Postprint: Generational Cumulative Effects of Temperature on Growth, Development, and Reproduction in the Red Morph of the Pea Aphid (Acyrthosiphon pisum)

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Abstract

To investigate the cumulative generational effects of temperature on the red morph of the pea aphid and provide a theoretical basis for ecological control measures against pea aphids, this study examined the development, fecundity, and life table parameters of the red morph of the pea aphid across three consecutive generations under five artificially controlled temperature conditions (12 °C, 17 °C, 22 °C, 25 °C, and 28 °C). The results showed that at 12 °C, the nymphal stage duration of the F2 generation was shortened by 16.0% and 6.8% compared to the F0 and F1 generations, respectively, whereas no significant differences in nymphal stage duration were observed among the three generations at 22 °C and 25 °C. At 12 °C, the generation time in the F2 generation was reduced by 10.5% and 12.4% compared to the F0 and F1 generations, respectively, while no significant differences in generation time were detected among the three generations under 17 °C, 22 °C, and 25 °C conditions. At 12 °C, the average fecundity of the F2 generation decreased compared to the F0 and F1 generations; however, under continuous high temperature of 25 °C, the decline in reproductive capacity was most pronounced, with the average fecundity of the F1 and F2 generations decreasing by 49.3% and 50.9% relative to the F0 generation, respectively, while at 22 °C, no significant differences in fecundity were observed among the F1, F2, and F0 generations. When the red pea aphid was reared continuously, adult body weight was least affected at 12 °C and 25 °C, showing no significant differences among the three generations; at 22 °C, the adult body weight of the F1 generation was significantly higher than that of the F0 and F2 generations, and at 12 °C, the body mass growth rate exhibited a trend of increasing progressively with generation number. With increasing generation number, the net reproductive rate (R0) decreased and the mean generation time (T) shortened under both 12 °C and 25 °C conditions; at

25 °C, the intrinsic rate of increase (rm) and finite rate of increase (λ) of the F1 and F2 generations both increased significantly compared to the F0 generation. These findings indicate that under continuous low- or high-temperature stress, the reproductive capacity of red pea aphid offspring declines with no significant changes in body weight, but developmental duration shortens while the intrinsic and finite rates of increase rise, demonstrating extremely strong environmental adaptability, which may be one of the reasons for its population increase.

Full Text

Abstract

To determine the cumulative effect of temperature on the growth, development, and reproduction of red pea aphid (*Acyrthosiphon pisum*), and further provide scientific theory for ecological pest management, we studied the life tables of three continuous generations through indoor observation under five temperature regimes (12 °C, 17 °C, 22 °C, 25 °C, and 28 °C). Results showed that the nymph stage of the F2 generation shortened by 16.0% and 6.8% compared with F0 and F1 generations at 12 °C. There was no significant difference among three generations at 22 °C and 25 °C. F2 generation time reduced by 10.5% and 12.4% compared with F0 and F1 at 12 °C. There was no significant difference among three filial generations at 17 °C, 22 °C, and 25 °C. The average reproduction of F2 generation was significantly lower than those of F0 and F1 at 12 °C. Offspring fertility also declined obviously under continuous high temperature of 25 °C. The average reproduction of F1 and F2 decreased by 49.3% and 50.9% respectively compared with F0. The fecundities of both F1 and F2 aphids were not significantly different compared with that of F0 at 22 °C. Continuous feeding and weight gain of red pea aphids were lowest at 12 °C and 25 °C among all treatments, with no significant difference in weight among three generations. The weight of F1 generation was significantly higher than those of F0 and F2 generations at 22 °C; furthermore, the body weight growth rate apparently increased with the number of generations at 12 °C. With increasing generations under 12 °C and 25 °C, net reproductive rate (R0) and generation time (T) of red pea aphid respectively declined and shortened. The intrinsic increase rate (rm) and finite increase rate (λ) of F1 and F2 generations increased significantly compared with F0 under 25 °C. This showed that under continuous low temperature or high temperature stress, offspring fertility of red pea aphid declined. However, developmental duration shortened with no significant changes in body weight. The intrinsic increase rate (rm) and finite increase rate (λ) increased, showing strong adaptive capacity to the environment. This was one of the reasons for the rise of filial populations of red pea aphid.

Keywords: Red *Acyrthosiphon pisum*; Temperature; Generation; Fertility; Body weight; Population; Accumulative effect

Introduction

Global climate warming caused by rising greenhouse gas concentrations has altered the carbon-to-nitrogen ratio and other nutritional components in host plants, indirectly affecting the life activities of phytophagous insects [1-4]. As poikilothermic animals, insects experience accelerated growth and development under climate warming, leading to earlier occurrence of agricultural pests [5]. Pea aphid (*Acyrthosiphon pisum*) is a major pest of legume crops [6-7] that feeds on phloem sap [8-9], causing malformed growth, premature senescence, and even plant death [10-11]. Additionally, aphid honeydew covering leaf surfaces impairs photosynthesis, while these insects can transmit numerous plant viruses and trigger disease epidemics, adversely affecting crops, forage, and vegetables [12-13]. Pea aphids exhibit strong reproductive capacity and prominent generational overlap, enabling year-round damage under suitable temperatures [14]. Notably, the proportion of red morph pea aphids is increasing annually, with field observations showing they appear later but persist longer than green morphs [15-16]. While temperature affects body color variation in *Sitobion avenae* [17] and UV conditions can induce intraspecific differentiation and DNA mutation [18-19], red morph pea aphids maintain their presence and increasing proportion despite high visibility that makes them vulnerable to predation. Therefore, investigating population dynamics and biological characteristics across generations is crucial for understanding how temperature influences red morph population patterns and cumulative effects.

Temperature is a key abiotic factor affecting aphid developmental rates and population dynamics. Previous research has demonstrated significant temperature-dependent variation in fecundity for *Diuraphis noxia* [20], with developmental rates of *Aphis gossypii* and pea aphid accelerating as temperature rises within certain ranges [21-22]. Studies have also shown that intrinsic growth rates of cereal aphids increase with temperature while population doubling time and generation time decrease [23]. Developmental duration of pea aphid varies significantly across host plants [24], and *Aphis citricola* shows shortened developmental stages at higher temperatures [25]. Research on cotton aphids revealed that developmental duration shortened rapidly with increasing temperature in the first generation, following a power function curve, while the second generation showed parabolic changes [26]. The optimal developmental temperature for three aphid species (*Aphis craccivora*, *Acyrthosiphon pisum*, and *Megoura japonica*) was identified as 19-23 °C [27], with red morph pea aphids showing significantly lower net reproductive rates above 24 °C compared to 16-20 °C, indicating that lower temperatures favor their growth [28]. However, systematic analysis of temperature’ s generational cumulative effects on red morph pea aphid development and reproduction remains lacking. This study investigated biological characteristics of red morph pea aphids across three continuous generations on broad bean (*Vicia faba*) to elucidate the cumulative impacts of temperature on population dynamics and provide theoretical foundations for ecological pest management.

1.1 Experimental Materials

Red morph pea aphids were collected in early May 2014 from unsprayed alfalfa (*Medicago sativa*) fields at Gansu Agricultural University. They were reared in an incubator at $(22\$\pm1)°C, withaphotoperiodofL : D = 16h : 8handhumidityof(60\pm\$10)\%$, feeding on 10 cm tall broad bean seedlings. Newborn nymphs within 6 h were selected for experiments.

1.2 Experimental Methods

Newborn nymphs were placed on potted broad bean plants (10 cm height) at a density of 10 nymphs per plant (2 plants per pot). A funnel-shaped white paper was wrapped around the plant base to collect shed skins. Plants were maintained at 6 °C, 12 °C, 17 °C, 22 °C, 25 °C, and 28 °C with (60\$±\$10)% humidity and L:D = 16 h:8 h, with three replicates per temperature. After F0 and F1 generations began reproducing, daily fecundity was recorded and newborn nymphs were removed periodically. Nymphs from the peak reproduction period of F0 and F1 generations were used to observe developmental duration and reproduction of F1 and F2 generations under identical conditions. Survival, molting times, and exuviae were recorded every 12 h for F0, F1, and F2 generations. First-instar nymphs (W1) and newly molted adults (W2) were weighed to calculate weight difference (dW), developmental duration (DD), and mean relative growth rate (MRGR).

1.3 Life Table Parameter Calculation

Population life tables were constructed for red morph pea aphids to determine population dynamic parameters including net reproductive rate (R0), mean generation time (T), intrinsic rate of increase (rm), and finite rate of increase (λ) [29].

1.4 Data Analysis

Statistical analysis was performed using SPSS 19.0 (Duncan' s new multiple range test), with tables prepared in Microsoft Excel 2007.

2.1 Effect of Temperature on Developmental Duration Across Generations

Red morph pea aphids completed development across 12-28 °C in the F0 generation, while F1 generation could not develop normally at 28 °C . For F0, F1, and F2 generations, nymph stage shortened as temperature increased within the 12–22 °C range. The F0 generation at 12 °C had a significantly longer nymph stage (16.92 d) than at other temperatures ($P<0.05$), with generation time decreasing as temperature rose and being significantly longer at 12 °C and 17 °C than at 22 °C, 25 °C, and 28 °C. In F1 and F2 generations, the nymph stage at 12 °C was significantly longer than at 17 °C, 22 °C, and 25 °C. The pattern of nymph stage and generation time across generations was consistent with that of F0, with lower temperatures resulting in longer generation times.

At 12 °C, the nymph stage shortened progressively across generations, with F2 decreasing by 16.0% and 6.8% compared to F0 and F1, respectively. At 17 °C, F2 nymph stage increased by 13.3% and 8.1% compared to F0 and F1, respectively. No significant differences in nymph stage were observed among generations at 22 °C and 25 °C. Adult stage showed similar patterns to nymph stage at 22 °C, while at 25 °C, F1 and F2 adult stages shortened significantly by 6.8% and 6.4% compared to F0. Generation time at 12 °C differed significantly between F2 and both F0 and F1 ($P<0.05$), with F2 shortening by 10.5% and 12.4%, respectively, while no significant differences occurred between F0 and F1. At 17 °C, 22 °C, and 25 °C, generation time showed no significant differences among generations.

2.2 Effect of Temperature on Fecundity Across Generations

Red morph pea aphid fecundity in F0, F1, and F2 generations initially increased then decreased with rising temperature, peaking at 22 °C [Figure 1: see original paper]. In the F0 generation, average fecundity differed significantly among 12 °C, 17 °C, 22 °C, and 25 °C treatments ($P<0.05$), with 28 °C severely inhibiting reproduction (average 15.92 nymphs). In F1 generation, average fecundity showed no significant difference between 12 °C and 25 °C, but differed significantly among other treatments ($P<0.05$). In F2 generation, fecundity at 22 °C differed significantly from the other three temperatures, while no significant differences were observed among 12 °C, 17 °C, and 25 °C.

Comparing fecundity across generations at the same temperature revealed that F2 average fecundity at 12 °C and 17 °C decreased significantly compared to F0 and F1, while F0 and F1 showed no significant differences. Specifically, F2 fecundity decreased by 30.6% and 27.4% compared to F0 and F1 at 12 °C, and by 28.4% and 24.9% at 17 °C. At 22 °C, F1 and F2 fecundity showed no significant differences from F0. However, at 25 °C, F1 and F2 average fecundity decreased by 49.3% and 50.9% compared to F0.

2.3 Effect of Temperature on Body Weight and Relative Growth Rate Across Generations

Adult weights of F0, F1, and F2 generations under different temperatures are shown in . The F0 generation reached maximum weight at 17 °C and 22 °C, significantly heavier than at 12 °C, 25 °C, and 28 °C ($P<0.05$), with no significant difference between 12 °C and 28 °C. For F1 and F2 generations, adult weight was significantly higher at 22 °C than at other temperatures ($P<0.05$). In F1 generation, weights at 12 °C, 17 °C, and 25 °C showed no significant differences ($P>0.05$), while in F2 generation, only weights at 12 °C and 25 °C showed no significant difference. Relative mean daily growth rates varied considerably across temperatures. The F0 generation exhibited the highest growth rate at 28 °C, which did not differ significantly from that at 22 °C but was significantly higher than at other temperatures ($P<0.05$). This resulted from shortened developmental duration at high temperatures, enabling rapid organic matter accumulation and faster weight gain. F1 and F2 generations showed consistent patterns, with significantly higher growth rates at 22 °C than at 12 °C, 17 °C, and 25 °C, as optimal temperature promoted heavier body weight combined with relatively short developmental duration, facilitating rapid weight gain.

Continuous rearing affected adult weight minimally at 12 °C and 25 °C, with no significant differences among the three generations. At 22 °C, F1 adult weight was significantly greater than F0 and F2 ($P<0.05$), while F0 and F2 showed no significant difference. Optimal temperature favored organic matter accumulation and weight gain, yet red morph pea aphids also grew well at relatively low and high temperatures, indicating strong temperature adaptation capacity. Relative mean daily growth rates across generations at the same temperature showed an increasing trend with generation number at 12 °C, with F1 and F2 increasing by 13.9% and 21.5% compared to F0, respectively. At 22 °C and 25 °C, no significant changes in relative growth rate occurred among F0, F1, and F2 generations. The ability of red morph pea aphids to grow well under continuous low temperature (12 °C) demonstrates that relatively cool conditions cannot completely suppress their development.

2.4 Effect of Temperature on Population Life Table Parameters Across Generations

Experimental population life tables were constructed based on age-specific survival and fecundity rates . Net reproductive rate (R0) of F0, F1, and F2 generations increased with temperature from 12 °C to 22 °C, then decreased at 25 °C, reaching maximum values at 22 °C for all generations. The lowest R0 (8.92) occurred in F0 at 28 °C. Mean generation time (T) of F0 initially shortened then lengthened as temperature increased from 12 °C to 28 °C (with 25 °C as the turning point), while T in F1 and F2 generally decreased with rising temperature from 12 °C to 25 °C. Intrinsic rate of increase (rm) in F0 increased then decreased with temperature from 12 °C to 28 °C, being significantly higher at 22 °C than at other temperatures ($P<0.05$). In F1, rm at 22 °C exceeded that at other temperatures, while no significant difference occurred between 12 °C and 17 °C. In F2, rm generally increased with temperature from 12 °C to 25 °C, though no significant difference existed between 22 °C and 25 °C. Finite rate of increase (λ) showed consistent patterns with rm across all generations and temperature treatments.

At 17 °C and 22 °C, net reproductive rate (R0) showed no significant changes across generations . However, at 12 °C, R0 in F2 decreased by 38.9% and 50.1% compared to F0 and F1, respectively. At 25 °C, R0 in F1 and F2 decreased by 49.7% and 50.2% compared to F0 ($P<0.05$). Mean generation time (T) at 12 °C and 25 °C shortened significantly in F1 and F2 compared to F0 ($P<0.05$), with no significant difference between F1 and F2. At 17 °C and 22 °C, T showed no significant differences between F0 and F2. Intrinsic rate of increase (rm) and finite rate of increase (λ) at 17 °C decreased significantly in F1 and F2 compared to F0 ($P<0.05$), with no significant differences between F1 and F2. At 22 °C, rm and λ showed no significant differences among F0, F1, and F2. At 25 °C, rm and λ increased significantly in F1 and F2 compared to F0 ($P<0.05$), with no significant differences between F1 and F2.

3 Discussion and Conclusion

Temperature is the primary factor determining insect developmental rates. Rising temperatures accelerate development across life stages, advancing initial appearance, migration timing, and population peaks. Between 1986 and 2006 in Gansu' s Gulang County, earlier occurrence of suitable temperatures advanced the migration of *Sitobion avenae* from low to high altitudes, increasing peak population densities and damage severity [30]. Extended growing seasons under warming climate benefit agricultural pests, with pea aphids showing similar patterns as major legume crop pests. Life table technology provides an important methodology for studying population dynamics mechanisms, evaluating pest control measures, developing predictive models, and implementing scientific pest management [31]. Therefore, applying this method to assess temperature effects on successive pea aphid generations is practical and reliable.

This study subjected red morph pea aphids to continuous temperature stress across three generations, obtaining biological parameters including developmental duration, fecundity, net reproductive rate, intrinsic rate of increase, and mean generation time to clarify temperature stress impacts and understand population increase mechanisms in Gansu Province. Results demonstrated substantial variation in growth, development, and reproduction across temperature regimes. Nymph stages of F0, F1, and F2 generations shortened as temperature increased from 12 °C to 22 °C, indicating that elevated temperatures accelerate developmental rates, likely by increasing enzyme and hormone activity to enhance biochemical reactions [32–34]. High temperature (28 °C) caused high mortality in F1 nymphs that failed to complete development, demonstrating inhibitory effects on growth and development, consistent with findings by Morgan et al. [21] and Du et al. [28]. At 12 °C, nymph stage shortened progressively across generations, while at 17 °C, F2 nymph stage extended compared to F0 and F1. No significant differences in generation time occurred among three generations at 17 °C, 22 °C, and 25 °C, but developmental duration shortened with increasing generation number at 12 °C, indicating that relatively low temperatures cannot suppress development and shortened development time facilitates population growth.

Fecundity of F0, F1, and F2 generations initially increased then decreased with rising temperature from 12 °C to 25 °C, with F0 fecundity dropping sharply at 28 °C. Average fecundity in F2 decreased compared to F0 and F1 at 12 °C and 17 °C, while the greatest decline in offspring fertility occurred under continuous high temperature (25 °C). Adult weight of F0, F1, and F2 generations reached maximum values at 22 °C. The highest relative mean daily growth rate in F0 occurred at 28 °C due to shortened developmental duration enabling rapid organic matter accumulation. F1 and F2 generations showed consistent patterns, with significantly higher growth rates at 22 °C than at 12 °C, 17 °C, and 25 °C, as optimal temperature promoted heavier body weight combined with relatively short developmental duration. Continuous rearing minimally affected adult weight at 12 °C and 25 °C, with no significant differences among generations. At 22 °C, F1 adult weight significantly exceeded F0 and F2, demonstrating that optimal temperature favors organic matter accumulation and weight gain. The increasing trend in growth rate with generation number at 12 °C indicates strong temperature adaptation capacity in red morph pea aphids.

Net reproductive rate (R0), mean generation time (T), intrinsic rate of increase (rm), and finite rate of increase (λ) are important parameters for evaluating population changes in specific environments [31]. Net reproductive rate (R0) of F0, F1, and F2 generations increased with temperature from 12 °C to 22 °C, then decreased at 25 °C, reaching maximum values at 22 °C. With increasing generations, R0 declined and T shortened under 12 °C and 25 °C conditions, with shortened generation time facilitating rapid population growth, possibly related to aphid stress responses [35-36]. At 25 °C, intrinsic rate of increase (rm) and finite rate of increase (λ) increased significantly in F1 and F2 compared to F0, potentially representing an r-strategist pest stress response where pea aphids rapidly increase population density to counteract potential high mortality under high temperature and drought conditions [23]. Under continuous low or high temperature stress, red morph pea aphid offspring fecundity declined, but developmental time shortened with no significant weight changes, while intrinsic and finite rates of increase increased, demonstrating strong environmental adaptability that may contribute to population increases.

This experiment investigated experimental population life tables of red morph pea aphids on broad bean plants grown under different temperatures, with results accurately reflecting developmental and population dynamic changes on plants or in fields. This study only examined temperature effects on biological parameters across three continuous generations. Further research is needed on temperature impacts on proteins, lipids, amino acids, and related physiological and molecular mechanisms to provide more reliable theoretical foundations for pea aphid forecasting and management.

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Note: Figure translations are in progress. See original paper for figures.