leaf area, water saturation deficit (WSD), osmotic potential, and chlorophyll fluorescence (F_v/F_m) were measured for nine second leaves per treatment when the aphids were transferred to the new plants. For the case of pulsed stresses, we measured the plant responses once the SWC reached 40% and at one week after the SWC was replenished to 70%. The details are given in Supplementary Materials S1.

Aphid life table study

The data collection procedures followed those described in Saska et al. (2021b) and were based on the ‘group design’ (Chang et al. 2016). Ten adult wingless virginoparae were placed on the plants in each pot (eight replicated pots per treatment) and were removed on the next day, when the number of neonates was reduced to 10 per pot to level the initial population sizes. Transparent polyethylene tubes enclosed all the plants in each pot to reduce the risk of aphid escape. The numbers of aphids, instars, and newly produced

offspring were recorded daily for each pot, and the neonate nymphs were removed. Due to space limitations and to facilitate manipulation, the aphids were transferred every week to new young plants (Akca et al. 2015; Saska et al. 2021b). The experiment was conducted in climatic chambers with a constant temperature of 21 (± 1) °C and a long-day photoperiod (16 h light/8 h dark) and lasted until the last aphid died (ca. six weeks).

Data analysis

The life table data were evaluated according to the age-stage, two-sex life table theory (Chi and Liu 1985; Chi 1988; Chi et al. 2020) by using the TWOSEX-MSChart program (Chi 2022a). The mathematical approaches that were used to calculate the life table and population parameters are summarized in Table 2. In the first step, the life table parameters were calculated based on the original aphid cohorts. The standard errors (SEs) for the parameters were estimated using 100,000 aphid cohorts that were generated by bootstrapping based on the original cohort (Polat Akkopru et al. 2015). Treatments were compared using a paired bootstrap test for individual life tables and population parameters (Mou et al. 2015; Wei et al. 2020). The population growth starting with 10 individuals was projected in the program

Table 2 Population parameters used in the age-stage, two-sex life table analysis

Parameter and equation	Explanation
$s_{xj} = \frac{n_{xj}}{n_{01}}$	Age-stage-specific survival rate (s_{xj}); x is age from birth, j is the stage. Thus, n_{xj} is the number of individuals who survived to age x and stage j . n_{01} is the initial number of new-born aphids with which the experiment was started
$l_x = \sum_{j=1}^{\beta} s_{xj}$	Age-specific survival rate (l_x); β is the number of life stages
$f_{xj} = \frac{N_x}{n_{xj}}$	Age-stage-specific fecundity (f_{xj}); N_x is the number of nymphs produced at age x
$m_x = \frac{\sum_{j=1}^{\beta} s_{xj} f_{xj}}{\sum_{j=1}^{\beta} s_{xj}}$	Age-specific fecundity (m_x)
$R_0 = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj} f_{xj} = \sum_{x=0}^{\infty} l_x m_x$	Net reproductive rate (R_0). Note that $R_0 = F \left(\frac{n_f}{n_{01}} \right)$, where F is mean fecundity, n_f is the number of individuals who reached the female stage f and n_{01} is the initial number of individuals at the beginning of the life table study
$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$	Intrinsic rate of increase (r) estimated by using the iterative bisection method and the Euler-Lotka equation with the age indexed from 0 (Goodman 1982)
$\lambda = e^r$	Finite rate of increase (λ)
$T = \frac{\ln R_0}{r}$	Mean generation time (T)
$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{\beta} s_{iy}^t s_{ij}'$	Life expectancy (e_{xj}); s_{iy}^t is the probability that an individual of age x and stage j can survive to age i and stage y by assuming that $s_{iy}' = 1$ (Chi & Su 2006)
$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{\beta} s_{iy}^t s_{ij}'$	Reproductive value (v_{xj}) (Tuan et al. 2014)
$\phi_{j,t} = \log \left(\frac{n_{j,t+1}}{n_{j,t}} \right)$ $\approx \log \left(\frac{\lambda n_{j,t}}{n_{j,t}} \right) = \log \left(\frac{\lambda n_{total,t}}{n_{total,t}} \right) = \log \lambda$	Growth rate of each stage between two consecutive days, where t is time (Huang et al. 2018). As a population approaches stable age-stage distribution, all stages ($n_{j,t}$) and the total population ($n_{total,t}$) will increase at the finite rate, λ

The equations come from the work of Chi and Liu (1985) and Chi (1988), unless stated otherwise. The SEs of the parameters were estimated using 100,000 bootstraps (Polat Akkopru et al. 2015)

TIMING-MSChart (Chi 2022b), following the method of Huang et al. (2018) (Table 2). The uncertainty of the predictions for each treatment was assessed according to Gharekhani et al. (2023): projections were repeated for 15 life tables of different percentiles taken from the 100,000 previously bootstrapped cohorts (namely, 0.025, 0.05, 0.1, 0.159, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.841, 0.9, 0.95, and 0.975 percentile). The 15 simulated population sizes at days 7, 14, 21, 28, 35, and 42 were used for bootstrapping the frequency distributions (100,000 bootstraps) in TIMING-MSChart, which were then compared by a paired bootstrap test (Gharekhani et al. 2023). In all of our previous studies using the same aphid–plant system, a stable age-stage distribution was achieved after 35–40 days (Saska et al. 2016, 2021b, 2023; Platková et al. 2020); therefore, we did not perform comparisons after this period.

Results

The plant morphophysiological traits showed the plant responses to the stress regimes applied (Supplementary materials S1). Based on the physiological traits, the highest stress levels were found on plants after stress pulses (corresponding to treatments 40-1, 40-2, and 40-3), which were followed by the continuous stress control (40C) and rewatered plants after the stress pulse (equivalent to 40-0), compared to the well-watered control (70C) (Supplementary materials S1). We could not find any notable damage to photosystem II, according to the F_v/F_m values. The morphological traits were most affected in the continuously stressed plants (Supplementary materials S1).

The experimental treatments affected the life table and population parameters of *M. dirhodum* (Fig. 1; Supplementary materials S2). The survival rates during the nymphal stage were rather high in all treatments and varied between 81 and 91% (Fig. 1a). The lowest survival was observed for the continuous drought control (40C), but none of the pairs of treatments were significantly different from each other (Fig. 1a). The age-stage-specific survival rates (s_{xj}) demonstrated that, due to the variations in the duration of development of particular stages, the nymphal stage overlapped with the adult stage (Supplementary materials S3: Fig. S1). Although the development times of *M. dirhodum* were generally short (7.5–8.5 days on average), there were significant differences across the treatments (Fig. 1b), and pulsed stress treatments timed before and early during aphid development (40–0 and 40–1, respectively) had the greatest negative effect on development times (Fig. 1b). The overall patterns across the treatments in adult (19–24 days on average) and total longevity (23–30 days on average) were very similar to those described above, i.e. the 40–0 and 40–1 treatments lived the longest (Fig. 1c, d).

The effect of drought timing on reproduction was not very prominent. The oviposition period (Fig. 1e) varied with the drought treatments in patterns that were similar to those described for nymphal development or longevity (Fig. 1b, d), but the differences were small (ca. 18–21 days on average). The fecundity was lowest under continuous stress control and highest under the pulsed stress treatment 40-0, i.e. on plants that had recovered from pulsed stress (Fig. 1f), but the difference between the two extremes was not very large (46–54 offspring female⁻¹; Supplementary materials S2: Table S2). Even though the fecundity was highest for the 40–0 treatment, it was not significantly different from that of the well-watered control 70C (Fig. 1f). Cumulative fecundity showed negative effects on fecundity in 40C from the onset of reproduction (Fig. 2). The patterns of differences between the remaining treatments were, however, variable depending on the time (Fig. 2). On day 35, when the production of the new offspring had already stopped, the cumulative fecundity was significantly greatest for 40–0, followed by the remaining three pulsed stress treatments and well-watered control, and lowest in the continuous stress treatment (Fig. 2). The age-specific survival rate (l_x), age-specific fecundity (m_x), net maternity ($l_x m_x$), and age-stage-specific life expectancy (e_{xj}) for each treatment are shown in Supplementary materials S3: Figs S2–S3. The highest age-stage reproductive value (v_{xj}) was estimated to occur at similar ages (e.g., 9–10 days) for all treatments (Supplementary materials S3: Fig. S4).

The values of the intrinsic rate of increase, r , and finite rate of increase, λ , pointed to rapid population growth of *M. dirhodum* under all treatments (Supplementary materials S2: Table S2) and ranged from 0.2674 to 0.2801 d⁻¹ in the case of r and from 1.3065 to 1.3232 d⁻¹ for λ . The lowest r and λ values were observed for the pulsed stress treatments 40-0 and 40-1, i.e. for plants that recovered from or were experiencing pulsed drought during nymphal development, which were significantly lower than the well-water control (Fig. 1g, h). Of the pulsed stress treatments, the highest r and λ values were observed for 40-3 (i.e. plants that experienced drought during the second week of reproduction), which were not significantly different from those of the well-watered control (Fig. 1g–h). The reproduction rates R_0 ranged from 37.8 to 48.5 offspring individual⁻¹ and were lowest under the continuous drought stress control and highest under the pulsed stress treatment 40-0 (Fig. 1i), with a difference of ca. 10.5 offspring individual⁻¹ between these two treatments (Supplementary materials S2: Table S2). The generation times T ranged between 13.5 and 14.5 days and were shortest for both control treatments (e.g. 40C and 70C) and for the pulsed stress treatment 40-3 (Fig. 1j). The values of T for the remaining drought stress treatments were significantly longer compared to both controls, being longest for the pulsed stress treatment 40-0 (Fig. 1j).

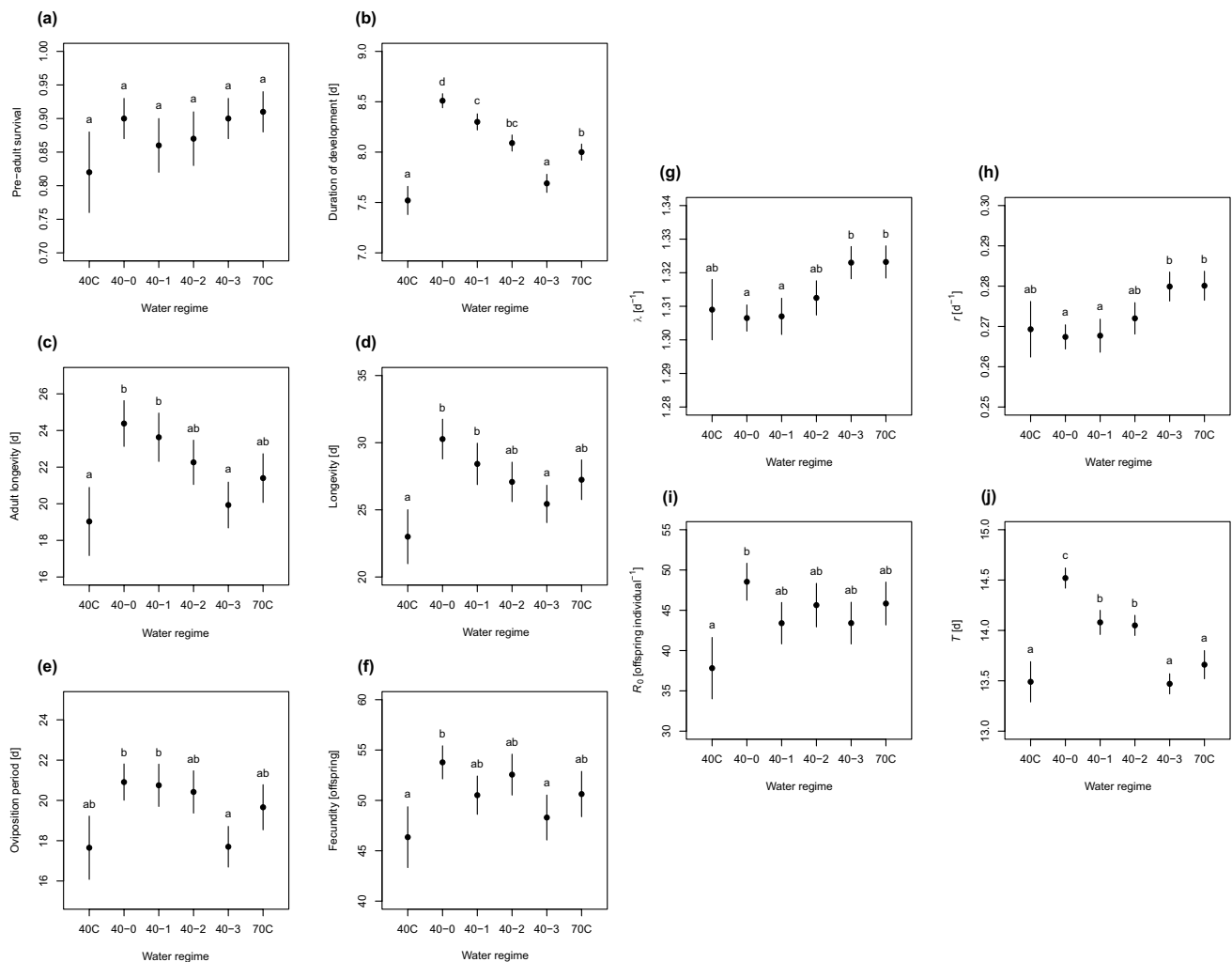


Fig. 1 Life table and population growth parameters for *Metopolophium dirhodum* reared on *Triticum aestivum* under the six water supply regimes. The vertical bars represent the standard errors of the means (SEs) estimated from 100,000 bootstraps. Treatments assigned the same letters do not differ significantly from each

other (paired bootstrap test). The values \pm SEs of all parameters can be found in Supplementary materials S2: Table S2, and differences between treatments with associated p values are shown in Supplementary materials S2: Table S3

The population growth curves (on a logarithmic scale) approached linearity after approximately 35 d (Fig. 3a) for all treatments, which suggests that the aphid populations had reached a stable age-stage distribution. The stable stage distributions were nearly identical for all treatments, as the populations consisted of $90.2 \pm 0.25\%$ nymphs and $9.8 \pm 0.24\%$ females. Although the growth curves seemed to not differ greatly across the treatments (Fig. 3a), the projected population sizes were significantly different for all the time points that were compared (Fig. 3a). The patterns in differences between treatments were notably different among the time points, but approaching the stable age-stage distribution, the overall pattern in the differences between treatments (Fig. 3a) resembled those of r and λ (Fig. 1g-h). This variation in between-group

differences over time occurred because the age-stage distribution fluctuated asynchronously due to prolonged nymph development in some treatments, namely the 40-0, 40-1, and 40-2 pulsed stress treatments (Fig. 1b). Consequently, the age-stage distributions fluctuated asynchronously between the treatments, and the peak in reproduction was delayed in those treatments (Fig. 3b). The projected population sizes after 35 d, when the stable age-stage distribution was reached, were greatest for the well-watered control (65,207 individuals) and pulsed stress treatment 40-3 (66,291), which were followed by the pulsed stress treatment 40-2 (48,270), continuous stress control (46,154), and pulsed stress treatments 40-1 (42,883) and 40-0 (39,661).

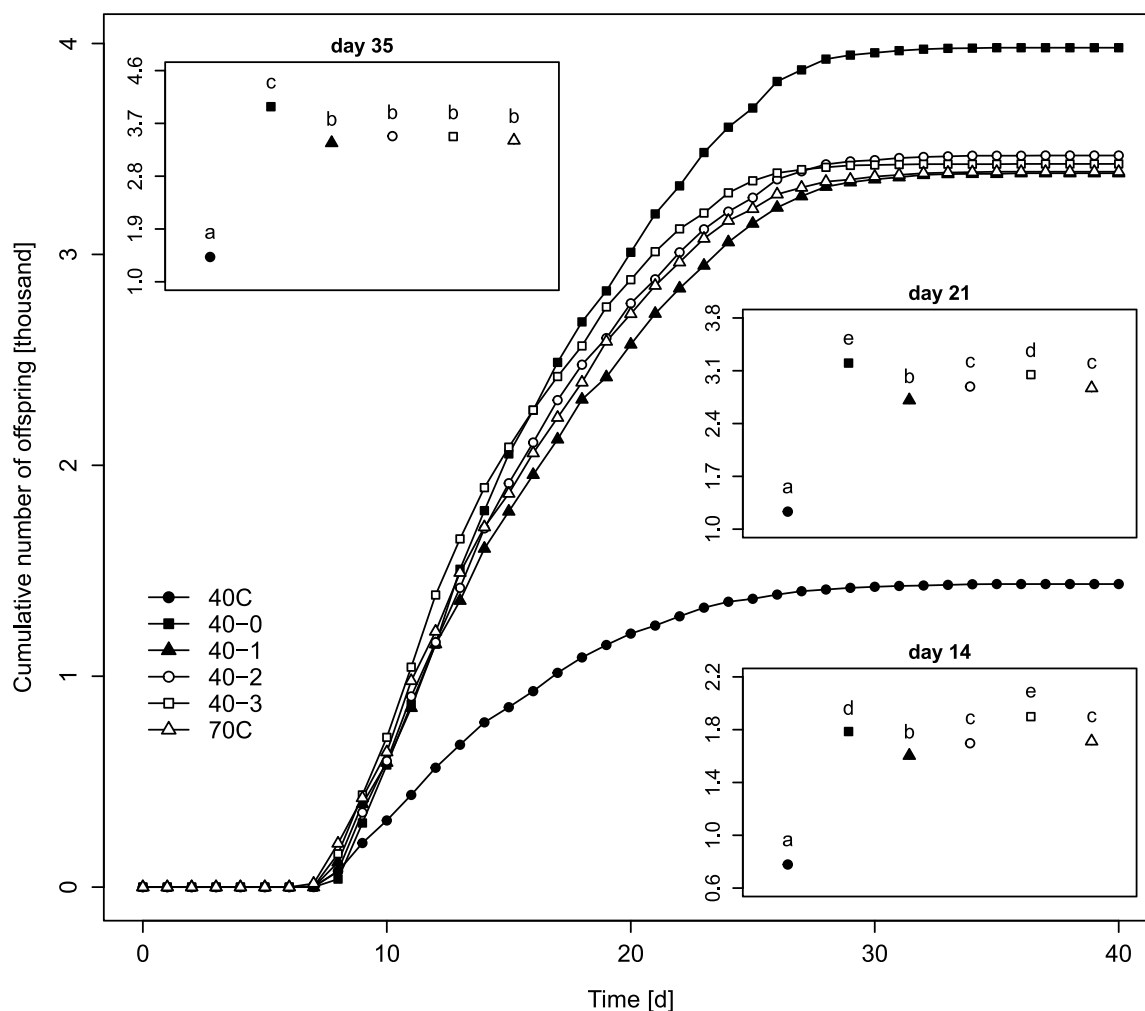


Fig. 2 Cumulative number of offspring (in thousand individuals) produced by cohorts of *Metopolophium dirhodum* on wheat subjected to six water supply levels. Inset figures show the treatment means for days 14, 21, and 35 after the beginning of the experiment. The

vertical bars represent SEs estimated from 100,000 bootstraps after Gharekhani et al. (2023). Treatments assigned the same letters do not differ significantly from each other (paired bootstrap test)

Discussion

The *pulsed stress hypothesis* (Huberty and Denno 2004) predicts that plants hosting fluid-feeding insects that are intermittently stressed by drought are more suitable hosts than well-watered plants or plants subjected to continuous drought. The support for this hypothesis in the literature is, however, inconsistent (Table 1). The test of the *pulsed stress hypothesis* in this study was based on a system consisting of young spring wheat as the host plant and the rose-grain aphid, *M. dirhodum*, as the fluid-feeding insect, and used the age-stage, two-sex life table. This test provided no evidence for the validity of this hypothesis at the population level for this study system and under the experimental conditions of this study. We also found evidence that the timing of the pulsed stress with regard to

the developmental phase of this aphid is important for the magnitude of its effect on population growth.

All the previous tests of the pulsed stress hypothesis were based on using only selected parameters. The advantage of the life table approach compared to collecting only a subset of parameters or following only a limited period of time is that life tables describe changes in the structure of the population and fecundity over time, from which the important parameters can be calculated (r , λ , R_0 , and T) and population projections can be made (Huang et al. 2018; Chi et al. 2020; Gharekhani et al. 2023). Although these predictions are based on data collected in controlled laboratory conditions (i.e. constant temperature, no predation, parasitism or diseases, and no immigration or emigration) and cannot be directly used for forecasting in the field where conditions are more variable, they are still relevant since they describe the potential of the population to grow

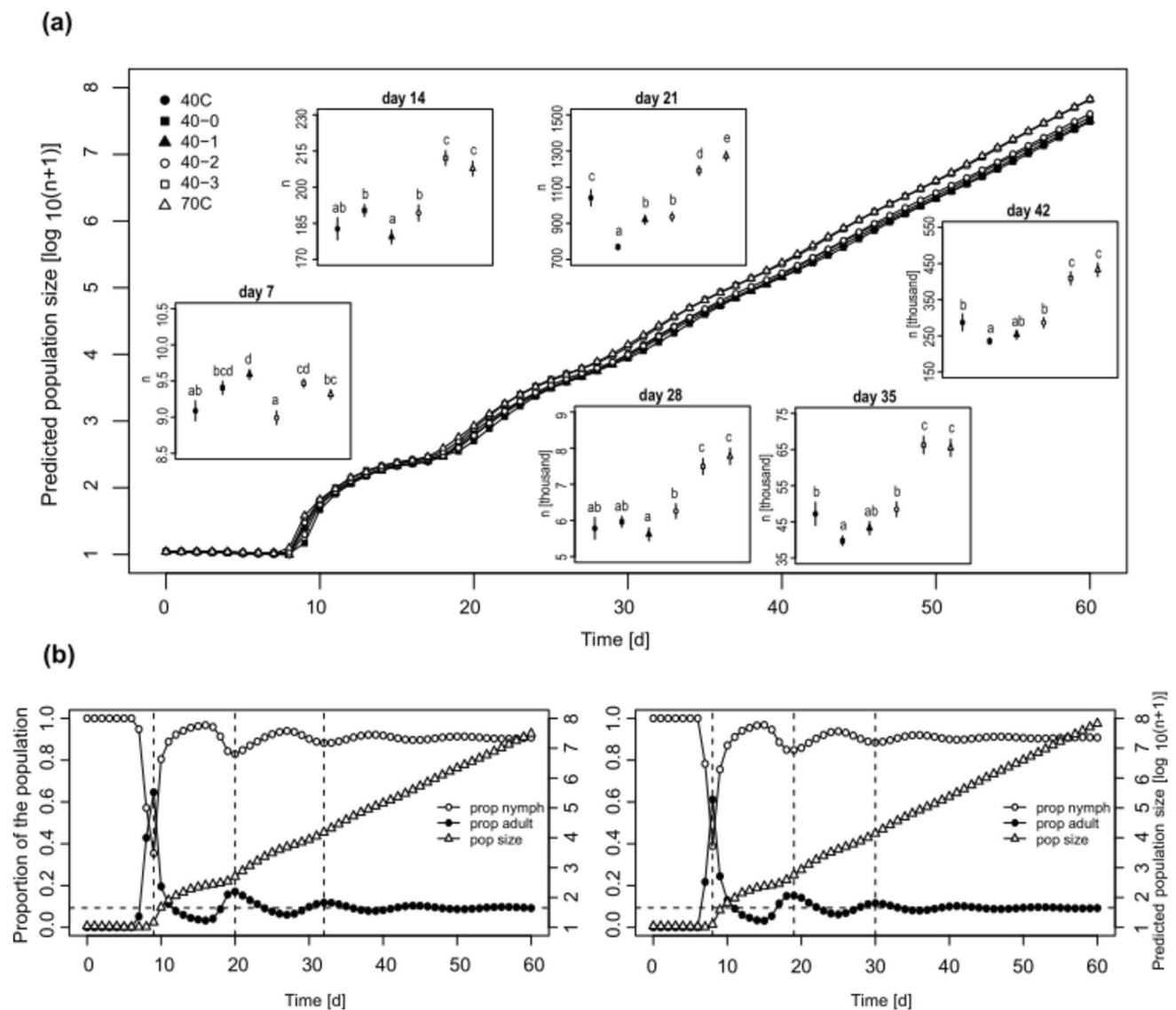


Fig. 3 Population projections and corresponding age-stage distributions for *Metopolophium dirhodum* reared on *Triticum aestivum* under six water supply regimes. The projections are based on the age-stage, two-sex life table theory. **a** Main figure: Predicted courses of population growth ($\log_{10}[n+1]$) for the six treatments. The relationships between time for $d \geq 35$ (after the stable age-stage distribution was reached) and the population sizes for the individual treatments are as follows. 40C: $(\log_{10}[n+1])=0.5415+0.1169d$, 40-0: $(\log_{10}[n+1])=0.5523+0.1154d$, 40-1: $(\log_{10}[n+1])=0.5440+0.1160d$, 40-2: $(\log_{10}[n+1])=0.5396+0.1177d$, 40-3: $(\log_{10}[n+1])=0.5446+0.1214d$, and 70C: $(\log_{10}[n+1])=0.5320+0.1216d$. Note that the slopes are equal to specific values of $\log_{10}(\lambda)$. Inset figures: Predicted population size (n)

for 7, 14, 21, 28, 35, and 42 days from the start of the experiment. The vertical bars represent the SEs estimated from 100,000 bootstraps after Gharekhani et al. (2023). Treatments assigned the same letters do not differ significantly from each other (paired bootstrap test). **b** Changes in the age-stage distribution for the treatments with slowest (40-0; left) and fastest (70C; right) population growth. Note that the magnitudes of the fluctuations (and thus the instability) decrease as stable age-stage distributions are achieved (the dashed horizontal line represents ca. 10% of adults in the population)

under the given combination of factors (Huang and Chi 2012).

Predicted population sizes can be compared at various times. This is very useful for several reasons. First, such a comparison may provide a straightforward measure of an effect. Second, it allows comparisons with other studies

because the time interval for which the aphid populations were followed greatly varied across the studies (Table 1). Third, how the timing of the comparison (or census) affects the conclusions can be assessed. Here, although some hints of the overall trend in differences between the treatments became visible after 14 days, there was still considerable

variation in the significance of these between-treatment differences until the stable age-stage distribution was reached. The patterns in differences between treatments in the predicted population sizes stabilized ca. from day 35 onwards, after the stable age-stage distribution was reached, and followed those of λ . Thus, the population sizes were predicted to be highest for the well-watered control and the 40–3 treatment and comparably lower for the remaining treatments. The lowest number of individuals was predicted for the 40–0 treatment. These results clearly show that the drought timing is important to determine its effect, and if it occurs later (e.g. three weeks after the establishment of the colony), the negative effects of the stress do not ensue. This is fully in accordance with our expectations and with earlier life-table-based results, which showed that the development of nymphs and the early reproduction period had the greatest effects on the rates of population growth (Lewontin 1965; Saska et al. 2021b; 2023). In contrast, Luo and Gilbert (2022) found for *Aphis nerii* reared on *Asclepias syriaca* that population maxima were reached earlier and were lower when the stress occurred 21 days after the beginning of the experiment. This difference may, however, arise because the study systems or the methods of data collection were different. Nevertheless, we can reject the pulsed stress hypothesis at the population level based on our data.

The length of time that the aphid populations were allowed to grow in past studies is, however, important for the relevance of the conclusions drawn from this type of data. Because the fluctuations in population size over time may be asynchronous among populations that are subjected to particular treatments, as in this study, conducting the census too early (e.g. 10–14 days in Mody et al. 2009, or 16 days in Pons et al. 2020) may affect the conclusions since the variability in the population structure was still high, and the population (and stage-specific) growth rate was unstable. We showed that before the stable age-stage distribution was achieved, even a small difference in the nymphal duration of development (1 day in the present study) caused an increase in generation time T and resulted in asynchrony in the population fluctuations across the treatments and consequently in differences between the treatments being time-dependent. Thus, comparing only the numbers of individuals across treatments but without examining the population structure before the stable stage distribution is reached can lead to different conclusions that the stress (or any factor of concern) would have on population growth.

Among the single parameters frequently assessed in the past studies, fecundity received particular attention because it provides a seemingly straightforward measure of an effect. The levels of mean fecundity were not affected by the pulsed stress treatments compared to the well-watered control in this study, which is also in contrast to the results of several earlier studies (Tariq et al. 2012; Banfield-Zanin and Leather

2015b,c). However, the way that fecundity is estimated varies markedly across studies. It usually accumulates over a limited number of days (Kennedy et al. 1958; Major 1990; Banfield-Zanin and Leather 2015c). The major limitation of using fecundity as the main or sole parameter for demonstrating an effect is that neither mortality nor the development rate is included in this measure, which both can compensate for a change in fecundity. This study provides a nice example of how choosing fecundity as the main or single measure of the effect of drought (or any other factor) may lead to improper conclusions on the overall effect of a studied factor on aphid populations. We observed significantly higher mean fecundity for the 40–0 pulsed stress treatment compared to the continuous stress control (but not to the well-watered control; Fig. 1f), which seems to provide support for the *pulsed stress hypothesis*. However, when uneven development rates and $l_x m_x$ curves (Supplementary materials S3: Fig. S2) were also considered and jointly manifested in λ , that particular treatment was found to be inferior for the aphids (Fig. 1g–h). At the population level, the conclusion is therefore opposite to that if only fecundity was used as the measure. Thus, using fecundity as the sole parameter has limited value for reaching conclusions at the population level. Additionally, it was evident that the parameters related to reproduction and development estimated in this study would have suggested contrasting conclusions (e.g. fecundity vs. development time) regarding the validity of the *pulsed stress hypothesis* if they had been considered alone. We therefore advocate collecting full life table data, if possible, to come to more solid conclusions about the effect of drought (or any other factor) on aphid populations.

Despite our abundant criticism of building comparisons solely on a subset of parameters, we acknowledge that collecting data for only selected life history or population parameters may still find some use if the research question is motivated by describing short-term responses of species (e.g. acute toxicity of pesticides in efficacy essays), if the species has little-known biology, if it is difficult to rear, has a long lifespan or its life cycle includes dormancy, even though some of these situations can also be approached at the population level. For example, incorporating diapause into life table research has been recently solved (Amir-Maafi et al. 2022). Toxicity may also manifest sublethally, which is worth studying at the population level to better understand the effects (Saska et al. 2016). The results based on selected parameters can also be utilized in meta-analyses (Huberty and Denno 2004; Leybourne et al. 2021). The authors that have chosen to collect or use only selected parameters in their studies should, however, in any case mention the limitations of their approach, bearing in mind that at the population level, other parameters might cancel out or reverse the trends they observe.

Some field data were also interpreted as supporting the *pulsed stress hypothesis*. Flint et al. (1996) and Sconiers and Eubanks (2017) observed in the field that aphids and whiteflies were more abundant on cotton plants immediately after they were watered after a period of drought stress. This may not, however, mean that these plants were more suitable for aphids; more likely, these plants had become more attractive to aphids due to the improved saturation, which resulted in higher colonization rates by dispersing aphids. This interpretation is supported by the preference experiments of Kennedy et al. (1958) that used *Aphis fabae* on *Euonymus europaeus* and *Vicia faba*, which showed a rapid and positive response of aphids to the rewatered plants. We conclude that using field abundance data alone is not a suitable approach for testing or supporting the *pulsed stress hypothesis*. Nevertheless, controlled field studies at the population level are needed to better understand aphid–plant interactions under climate change scenarios, including drought.

There are possible limitations of the approach used in this study, which may limit the translation of our results to the field. This is particularly associated with the weekly transfer of aphids to new young plants, which may to some extent interrupt the tight relationship between plants and aphids. A large body of literature is based on the transference of insects from plant to plant or from leaf to leaf (Schoonhoven et al. 2005). It is possible that transferring aphids is stressful for them and may worsen their performance. In contrast, providing a constant supply of young plant material that has been previously non-infested may provide better food resources and, in this way, improve performance. It would be useful to conduct a comparative life table study focusing on the possible effects of these transfers on population growth. Nevertheless, cereal aphids leave the plants regularly in the field and naturally disperse by means of walking (Ben-Ari et al. 2015); therefore, transferring aphids in our experiment has some biological basis since aphids often might not stay for their entire lifetime on a single host. Our study considered only a single pulse of stress. This is a simplified situation compared to the field, where plants likely experience multiple stress events during the growing season or the stress periods are longer (Mittler 2006). Of the available studies (Table 1), several included multiple pulses of drought (e.g. Tariq et al. 2012; Simpson et al. 2012; Pons et al. 2020), with inconsistent results. Studies are needed to reveal how aphids respond to single compared to multiple pulses of stress at the population level.

In summary, our data do not provide support for the validity of the *pulsed stress hypothesis* for this study system at the population level because pulsed stress did not improve the performance or population growth of *M. dirhodum* on spring wheat compared to the well-watered control. The support for the *pulsed stress hypothesis* in the literature is largely based on short-term effects, while we stress that the effects

at the population level are more important. We conclude that the general validity of the *pulsed stress hypothesis* remains questionable since solid support at the population level is currently lacking.

Author contribution

PS, JS, PV, and SJT done conceptualization; JS, HP, KK, and PV collected the data; PS and HP performed formal analysis; PS did writing—original draft preparation; all authors contributed to writing—review and editing; PS and SJT were involved in funding acquisition.

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Declarations

Conflict of interest The authors have declared no conflicts of interest.

Data availability Data available at <https://doi.org/https://doi.org/10.5281/zenodo.6299859>.

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