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# Effects of Organic and Synthetic Fertiliser on Insect Herbivore Populations in Quinoa

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## ABSTRACT

Fertilisers are used in agriculture to promote crop productivity. There are many nutrient sources in fertilisers, and different sources cause variation in plant defence and pest tolerance. Assessing how pests respond to different types of fertilisers is key to develop integrated pest management programs. Here, we assessed how two fertilisers applied to quinoa (*Chenopodium quinoa* Willd.) affected cowpea aphid (*Aphis craccivora* Koch.) and *Lygus spp.* survival and reproduction. Quinoa is a newly introduced crop in the USA, and fertiliser regimes using organic or synthetic nitrogen sources are being evaluated. We quantified growth and survival of each pest on organic- and synthetic-fertilised quinoa for two varieties in cages and the open field. We also quantified gene expression associated with three phytohormones involved in chemical defence to identify potential mechanisms of treatment effects. In cages, organic-fertilised quinoa had the fewest aphids and lowest *Lygus* survival. However, the effects were weaker in the open field, where aphids were marginally less abundant on organic-fertilised plants and no effects of fertiliser on *Lygus* were observed. There was also evidence for fertiliser altering defence gene expression, suggesting a possible mechanism impacting pest behaviour and fitness. Overall, our study shows that fertilisers from different sources may provide varying levels of pest control in quinoa crops.

## 1 | Introduction

Fertilisers are a staple of agriculture that affect crop productivity and pest tolerance (Herms 2002, Altieri and Nicholls 2003, Pope et al. 2012, Rowen, Tooker, and Blubaugh 2019). Nitrogen fertilisation, for example, may decrease plant tolerance to insects by increasing nutrient levels and promoting extended feeding bouts (Herms 2002, Yardim and Edwards 2003). Fertilisers also cause morphological changes to crops, such as altering the growth rate and epicuticle thickness, which, in turn, impacts the ability of pests to consume plants (Altieri and Nicholls 2003). Given the complexity of these direct and indirect effects on plants and pests, it has been widely debated how fertiliser treatments will affect arthropod communities in crop systems (Butler, Garratt, and Leather 2012).

Many pest management strategies affect soil fertility. Increased nitrogen from fertilisers often increases attractiveness of plants to pests, but certain organic fertilisers have been shown to mitigate this effect by also promoting plant tolerance to pests (Altieri and Nicholls 2003; Rowen, Tooker, and Blubaugh 2019). Soils with high organic matter often also support diverse communities of organisms that deter or consume pests (Altieri and Nicholls 2003, Rowen, Tooker, and Blubaugh 2019) as well as symbiotic microbes that alter plant growth and defence (Thaler and Bostock 2004; Staley

et al. 2010; Rowen, Tooker, and Blubaugh 2019). Despite these predictions, studies assessing the effects of organic and synthetic fertilisers on insect pests have contradictory results. On cabbage, collards and corn, herbivores had higher survival and reproduction on plants grown with synthetic rather than organic fertiliser (Eigenbrode and Pimentel 1988, Morales et al. 2001, Hsu, Shen, and Hwang 2009). However, other studies show impacts of organic and synthetic fertilisers vary across pest species (Yardim and Edwards 2003; Staley et al. 2010). Because growers are increasingly converting their agricultural land to organic production (Skorbiansky, Carlson, and Spalding 2023), considering how fertilisers may impact multiple common pests is critical when developing integrated pest management strategies for crops.

Effects of fertilisers on pests depend on whether they alter plant traits such as secondary metabolite production, which vary by crop variety. Quinoa (*Chenopodium quinoa* Willd.), for example, has hundreds of varieties bred for abiotic and pest tolerance and yield (Aguilar and Jacobsen 2003; Peterson et al. 2015). In the US, quinoa is grown commercially in Washington, Oregon, California and Colorado, and varieties are being developed to suit these regions (Peterson et al. 2015; Aluwi, Murphy, and Ganjyal 2017; Goldberger and Detjens 2019). Common pests in these areas are aphids, *Lygus* and stem-boring flies, which can cause up to 100% yield loss (Oeller et al. 2021; Szczepaniec and Alnajjar 2023). The Pacific region leads in organic acreage (Skorbiansky, Carlson, and Spalding 2023); thus, there is interest in the link between quinoa cultivation and organic agriculture. Trials are being conducted to determine optimal fertilisation regimes that promote growth of different quinoa varieties. However, interactions between crop variety and nitrogen source could impact not only crop growth and yield but also insect pests in the system, which should be considered in pest management (Hsu, Shen, and Hwang 2009).

Our study assessed the ecological effects of organic and synthetic fertiliser inputs on pest populations in two quinoa varieties. Our trials were conducted in the Pacific Northwest USA, where quinoa is being introduced as a crop and trials examining effects of organic as compared to synthetic fertiliser sources on quinoa growth are being conducted. We first used experiments to test the effects of organic and synthetic fertilisers on population growth and survival of two pests, cowpea aphid (*Aphis craccivora*) and *Lygus* bugs (*Lygus spp.*), on quinoa grown in greenhouse and open-field common garden studies. We complemented these studies by assessing induced defence gene expression to assess the potential mechanisms by which fertiliser treatments impacted pest populations. These studies can aid in identifying potential indirect costs or benefits of particular fertiliser sources beyond effects on plant yield or quality.

## 2 | Methods

### 2.1 | Effects of Fertiliser Source and Variety on Aphid Population Growth

We ran a greenhouse experiment to assess the effects of fertiliser and variety on aphids in quinoa. There were three fertiliser treatments: (i) organic chicken manure (Perfect Blend 4–4-4, Othello, WA), (ii) synthetic granular (Osmocote 14–14-14, Scotts, Marysville, OH) and (iii) a control with no fertiliser, and two quinoa varieties: (i) Titicaca and (ii) Cherry Vanilla. There were eight replicates for each treatment combination, for 48 total replicates (3 fertilisers × 2 varieties × 8 replicates). We standardised to 2 g N for each 3 L pot of soil for each fertiliser (Peterson and Murphy 2014). Titicaca is a high saponin variety with nearly three times the total saponin content as Cherry Vanilla, a low saponin variety (16.8 vs. 5. 8 mg/g, Medina-Meza et al. 2016). Saponins are secondary metabolites that may be chemical pest deterrents (Valoy, Reguilón, and Podazza 2015; Medina-Meza et al. 2016; Oeller et al. 2021).

In the greenhouse (16:8 h light: dark; 21°C–24°C light; 16°C–18°C dark), 10 seeds were planted per pot and thinned to one plant 10 days later. After 4 weeks, plants were placed in individual mesh cages (50 × 50 × 95 cm, BugDorm Insect Cages, MegaView Science, Taiwan). Five adult cowpea aphids of the same age were placed on a leaf on the top third of each plant. After 24 h, an initial count was taken of aphids and two leaves from the top second node of five plants without aphids were collected, wrapped in foil, frozen in liquid nitrogen and stored at −80°C to assess 'pre-aphid' levels of jasmonic acid, salicylic acid and abscisic acid. Final aphid counts were taken 9 days later, which allowed enough time for a complete generation to occur, and after which plant leaves were sampled similarly to the 'pre-aphid' plants for assessment of chemical phytohormone signalling after exposure to aphid feeding, that is, 'post-feeding' (Clark et al. 2019). The experiment was conducted in two temporal blocks with block 1 from 16 February to 24 February 2019 and block 2 from 30 March to 7 April 2019.

### 2.2 | Effects of Fertiliser Source and Variety on Lygus Survival and Reproduction

A second experiment was conducted in field cages to assess the effects of fertiliser and variety on *Lygus* bug survival and reproduction. A field experiment was necessary due to our inability to establish a *Lygus* colony in greenhouses. We used the same fertiliser treatments (organic, synthetic, none), which were crossed with two quinoa varieties: (i) Titicaca and (ii) Cherry Vanilla. We had eight replicates of each combination, for 48 cages in total (3 fertilisers × 2 varieties × 8 replicates). Ten seeds were planted per pot and thinned to one plant 10 days later, after which pots were placed in the ground at the Spillman Agronomy Farm in Pullman, WA with a mesh cage (35 × 35 × 60 cm, BugDorm Insect Cages, MegaView Science, Taiwan) placed over each. *Lygus hesperus* was collected in an adjacent quinoa field, and eight adults were placed on each plant. We attempted to include four females and four males by observing the abdomen, as male *Lygus* have a more tapered abdomen (Mueller, Summers, and Goodell 2003); however, we could not always discern below the wings without overhandling specimens and killing them, and there may have been some variation. After 24 h, an initial count was taken of surface eggs and adults, after which counts were taken every 2 days for 9 days. Identical to the aphid experiment, tissue samples were collected and stored before and after *Lygus* bug presence to analyse jasmonic acid, salicylic acid and abscisic acid signalling both 'pre-*Lygus*' and 'post-*Lygus*'. The experiment was conducted over two temporal blocks, with

block 1 from 16 July to 24 July 2019 and block 2 from 30 July to 7 August 2019.

### 2.3 | Effects of Fertiliser and Variety on Pests in a Common Garden Field Experiment

We also conducted an open field experiment to test the effects of fertiliser and variety on aphid and *Lygus* populations at Spillman Agronomy Farm. This farm is surrounded by wheat, chickpea, canola and alfalfa, which can be sources of aphids and *Lygus* to quinoa. Twelve plots were laid out in a split-plot randomised block design with fertiliser (organic, synthetic or none) applied to the whole plot and quinoa variety (Cherry Vanilla or Titicaca) as subplots. The same prior fertiliser treatments were used: (i) organic, (ii) synthetic or (iii) none. Each fertiliser plot contained four 2.77 $m^2$ variety subplots (two of each variety) divided by a 2 m buffer, resulting in 48 total replicates across fertiliser and variety treatment combinations. Soil samples from eight locations in the field were collected prior to fertiliser application with a hand-operated soil auger at 25 cm, and the soil was determined to have 84 kg N per ha on average (Soiltest, Moses Lake, WA). We standardised the amount of nitrogen applied per plot to 56 kg N per ha (Peterson and Murphy 2014). Fertilisers were broadcast on each plot and tilled into the soil using a rototiller for 1 week before planting on 8 May 2019. Control plots were tilled, but no fertiliser was applied.

Seeds were hand-planted on 15 May 2019 and thinned to 50 plants per plot 1 month later. All plots were weeded weekly. Visual observations of *A. craccivora*, *Lygus hesperus* and *L. elisus* were taken weekly on 10 random plants per plot across the season (Staley et al. 2010). *Lygus* adults were counted exactly, but due to high numbers, *A. craccivora* populations were measured by counting how many of the 10 plants were infested (100 or more individuals) with aphids. Observations of pest identity and abundance were taken weekly from 1 July to 26 August 2019.

### 2.4 | Effects of Fertilisers on Induced Defence Gene Transcript Expression

To test a potential mechanism of fertiliser effects on pest populations, we ran bioassays on plant tissue samples collected from 'pre' and 'post' aphid and *Lygus* in their respective experiments. Bioassays quantified defence gene transcripts reflective of jasmonic acid (*WRKY33*), salicylic acid (*EP3*) and abscisic acid (*ABA4*) phytohormones; each is involved in hormone biosynthesis (Rollano-Peñaloza et al. 2022). Tissue samples from the experiments were ground using a mortar and pestle in liquid $N_2$. One hundred milligrams of homogenised tissue was used for total RNA extraction using Promega SV kits (Promega, Madison, WI) and cDNA was synthesised from 1 μg of total RNA using Bio-Rad iScript kits. Gene-specific primers (Table 1) were used in qRT-PCR reactions (10 μl) containing 3 μL of ddH2O, 5 μL of iTaq Univer SYBR Green Supermix, 1 μL of diluted primer mix (forward and reverse, 10 μM) and 1 μL of diluted (1:25) cDNA template. The qRT-PCR programme had a 3-min denaturation at 95°C followed by 40 cycles of denaturation at 95°C for 15 s, annealing for 30 s at 60°C and extension for 30 s at 72°C. For melting curves, a dissociation step cycle was used (55°C for 10 s and 0.5°C for 10 s until 95°C). The transcript abundance of *CqWRKY33* (jasmonic acid gene; *WRKY* transcription factor), *CqEP3* (salicylic acid gene; *endochitinase EP3-like*) and *CqABA4* (abscisic acid gene; gene encoding Protein ABA DEFICIENT 4) were then calculated using the delta–delta Ct method, (2–ΔΔCt) with *CqActin* as a housekeeping gene (Livak and Schmittgen 2001; Kozera and Rapacz 2013).

### 2.5 | Statistical Analysis

All analyses were conducted in R v. 3.6.2 (R Core Team 2020), with post hoc tests using the emmeans package (Lenth 2016). For the aphid experiment, we fit generalised linear mixed models (GLMM) using the lme4 package (Bates et al. 2015) to assess the effects of fertiliser and variety on aphid growth rates, with cage as a random effect and aphids modelled with a negative binomial distribution (Long 1997). For the *Lygus* experiment, a mixed Cox proportional hazards model (Cox 1972) was used to assess effects of fertiliser, variety and their interaction on survival; cage was a random effect. Negative binomial regressions were used to test effects of quinoa variety and fertiliser on the amount of *Lygus* eggs laid; day and cage were random effects. Significance tests were performed with the 'car' package (Fox and Weisberg 2018). For the common garden experiment, negative binomial models were used to analyse the effects of variety and fertiliser on aphid and *Lygus* abundance. Separate models were conducted with number of aphid-infested plants or number of *Lygus* as the responses. In all models, variety and fertiliser

**TABLE 1** | List of quinoa primers used for this study.

| Gene | Primer sequences (5′-3′) | NCBI accession No. | Amplicon size | Reference |
|---|---|---|---|---|
| *ABA4* FP | CCTTCTGTACGCTTATCTTCTGT | XM_021907877.1 | 143 bp | Morales et al. 2017 |
| *ABA4* RP | GAATCCATGCTGATGCTAATGTC | | | |
| *EP3* FP | CCTTCTTTGCTCATGTCACCC | XM_021895224.1 | 164 bp | Rollano-Peñaloza et al. 2022 |
| *EP3* FP | CTGCTCCATAGTTGTAGTTCCA | | | |
| *WRKY33* FP | TCCTTTACACCTGAGACATCCT | XM_021910261.1 | 126 bp | Rollano-Peñaloza et al. 2022 |
| *WRKY33*RP | ACTGTTCTGTTACCATACCCTGAC | | | |
| *Actin* IFP | TACCACAGGTATCGTGCTTGACTC | XM_021904103.1 | 113 bp | Rollano-Peñaloza et al. 2022 |
| *Actin* RP | GATCACGTCCGGCAAGATCC | | | |

were fixed effects, and week and cage were included as random effects.

To evaluate the effects of fertiliser and variety on the relative gene transcript expression of phytohormones *ABA4*, *EP3* and *WRKY33*, we ran separate generalised linear models (GLM) with gene transcript expression as the response and fertiliser, variety, insect presence (pre or post insect presence) and their interaction as fixed effects. Analyses for defensive gene expression were run on cycle threshold values (Ct), and $2^{-\Delta\Delta Ct}$ (relative expression) was calculated using estimates from the models. Estimated marginal mean of Ct values and standard error of the mean were generated using the emmeans package (Lenth et al. 2016). Methodology for $2^{-\Delta\Delta\mathbf{Ct}}$ followed Rao et al. (2013) and Kozera and Rapacz (2013) using the housekeeping gene *Actin*.

## 3 | Results

### 3.1 | Effects of Fertiliser and Variety on Aphid Population Growth

*Aphis craccivora* population growth was affected by fertiliser ($\chi^2 = 6.19$, $p = 0.045$) but not quinoa variety ($\chi^2 = 0.064$, $p = 0.79$) (Figure 1). After 9 days, aphid abundance on quinoa plants grown with synthetic fertiliser was higher than on plants grown in organic and no fertiliser (Figure 1).

### 3.2 | Effects of Fertiliser and Variety on Lygus Survival and Reproduction

*Lygus* survival was higher on Titicaca than Cherry Vanilla ($Z = -2.78$, $p = 0.0054$) (Figure 2a), and on organic compared to synthetic or control plants ($Z = 3.09$, $p = 0.0020$) (Figure 2b), but there was no interaction ($Z = 0.58$, $p = 0.56$). *Lygus* egg counts were also higher on Titicaca than on Cherry Vanilla ($\chi^2 = 36.5$, $p < 0.001$) (Figure 3a), and more *Lygus* eggs were laid on control plants compared to plants grown with either organic or synthetic fertiliser (Figure 3b).

### 3.3 | Common Garden Field Experiment

*Aphis craccivora* populations were also not significantly affected by quinoa variety ($p > 0.10$ for each effect) but were marginally impacted by fertiliser treatment (Figure 4A). There were marginally fewer *A. craccivora* on quinoa grown with organic fertiliser than synthetic or no fertiliser ($Z = -1.75$, $p = 0.08$) (Figure 4A). *Lygus* populations were also not affected by quinoa variety, fertiliser treatment or interactions between the two in the common garden experiment ($p > 0.05$ for each effect) (Figure 4B).

### 3.4 | Effects of Fertiliser and Variety on Induced Defensive Gene Expression

In the aphid experiment, both fertiliser treatments had lower *WRKY33* gene transcript levels than the control ($\chi^2 = 7.59$, $p = 0.022$), but did not affect *ABA4* or *EP3* expression ($p > 0.10$ for both) (Figure 5). Quinoa variety also affected *WRKY33* ($\chi^2 = 9.48$, $p = 0.002$), with higher gene transcript levels on Cherry Vanilla than Titicaca (Figure 5); variety did not affect *ABA4* or *EP3* ($p > 0.10$ for both). The interaction between fertiliser and variety mediated *WRKY33* expression ($\chi^2 = 7.26$, $p = 0.026$), with stronger effects of fertiliser on Cherry Vanilla than Titicaca, but there was no interaction for *ABA4* or *EP3* ($p > 0.10$ for both) (Figure 5). Aphid presence affected the expression of *ABA4* ($\chi^2 = 13.39$, $p < 0.001$), *EP3* ($\chi^2 = 85.29$, $p < 0.001$) and *WRKY33* ($\chi^2 = 19.87$, $p < 0.001$), with higher expression of each gene transcript after aphids were present (Figure 5).

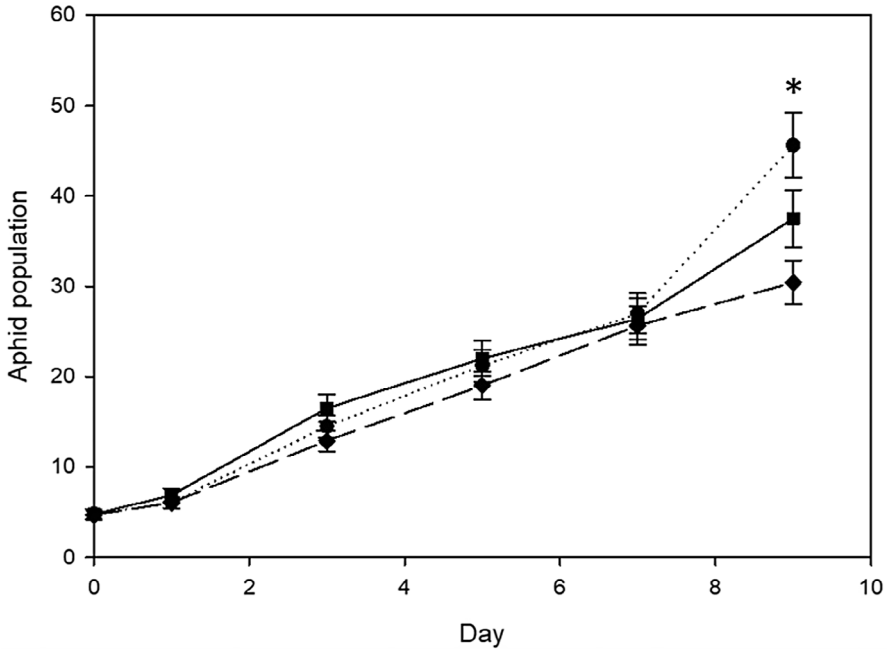


**FIGURE 1** | Aphid populations on quinoa grown with organic, synthetic and no fertiliser over 9 days in a greenhouse experiment. Shown are mean (± SE) for each time point counts were made.

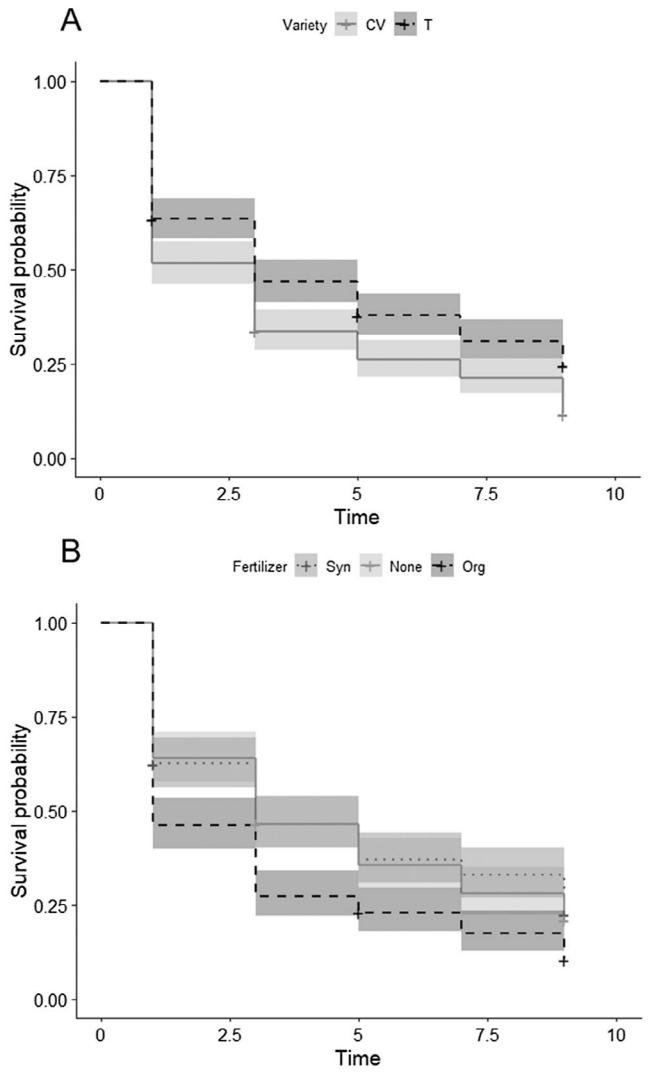


**FIGURE 2** | Survival probability of *Lygus* spp. over 9 days on (A) two quinoa varieties (CV = Cherry Vanilla, T = Titicaca) grown with (B) organic, synthetic or no fertiliser in a field experiment.

In *Lygus* field experiments, fertiliser treatments affected *ABA4* ($\chi^2 = 16.77$, $p < 0.001$) and *WRKY33* expression ($\chi^2 = 64.92$, $p < 0.001$), with the highest levels of both gene transcripts on control plots, and no difference between the two fertiliser sources (Figure 6). Fertilisers did not affect *EP3* expression ($\chi^2 = 0.83$, $p = 0.65$) (Figure 5). Variety, *Lygus* presence and the interaction between fertiliser and variety did not affect *ABA4*, *EP3* or *WRKY33* ($p > 0.10$ for all) (Figure 6).

## 4 | Discussion

We found variable fertiliser effects on pest survival, reproduction and abundance, although in general quinoa treated with organic fertiliser had lower pest numbers than plants treated with synthetic or no fertiliser. This was shown clearly in greenhouse and field cage experiments, while results were less clear in the open field experiment. The stronger effects observed in cages may partially reflect the effects of residual nitrogen in field soil before fertilisers were applied; it is also possible that allowing pests to colonise plants naturally did not challenge plants sufficiently compared to manual addition of pests in cages. Our results add to the literature suggesting that organic fertilisers may benefit plants by increasing pest tolerance or reducing attractiveness to pests (Kowalski and Visser 1979; Kajimura et al. 1995; Phelan, Mason, and Stinner 1995; Yardim and Edwards 2003). A potential trade-off is that synthetic fertilisers can greatly increase quinoa yields (Schulte Auf'm Erley, Kaul, Kruse, and Aufhammer 2005). The decisions growers make about which fertiliser product to apply should, thus, depend on risk from pests contrasted against potential lost yield.

Adding nitrogen to soil can affect a variety of plant traits that may indirectly affect pests. For example, applying fertilisers to soil can increase quinoa seed nitrogen and protein levels and may potentially make plants more attractive to pests that benefit from higher nitrogen availability (Kakabouki et al. 2018). However, in other crops, reduced pest populations have been seen organically compared to conventionally fertilised plants (Kowalski and Visser 1979, Kajimura et al. 1995, Phelan, Mason, and Stinner 1995, Yardim and Edwards 2003). One potential mechanism underlying this effect is that organic fertilisers, such as manure and vermicompost, can provide beneficial bacterial and fungal microbes that directly and indirectly augment plant defences against pests (Cardoza 2011; Alyokhin and Gross 2013; Pangesti et al. 2015; Rowen, Tooker, and Blubaugh 2019). Organic fertilisers can affect plants in other ways, like slowing macronutrient uptake, making them less attractive hosts than synthetically fertilised plants (Altieri and Nicholls 2003; Rowen, Tooker, and Blubaugh 2019). Fertilisers can also cause morphological changes to crops, affecting growth rate and thickness of epicuticle, which affects pest feeding and plant selection (Altieri and Nicholls 2003).

In the aphid and *Lygus* survival experiments, plants treated with no fertiliser had higher expression of the jasmonic acid gene transcript (*WRKY33*) than plants treated with either fertiliser. The abscisic acid gene transcript (*ABA4*) was also upregulated in control treatments in the *Lygus* survival experiment. Both the jasmonic and abscisic acid hormone pathways are believed to protect plants against herbivores (Thaler and Bostock 2004; Szczepaniec and Finke 2019), but we did not observe lower survival of aphids or *Lygus* on control plants despite higher gene transcript levels. Our results, thus, suggest that phytohormones are not the main mechanism by which fertilisers affected pests. Instead, it may be that plants grown in untreated soil had greater levels of both hormones because higher pest densities in these treatments caused plants to increase allocation of resources to defence (Thaler and Bostock 2004, Szczepaniec and Finke 2019). This is supported by the fact that all defence genes were induced by aphids, although there was no increased defence gene expression after *Lygus* feeding. Although it is not clear why aphids induced gene transcripts more than *Lygus*, it may be due to their feeding differences; aphids feed passively on phloem (Moran and Thompson 2001; Zhu-Salzman et al. 2004), while *Lygus* are mesophyll feeders that inject salivary enzymes to liquefy plant tissue prior to ingestion (Agustí and Cohen 2000; Rodriguez-Soana et al. 2002).

While the strongest treatment effects across our experiments were due to fertilisers, *Lygus* bug survival and egg counts were also affected by quinoa variety, with lower survival

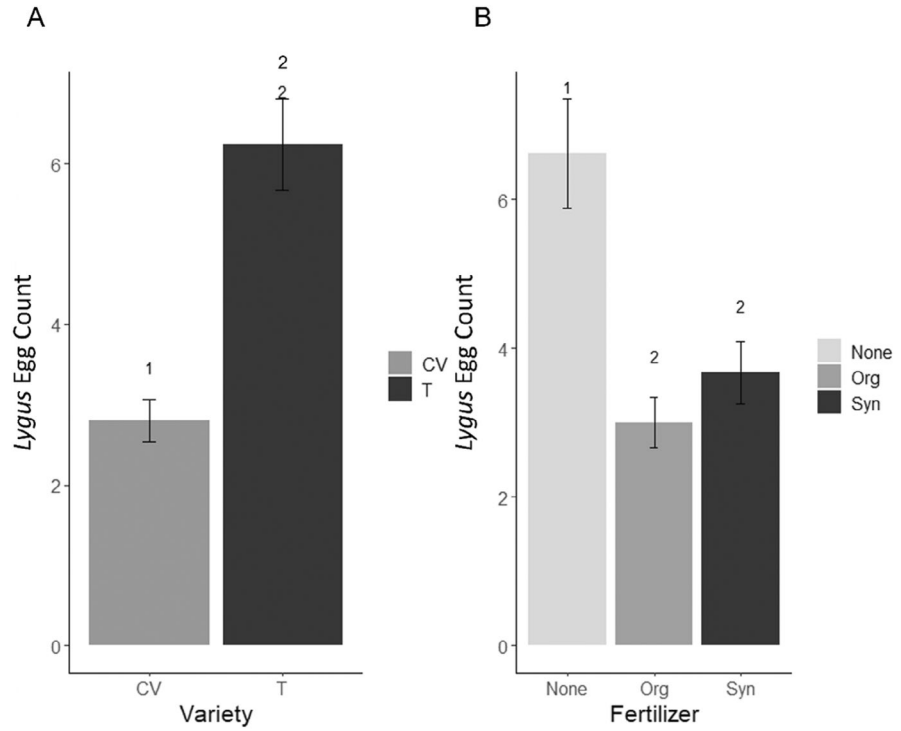


**FIGURE 3** | The number of *Lygus* spp. eggs on (A) two quinoa varieties (CV = Cherry Vanilla, T = Titicaca) grown with (B) organic, synthetic or no fertiliser in a field experiment. Each bar shows a mean ± SE, and numbers indicate significant differences between treatments ($\alpha = 0.05$).

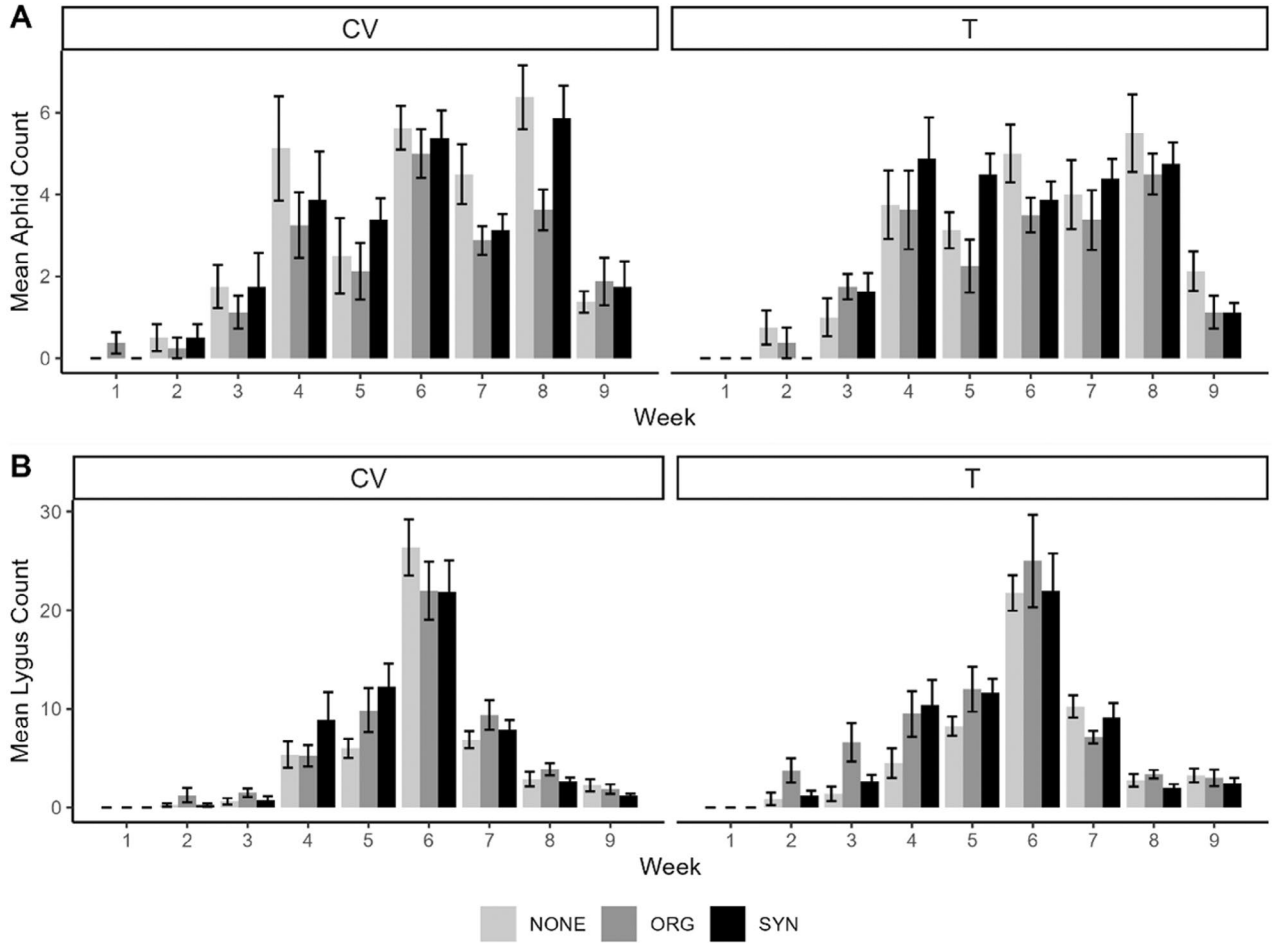


**FIGURE 4** | Mean weekly counts for (A) aphids and (B) *Lygus* spp. on quinoa plants grown with organic, synthetic or no fertiliser for two varieties (CV = Cherry Vanilla, T = Titicaca) in a common garden experiment.

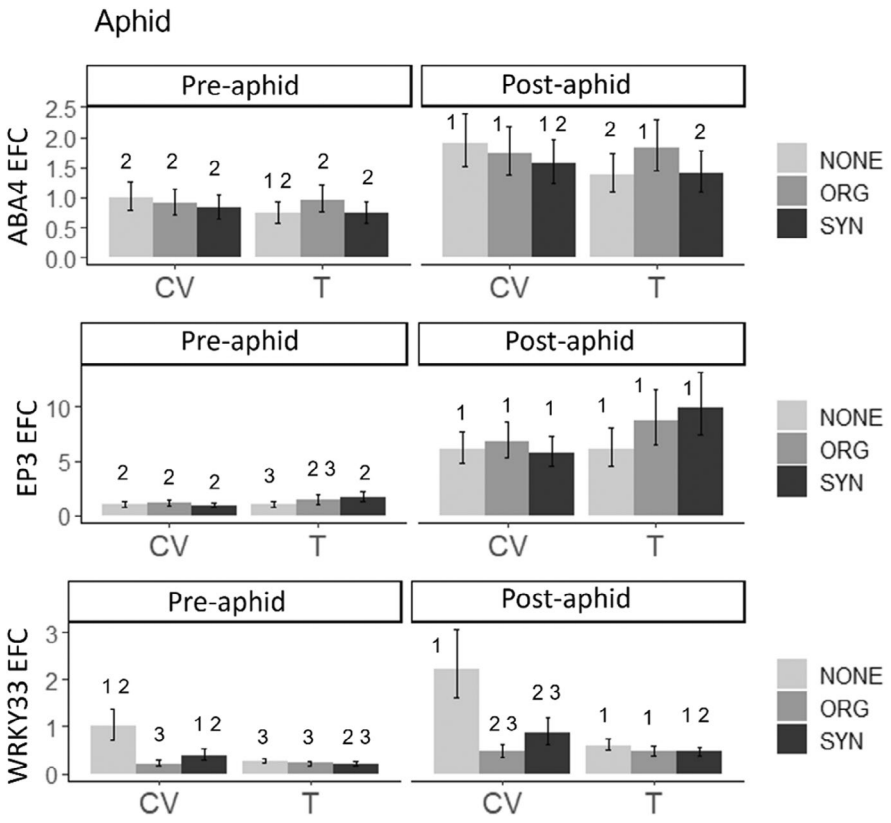


**FIGURE 5** | Differences in expression fold change (EFC) of genes *ABA4*, *EP3* and *WRKY33* in quinoa plants grown with organic, synthetic or no fertiliser preaphid and postaphid presence for two quinoa varieties (CV = Cherry Vanilla, T = Titicaca). Each bar shows a mean ± SE, and numbers indicate significant differences between treatments ($\alpha = 0.05$).

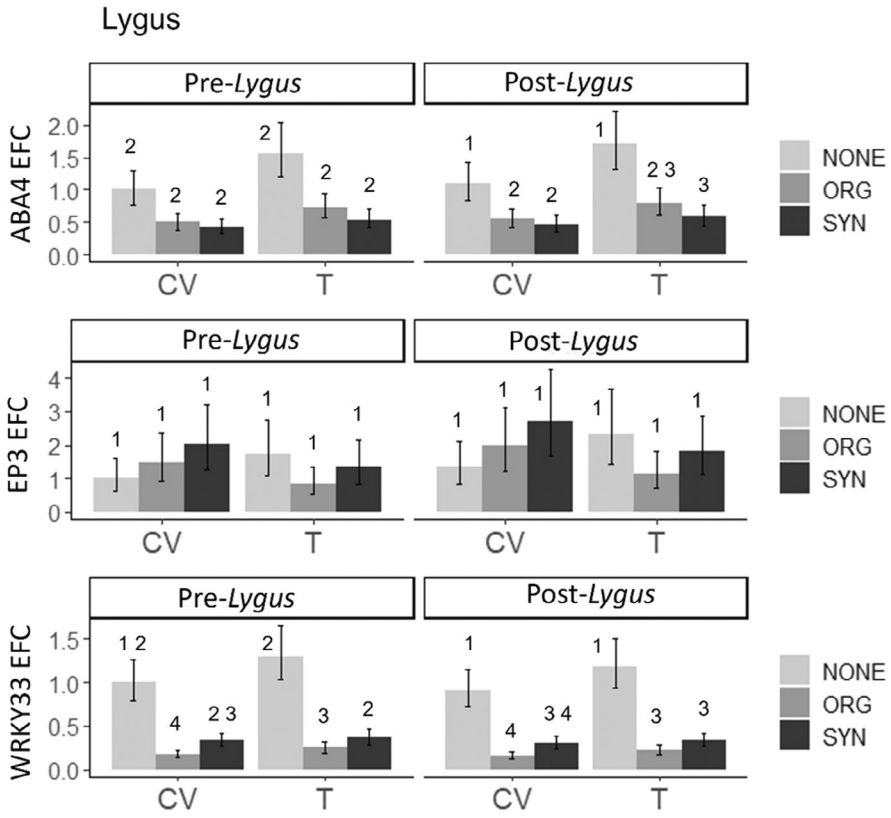


**FIGURE 6** | Differences in expression fold change (EFC) of genes *ABA4*, *EP3* and *WRKY33* in quinoa plants grown with organic, synthetic or no fertiliser pre-*Lygus* and post-*Lygus* presence for two varieties (CV = Cherry Vanilla, T = Titicaca). Each bar shows a mean ± SE, and numbers indicate significant differences between treatments ($\alpha = 0.05$).

and egg counts on Cherry Vanilla compared to Titicaca. In contrast, there was no effect of variety on aphid reproduction. We chose the two varieties based in part on their saponin content, as Titicaca is considered a high saponin variety (16.75 mg/g total saponins) and Cherry Vanilla is considered a low saponin variety (5.78 mg/g total saponins) (Medina-Meza et al. 2016). While it is theorised that saponins are a potential pest deterrent (Valoy, Reguilón, and Podazza 2015; Medina-Meza et al. 2016; Oeller et al. 2021), Yábar, Gianoli, and Echegaray (2002) found that high saponin varieties had higher pest abundances, including aphids, than low saponin varieties. Feeding differences between *Lygus* and aphids might also mitigate the impact of saponins as a pest deterrent. Our results also reflect this finding, although more experiments would be needed to demonstrate a causal relationship between saponins and pest levels. However, there are many other differences between the two varieties, such as size, colour and flower density, as well as plant defences that may have mediated these differences.

Our results suggest that when cost-effective, and if there is not a sufficient yield gap, growers may achieve better pest management outcomes with organic compared to conventional fertilisers. However, agronomic outcomes may depend on the dominant pest in a field and the quinoa variety being planted. More work is also needed to explore how variation in fertiliser treatments might affect quinoa productivity and pest management across realistic environmental contexts. For example, fertilisers may interact with soil texture, soil moisture and soil organic matter to affect pest outcomes. Despite these complexities, our study shows that careful selection of fertiliser regimes and variety are important components of an integrated pest management plan that can aid in promoting plant tolerance to pests across environmental contexts.

### Author Contributions

**Liesl Oeller** contributed to writing – original draft, writing – review and editing, conceptualisation, methodology, investigation and data curation. **Benjamin W. Lee** was involved in formal analysis and visualisation. **Saumik Basu** contributed to the methodology and data curation. **Kevin M. Murphy** contributed to conceptualisation, resources and funding acquisition. **David W. Crowder** was involved in supervision, conceptualisation, funding acquisition, writing – original draft, writing – review and editing.


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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

Data and code used for analysis are available upon request from Figshare (10.6084/m9.figshare.26792539) and will be made publicly available in this repository pending acceptance of this manuscript.

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