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Research Article

Interactive effects of irrigation and nitrogen regimes on *Rhopalosiphum padi* demography in drought-tolerant and drought-sensitive barley cultivars

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ABSTRACT- Sustainable control of cereal aphids under climate change requires a mechanistic understanding of how water and nutrient management interact with host drought tolerance to shape pest demography. The oat leaf aphid, *Rhopalosiphum padi* L., is a persistent constraint in cereal systems, yet its responses to combined abiotic and nutritional stress remain unclear. We evaluated irrigation and nitrogen effects on aphid life history across two barley cultivars differing in drought sensitivity. Plants were grown under three soil moisture levels (100%, 75%, and 50% field capacity) and three nitrogen rates (0, 75, and 150 mg N kg^{-1} soil), and aphid demographic parameters were quantified using the age–stage, two-sex life table. The design quantified non-linear interactions among host drought tolerance, water availability, and nitrogen supply. The drought-tolerant cultivar 'Sararood' constrained aphid development and reproduction, particularly under water deficit, resulting in prolonged development and reduced intrinsic rates of increase (*r*), from 0.2272 d^{-1} on 'Afzal' under optimal irrigation to 0.0090 d^{-1} on 'Sararood' under severe water stress. In contrast, aphids on the drought-sensitive cultivar 'Afzal' showed rapid population growth under full irrigation but showed collapse under drought. Nitrogen effects were context-dependent and interacted with both moisture regime and cultivar physiology; while nitrogen fertilization had negligible effects on developmental duration, it reduced the intrinsic rate of increase under severe drought in 'Afzal'. Notably, moderate irrigation combined with moderate nitrogen on 'Sararood' minimized aphid population growth, a resource-efficient regime. These results highlight co-optimization of cultivar choice with precision irrigation and fertilization as a climate-smart integrated pest management (IPM) strategy.

INTRODUCTION

Insect herbivores persist as a critical biotic constraint on global agricultural productivity, accounting for an estimated 15% annual yield loss in major cropping systems (Maxmen, 2013). The bird cherry-oat aphid, *Rhopalosiphum padi* L., a globally pervasive pest of cereal crops, inflicts substantial yield losses through direct feeding and viral pathogen transmission (Finley and Luck, 2011; Yang et al., 2025). Its population dynamics are fundamentally structured by soil moisture availability, which regulates host plant nutrient status, turgor pressure, and constitutive defensive responses (Huberty and Denno, 2004; Jamieson et al., 2012). While irrigation and soil fertility represent the two primary levers of agronomic management, their integrated and potentially synergistic impacts on pest population dynamics remain insufficiently quantified, especially across different host plant genotypes (Subedi et al., 2023; Nega, 2025).

Contemporary agricultural intensification, defined by high-input synthetic fertilization and expansive monocultures, has fundamentally reconfigured agroecosystem ecology, frequently exacerbating herbivore pressure on staple grains by altering bottom-up regulatory forces (Tilman et al., 2011; Hamann et al., 2021). Additionally, soil moisture variability, and specifically water-induced plant stress, exerts a profound yet context-dependent influence on plant–insect interactions by directly modulating host plant physiology and nutritional composition. Inorganic nitrogen (N) fertilization, a cornerstone of intensive agriculture, dramatically reshapes host plant nutritional physiology, frequently enhancing the fitness of phloem-feeding aphids (Nevo and Coll, 2001; Tamburini et al., 2018; Kansman et al., 2020). This is driven by elevated phloem amino acid concentrations and altered plant carbon-to-nitrogen ratios, which can accelerate aphid development and increase reproduction (Nevo and Coll, 2001; Tamburini et al., 2018; Sun et al., 2020). Similarly, water availability critically determines physiological alterations in host plants—including shifts in phloem composition and turgor pressure—that directly affect aphid performance (Huberty and Denno, 2004; Nachappa et al.,

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2016; Xie et al., 2022). Given the intrinsic linkage between soil moisture and nutrient bioavailability (Lal, 2020; Xing et al., 2024), irrigation and fertilization likely interact in complex, non-linear ways to shape aphid populations. Yet, empirical studies systematically dissecting these interactions across co-varying gradients remain scarce (Tamburini et al., 2018; Zaffaroni et al., 2020), limiting predictive frameworks for managed ecosystems.

Population dynamics of *R. padi* are highly sensitive to abiotic and nutritional factors, with outbreaks often linked to specific irrigation and nitrogen regimes (Ahmad et al., 2016; Aleosfoor et al., 2023). Critically, the host plant genotype is a fundamental mediator of these effects; however, it is unclear how barley cultivars with divergent drought tolerance modulate the interactive effects of water and nitrogen on *R. padi* demography.

Although water stress and nitrogen availability independently alter *R. padi* performance (Ponder et al., 2001; Hale et al., 2003), their concurrent effects are poorly understood. This study tests the hypothesis that irrigation and nitrogen regimes interact to shape *R. padi* population dynamics, and that this interaction is mediated by host cultivar drought tolerance. Using a multifactorial design, we aimed to: (I) quantify the individual and interactive effects of nitrogen and water stress on aphid population growth, (II) evaluate their impact on key demographic traits, and (III) assess the role of barley cultivar drought tolerance in mediating these effects. This integrative approach provides a foundation for optimizing agronomic practices to enhance resilience against aphid outbreaks in climate-adaptive cereal production.

MATERIALS AND METHODS

Insect rearing

A laboratory colony of *R. padi* was established from individuals collected at the Plant Protection Research Center, School of Agriculture, Shiraz University (29°43′N, 52°35′E). Single aphids were transferred with a fine camel-hair brush to Nik barley seedlings maintained in ventilated cages under greenhouse conditions (24 ± 1 °C, 60 ± 5% relative humidity (RH), and 16:8 light: dark (L:D) photoperiod). The colony was renewed weekly by infesting new seedlings to maintain vigor.

Plant cultivation

Barley (*Hordeum vulgare* L.) plants were grown under controlled greenhouse conditions using three cultivars: 'Karoon' (for aphid colony establishment), experimental cultivars 'Afzal' (drought-sensitive), and 'Sararood' (drought-tolerant). For experiments, eight seeds per cultivar were sown in 2-kg pots containing a 1:1 (w/w) mixture of sterilized sand and field soil. Seedlings were thinned to four plants pot^{-1} at the three-leaf stage (~2 weeks post-sowing). Each treatment comprised 40 replicate pots (n = 40), where one pot served as one experimental unit, containing four plants from which one individual plant was selected for aphid monitoring (n = 40 aphids treatment^{-1}). Soil field capacity was determined gravimetrically as 20% (w/w) using a pressure plate apparatus (Soil Science Department, Shiraz University).

Experimental design and treatments

The present study was conducted using a factorial arrangement within a completely randomized design. The factorial design included two barley cultivars ('Afzal' and 'Sararood'), three irrigation regimes (50%, 75%, and 100% FC), and three nitrogen fertilizer levels (0, 75, 150 mg N kg^{-1} soil), resulting in a total of 18 treatments (Table 1). Each treatment was replicated 40 times.

Table 1. Factorial experimental design showing the combinations of barley cultivar, irrigation regime (% of field capacity, FC), and nitrogen (N) fertilization level, with corresponding treatment abbreviations

No.	Cultivar	Irrigation (%)	Fertilizer level (mg kg^{-1})	Abbreviation
1	Afzal	50	0	A50N0
2	Afzal	50	75	A50N75
3	Afzal	50	150	A50N150
4	Afzal	75	0	A75N0
5	Afzal	75	75	A75N75
6	Afzal	75	150	A75N150
7	Afzal	100	0	A100N0
8	Afzal	100	75	A100N75
9	Afzal	100	150	A100N150
10	Sararood	50	0	S50N0
11	Sararood	50	75	S50N75
12	Sararood	50	150	S50N150
13	Sararood	75	0	S75N0
14	Sararood	75	75	S75N75
15	Sararood	75	150	S75N150
16	Sararood	100	0	S100N0
17	Sararood	100	75	S100N75
18	Sararood	100	150	S100N150

Application of urea nitrogen fertilizer

Nitrogen was applied as urea at three rates: 0, 75, and 150 mg N kg^{-1} soil. The urea fertilizer (Kermanshah Petrochemical Industries Company, Iran) was dissolved in deionized water and uniformly incorporated into the sterilized bulk soil of each pot prior to sowing to ensure homogeneous nitrogen availability. The treated soil was then thoroughly mixed and allowed to equilibrate for 24 h before planting.

Application of water stress

The field capacity (FC) of the experimental soil was determined to be 20% (w/w). Accordingly, the amount of water required to bring the soil to FC was calculated as 200 mL kg^{-1} soil. Until the four-leaf stage, all plants were maintained at FC by daily weighing and replenishing water loss. Thereafter, irrigation treatments were imposed: control plants continued to receive 100% FC, while water-stress (WS) treatments received either 75% or 50% of the water required to reach FC. Soil moisture was maintained at these target levels by daily pot weighing, and the calculated water volume was applied using graduated cylinders.

Life table study

Age-synchronized first-instar nymphs (≤ 12 h old) were used as experimental starting stage. Leaf cages were constructed from Petri dishes (90 mm diameter) with mesh-covered ventilation holes (800 mesh) in lids and lateral slits for barley leaf insertion, mounted on wooden stands. Fifty gravid adult females were confined individually in cages on barley plants for 24 h to produce nymphs. Adults were then removed, leaving one nymph per cage; this nymph developed to adulthood, and its progeny served as the experimental cohort.

Five days after plants reached the four-leaf stage (~31 days post-sowing for 'Afzal'; ~35 days for 'Sararood'), one cage containing a single first-instar nymph was affixed to the third leaf of each of the four plants per pot (n = 40 aphids $treatment^{-1}$). Daily observations recorded nymphal development, mortality, and exuviation (molted skins) until adulthood. Reproductive output was then monitored daily—nymphs counted and removed—until aphid death.

Life table analysis

Demographic parameters were calculated using the age-stage, two-sex life table method (Chi, 1988; Chi and Liu, 1985) as implemented in TWOSEX-MSChart program (Chi, 2025). Raw life history data consisted of individual aphid records (n = 40 aphids per treatment), where each first-instar nymph placed on a unique plant within a replicate pot served as an independent observation. Life table parameters were constructed directly from these individual-level data without prior averaging per pot or per plant, following standard age-stage methodology that preserves cohort variability. To accurately assess parameter variability and statistical significance, a non-parametric bootstrap technique (Efron and Tibshirani, 1993; Wei et al., 2020) with 100,000 replicates was applied, enabling precise estimation of the means and standard errors (Chi et al., 2022). Statistical comparisons of population parameters, developmental durations, and fecundity among treatments were performed using bootstrap-based pairwise analyses at the 5% significance level (TWOSEX-MSChart, version 2025). Given the stage-structured nature of age-stage life table data and the non-parametric bootstrap approach employed, formal parametric tests of interaction effects (e.g., two-way ANOVA) were not feasible; thus, only main effects of cultivar, irrigation, and nitrogen were statistically evaluated via pairwise bootstrap tests. Potential interactive patterns among treatments were instead discerned and interpreted qualitatively from treatment-specific trends and graphical representations of demographic parameters across factor combinations. Graphs were created in SigmaPlot 14.0.

RESULTS

Duration of developmental stages

Developmental times of *R. padi* were predominantly driven by host cultivar and irrigation regime, with nitrogen fertilization having negligible effects (Table 2). Aphids reared on the drought-sensitive cultivar 'Afzal' completed pre-adult development significantly faster than those on the drought-tolerant 'Sararood', regardless of treatment. Pre-adult duration ranged from 8.16–8.80 days on 'Afzal', compared to 11.14–12.16 days on 'Sararood'.

Water stress acted as a major constraint, shortening both development and adult lifespan. Under severe water stress (50% FC), pre-adult development was fastest and adult female longevity was most reduced in both cultivars. For example, longevity on 'Afzal' at 50% FC ranged from 33.80–35.17 days, and on 'Sararood' from 30.62–34.31 days. Increasing irrigation to 75% and 100% FC progressively extended both developmental time and longevity.

In contrast, nitrogen level (0–150 mg N kg^{-1}) did not significantly alter the duration of any developmental stage within a given irrigation regime for either cultivar. This confirms that under these experimental conditions, host plant genotype and water availability are the primary determinants of *R. padi* developmental physiology, while the influence of nitrogen is minimal. While aphid longevity generally differed between the two cultivars, these patterns were strongly modulated by the interplay of irrigation and nitrogen regimes. Under optimal irrigation (100% FC), female longevity was generally longer on 'Sararood' than on 'Afzal'. However, under severe water deficit (50% FC), this trend was altered, with 'Sararood' exhibiting significantly reduced longevity that was often comparable to or lower than that observed on 'Afzal' at certain nitrogen levels. Thus, the demographic impact of the host cultivar is context-dependent, being contingent upon the severity of the water stress and nitrogen supply. The most pronounced reduction in female longevity occurred under the 50% FC regime across all nitrogen treatments.

Population growth of R. padi in response to host cultivar, irrigation regime, and nitrogen fertilization

Host cultivar and irrigation regime were the dominant drivers of *R. padi* population growth parameters, while nitrogen fertilization had secondary, context-dependent

effects (Table 3). Across all treatments, aphids reared on the drought-sensitive cultivar 'Afzal' exhibited higher intrinsic rate of increase (r), finite rate of increase (λ), and net reproductive rate (R_0), and a shorter mean generation time (T), compared to on the drought-tolerant cultivar 'Sararood'. This demonstrates a strong host-plant-mediated constraint on aphid population performance across all treatment combinations. For example, under optimal irrigation (100% FC, 0 mg N kg^{-1}), r and R_0 were 0.2272 d^{-1} and 78.67 offspring per individual on 'Afzal' versus 0.1557 d^{-1} and 66.32 offspring on 'Sararood', respectively.

Water availability strongly modulated aphid performance. Severe water stress (50% FC) markedly reduced r, λ, and R_0 on both cultivars, with values increasing progressively as irrigation rose to 75% and 100% FC. This response was particularly pronounced on 'Sararood', where r plummeted to 0.0090 d^{-1} under severe stress (50% FC, 0 N). T was generally shorter under water-limited conditions and longer under optimal irrigation.

The effects of nitrogen fertilization were contingent on water availability. On 'Afzal', high nitrogen input (150 mg N kg^{-1}) under water stress suppressed r and R_0 (e.g., r decreased from 0.1857 to 0.1660 d^{-1} at 50% FC). In contrast, under 100% FC, nitrogen levels did not negatively affect growth parameters; R_0 even increased numerically with higher nitrogen, suggesting sufficient water buffers potential negative effects. On 'Sararood', nitrogen-induced changes in demographic parameters were minor and inconsistent across irrigation regimes.

Overall, host cultivar and water availability are the principal factors shaping the population growth potential of *R. padi*, whereas nitrogen fertilization within the tested range exerts a comparatively minor and context-dependent influence. The consistently lower r, λ, and R_0, coupled with a longer T on 'Sararood', indicate that cultivar-mediated host quality strongly constrains aphid population increase.

Duration of the pre-reproductive periods and fecundity

Adult pre-reproductive period (APRP) (days), and the total pre- reproductive period (TPRP), nymph production days (NPD), and fecundity of *R. padi* are summarized in Table 4. Cultivar effects dominated reproductive traits across treatments. Aphids on drought-sensitive 'Afzal' showed consistently shorter APRP (2.60–3.02 days) and TPRP (11–12 days) than on drought-tolerant 'Sararood' (APRP: 3.10–4.94 days; TPRP: 15–16 days), indicating delayed reproductive maturation on 'Sararood'.

Irrigation regime strongly influenced reproductive output. Severe water stress (50% FC) reduced fecundity ('Afzal': 37–49 nymphs female^{-1}; 'Sararood': 10–13 nymphs female^{-1}) and shortened NPD ('Afzal': ~26–27 days). Optimal irrigation (100% FC) maximized fecundity 'Afzal': ~96 nymphs female^{-1}; 'Sararood': ~69–72 nymphs female^{-1}) and extended NPD (~28–31 days).

Nitrogen effects were context-dependent and secondary. On 'Afzal', moderate to high N under optimal irrigation caused a slight, non-significant increase in fecundity ($P > 0.05$), whereas the same N levels under water stress non-significantly suppressed fecundity relative to the N-free control ($P > 0.05$). On 'Sararood', N effects remained minor ($P > 0.05$) across irrigation regimes, although moderate nitrogen occasionally showed non-significant enhancement of fecundity under favorable irrigation.

In summary, reproductive performance was primarily governed by host cultivar and irrigation. The drought-sensitive 'Afzal' supported faster reproduction and higher fecundity, whereas the drought-tolerant 'Sararood' imposed greater constraints, particularly under water deficit.

Nitrogen fertilization (75 and 150 mg N kg^{-1}) partially mitigated mortality under severe WS, although survival rates did not reach those observed under 100% or 75% FC, indicating that elevated nitrogen can alleviate but cannot fully compensate for the detrimental effects of drought on aphid survival (Leybourne et al., 2021; Kansman et al., 2022).

On the drought-tolerant cultivar 'Sararood', early nymphal instars (N1-N2) exhibited high survival across all irrigation regimes, with only a slight reduction under severe water stress (50% FC). Moderate (75 mg N kg^{-1}) and high (150 mg N kg^{-1}) nitrogen levels further improved early-instar survival under well- and moderately irrigated conditions. Fourth-instar nymphs (N4), however, proved highly sensitive to drought, exhibiting substantial mortality at 50% FC— albeit partially ameliorated by nitrogen supplementation. Female survival mirrored these trends, peaking under full irrigation and high nitrogen, and under water deficit (Fig. 1). These patterns on 'Sararood' suggest cultivar-mediated stability in aphid performance under moderate water limitation when nitrogen is adequate.

On the drought-sensitive cultivar 'Afzal', survival remained high under 100% FC, with 150 mg N kg^{-1} yielding optimal outcomes. Survival declined progressively at 75% FC and plummeted under severe stress (50% FC), irrespective of nitrogen level. Early instars (N1–N2) displayed moderate drought tolerance, whereas late instars (N3–N4) suffered high mortality—particularly at low nitrogen levels. Adult females exhibited parallel declines under water-limited conditions (Fig. 2).

On 'Afzal' cultivar (Fig. 3), l_x declined progressively with decreasing soil moisture, with the steepest reduction under 50% FC. At 100% FC, l_x decreased during the initial 10 days, reflecting early-instar mortality, after which survivorship remained relatively stable until approximately days 38–40, followed by a sharp decline associated with the onset of senescence. Under 75% and 50% FC, the l_x curves showed accelerated mortality, with the most pronounced decline occurring under severe stress. Nitrogen fertilization modulated these patterns; the highest N rate (150 mg N kg^{-1} soil) partially mitigated the survival reductions at 75% FC, but could not compensate for the severe mortality at 50% FC. Both f_x and m_x peaked during early adulthood and were maximized under full irrigation combined with high nitrogen. They were strongly suppressed by water deficit, particularly at 50% FC across all N levels. Correspondingly, the net reproductive maternity ($l_x m_x$) was highest under no WS and elevated nitrogen, with peaks becoming delayed and diminished as WS intensified.

On the drought-tolerant cultivar 'Sararood' (Fig. 4), *R. padi* survival rates exhibited relative resilience to moderate WS, with survivorship at 75% FC moderately reduced compared to full irrigation (100% FC) but remaining substantially higher than under severe WS (50% FC). Although survival declined at 50% FC, the reduction was less severe than on 'Afzal', reflecting the cultivar's inherent drought tolerance. The fecundity parameters (f_x and m_x) on 'Sararood' exhibited notable stability across irrigation regimes: reduced soil moisture (75% and 50% FC) decreased fecundity relative to

100% FC, but these declines were moderate and less severe than those recorded on 'Afzal'. The age-specific fecundity curves under WS maintained discernible peaks, indicating persistent reproductive activity. Correspondingly, age-specific maternity ($l_x m_x$) displayed clear peaks under full irrigation and high nitrogen; although peak height was attenuated under WS, it remained substantial and biologically meaningful, indicating preserved reproductive potential.

Across all treatments, adult female aphids consistently exhibited the highest e_{xj} compared to the corresponding nymphal instars, a demographic pattern consistent with the alignment of reproductive investment and extended residual lifespan in aphids (Fig. 5 and Fig. 6). Notably, this pattern was robust irrespective of irrigation or soil nitrogen level, reflecting an inherent demographic advantage for mature females. Under 100% FC, e_{xj} was maximized for both nymphs and adults in both cultivars. The magnitude of this increase, however, was more substantial on the drought-tolerant 'Sararood', particularly under combined high nitrogen fertilization, where aphids achieved the greatest life expectancy, indicating a positive effect of resource abundance on population persistence. Reduced significantly reduced aphid life expectancy, with the degree of decline being cultivar-dependent. On 'Sararood', e_{xj} declined progressively as WS intensified (100% FC > 75% FC > 50% FC). A similar declining trend occurred on 'Afzal' but was more severe. In particular, aphids on 'Afzal' under severe water stress combined with no nitrogen supplementation (A50N0) showed the steepest reductions in e_{xj}, indicating heightened vulnerability of aphid cohorts to compounded abiotic stress on this drought-sensitive cultivar. By contrast, 'Sararood' consistently supported higher e_{xj} values across all treatments, demonstrating a cultivar-mediated buffering effect against the negative impacts of water and nutrient stress on aphid longevity.

Table 2. Effects of irrigation regimes and nitrogen fertilizer levels on the mean (± SE) pre-adult developmental duration and total female longevity of *Rhopalosiphum padi* (L.) on two barley cultivars ('Afzal': drought-sensitive; 'Sararood': drought-tolerant) under greenhouse conditions

Cultivar	Irrigation (%)	Fertilizer level (mg kg^{-1})	1st Nymph duration (days)	2nd Nymph duration (days)	3rd Nymph duration (days)	4th Nymph duration (days)	pre-adult developmental time (days)	Adult female longevity (days)
Afzal	50	0	2.15 $^{bA\beta}$ ± 0.06	1.94 $^{bA\alpha}$ ± 0.08	1.70 $^{bA\alpha}$ ± 0.09	2.48 $^{bA\alpha}$ ± 0.09	8.28 $^{bA\alpha}$ ± 0.12	35.17$^{aA\beta}$ ± 0.92
Afzal	50	75	2.35 $^{bA\alpha}$ ± 0.07	1.97 $^{bA\alpha}$ ± 0.08	1.71 $^{bA\beta}$ ± 0.08	2.30 $^{bA\alpha}$ ± 0.10	8.16 $^{bA\beta}$ ± 0.10	33.80$^{aA\gamma}$ ± 0.79
Afzal	50	150	2.17 $^{bA\beta}$ ± 0.05	1.77 $^{bA\alpha}$ ± 0.08	1.94 $^{bA\alpha}$ ± 0.08	2.47 $^{bA\alpha}$ ± 0.08	8.35 $^{bA\alpha}$ ± 0.12	34.52 $^{aA\beta}$ ± 0.72
Afzal	75	0	2.37 $^{bA\alpha}$ ± 0.08	1.90 $^{bA\alpha}$ ± 0.05	1.90$^{bAB\alpha}$ ± 0.06	2.36 $^{bA\alpha}$ ± 0.10	8.52 $^{bA\alpha}$ ± 0.12	37.10 $^{bA\alpha}$ ± 0.72
Afzal	75	75	2.32 $^{bA\alpha}$ ± 0.07	1.90 $^{bA\alpha}$ ± 0.07	2.05 $^{bA\alpha}$ ± 0.09	2.27 $^{bA\alpha}$ ± 0.08	8.51 $^{bA\alpha}$ ± 0.15	36.81 $^{bA\beta}$ ± 0.63
Afzal	75	150	2.40 $^{bA\alpha}$ ± 0.07	1.87 $^{bA\alpha}$ ± 0.07	1.71 $^{bB\alpha}$ ± 0.09	2.39 $^{bA\alpha}$ ± 0.10	8.36 $^{bA\alpha}$ ± 0.11	36.21 $^{bA\alpha}$ ± 0.93
Afzal	100	0	2.27 $^{bA\alpha}$ ± 0.07	1.90 $^{bA\alpha}$ ± 0.08	1.97$^{bA\alpha}$ ± 0.10	2.42 $^{bA\alpha}$ ± 0.08	8.52 $^{bA\alpha}$ ± 0.13	35.81 $^{bB\alpha}$ ± 0.60
Afzal	100	75	2.47 $^{bA\alpha}$ ± 0.07	2.00 $^{bA\alpha}$ ± 0.09	1.84 $^{bA\alpha}$ ± 0.10	2.47 $^{bA\alpha}$ ± 0.09	8.80 $^{bA\alpha}$ ± 0.15	39.27 $^{bA\alpha}$ ± 0.52
Afzal	100	150	2.40 $^{bA\alpha}$ ± 0.07	1.85 $^{bA\alpha}$ ± 0.07	1.87 $^{bA\alpha}$ ± 0.09	2.39 $^{bA\alpha}$ ± 0.07	8.52 $^{bA\alpha}$ ± 0.10	38.10 $^{bA\alpha}$ ± 0.70
Sararood	50	0	2.79 $^{aA\gamma}$ ± 0.11	2.74 $^{aA\alpha}$ ± 0.07	2.94 $^{aA\alpha}$ ± 0.10	2.94 $^{aA\beta}$ ± 0.13	11.14 $^{aA\beta}$ ± 0.16	34.31 $^{aA\beta}$ ± 0.61
Sararood	50	75	2.87 $^{aA\beta}$ ± 0.12	2.57 $^{aA\beta}$ ± 0.08	2.79 $^{aA\alpha}$ ± 0.09	3.05 $^{aA\alpha}$ ± 0.09	11.33 $^{aA\beta}$ ± 0.14	31.86 $^{aB\gamma}$ ± 0.92
Sararood	50	150	3.00 $^{aA\alpha}$ ± 0.13	2.70 $^{aA\alpha}$ ± 0.08	2.80 $^{aA\alpha}$ ± 0.09	3.00 $^{aA\beta}$ ± 0.08	11.42 $^{aA\beta}$ ± 0.10	30.62 $^{bB\gamma}$ ± 0.86
Sararood	75	0	3.50 $^{aA\alpha}$ ± 0.11	2.72 $^{aA\alpha}$ ± 0.10	2.64 $^{aA\alpha}$ ± 0.11	3.18 $^{aA\alpha}$ ± 0.13	12.16 $^{aA\alpha}$ ± 0.19	51.32 $^{bA\alpha}$ ± 1.17
Sararood	75	75	3.25 $^{aAB\alpha}$ ± 0.11	2.66 $^{aA\alpha}$ ± 0.09	2.81 $^{aA\alpha}$ ± 0.12	3.25 $^{aA\alpha}$ ± 0.10	12.11 $^{aA\alpha}$ ± 0.18	47.58 $^{aB\beta}$ ± 1.15
Sararood	75	150	3.17 $^{aB\alpha}$ ± 0.11	2.65 $^{aA\alpha}$ ± 0.09	2.81 $^{aA\alpha}$ ± 0.10	3.24 $^{aA\alpha}$ ± 0.12	11.91 $^{aA\alpha}$ ± 0.17	47.43 $^{aB\beta}$ ± 1.11
Sararood	100	0	3.12 $^{aA\beta}$ ± 0.11	2.76 $^{aA\alpha}$ ± 0.10	2.50 $^{aA\alpha}$ ± 0.10	3.44 $^{aA\alpha}$ ± 0.11	11.84 $^{aA\alpha}$ ± 0.14	54.34 $^{aAB\alpha}$ ± 1.31
Sararood	100	75	3.17 $^{aA\alpha}$ ± 0.12	2.89 $^{aA\alpha}$ ± 0.09	2.52 $^{aA\alpha}$ ± 0.10	3.29 $^{aA\alpha}$ ± 0.10	11.81 $^{aA\alpha}$ ± 0.14	53.05 $^{aB\alpha}$ ± 1.07
Sararood	100	150	3.29 $^{aA\alpha}$ ± 0.14	2.75 $^{aA\alpha}$ ± 0.10	2.67 $^{aA\alpha}$ ± 0.10	3.44 $^{aA\alpha}$ ± 0.09	12.13 $^{aA\alpha}$ ± 0.19	56.86 $^{aA\alpha}$ ± 0.91

Different lowercase letters in columns indicate significant differences between cultivars within the same irrigation and fertilizer levels; different uppercase letters indicate significant differences among irrigation levels within the same cultivar and fertilizer level; different lowercase Greek letters indicate significant differences among fertilizer levels within the same cultivar and irrigation regimes ($P < 0.05$) based on bootstrap comparisons.

Table 3. Effects of irrigation regimes and nitrogen fertilizer levels on key population growth parameters including intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), and mean generation time (T) of *Rhopalosiphum padi* (L.) on two barley cultivars ('Afzal': drought-sensitive; 'Sararood': drought-tolerant) under greenhouse conditions

Cultivar	Irrigation (%)	Fertilizer level (mg kg^{-1})	Intrinsic rate of increase (r) (d^{-1})	Finite rate of increase (λ) (d^{-1})	Net reproductive rate (R_0) (offspring/ individual)	Mean generation time (T) (days)
Afzal	50	0	0.1857 $^{aA\gamma}$ ± 0.0044	1.2041 $^{aA\gamma}$ ± 0.0055	42.52 $^{aA\gamma}$ ± 2.82	20.18 $^{bA\alpha}$ ± 0.27
Afzal	50	75	0.1825 $^{aA\gamma}$ ± 0.0043	1.2002 $^{aA\gamma}$ ± 0.0051	39.05 $^{aA\gamma}$ ± 2.33	20.07 $^{bA\alpha}$ ± 0.31
Afzal	50	150	0.1660 $^{aB\gamma}$ ± 0.0048	1.1806 $^{aB\gamma}$ ± 0.0057	31.62 $^{aB\gamma}$ ± 2.34	20.79 $^{bA\alpha}$ ± 0.32
Afzal	75	0	0.1994 $^{aA\beta}$ ± 0.0036	1.2207 $^{aA\beta}$ ± 0.0044	57.02 $^{aA\beta}$ ± 2.44	20.27 $^{bA\alpha}$ ± 0.26
Afzal	75	75	0.1940 $^{aA\beta}$ ± 0.0037	1.2141 $^{aA\beta}$ ± 0.0045	52.32 $^{aA\beta}$ ± 2.55	20.39 $^{bA\alpha}$ ± 0.29
Afzal	75	150	0.1884 $^{aB\beta}$ ± 0.0035	1.2073 $^{aB\beta}$ ± 0.0042	46.22 $^{aB\beta}$ ± 2.37	20.34 $^{bA\alpha}$ ± 0.22
Afzal	100	0	0.2272 $^{aA\alpha}$ ± 0.0039	1.2551 $^{aA\alpha}$ ± 0.0049	78.67 $^{aA\alpha}$ ± 3.46	19.20 $^{bB\beta}$ ± 0.27
Afzal	100	75	0.2202 $^{aA\alpha}$ ± 0.0049	1.2464 $^{aA\alpha}$ ± 0.0062	86.15 $^{aA\alpha}$ ± 4.82	20.22 $^{bA\alpha}$ ± 0.31
Afzal	100	150	0.2252 $^{aA\alpha}$ ±0.0032	1.2526 $^{aA\alpha}$ ± 0.0041	88.40 $^{aA\alpha}$ ± 3.78	19.89 $^{bA\beta}$ ± 0.19
Sararood	50	0	0.0090 $^{bA\gamma}$ ± 0.0031	1.0945 $^{bA\gamma}$ ± 0.0034	11.10 $^{bA\gamma}$ ± 0.83	26.64 $^{aA\beta}$ ± 0.38
Sararood	50	75	0.0087 $^{bA\gamma}$ ± 0.0029	1.0913 $^{bA\gamma}$ ± 0.0032	9.27 $^{bA\gamma}$ ± 0.63	25.48 $^{aB\gamma}$ ± 0.42
Sararood	50	150	0.0088 $^{bA\gamma}$ ± 0.0029	1.0922 $^{bA\gamma}$ ± 0.0032	9.50 $^{bA\gamma}$ ± 0.70	25.51 $^{aB\beta}$ ± 0.42
Sararood	75	0	0.1335 $^{bA\beta}$ ± 0.0029	1.1428 $^{bA\beta}$ ± 0.0033	48.15 $^{bA\beta}$ ± 2.82	29.00 $^{aA\alpha}$ ± 0.47
Sararood	75	75	0.1251 $^{bB\beta}$ ± 0.0030	1.1333 $^{bB\beta}$ ± 0.0034	37.75 $^{bB\beta}$ ± 2.55	29.00 $^{aA\alpha}$ ± 0.47
Sararood	75	150	0.1278 $^{bAB\beta}$ ± 0.0030	1.1363 $^{bAB\beta}$ ± 0.0034	34.70 $^{bB\beta}$ ± 2.05	27.72 $^{aB\alpha}$ ± 0.43
Sararood	100	0	0.1557 $^{bA\alpha}$ ± 0.0027	1.1685 $^{bA\alpha}$ ± 0.0031	66.32 $^{bA\alpha}$ ± 3.18	26.92$^{aB\beta}$ ± 0.37
Sararood	100	75	0.1572 $^{bA\alpha}$ ± 0.0027	1.1702 $^{bA\alpha}$ ± 0.0032	66.45 $^{bA\alpha}$ ± 3.58	26.68 $^{aB\beta}$ ± 0.30
Sararood	100	150	0.1442 $^{bB\alpha}$ ± 0.0030	1.1552 $^{bB\alpha}$ ± 0.0035	61.90 $^{bA\alpha}$ ± 3.64	28.59 $^{aA\alpha}$ ± 0.41

Different lowercase letters in columns indicate significant differences between cultivars within the same irrigation and fertilizer levels; different uppercase letters indicate significant differences among irrigation levels within the same cultivar and fertilizer level; different lowercase Greek letters indicate significant differences among fertilizer levels within the same cultivar and irrigation regimes ($P < 0.05$) based on bootstrap comparisons.

In 'Afzal', optimal irrigation at 100% FC coupled with increasing nitrogen levels (0, 75, and 150 mg N kg^{-1}) enhanced v_{xj} (Fig. 7). Well-watered conditions hastened first female emergence and reproductive onset, boosting lifetime fecundity. Intensifying WS (75% → 50% FC) sharply curtailed reproductive output while extending TPRP (~11.29–11.38 days), signaling delayed maturation and impaired fecundity; nitrogen partially offset these deficits, sustaining higher reproduction under enriched conditions (Fig. 7).

Contrastingly, 'Sararood' sustained greater reproductive values across water stress gradients (Fig. 8), despite protracted TPRP (15.03 to 16.64 days) reflecting extended pre-reproductive development. Nitrogen enhanced fecundity and longevity under water stress without shortening TPRP, indicative of adaptive resource partitioning prioritizing survival and reproductive endurance under resource limitation. Under optimal irrigation, the reproductive parameters peaked, but differences between nitrogen levels were less pronounced than in 'Afzal', suggesting that the inherent drought tolerance of 'Sararood' moderates aphid performance independently of soil fertility (Fig. 8).

This study clarifies how concurrent water limitation and nitrogen enrichment jointly structure the life history and demographic potential of *R. padi* on barley cultivars with contrasting drought tolerance, thereby refining current frameworks on aphid responses to combined abiotic and nutritional stress. Moving beyond single-factor models, our results demonstrate that aphid demographic responses are not governed by single factors but emerge from cultivar-specific physiological landscapes that modulate bottom-up forces under abiotic stress. By explicitly integrating irrigation, nitrogen inputs, and host drought tolerance within an age–stage, two-sex life-table framework, the present greenhouse study identifies treatment-dependent demographic responses under controlled conditions. However, these patterns should be interpreted as mechanistic evidence generated in a simplified experimental system rather than direct estimates of field outbreak dynamics, where spatial heterogeneity, fluctuating weather, soil complexity, and biotic interactions may substantially modify realized population trajectories.

Table 4. Effects of irrigation regimes and nitrogen fertilizer levels on adult pre-reproductive period (APRP), total pre-reproductive period (TPRP), nymph production days (NPD), and fecundity (nymphs /female) of *Rhopalosiphum padi* (L.) on two barley cultivars ('Afzal': drought-sensitive; 'Sararood': drought-tolerant) under greenhouse conditions

Cultivar	Irrigation (%)	Fertilizer level (mg kg^{-1})	APRP (days)	TPRP (days)	NPR (days)	Fecundity (nymphs/female)
Afzal	50	0	3.00 $^{bA\alpha}$ ± 0.17	11.29 $^{bA\alpha}$ ± 0.21	27.00 $^{aA\alpha}$ ± 0.58	48.60 $^{aA\gamma}$ ± 1.40
Afzal	50	75	3.16 $^{bA\alpha}$ ± 0.17	11.33 $^{bA\alpha}$ ± 0.19	25.88 $^{aB\gamma}$ ± 0.53	43.38 $^{aB\gamma}$ ± 1.17
Afzal	50	150	3.02 $^{bA\alpha}$ ± 0.19	11.38 $^{bA\alpha}$ ± 0.23	27.47 $^{aA\beta}$ ± 0.58	37.20 $^{aC\gamma}$ ± 1.25
Afzal	75	0	3.07 $^{bA\alpha}$ ± 0.18	11.61 $^{bA\alpha}$ ± 0.21	27.86 $^{bA\alpha}$ ± 0.57	60.02 $^{aA\beta}$ ± 1.37
Afzal	75	75	2.97 $^{bA\alpha}$ ± 0.17	11.49 $^{bA\alpha}$ ± 0.20	28.70 $^{bA\beta}$ ± 0.53	56.56 $^{aA\beta}$ ± 1.13
Afzal	75	150	2.89 $^{bA\alpha}$ ± 0.17	11.26 $^{bA\alpha}$ ± 0.17	28.28 $^{bA\beta}$ ± 0.77	48.65 $^{aB\beta}$ ± 1.74
Afzal	100	0	2.60 $^{bA\beta}$ ± 0.14	11.13 $^{bA\alpha}$ ± 0.20	27.63 $^{bB\alpha}$ ± 0.53	82.81 $^{aB\alpha}$ ± 2.04
Afzal	100	75	2.80 $^{bA\alpha}$ ± 0.16	11.61 $^{bA\alpha}$ ± 0.23	30.88 $^{bA\alpha}$ ± 0.64	95.72 $^{aA\alpha}$ ± 1.70
Afzal	100	150	2.78 $^{bA\alpha}$ ± 0.16	11.32 $^{bA\alpha}$ ± 0.16	30.26 $^{bA\alpha}$ ± 0.58	93.05 $^{aA\alpha}$ ± 2.13
Sararood	50	0	4.94 $^{aA\alpha}$ ± 0.30	16.09 $^{aA\alpha}$ ± 0.33	25.17 $^{aA\beta}$ ± 0.79	12.68 $^{bA\gamma}$ ± 0.59
Sararood	50	75	4.69 $^{aA\alpha}$ ± 0.28	16.09 $^{aA\alpha}$ ± 0.30	21.75 $^{bB\gamma}$ ± 0.84	10.35 $^{bB\gamma}$ ± 0.44
Sararood	50	150	4.57 $^{aA\alpha}$ ± 0.21	16.00 $^{aA\alpha}$ ± 0.26	20.77 $^{bB\gamma}$ ± 0.80	10.85 $^{bB\gamma}$ ± 0.43
Sararood	75	0	4.43 $^{aA\alpha}$ ± 0.19	16.59 $^{aA\alpha}$ ± 0.27	37.78 $^{aA\alpha}$ ± 0.97	52.05 $^{bA\beta}$ ± 1.94
Sararood	75	75	4.52 $^{aA\alpha}$ ± 0.22	16.64 $^{aA\alpha}$ ± 0.30	35.58 $^{aA\beta}$ ± 1.05	41.94 $^{bB\beta}$ ± 1.77
Sararood	75	150	4.18 $^{aA\alpha}$ ± 0.21	16.11 $^{aA\alpha}$ ± 0.28	34.97 $^{aA\beta}$ ± 0.94	37.51 $^{bC\beta}$ ± 1.39
Sararood	100	0	3.50 $^{aA\beta}$ ± 0.17	15.34 $^{aA\beta}$ ± 0.23	40.07 $^{aB\alpha}$ ± 1.02	69.81 $^{bA\alpha}$ ± 2.23
Sararood	100	75	3.10 $^{aA\beta}$ ± 0.17	15.03 $^{aA\beta}$ ± 0.18	40.97 $^{aB\alpha}$ ± 0.88	71.83 $^{bA\alpha}$ ± 3.11
Sararood	100	150	3.44 $^{aA\beta}$ ± 0.18	15.58 $^{aA\alpha}$ ± 0.26	45.05 $^{aA\alpha}$ ± 0.83	68.77 $^{bA\alpha}$ ± 1.81

Different lowercase letters in columns indicate significant differences between cultivars within the same irrigation and fertilizer levels; different uppercase letters indicate significant differences among irrigation levels within the same cultivar and fertilizer level; different lowercase Greek letters indicate significant differences among fertilizer levels within the same cultivar and irrigation regimes ($P < 0.05$) based on bootstrap comparisons.

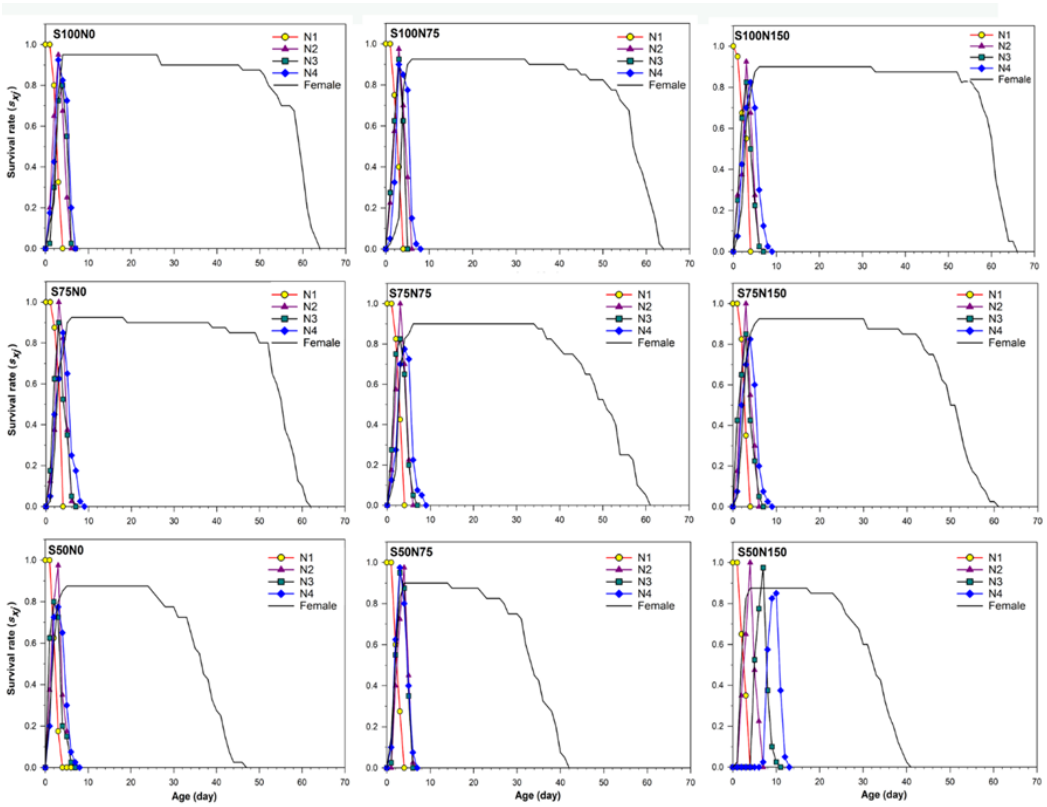

Fig. 1. Age-stage survival (s_{xj}) of *Rhopalosiphum padi* on drought-tolerant 'Sararood' cultivar under water stress, across different irrigation regimes (100%, 75%, and 50% field capacity) and nitrogen levels (0, 75, and 150 mg N kg^{-1} soil). N1: first-instar nymph; N2: second-instar nymph; N3: third-instar nymph; N4: fourth-instar nymph.

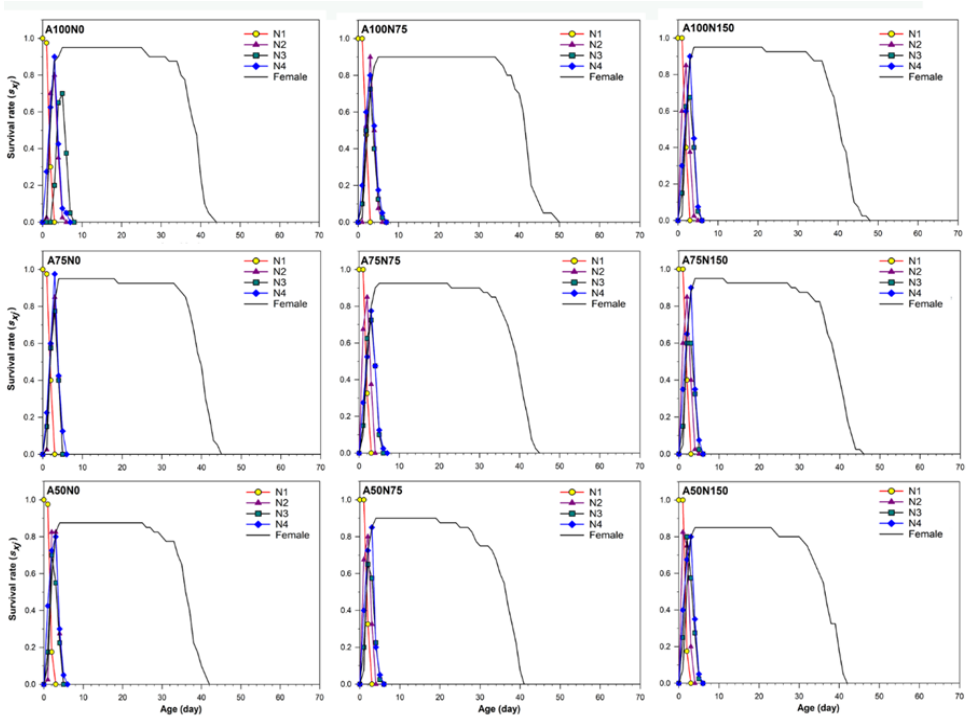

Fig. 2. Age-stage survival (s_{xj}) of *Rhopalosiphum padi* on drought-sensitive 'Afzal' cultivar under water stress, across different irrigation regimes (100%, 75%, and 50% field capacity) and nitrogen levels (0, 75, and 150 mg N kg^{-1} soil). N1: first-instar nymph; N2: second-instar nymph; N3: third-instar nymph; N4: fourth-instar nymph.

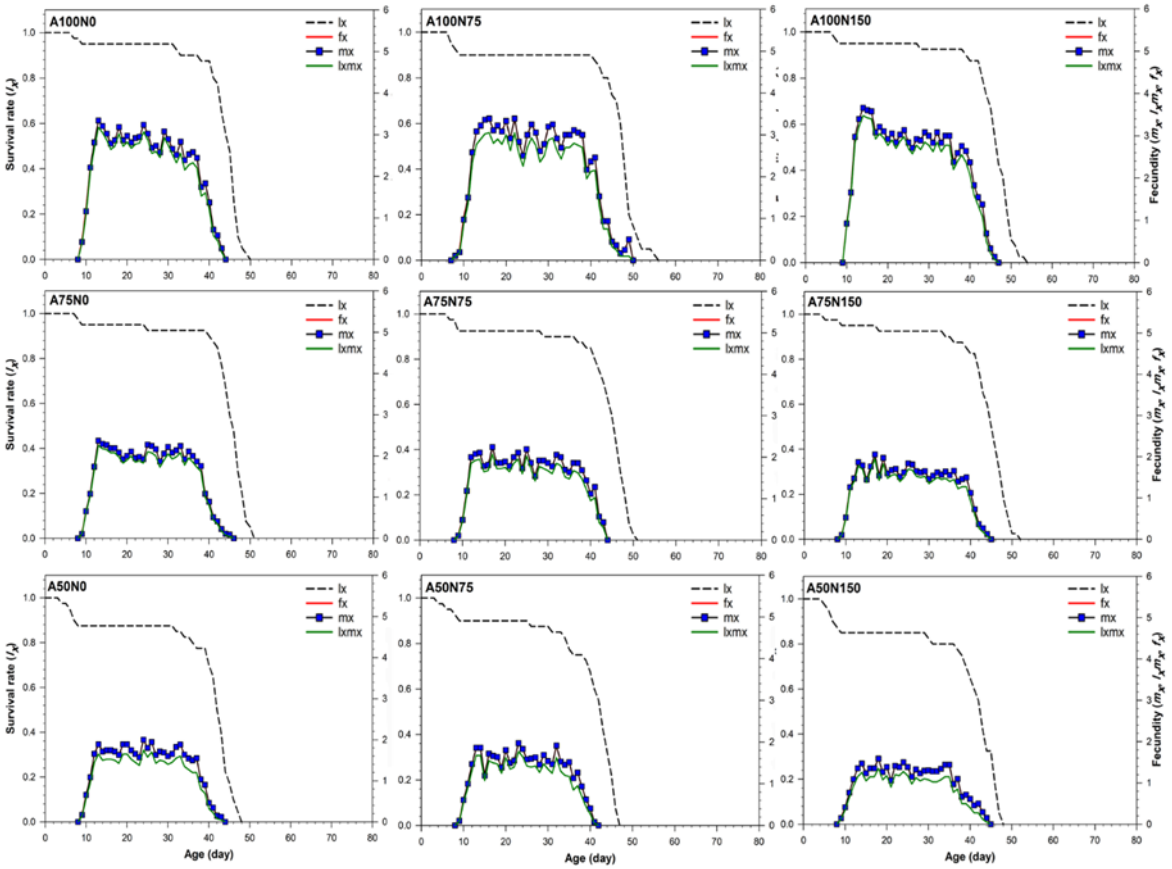

Fig. 3. Age-specific survival rate (l_x) and age-specific fecundity (m_x) of *Rhopalosiphum padi* on drought-sensitive 'Afzal' cultivar under different irrigation regimes (100%, 75%, and 50% field capacity) and nitrogen levels (0, 75, and 150 mg Nkg^{-1} soil).

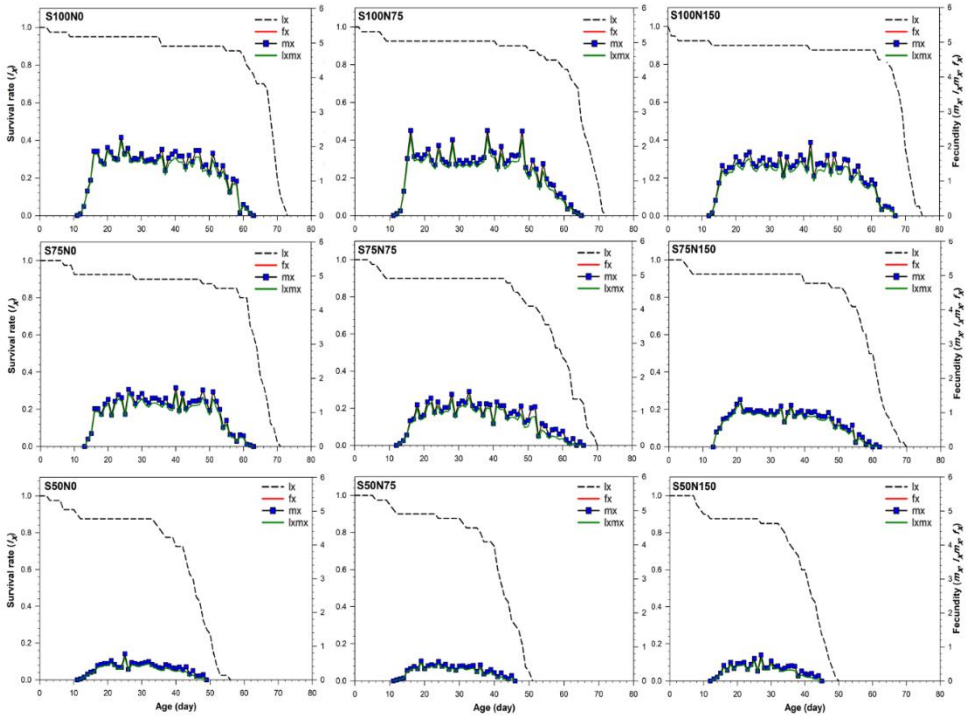

Fig. 4. Age-specific survival rate (l_x) and age-specific fecundity (m_x) of *Rhopalosiphum padi* on drought-tolerant 'Sararood' cultivar under different irrigation regimes (100%, 75%, and 50% field capacity) and nitrogen levels (0, 75, and 150 mg Nkg^{-1} soil).

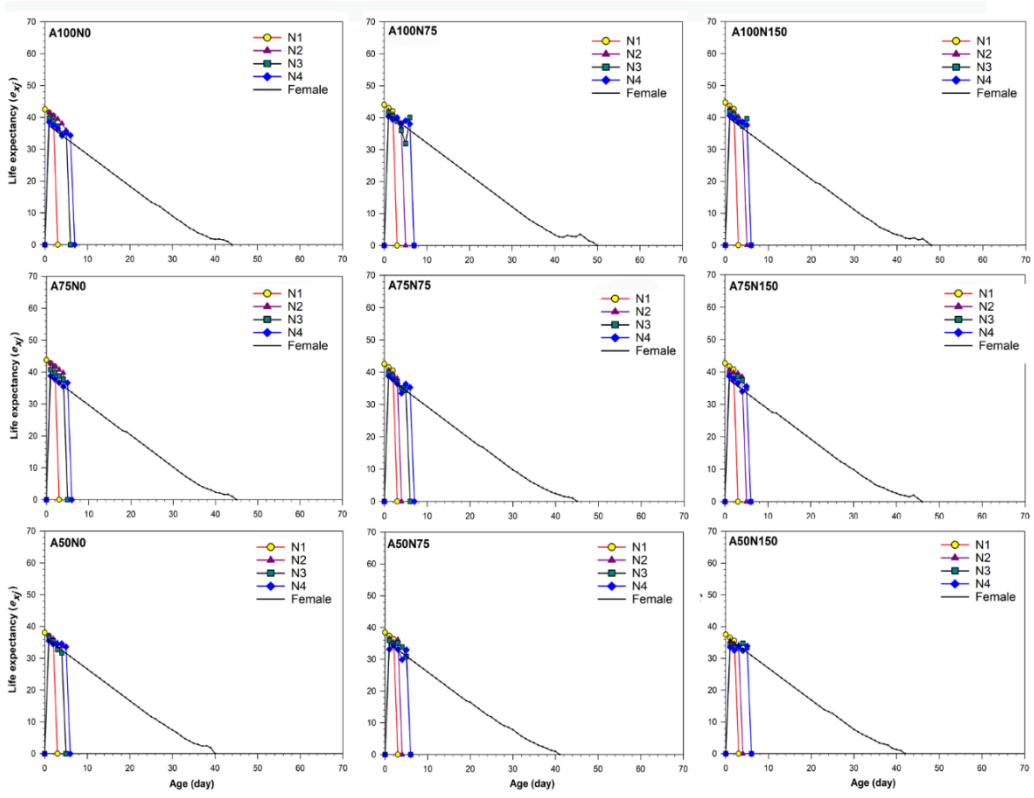

Fig. 5. Age-specific life expectancy (e_{xj}) of *Rhopalosiphum padi* on drought-sensitive 'Afzal' cultivar under water stress, across different irrigation regimes (100%, 75%, and 50% field capacity) and nitrogen levels (0, 75, and 150 mg Nkg^{-1} soil). N1: first-instar nymph; N2: second-instar nymph; N3: third-instar nymph; N4: fourth-instar nymph.

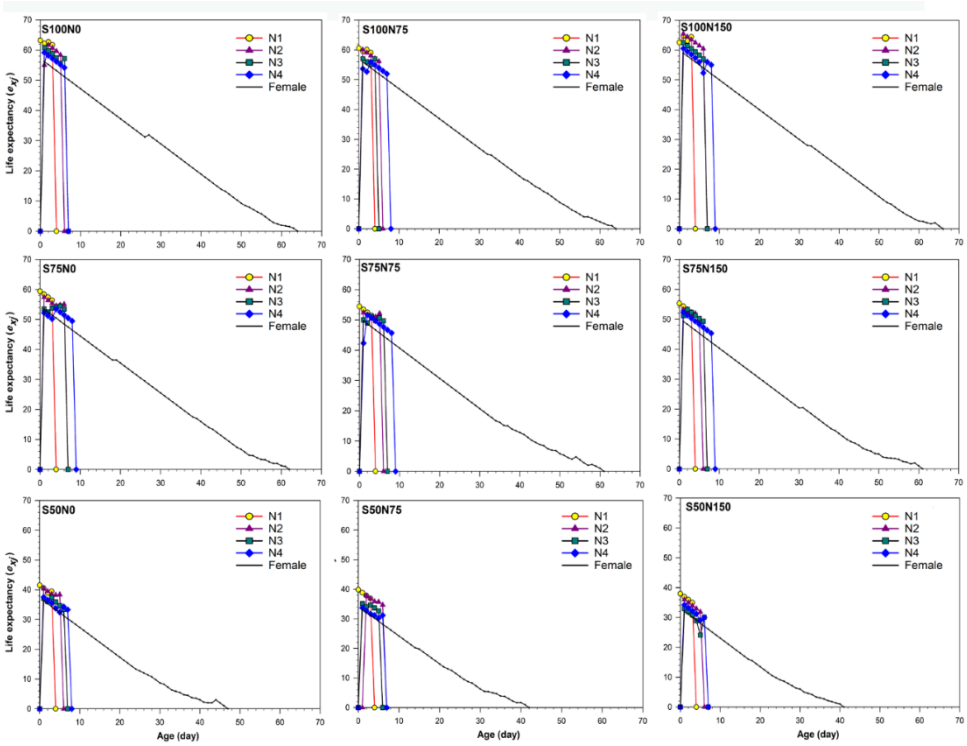

Fig. 6. Age-specific life expectancy (e_{xj}) of *Rhopalosiphum padi* on drought-tolerant 'Sararood' cultivar under water stress, across different irrigation regimes (100%, 75%, and 50% field capacity) and nitrogen levels (0, 75, and 150 mg N kg^{-1} soil). N1: first-instar nymph; N2: second-instar nymph; N3: third-instar nymph; N4: fourth-instar nymph.

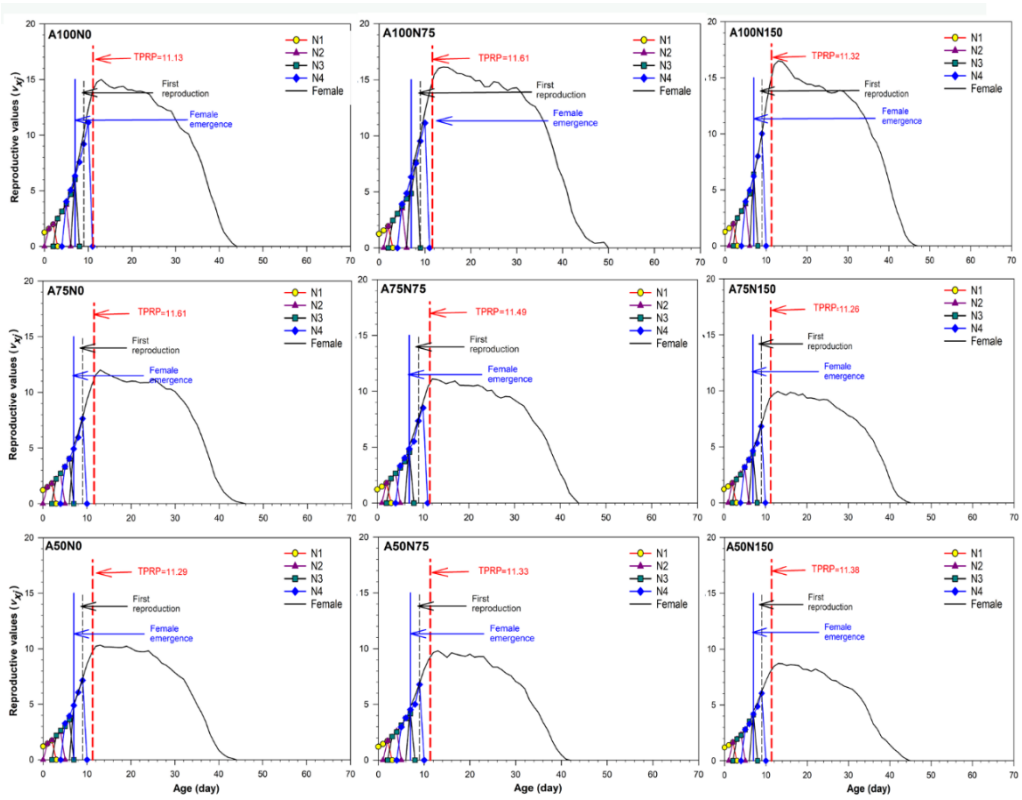

Fig. 7. Age-stage-specific reproductive rate (v_{xj}) of *Rhopalosiphum padi* on drought-sensitive 'Afzal' cultivar under different irrigation regimes (100%, 75%, and 50% field capacity) and nitrogen levels (0, 75, and 150 mg N kg^{-1} soil). TPRP: Total pre-reproductive period; N1: first-instar nymph; N2: second-instar nymph; N3: third-instar nymph; N4: fourth-instar nymph.

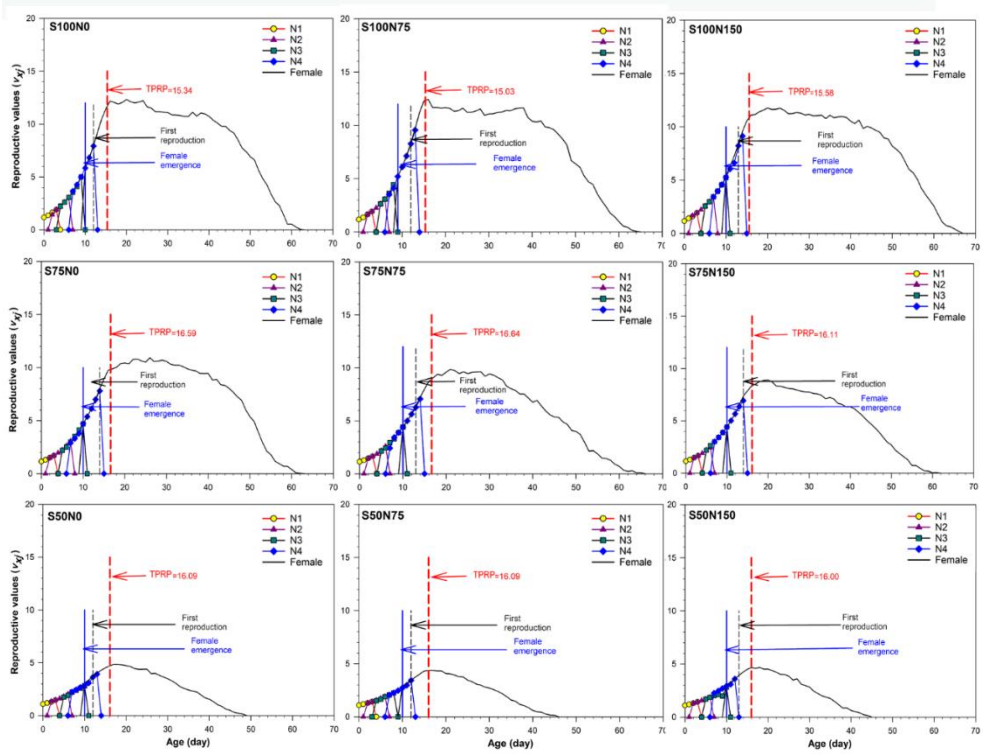

Fig. 8. Age-stage-specific reproductive rate (v_{xj}) of *Rhopalosiphum padi* on drought-tolerant 'Sararood' cultivar under different irrigation regimes (100%, 75%, and 50% field capacity) and nitrogen levels (0, 75, and 150 mg N kg^{-1} soil). TPRP: Total pre-reproductive period; N1: first-instar nymph; N2: second-instar nymph; N3: third-instar nymph; N4: fourth-instar nymph.

DISCUSSION

The stark contrast in aphid development and longevity between the drought-sensitive 'Afzal' and drought-tolerant 'Sararood' underscores the primacy of host genotype. The accelerated development on 'Afzal' likely reflects a more accessible nutritional profile or attenuated inducible defenses, whereas the protracted development on 'Sararood' suggests stronger constitutive or stress-induced resistance mechanisms, aligning with reports that drought-tolerant plants often exhibit enhanced biochemical defenses that impair herbivore performance (Kansman et al., 2022; Stallmann et al., 2022). Water stress exerted a clear detrimental impact on aphid longevity and developmental timings, consistent with reports showing that drought-induced shifts in phloem sap osmotic potential, nutrient balance, and secondary metabolite profiles impair aphid feeding efficacy and reduce survival (Zaffaroni et al., 2020; Leybourne et al., 2021; Sadras et al., 2025). In this context, 'Sararood' can be viewed as a "resistant but resource-stable" host, on which *R. padi* experiences slower development and extended survival under benign conditions, but faces accelerated life-history schedules when water becomes limiting, indicating that the same drought-tolerance traits that secure plant performance simultaneously constrain aphid demographic expansion.

Notably, the acceleration of pre-adult development in *R. padi* on 'Sararood' under severe water deficit suggests an adaptive plastic response, whereby aphids shorten development to complete reproduction on a deteriorating host, a pattern that mirrors stress-induced life-history acceleration reported in other aphid–host systems (Dardeau et al., 2015; Gebretsadik et al., 2025). Such plasticity implies that drought-tolerant cultivars do not simply diminish aphid fitness, but also select for altered developmental schedules, potentially reshaping phenological synchrony with natural enemies and virus transmission windows in water-limited agroecosystems.

Contrary to expectations, nitrogen fertilization at the tested levels did not significantly influence aphid developmental durations or longevity across irrigation treatments and cultivars, an observation harmonizing with literature emphasizing the dominant influence of moisture availability over nitrogen in regulating aphid life history traits (Pons and Tatchell, 1995; Quandahor et al., 2023). However, the interaction where severe WS induced developmental reductions regardless of nitrogen input in 'Sararood' points to complex, non-additive physiological effects that merit additional biochemical investigation. These findings stress that nitrogen's influence on aphids is context-dependent, varying with host genotype, water availability, and possibly timing and form of nutrient application (Dardeau et al., 2015). The absence of strong nitrogen effects on development underlines that, under realistic irrigation regimes, water management remains the primary agronomic lever for modulating aphid generation time, whereas nitrogen chiefly acts by reshaping reproductive investment and cohort persistence.

The marked decline in female longevity with increasing water stress across cultivars, especially severe in 'Afzal', implicates altered phloem composition via drought-induced osmotic shifts and secondary metabolite accumulation as critical factors limiting aphid survival and reproduction (Huberty and Denno, 2004; Leybourne

et al., 2021). In contrast, 'Sararood'-supported populations exhibited extended pre-reproductive periods and delayed maturation, a pattern consistent with adaptive life-history "slowing" that reduces immediate fecundity but may buffer populations under chronic resource limitation (Gebretsadik et al., 2025). Under full irrigation, nitrogen fertilization within the tested agronomic range had only marginal effects on key demographic parameters (r, λ, and R_0), especially in 'Afzal', corroborating the view that sufficient water availability can mask or dilute nitrogen-driven changes in phloem-feeder performance (Pons and Tatchell, 1995; Sagers and Goggin, 2007). Together, these patterns indicate that in well-watered systems the barley–aphid interaction is primarily vigor-driven, whereas under water deficit it becomes defense-driven, with nitrogen inputs tipping the balance towards either tolerance or resistance depending on cultivar physiology; however, confirmation in field setting with natural enemy communities is needed.

Under moderate and severe water stress, however, high nitrogen in 'Afzal' paradoxically depressed r, λ, and R_0, diverging from classical resource concentration predictions (Mattson, 1980; Throop and Lerdau, 2004) and instead supporting emerging evidence that elevated nitrogen under drought amplifies defensive chemistry or disrupts phloem osmotic balance to the detriment of aphids (Iqbal et al., 2020; Leybourne et al., 2021). This "defense intensification" scenario suggests that nitrogen-enriched, drought-stressed 'Afzal' becomes a physiologically unstable host in which high nutritional potential is offset by enhanced chemical or physical barriers, producing steep demographic collapses rather than gradual declines. These combined patterns indicate that nitrogen's effects on aphids cannot be interpreted independently of water status and host genotype.

The drought-tolerant 'Sararood' exhibited more nuanced and often non-linear demographic responses to nitrogen across moisture gradients, with high nitrogen under full irrigation slightly reducing r and λ but not consistently altering R_0 or T. Under moderate water stress, demographic parameters were most suppressed at intermediate nitrogen, while the highest nitrogen level did not uniformly intensify declines, hinting at threshold or saturating responses in plant physiological adjustment to combined water–nitrogen stress. This non-linearity implies that, for drought-tolerant cultivars, nitrogen regimes can be tuned to maintain yield while keeping aphid growth near or below replacement, offering a realistic lever for "nutritional steering" within IPM. Across all regimes, 'Sararood' -hosted aphids maintained longer generation times than those on 'Afzal', supporting a reinterpretation of the plant vigor hypothesis (Price, 1991) under drought: in stress-tolerant cultivars, resistance traits and slower host growth can decouple plant vigor from herbivore success, such that "vigorous" plants in terms of yield or drought performance do not necessarily favor aphids. The persistent decline in r, λ, and R_0 with increasing water stress on both cultivars confirms water limitation as the dominant abiotic constraint, yet the magnitude and shape of these declines remained genotype-specific, underlining the importance of genotype-by-environment interactions in aphid population regulation (Lee et al., 2012; Grinnan et al., 2013; Hancock et al., 2015; Jamieson et al., 2017).

Age-stage survival (s_{xj}) declined steeply under moderate and especially severe water stress on both cultivars, confirming drought as a key constraint on aphid cohort persistence, consistent with prior work on *R. padi* and other cereal aphids (Ponder et al., 2001; Kansman et al., 2022; Liu et al., 2023). However, these survival dynamics were quantified in the absence of predators and parasitoids, which are known to interact with drought in field and mesocosm settings (e.g., influencing aphid distribution and top-down regulation). On 'Afzal', survival curves under 50% field capacity collapsed regardless of nitrogen level, indicating that water stress overrides any potential nutritional benefit and can even convert high nitrogen into a liability via enhanced mortality (Coley et al., 1985; Guo et al., 2024; Li et al., 2024). In 'Sararood', survival patterns were more stable across nitrogen treatments under well-watered and moderately stressed conditions, suggesting that drought-tolerant physiology buffers aphids against nitrogen-driven fluctuations in host quality while offering little protection under severe water deficit. This buffering capacity is particularly evident in the comparatively slower erosion of e_{xj} and v_{xj} under stress, implying that 'Sararood' moderates the speed, rather than the inevitability, of demographic decline when resources become limiting. The muted divergence among nitrogen levels in survival curves of 'Sararood', compared with the pronounced nitrogen-related separation in 'Afzal', points to intrinsic cultivar traits—such as tighter regulation of phloem nutrients and defense metabolites—that dampen the expression of nitrogen effects on aphids (Aleosfoor et al., 2023; Sadras et al., 2025).

Patterns in age-specific survival (l_x), fecundity (m_x), maternity ($l_x m_x$), life expectancy (e_{xj}), and reproductive value (v_{xj}) collectively show that optimal irrigation maximizes survival, reproductive output, and future reproductive potential in both cultivars but more so in 'Afzal', where well-watered, nitrogen-enriched plants supported high fecundity and earlier, more pronounced peaks of m_x and $l_x m_x$. Under water stress, these peaks were suppressed and delayed, with nitrogen only partially offsetting the losses and sometimes aggravating mortality, again highlighting that added nitrogen cannot rescue aphid populations from drought-induced host deterioration (Jamieson et al., 2012; Leybourne et al., 2021). The contrasting temporal profiles of v_{xj} on 'Afzal' and 'Sararood' reveal two distinct demographic strategies from the pest's perspective: rapid, front-loaded reproduction on susceptible hosts versus extended, low-intensity reproduction on resistant hosts, each with different implications for early-season monitoring thresholds and timing of control measures. In 'Sararood', age-specific fecundity curves under water limitation retained clear but lower peaks, and e_{xj} remained comparatively higher than in 'Afzal' across stress treatments, indicating that this cultivar provides a more temporally stable, though less fecundity-promoting, resource environment. The longer total pre-reproductive periods on 'Sararood', combined with sustained reproductive values under stress, support an interpretation of host-mediated life-history "stretching,"

in which aphids trade rapid population expansion for persistence under suboptimal conditions (Hamann et al., 2021; Sun et al., 2022).

From an applied perspective, these cultivar- and environment-specific trajectories translate into distinct outbreak risks under tested conditions, nonetheless, direct translation to field management requires caution due to the pot-scale limitations (e.g., restricted root volume and uniform microclimate), the absence of natural enemies, and evaluation of only one aphid species. On 'Afzal', high population growth rates and fecundity under full irrigation across nitrogen levels imply elevated outbreak potential in fertile, well-watered systems, consistent with resource availability frameworks linking nitrogen enrichment to aphid success (Sadras et al., 2021). Under drought, the sharp demographic collapse on 'Afzal' suggests that water-saving strategies may inadvertently reduce aphid pressure but at the cost of increased crop vulnerability, underscoring a trade-off between pest suppression and plant stress (Huberty and Denno, 2004; Nachappa et al., 2016; Tamburini et al., 2018; Zaffaroni et al., 2020). These trade-offs highlight the need for irrigation scheduling that explicitly weighs yield stability against expected aphid pressure, rather than treating water management and pest management as independent decision layers. 'Sararood', by contrast, combines greater yield stability under water limitation (as shown in previous work) with markedly reduced aphid performance, offering a dual benefit of drought resilience and intrinsic pest suppression (Aleosfoor et al., 2023; Tack and Roslin, 2011; Stone et al., 2018). These properties strongly support incorporating drought-tolerant, aphid-constraining cultivars into climate-resilient IPM strategies, where cultivar choice is explicitly matched to expected water availability and aphid pressure (Bayendi Loudit et al., 2018; Kansman et al., 2022; Carvajal Acosta et al., 2023; Sadras et al., 2025), pending field-scale confirmation that accounts for multitrophic interactions.

At a broader conceptual level, our findings emphasize that single-factor approaches—focusing on either water or nitrogen in isolation—are insufficient to predict aphid population trajectories under realistic climate and management scenarios (Grinnan et al., 2013; Hancock et al., 2015; Jamieson et al., 2017; McCaw et al., 2024). The observed non-linear and sometimes antagonistic interactions between drought and nitrogen, modulated by cultivar, align with contemporary views of plant–insect systems as governed by multi-dimensional stress gradients rather than simple resource surpluses or deficits (Jamieson et al., 2012; Sadras et al., 2025). By explicitly coupling water–nitrogen regimes with cultivar-specific drought physiology in an age–stage, two-sex life-table analysis, this study provides a mechanistic scaffold that can inform for next-generation predictive models that can inform precision irrigation–fertilizer scheduling and cultivar deployment under climate change. Such models will ultimately require integration of field data incorporating natural enemies, virus epidemiology, and larger-scale plant architecture to achieve robust predictive power. By integrating stage-structured survival and fecundity via the $l_x m_x$ and v_{xj} frameworks, this work provides a mechanistic demographic basis for next-generation models of aphid dynamics under climate change, in which cultivar-specific drought physiology, water–nitrogen coupling, and aphid life-history plasticity are explicitly represented (Chi, 1988; Chi and Liu, 1985; Chi et al., 2022).

CONCLUSION

In conclusion, this study demonstrates that soil moisture, nitrogen fertilization, and host drought tolerance jointly determine *R. padi* population dynamics, highlighting drought-tolerant barley cultivars such as 'Sararood' as potential pivotal components of sustainable IPM strategies that can simultaneously stabilize yield and suppress aphid population growth. Cultivar-specific responses show that such varieties constrain aphid development and fecundity under water limitation, while the context-dependent effects of nitrogen emphasize the need for tightly integrated nutrient–irrigation strategies that safeguard productivity without exacerbating pest pressure. Together, these insights provide a robust mechanistic basis for breeding and precision IPM programs and call for upscaling these greenhouse-derived demographic patterns to field-level, multi-trophic settings to develop predictive, decision-support tools capable of guiding aphid management in increasingly water-limited and climatically variable cereal systems.

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CRediT AUTHORSHIP CONTRIBUTION STATEMENT

Conceptualization: Maryam Aleosfoor; Conducted experiments: Khatereh Zohrabi dehdezi; Methodology: Maryam Aleosfoor and Lida Fektrat; Formal analysis: Maryam Aleosfoor, Lida Fekrat, and Aurang Kavousi; Writing—original draft preparation: Lida Fekrat, Maryam Aleosfoor, and Aurang Kavousi; Writing—review and editing: Lida Fekrat, Maryam Aleosfoor, and Aurang Kavousi; Supervision: Maryam Aleosfoor; Project administration: Maryam Aleosfoor; Funding acquisition: Maryam Aleosfoor.

DECLARATION OF COMPETING INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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