



## Soil Nutrient Enrichment Alters Trophic Linkages and Predator Efficiency in Cowpea-Aphid-Ladybird Systems

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### ABSTRACT

Soil nutrient management can strongly influence interactions among plants, herbivores, and natural enemies. This study examined how organic and inorganic soil amendments affect tritrophic interactions among cowpea (*Vigna unguiculata* L. Walp.), the aphid *Aphis craccivora* Koch, and the predatory ladybird *Cheilomenes sexmaculata* Fabricius under semi-field conditions. Plants were grown in control, vermicompost, and NPK-treated soil to evaluate plant growth, aphid fitness, development of predator and its performance. Vermicompost significantly increased the number of leaflets per plant which reflected enhanced vegetative growth, while differences in leaflet shape were qualitative. It also enhanced the aphid fitness due to improved host quality. The total developmental period was significantly shortened and predation efficiency was highest at various prey densities in vermicompost treatment. Overall, vermicompost improved plant vigour and predator performance through improved prey quality, demonstrating a cascade effect across trophic levels. These results highlight vermicompost as a sustainable alternative to chemical fertilizers for promoting natural pest regulation and maintaining ecological balance in cowpea agroecosystems.

**KEY WORDS:** Tritrophic interactions, Soil fertilization, Vermicompost, NPK, *Cheilomenes sexmaculata*

### INTRODUCTION

Fertilizers play a crucial role in maintaining soil fertility (de Oliveira *et al.*, 2023; Liu *et al.*, 2023) and sustaining agricultural productivity (Liu *et al.*, 2021; Krasilnikov *et al.*, 2022). They provide adequate soil nutrition which support plant growth (Leghari *et al.*, 2016; Muhammad *et al.*, 2022), yield (dos Santos Sousa *et al.*, 2022; Tang, 2025), and resilience to pest attack (Altieri *et al.*, 2012; Gómez-Trejo *et al.*, 2021; Rajareddy *et al.*, 2024). However, the type and source of nutrients supplied to the soil can determine not only plant performance but also the interactions between herbivorous pests and their natural enemies (Pekas & Wäckers, 2020; Horgan *et al.*, 2022). In tritrophic systems, the plants, herbivores, and predators are interconnected and fertilizer-induced changes at the soil level are capable of influencing biological processes across all three trophic levels (Zhu *et al.*, 2020; Gorji *et al.*, 2023). Among various soil amendments, organic and

inorganic fertilizers are the most widely used (Hernandez *et al.*, 2021; Garbowski *et al.*, 2023; Prashar *et al.*, 2025). Organic fertilizers, such as vermicompost are known to improve soil structure, water-holding capacity, and microbial activity (Chatterjee *et al.*, 2020; Oyege & Balaji Bhaskar, 2023). They release nutrients slowly and promote balanced plant growth (Iqbal *et al.*, 2024; Hossain *et al.*, 2025). In contrast, inorganic fertilizers, such as NPK formulations provide nutrients rapidly but alter soil chemistry (Liu *et al.*, 2017; Mi *et al.*, 2018) and plant physiology differently (Liu *et al.*, 2024; Sai & Paswan, 2024).

The contrasting nutrient release patterns and effects of these fertilizers can lead to substantial differences in plant vigour, leaf structure, and biochemical composition. Such variations are especially relevant for cowpea (*Vigna unguiculata* L. Walp.), a major leguminous crop grown throughout tropical and subtropical regions (Vendramini *et al.*, 2012; Sindha *et al.*, 2024), which is highly responsive

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to soil nutrient management (Aechra *et al.*, 2017; Abd El Lateef *et al.*, 2018). The morphological traits of plants; such as the number of leaves and the leaf length-to-width ratio, reflect its overall vigour (Sibhatu, 2016; Jagadale *et al.*, 2017) and influence the feeding behaviour and reproductive potential of herbivorous insects (Agrawal, 2004; Ruhnke *et al.*, 2009; Chaudhary *et al.*, 2018; Münzbergová & Skuhrovec, 2020; González-Carrera *et al.*, 2025). Improved nutrient availability generally promotes lush plant growth (Nadeem *et al.*, 2018; Kafle *et al.*, 2023), but it may also make plants more suitable hosts for sap-feeding pests by enhancing nutrient quality in the phloem (Joern & Behmer, 2012; Ebeling *et al.*, 2022).

Among these pests, the cowpea aphid, *Aphis craccivora* Koch (Hemiptera: Aphididae) is one of the most destructive species which causes leaf curling, stunted growth, and substantial yield losses in cowpea (Choudhary *et al.*, 2017; Ghosh, 2020; Mohamed *et al.*, 2021). Its development, fecundity, and longevity are closely tied to host plant quality (Borowiak-Sobkowiak *et al.*, 2017; Ríos Martínez & Costamagna, 2018). Plants grown in nutrient-rich soil, particularly under high nitrogen availability support faster aphid reproduction and longer survival (Gao *et al.*, 2018; Mousa *et al.*, 2019). Thus, fertilizer-induced changes in plant quality can directly alter aphid population dynamics and pest pressure in the agricultural fields.

The consequences of soil fertility also extend to higher trophic levels particularly to predatory ladybird beetles (Hosseini *et al.*, 2018; Aguilera *et al.*, 2021), such as *Cheilomenes sexmaculata* Fabricius (Coleoptera: Coccinellidae), which are key biological control agents of aphids. The growth of predator and its feeding efficiency depend on the abundance and nutritional quality of its prey (Zhu *et al.*, 2020). High-quality aphids supported by nutrient-enriched plants may accelerate predator development and increase the consumption rate. Conversely, nutrient imbalances can prolong the developmental period or reduce the feeding efficiency. Assessing parameters such as the total developmental period (TDP) and percent prey consumption provides a clear measure of how soil nutrient amendments influence biological control potential through tritrophic interactions.

The present study evaluates the impact of two types of soil amendments; vermicompost (organic) and NPK (inorganic) on the performance of cowpea *V. unguiculata*, its pest *A. craccivora*, and the predator *C. sexmaculata*. It aims to understand how differences in soil nutrient sources shape plant growth, aphid fitness, development of the

predator and its predation efficiency within a tritrophic framework.

## MATERIALS AND METHODS

### Experimental design

The study was conducted under semi-field conditions in University of Lucknow (26.86° N, 80.93° E) area to evaluate the influence of soil nutrient amendments on cowpea (*V. unguiculata*) growth, aphid (*A. craccivora*) performance, and development of predator (*C. sexmaculata*) and its predation efficiency. Experiments were carried out in cubical mesh cages (250 µm; 0.5×0.5 m) under natural photoperiod 11.5L: 12.5D with recorded temperature and relative humidity 26.8 ± 2°C and 63.4 ± 5%, respectively during the experimental duration from October 2022 to April 2023.

### Assessment of various trophic levels

**Plant growth assessment :** *Vigna unguiculata* seeds were individually sown in plastic pots (8 × 6 inches) filled with autoclaved sterile soilrite to prevent microbial and pest contamination. Plants were maintained under natural environmental conditions and grown to the third or fourth trifoliate stage for the experiments. Treatments included control, vermicompost (1.8 t/ha), and NPK (131.6 kg/ha) amendments (TNAU Agritech portal, 2022) in soilrite. All plants were watered daily to maintain uniform soil moisture. Plant growth was evaluated by recording the number of leaves (compound leaflets) per plant and the leaflet length-to-width (L: W) ratio as an indicator of vegetative growth. The L: W ratio is measured using ImageJ (version 1.52a) software. Each treatment was replicated thirty times. Total 90 replicates were used.

**Aphid fitness evaluation :** *Aphis craccivora* individuals were collected from local *Lablab purpureus* (L.) Sweet fields and maintained on cowpea plants to establish clonal colonies. Offspring from a single gravid aphid were used for all experiments to ensure uniformity.

**Fecundity:** A single gravid aphid (30 per treatment) was confined to a target leaflet using fine mesh insect-rearing bags. The total number of offspring produced over seven consecutive days was recorded to assess reproductive potential under different plant nutrient conditions. Total 90 replicates were used.

**Longevity:** First instar aphids were individually confined to leaflets using fine mesh insect rearing bag and monitored daily until death. The experiment was replicated 30 times for each treatment (n=90).

These parameters provided insights into how plant nutritional status affects aphid population growth and survival.

### Development and Predation efficiency

Adult *C. sexmaculata* were collected from *L. purpureus* plants from the local agricultural fields of Barabanki, India (26°93' N, 81°18' E). The collected adults were paired and reared for three successive generations in plastic beakers (14.5 × 10.5 cm<sup>2</sup>) covered with muslin cloth fastened with rubber bands. The rearing was carried out under natural environmental conditions corresponding to the experimental period within cubical mesh cages. They were provided with an *ad libitum* supply of *A. craccivora* reared on *V. unguiculata* maintained under the identical semi-field conditions to establish the stock culture. Eggs were collected daily and the resulting neonates were reared to adulthood. Periodic introduction of wild beetles was performed to maintain genetic diversity and prevent inbreeding. All the requisite stages used in the experiments were obtained from these established colonies.

### Developmental period

The developmental period of *C. sexmaculata* was recorded for each treatment to assess the influence of prey availability and plant nutrient status on predator growth. The duration of the eggs (incubation period), larvae (from first instar to fourth instar), pre-pupal and pupal stages (immature developmental period) were monitored individually. Eggs (E), first instar (L1), and second instar (L2) larvae were maintained on leaves of *V. unguiculata* plants infested with *A. craccivora* enclosed inside insect-rearing bags to prevent larval dispersal due to their small sizes within cubical mesh cages. The third (L3) and fourth (L4) instar larvae being highly voracious and mobile were reared directly on aphid-infested *V. unguiculata* plants within cubical mesh cages. Throughout the experiment, predators were provided with an *ad libitum* supply of *A. craccivora* reared on *V. unguiculata* plants from the corresponding soil treatment. Subsequently, the total developmental period (TDP) from egg to newly emerged adult was calculated for each treatment. The experiment was replicated 30 times per treatment (n=90).

### Percent prey consumption

Prior to the experiment, adult beetles were starved for 24 hours to standardize hunger. Five different densities of third instar *A. craccivora* nymphs (50, 100, 200, 300, and 400) were applied to leaflets of *V. unguiculata* plants within cubical mesh cages. Third instar aphids were used to minimize reproduction during the 24-hour predation period. After introducing the requisite number of aphids, a single adult beetle was released into each cage. After 24 hours, beetles were removed and the remaining live aphids were counted. The number of aphids consumed was recorded and percent prey consumption was calculated for each

adult beetle at each aphid density. The experiment was replicated 20 times (n=100) for each aphid density. Total replicates were 300 for all treatments.

### Statistical analyses

Data on plant growth (number of leaflets per plant and length-to-width ratio of leaflets), aphid fitness (fecundity and longevity), along with growth of predator (immature developmental durations and TDP) and its performance (percent predation at different aphid densities) were tested for normality using the Shapiro-Wilk test. All the datasets were found to be non-normally distributed. Differences among soil treatments (control, vermicompost, and NPK) were analysed using the Kruskal-Wallis H test. Pairwise comparisons were conducted for significant differences using the Bonferroni post hoc test. All analyses and graphical outputs were conducted using IBM SPSS (Version 27.0) software.

## RESULTS

### Effects of soil treatment on *V. unguiculata* growth

The number of leaflets per plant varied significantly among soil treatments ( $H = 48.948$ ,  $df = 2$ ,  $p < 0.001$ ). Plants grown in vermicompost-amended soil showed the highest number of leaflets followed by NPK-treated and control plants (Fig. 1). In contrast, although the leaflet length-to-width ratio did not differ significantly among treatments ( $H = 3.849$ ,  $df = 2$ ,  $p = 0.146$ ), yet noticeable differences in leaflet shape were observed. Leaflets of control plants were slightly more elongated *i.e.* lanceolate ( $1.88 \pm 0.06$ ), whereas those of NPK ( $1.76 \pm 0.07$ ) and vermicompost ( $1.75 \pm 0.07$ ) treatments appeared broader and more ovate in shape (Fig. 2).

### Effect of soil treatment on *A. craccivora* fitness

Aphid fecundity differed significantly among soil treatments ( $H = 240.405$ ,  $df = 2$ ,  $p < 0.001$ ). The highest fecundity was observed in aphids reared on vermicompost-grown plants, followed by those on NPK-treated and control plants (Fig. 3). Similarly, aphid longevity also varied significantly among treatments ( $H = 63.056$ ,  $df = 2$ ,  $p < 0.001$ ), with the longest lifespan recorded in the vermicompost treatment, followed by NPK and control. (Fig. 4).

### Effect of soil treatment on development and predation efficiency of *C. sexmaculata*

The developmental durations of the immature stages of *C. sexmaculata* showed minor variations among soil treatments, although most differences were statistically non-significant. The egg stage (incubation period) was shortest in the vermicompost treatment, followed by NPK

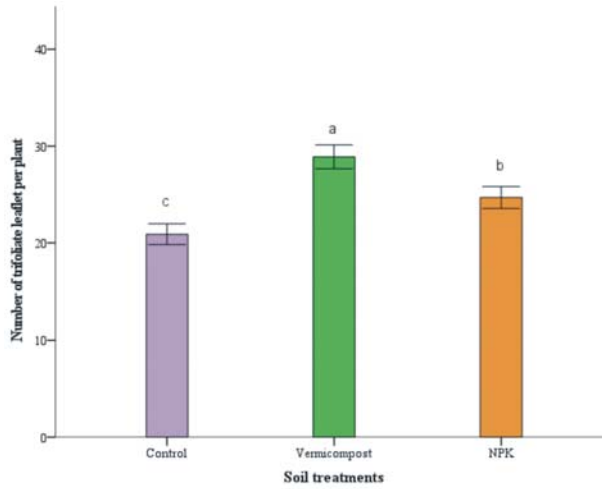


Fig. 1: Number of trifoliolate leaflets per *V. unguiculata* plant grown under control, vermicompost-amended, and NPK-amended soils. Bars represent mean  $\pm$  SE. Different letters above the bars indicate significant differences among treatments ( $p < 0.05$ ).

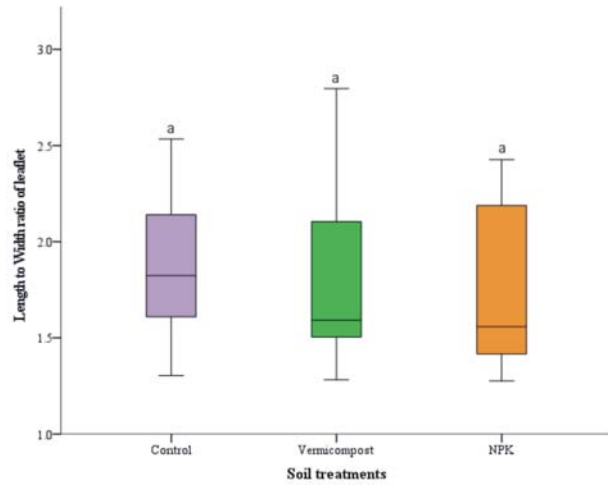


Fig. 2: Box plots showing the leaflet length-to-width ratio for *V. unguiculata* plants grown under control, vermicompost-amended, and NPK-amended soils. The centre line within each box represents the median, the box shows the interquartile range, and whiskers extend to the full data range. Similar letters denote no significant difference.

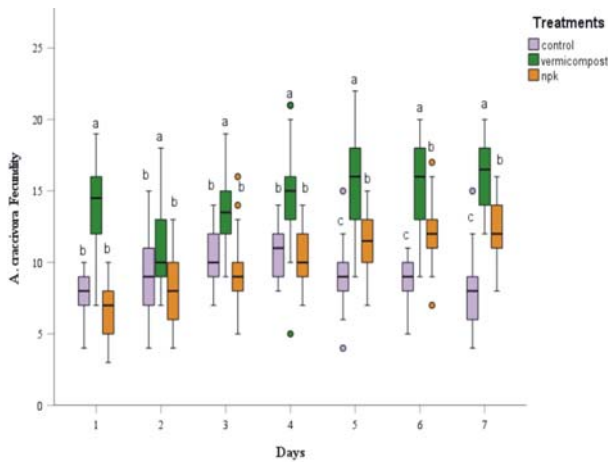


Fig. 3: Box plots showing aphid *A. craccivora* fecundity in control, vermicompost-amended, and NPK-amended soil treatments. The centre line within each box represents the median, the box indicates the interquartile range, and whiskers extend to the full data range. Circles represent outliers. Different letters above the boxes denote significant differences among treatments ( $p < 0.05$ ), whereas similar letters indicate no significant difference.

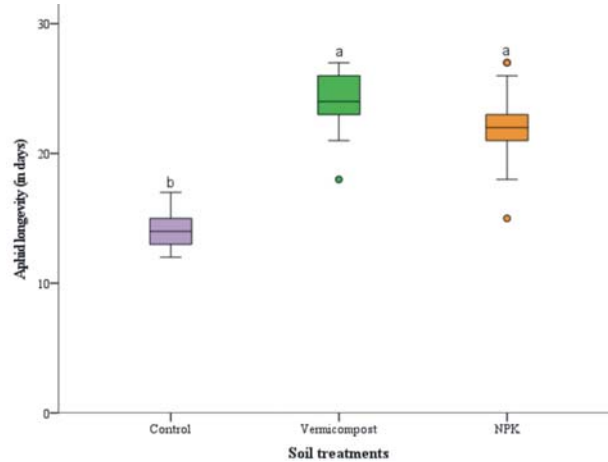


Fig. 4: Box plots showing aphid *A. craccivora* longevity in control, vermicompost-amended, and NPK-amended soil treatments. The centre line within each box represents the median, the box indicates the interquartile range, and whiskers extend to the full data range. Circles represent outliers. Different letters above the boxes denote significant differences among treatments ( $p < 0.05$ ), whereas similar letters indicate no significant difference.

and control, but this variation was not significant ( $H = 4.628$ ,  $df = 2$ ,  $p = 0.099$ ). Similarly, the first, second, third, and fourth-instar larval durations did not differ significantly among treatments ( $H = 1.171 - 4.684$ ,  $df = 2$ ,  $p > 0.05$ ). The pre-pupal ( $H = 2.000$ ,  $df = 2$ ,  $p = 0.368$ ) and pupal ( $H = 2.866$ ,  $df = 2$ ,  $p = 0.239$ ) durations also exhibited no significant variation (Fig. 5). However, the total developmental period (egg-to-adult) varied significantly among treatments ( $H = 10.850$ ,  $df = 2$ ,  $p = 0.004$ ) where vermicompost had the shortest total developmental period (35.73 days), followed by NPK (43.87 days) and control (56.90 days) (Fig. 6).

The predation efficiency (percent consumption) at individual prey densities showed clear variation across treatments. At prey density 50, the percent consumption was highest under vermicompost, followed by NPK and control, with a significant difference among treatments ( $H = 6.310$ ,  $df = 2$ ,  $p = 0.043$ ). A similar trend was evident at prey density 200 ( $H = 7.613$ ,  $df = 2$ ,  $p = 0.022$ ), 300 ( $H = 13.004$ ,  $df = 2$ ,  $p = 0.002$ ), and 400 aphids ( $H = 12.291$ ,  $df = 2$ ,  $p = 0.002$ ), whereas at 100 aphids, the difference among treatments was not significant ( $H = 5.466$ ,  $df = 2$ ,  $p = 0.065$ ). Although the cumulative percent consumption at all the prey densities of *C. sexmaculata* was recorded to be non-significant ( $H = 5.069$ ,  $df = 2$ ,  $p = 0.079$ ) yet the overall trend indicated that soil enrichment enhanced the predator's feeding efficiency in vermicompost treatment from NPK and control (Fig. 7).

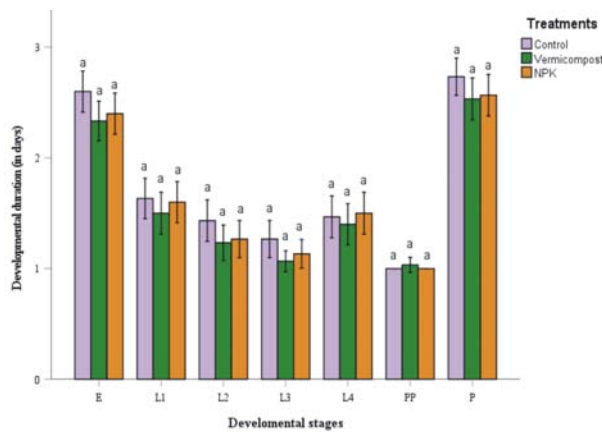


Fig. 5: Duration of immature developmental stages (E-egg, L1 to L4- larval instars, PP- pre-pupa, P- Pupa) of *C. sexmaculata* reared on *A. craccivora* from control, vermicompost-amended, and NPK-amended soils. Bars represent mean  $\pm$  SE. Similar letters above bars denote no significant difference.

## DISCUSSION

This study highlights the effects of soil nutrient management in tritrophic interactions among the leguminous crop *V. unguiculata*, the aphid *A. craccivora*, and the predatory ladybird beetle *C. sexmaculata*. The results clearly indicate that organic amendment via vermicompost enhanced plant morphological traits, improved aphid fitness, shortened predator developmental period and increased the percent consumption. Ecological theory predicts that changes in resource availability at the plant level can propagate upward through trophic levels and influence herbivore and natural-enemy dynamics (Price *et al.*, 1980). In this system, vermicompost appears to promote a more favourable tritrophic linkage than conventional NPK fertilizer highlighting to its potential role in ecologically grounded pest management strategies.

The significant increase in the number of leaflets per plant in vermicompost-amended soil reflects improved nutrient availability (Adilođlu *et al.*, 2018), microbial activities (Arancon *et al.*, 2004) and soil structure (Ceritođlu *et al.*, 2018) compared to chemical fertilizer (NPK) or control conditions. Vermicompost is known to enhance plant vegetative growth through the slow release of plant growth promoting substances, such as humic acids (Rehman *et al.*, 2023) and phytohormones (Arancon *et al.*, 2004). The improved root-shoot balance due to better soil structure, microbial activities and nutrient uptake likely

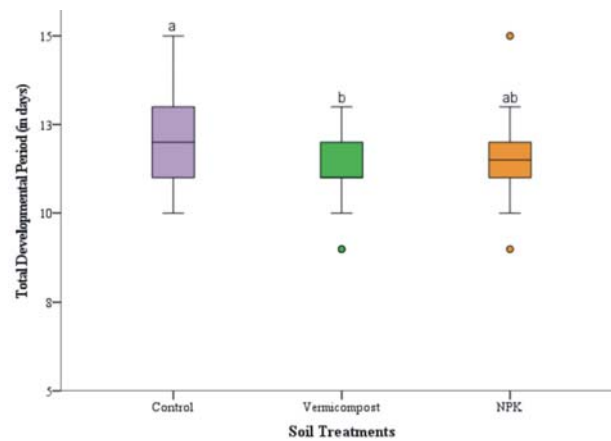


Fig. 6: Box plots showing total developmental duration (from egg to newly emerged adult) of *C. sexmaculata* reared on *A. craccivora* from control, vermicompost-amended, and NPK-amended soils. The centre line within each box represents the median, the box indicates the interquartile range, and whiskers extend to the full data range. Circles represent outliers. Different letters above the boxes denote significant differences among treatments ( $p < 0.05$ ), whereas similar letters indicate no significant difference.

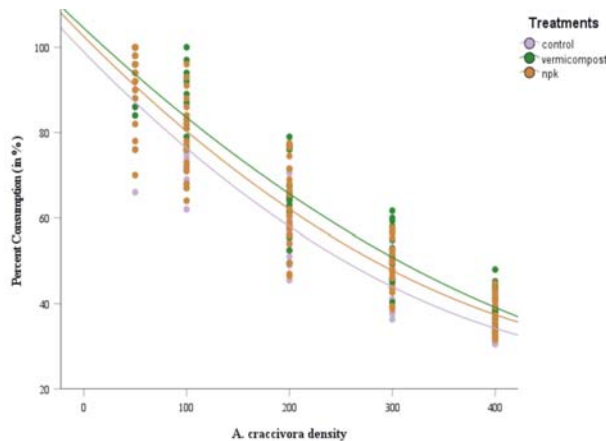


Fig.7: Percent consumption of *C. sexmaculata* at varying *A. craccivora* densities under control, vermicompost-amended, and NPK-amended soil treatments. Each point represents mean  $\pm$  SE.

contributed to the higher leaflet production observed in this treatment.

Although the leaflet length-to-width (L: W) ratios were non-significant between treatments yet there were noticeable morphological differences present *viz.* control plants produced slightly more elongated and lanceolate leaflets, while NPK and vermicompost treatments had somewhat broader and ovate leaflets. Such shape trends can indicate phenotypic plasticity in response to nutrient regimes. Broader ovate leaflets under enriched soils may increase light capture and photosynthetic efficiency (Niinemets & Sack, 2006; Shi, Yu & Niinemets, 2020), which in turn could indirectly influence the herbivore quality (Campo & Dirzo, 2003).

Aphid fecundity and longevity were significantly enhanced on vermicompost-grown plants which validates the notion that host plant nutritional status is a key determinant of herbivore performance (Awmack & Leather, 2002; Züst & Agrawal, 2017). Plants with superior nitrogen content promote aphid reproduction by improving phloem sap quality (Rousselin *et al.*, 2016). Vermicompost treatment at the soil level likely elevated soluble nitrogen levels and amino acids in cowpea phloem, thereby enhancing aphid reproductive potential and survival. Hosseini *et al.* (2018) found that increasing nitrogen fertilization of cucumber increased the nutritional content of aphids and altered predator foraging responses. The shorter aphid lifespan on control plants suggests suboptimal nutrition or increased plant defensive compounds under nutrient-limited conditions. Moreover, organic amendments (including vermicompost) and organic management frequently improve plant vigour and nutrient availability and these factors can increase

herbivore performance in some systems (Blouin *et al.*, 2019), however effects are species and context-dependent (Arancon *et al.*, 2004). In the present study, vermicompost likely created a more balanced nutritional environment that supported aphid fecundity and longevity better than NPK and control condition, while sustaining higher predator efficiency indicating a stabilizing effect across trophic levels.

The development and predation efficiency of *C. sexmaculata* were influenced by soil enrichment, though the degree of impact varied among parameters. Immature developmental durations exhibited small variations across treatments, with non-significant differences in egg, larval, pre-pupal or pupal stages. However, the slight reductions across multiple immature stages under vermicompost treatment likely accumulated and resulted in a significantly shorter total developmental period (Farhadi *et al.*, 2010). Such bottom-up effects, where soil amendments influence plant vigour and consequently herbivore and predator fitness, have been widely documented in tritrophic systems (Fallahpour *et al.*, 2020; Aguilera *et al.*, 2021). The shorter total developmental period in vermicompost-treated plants aligns with the earlier reports which indicate that organically enriched soils enhance plant nutritional quality and secondary metabolites which promote aphid growth and provide superior prey for predatory coccinellids (Chen *et al.*, 2010; Hosseini *et al.*, 2018). Conversely, the longer developmental period observed in the control treatment reflects nutrient limitation at the base trophic level, which propagates upward through the food chain and delays predator maturation (Chen *et al.*, 2015).

The predation efficiency of *C. sexmaculata* varied among soil treatments with the highest consumption recorded on aphids from vermicompost-treated plants, followed by NPK and control. Significant differences at most prey densities (50, 200, 300, and 400 aphids) indicate that organic amendments can enhance predator foraging efficiency by improving prey availability and host-plant nutrient status (Patel *et al.*, 2014; Blouin *et al.*, 2019). At the intermediate density of 100 aphids, consumption did not differ significantly, likely due to behavioural adjustments such as altered search patterns or patch switching, and moderate prey densities reducing effective encounters through aggregation or refuges (Jeschke *et al.*, 2002)

Vermicompost enhances plant nitrogen and amino acid content (Arancon *et al.*, 2004) due to its richness in humic substances and microbial metabolites which likely improves aphid nutritional quality and consequently, predator feeding efficiency. Although cumulative consumption across all densities was not statistically

significant, yet the overall trend clearly favoured vermicompost over NPK and control. These results are consistent with previous studies showing that nutrient-enriched host plants produce higher-quality prey (Nevo & Coll, 2001), which increases prey consumption (Hosseini *et al.*, 2018) and supports better developmental and reproductive performance of coccinellids (Obrycki *et al.*, 2009; Shah & Khan, 2014). In the present study, the moderate increase observed under NPK treatment suggests that inorganic enrichment can also enhance predator performance, though not as effectively as vermicompost, possibly due to differences in nutrient balance and soil microbial activity (Arancon *et al.*, 2004).

## CONCLUSIONS

This study establishes that soil nutrient management plays a pivotal role in shaping tritrophic interactions. Vermicompost significantly enhanced *V. unguiculata* growth and supported effective biological control of *A. craccivora* through improved performance of *C. sexmaculata*. Although NPK fertilization also enhanced plant, pest, predators development and performance but its overall ecological benefits were limited compared to vermicompost.

Hence, vermicompost emerges as an ecologically sustainable soil fertilizer that strengthens plant health, maintains predator efficiency, and facilitates natural pest suppression. Promoting organic nutrient sources such as vermicompost can reduce dependence on chemical fertilizers which also aligns with integrated pest management (IPM) principles, and contribute to resilient agroecosystems.

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