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Article

Nitrogen and plant growth regulator affect plant detoxification metabolism and tritrophic interactions among *Triticum aestivum*, *Sitobion avenae* and *Aphelinus asychis*

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With 8 figures and 1 table

Abstract: The application of nitrogen fertilizers and plant growth regulators (PGRs) are common agronomic practices in wheat production. To investigate the influence of these two factors on a wheat banker plant system and the associated tritrophic interactions, we exogenously applied 0, 50, 150 or 250 mg/L indole-3-acetic acid (IAA) on wheat seedlings cultivated in Hoagland Nutrient Solutions spiked with 0, 640, 1280 or 1920 mg/L NH_4NO_3, and examined performance and biochemical response mechanisms of plants and insects. Results indicated that the application of 1280 mg/L NH_4NO_3 coupled with 150 mg/L IAA increased leaf area of wheat seedlings significantly. In addition to the lower water content, more photosynthetic pigments and higher activity of polyphenol oxidase (PPO), peroxidase (POD) and catalase (CAT) were also detected within this treatment. However, wheat plants with the greatest leaf area did not produce heavier *Sitobion avenae*. Aphids feeding on seedlings applied with 1920 mg/L NH_4NO_3 coupled with 0 or 50 mg/L IAA treatments showed larger body weight difference, more trehalose and relatively higher activity of detoxification and metabolic enzymes. Moreover, not only did this treatment support the largest aphids, but also medium weight aphids produced the largest parasitoids *Aphelinus asychis*, which were produced from seedlings with 1280 mg/L NH_4NO_3 and 250 mg/L IAA, 1920 mg/L NH_4NO_3 and 50 mg/L IAA and 640 mg/L NH_4NO_3 and 50 mg/L IAA. This study provided baseline data for regulating the application of nitrogen and PGRs for optimization of banker plant systems. Moreover, the manipulation of growth conditions of wheat must be considered when comparing different approaches to Integrated Pest Management.

Keywords: Fertilizer, Phytohormone, Indole-3-acetic acid (IAA), banker plant, Integrated Pest Management

1 Introduction

In natural ecosystems, tritrophic interactions are affected by many factors including the quality, diversity and spatial distribution of host plants (Raupp et al. 2010; Davis & Hofstetter 2012; Hoysted et al. 2018; Hohenstein et al. 2019; Thomine et al. 2020a; 2020b), performance of herbivorous arthropods (Bisane et al. 2013; Burghardt & Tallamy 2013; Louis & Shah 2013), parasitoid diet breath (Desneux et al. 2009; Monticelli et al. 2019a; 2019b), habits of parasitoids and predators (Lane et al. 1999; Schöller & Flinn 2000; Kennedy 2003; Rehman & Powell 2010), inter-species competition (Stout et al. 2006; Gripenberg et al. 2010; Chailleux et al. 2014), the physical environment (Ozawa et al. 2012) and xenobiotics such as pesticides (Desneux et al. 2007). In practice, the application of nitrogen fertilizer helps meet global food demand and nitrogen is not only a necessary nutritional element of plants but also the regulatory factor for direct and indirect defense (Stevens et al. 2004; Chen & Ni 2011; Bogaert et al. 2017) which affects the nutritional quality and defense levels of plants. It is also widely documented as an abiotic factor triggering bottom-up effects which impacts the survival and development of some lepidopteran insects (Han et al. 2018; 2019) and may result in

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differing quality of hosts for parasitoids (Benrey & Denno 1997; Williams 1999). Additionally, the appropriate application of nitrogen supports sustainable pest management theory that requires the consideration of both economic and environmental sustainability (Clark & Tilman 2008; Stevens et al. 2004; 2006; Bobbink et al. 1998; 2010; Throop and Lerdau 2004; Rashid et al. 2017). Therefore, to obtain positive effects on biocontrol service, appropriate nitrogen levels should be applied to reduce bottom-up effects on the fitness and interactions among higher trophic levels (Chesnais et al. 2016; Dong et al. 2018; Han et al. 2020).

Plant growth regulators (PGRs) are also widely used to adjust the branching, growth rate, coloring, reproduction and flowering times of plants (Basra 2000; Prado & Frank 2013; Waqas et al. 2017). Previous studies revealed that certain levels of PGRs had the potential to reduce insect populations by reducing fecundity, viability and increasing their development time (Kaur & Rup 2002; 2003; Uçkan et al. 2008; Pineda et al. 2009; Ryalls et al. 2016). Conversely, some studies indicated opposite results. PGRs could alter the abundance, fitness or efficacy of parasitoids by affecting the quality of insect hosts (Coffelt et al. 1993). However, the specific effect of PGRs on tritrophic interactions has rarely been studied. For instance, N-dimethylaminosuccinamic and chlormequat chloride acid reduced the body size of aphids (Honeyborne 1969) and, as a consequence, the size of parasitoids living on smaller hosts may also decrease (Sampaio et al. 2008). Indole-3-acetic acid (IAA) is one of the most important phytohormones in plants, stimulating cell elongation and growth by increasing cell wall plasticity and is widely used in promoting leaf growth and lateral root accumulation in agriculture and horticulture. *Apanteles galleriae* Wilkinson, for example, was reported to show a longer developmental period and a shorter adult life when parasitized on *Achoria grisella* F. fed with artificial diets with spiked IAA (Uçkan et al. 2011). Given that nitrogen fertilizer and PGRs are both frequently used in agriculture, it is important to investigate the influence of the combination of these two factors in crop production.

In a wheat-aphid-parasitoid system, nitrogen and PGR application regimes could change the level of chemical constitutive defense and the nutritional condition of wheat (Dudareva et al. 2004; Cory & Hoover 2006; De Vos et al. 2005). Leaf area (Asseng et al. 2003) and free water content (Nielsen & Vigil 2005; Jacobs et al. 1998; Nachappa et al. 2016) are both important indices of nutrition in wheat and pest fitness is closely related to plant nutritional condition (Han et al. 2014; 2015; 2016; Dong et al. 2018). The concentration of chlorophyll and carotenoids in leaves reflect the level of photosynthesis in plants which are essential for plant growth and development (Moharekar et al. 2003; Heng-Moss et al. 2003; Sairam & Saxena 2000). Besides these nutritional factors, secondary metabolites can be also produced to defend plants from biotic attack and abiotic stress, such as fertilizer deficiency and drought (Chen et al. 2010; Winter & Rostas 2010; Di et al. 2018). This includes detoxification enzymes such as superoxide dismutases (SOD) (Gao et al. 2013), polyphenol oxidase (PPO) (Mayer 2006; Kruzmane et al. 2002; Thipyapong et al. 2004; Constabel & Barbehenn 2008), peroxidase (POD) (Lagrimini 1991; Cao & Liu 2014) and catalase (CAT) (Slaughter & O'Brien 2000; Mittler 2002). These substances were documented to be effective on several plants fed upon by *Bemisa tabaci* Gennadius (Di et al. 2018) and aphids feeding on wheat with a potassium and IAA application (Di et al. 2014). Benzoxazinoids are also documented as the dominant secondary metabolites in cereals mediating plant resistance to herbivorous insects (Li et al. 2018), but whether those are also triggered by nitrogen and IAA application is unclear. Furthermore, the co-evolution of herbivorous pests and their host plants involves the development of defending strategies. Variation in chemical defense and nutrition in wheat may lead to changes of growth conditions (DW, trehalose, total protein, etc.), digestive ability (trehalase, sucrase, amylase, etc.) and detoxification ability (SOD, AKP, CAT, POD, etc.) (Mittler 2002; Chen 2008; Zhu-Salzman et al. 2008; Slaughter & O'Brien 2000; Matés & Sánchez-Jiménez 1999) of the aphid *Sitobion avenae* (F.), a widely-spread agricultural pest feeding on plants that causes significant economic loss (Kang et al. 2018). Secondary metabolite substances in plants can regulate levels of digestive and detoxification enzymes in insects (Di et al. 2018). Thus, it is important to examine enzymes in aphids and plants, which may provide information on the response mechanisms after regulating nitrogen and IAA levels in plants.

Aphelinus asychis (Walker) (Hymenoptera: Aphelinidae) is a single-parasitic parthenogenetic polyphagous parasitoid which feeds on various aphids including *Myzus persicae* (Sulzer), *Lipaphis erysimi* (Kaltenbach), *Brevicoryne brassicae* (L.), *Sitobion avenae* (Fabricius) and *Aphis gossypii* (Glover) (Zhu & Fang 2009; Byeon et al. 2009; Wang et al. 2016) and is a widely used biological control agent (Boivin et al. 2012; Wang et al. 2016). The body-size, nutrient levels and stress resistance of *A. asychis* are specifically connected with growth conditions and the detoxification ability of its hosts (Rehman & Powell 2010). For example, the aphid parasitoid *Aphidius ervi* (Haliday) was negatively affected when parasitizing on *S. avenae* on water stressed wheat via bottom-up effects (Nguyen et al. 2018). In practice, information on responses to the dosage of nitrogen and PGRs would assist pest management in the field or in greenhouses. As a banker plant system (Hopper et al. 1993; Frank 2010; Ohta & Honda 2010), the complex interactions in a wheat-aphid-parasitoid system needs to be examined to reduce expensive releases of parasitioids for biological control (Parolin et al. 2012).

In this study, Hoagland's solution (Hoagland & Arnon 1950) was hydroponically used to meet the nutrient demands of the plants. Leaf area, water content, chlorophyll, carotenoid, SOD, PPO, POD and CAT of wheat were measured to quantify the nutritional content and secondary metabolites of wheat. Meanwhile, DW, trehalose, total protein, SOD, AKP, CAT, POD, trehalase, sucrase and amylase of aphids were examined to test growth conditions and detoxification ability of aphids. Body-length, trehalose, total protein, SOD, AKP, trehalase, sucrase and amylase of parasitoids were assayed to clarify the adaptability of parasitoids raised on aphids under different plant conditions.

2 Materials and methods

2.1 Plant treatments and inoculation of insects

Wheat seeds (*T. aestivum* var. Mingxian 169) were grown in plastic pots (9 cm diameter, 20 seedlings per pot) with vermiculite (cleaned two times with 10% HCl and distilled water); the temperature fluctuated daily from 22 ± 1 °C at night to 27 ± 1 °C during the day in the growth chamber (RXZ, Ningbo, 14 L: 10 D, RH 70 ± 5%). All seedlings were maintained on standard Hoagland's solution amended with one of four treatment levels of nitrogen (0, 640, 1280 or 1920 mg/L NH_4NO_3) and 50 mL of the solution was added to pots every other day. After one week, distilled water solution containing 0, 50, 150 or 250 mg/L IAA (IB0723, Sangon Biotech, Shanghai, China) was sprayed on wheat seedlings in a spray tower (7 mL, 0.5 bar, settled for 30 s) (Potter, Burkard Manufacturing Co. Ltd, UK). The experimental design is summarized in Table 1.

Aphids (*S. avenae*) and parasitoids (*A. asychis*) were obtained from colonies maintained at the Key Laboratory of Applied Entomology, Yangling, China. The aphids were reared on wheat variety Mingxian 169 for more than 5 generations and starved for 2 h before inoculation. Twelve hours after IAA spraying, 5 first-instar aphids from the laboratory colony were inoculated onto one wheat seedling (100 first-instar aphids in total for the 20 seedlings in a pot) using a fine brush to establish a new colony for each treatment and 16 separate colonies were established. For each colony, one pot with 20 wheat plants and 100 aphids were placed in separate insect cages (60×60×60 cm, 80 mesh net) and maintained in the growth chamber as described above. Three weeks after aphid inoculation, 100 mummified aphids of *A. asychis* were added to each cage. After two weeks, mummified aphids were collected for analysis from each cage.

2.2 Measurement of leaf area, water content, chlorophyll and carotenoid content of wheat

Plants were grown separately and sprayed as described above. The area of the first leaf was carefully measured with a Portable Leaf Area Meter (Li-3000c, LI-COR Biosciences, USA) and each treatment was replicated 15 times. To measure water content, 1g of leaves were accurately weighed on an analytical balance (AL204, Metter-Toledo, Switzerland) after being oven-dried at 60 °C for 24 h. Water content was calculated according to Jacobs et al., 1998 (n = 10). After drying, 0.1 g of leaves were cut into small pieces (0.5 cm long), placed in 15 mL tubes with 10 mL 96% alcohol solution and sealed with parafilm. To determine chlorophyll and carotenoid content, leaf pieces were placed in the dark for 24 h. The mixture was then centrifuged at 1,500 g (High-speed refrigerated centrifuge CR22GIII, HITACHI, Japan) for 10 min at 25 °C and the supernatant was transferred to 48-well plates (Corning, USA) to measure OD_{665}, OD_{649} and OD_{470} in a Microplate Reader (Tecan Infinite M200, Tecan Group Ltd, Mnnedorf, Switzerland). Each well contained 150 µL supernatant. Chlorophyll and carotenoid contents were calculated following the methods of Porra *et al.*, 1989 (n = 10). Calculations are as follows:

$$WaterContent = \frac{FreshWeight - DryWeight}{FreshWeight}\%$$

$$C_{Chlorophylla} = 13.95A_{665} - 6.88A_{649}$$

$$C_{Chlorophyllb} = 24.96A_{649} - 7.32A_{665}$$

$$C_{Chlorophyll} = C_{Chlorophylla} + C_{Chlorophyllb}$$

$$C_{Carotenoid} = {1000A_{470} - 2.05C_{Chlorophylla} - 114.8C_{Chlorophyllb}} \big/ {245}$$

2.3 Weight difference (DW) of aphids and body measurements of parasitioids

For measuring aphid DW, one wheat plant was grown in a small pot (2 cm in diameter) and sprayed with IAA using the same spray tower (0.35 mL, 0.3 bar, settled for 40 s) as described above. Each plant was inoculated with 5 adult aphids from the laboratory colony. To prevent aphids from climbing on other plants, each plant was covered with a transparent cylindrical cage (35 cm high, 4.0 cm in diameter) made with plastic board and the top was covered with 80 mesh gauze. Adults and newly emerged aphids were removed with only one first-instar aphid remaining on the plant. The average weight of the removed first-instar aphids was used as the initial weight from each plant separately. The final weight of the aphid left on the plant was measured when it reached the adult stage and before offspring were produced. All weights were measured using a scale reading to part per million (MSA3.6P, Sartorius, Germany) and each treatment was replicated ten times.

Table 1. Experimental design.

Treatment	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
IAA (mg/L)	0	0	0	0	50	50	50	50	150	150	150	150	250	250	250	250
NH_4NO_3 (mg/L)	0	640	1280	1920	0	640	1280	1920	0	640	1280	1920	0	640	1280	1920

Mummified aphids collected from each colony were placed in 2000 mL beakers, covered with 80 mesh gauze and maintained in growth chambers under conditions as described above (22 ± 1 °C at night to 27 ± 1 °C during day, 14 L : 10 D, RH 70 ± 5%). After 2 weeks, newly emerged adult females were randomly chosen to measure body-length and head-width under a stereo microscope (SteREO Discovery V12, Zeiss, Germany). Twenty females were measured for each treatment.

2.4 Sampling and measuring of secondary metabolites

Wheat plants sampled to measure the secondary metabolites were planted and sprayed with IAA as described in 2.1. Wheat tissue (0.5 g) was quickly cut and weighed from the second leaf of the trefoil-stage of healthy wheat plants and was quickly ground to powder in porcelain mortar under liquid nitrogen. The powder was immediately transferred into a 10 mL centrifuge tube with 9 mL 0.1 M PBS (pH 7.4). The mixture was centrifuged at 4,000 g for 20 min at 4 °C and 500 µL liquid supernatant was transferred to 1.5 mL microcentrifuge tubes and stored at –80 °C for use. This was repeated 10 times for every treatment.

Aphids sampled for measuring the secondary metabolites were acquired from the wheat plants used when measuring the aphid DW (above). Ten plants grown in the small pots were sprayed with IAA as described in 2.3. Each plant was then inoculated with five adult aphids from the laboratory colony and removed immediately after producing offspring. Aphids were then allowed to grow on the plants for three weeks and each plant was covered with a cylindrical cage as described above. Five 5th-instar aphids feeding on wheat were chosen randomly from each plant and were ground in 1.5 mL microcentrifuge tubes with 200 µL 0.9% NaCl distilled water solution on ice using a disposable plastic tissue grinding pestles (70 mm in length, Sangon Biotech, Shanghai, China) in each treatment. The mixture was centrifuged at 3,000 g (High-tech centrifuge CT15RE, Japan) for 10 min at 4 °C and the supernatant was stored in the freezer at –80 °C until later use. Ten replicates were conducted for each treatment. The parasitoids sampled for measuring the secondary metabolites were from the colonies from each treatment. Ten newly emerged adult female parasitoids were randomly chosen from the beaker and quickly ground in 1.5 mL tubes under liquid nitrogen. After being ground, 100 µL 0.01 M PBS (pH 7.2) was added and the mixture was centrifuged at 2,000 g for 10 min at 4 °C. Supernatant was stored in the freezer at –80 °C until later use. Each treatment was repeated for five times.

Activity or the amount of trehalose, total protein, SOD, AKP, trehalase, sucrase and amylase were tested according to the method by Zhang et al. 2014 and Di et al. 2018. For assaying the activity of PPO in wheat leaves, 10 µL supernatant was added to 200 µL catechol (20 mM, dissolved in 0.1 M PBS, pH = 7.4) in 96-well plates using a multichannel pipette and increases in optical density at 410 nm (OD_{410}) were immediately determined for 90 s in a microplate reader (Tecan Infinite M200; Tecan Group, Männedorf, Switzerland). Activity of PPO was expressed as ΔOD_{410}/min/g (FW) (Deng et al. 2013). For POD, 5 mM guaiacol and 1 mM hydrogen peroxide in PBS (0.1 M, pH = 7.4) were used as substrates, and 10 µL supernatant from wheat or 20 µL supernatant from aphids was added. The activity was expressed as ΔOD_{470}/min/g (FW) or ΔOD_{470}/min/g (total protein) (Cao & Liu 2014). Analysis of CAT followed the method of Slaughter & O'Brien (2000) with minor modifications. Five µL supernatant from wheat or 10 µL supernatant from aphids was added into 50 µL 25 mM H_2O_2. The mixture was incubated for 3 min at 25 °C, 180 µL 200 mM ammonium molybdate was added and OD_{405} was immediately measured. Activity of CAT was defined as ΔOD_{405}/min/g (FW) or ΔOD_{405}/min/g (total protein).

2.5 Data analyses

All data were checked for assumptions of homogeneity of variances. In the case of percentages (water content of wheat), data were normalized using an arcsine square root transformation. The main effects of the two independent factors, IAA and NH_4NO_3, and the interactions of the two factors on the testing variables, including leaf area and water content of wheat, weight differences of aphids, body length of *A. asychis*, content of Chlorophyll a+b and carotenoid content or activity of secondary metabolites, were analyzed by factorial-ANOVA at $P < 0.05$, and means were compared using Tukey's posthoc comparisons ($P < 0.05$). Correlation analysis among parameters from wheat, aphids and parasitoids was performed by calculating Pearson's correlation coefficient of bivariate variables. All analyses were performed using SPSS (version 25.0, Chicago, IL, USA).

3 Results

3.1 Effect of NH_4NO_3 and IAA on wheat

The results indicated the main effect of NH_4NO_3 ($F = 332.5$; df = 3, 224; $P < 0.001$; $F = 86.29$; df = 3, 144; $P < 0.001$) and IAA ($F = 244.6$; df = 3, 224; $P < 0.001$; $F = 17.27$; df = 3, 144; $P < 0.001$), together with the interaction between factors ($F = 17.69$; df = 3, 224; $P < 0.001$; $F = 43.8$; df = 9, 144; $P < 0.001$), were statistically significant for both leaf area and water content. Specifically, leaf area of wheat was greatest when 1280 mg/L NH_4NO_3 and 150 mg/L IAA was used, but lowest when none of the two factors were applied ($P <$ 0.001) (Fig. 1). Water content of wheat was maximal with 640 mg/L NH_4NO_3, 0 mg/L (or 250 mg/L) IAA and minimal when 0 mg/L NH_4NO_3 and 150 mg/L IAA was applied ($P <$ 0.001) (Fig. 2).

When examining photosynthetic pigments (Fig. 3), N ($F = 923.7$; df = 3, 144; $P < 0.001$) had the greatest effects on chlorophyll but IAA ($F = 1.402$; df = 3, 144; $P = 0.245$)

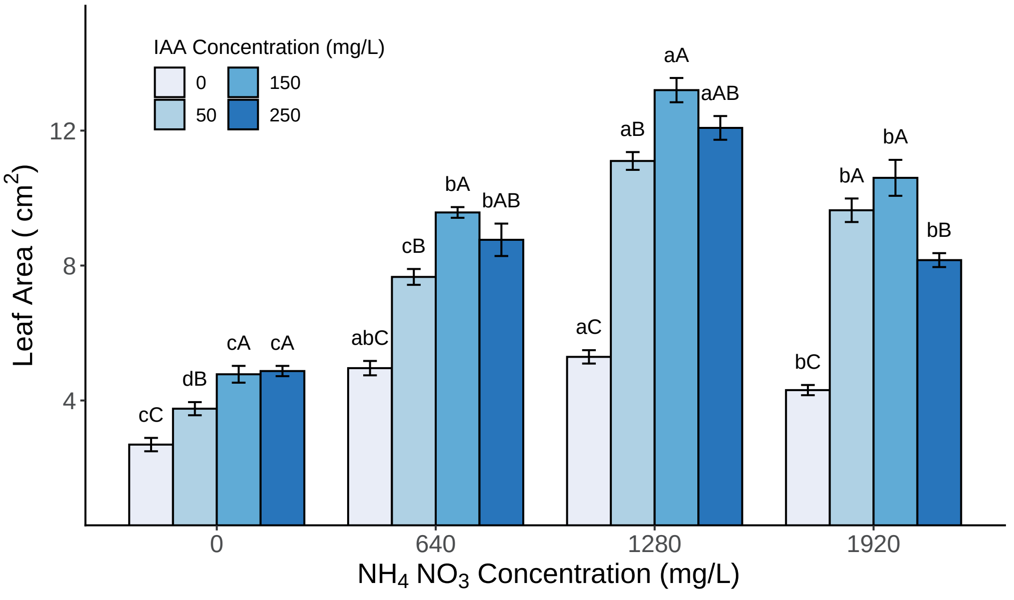

Fig. 1. Leaf area (cm²) of *Triticum aestivum* treated with combinations of NH_4NO_3 and IAA. The same lowercase letters on column in the same color mean no significant difference under different N levels. Different capital letters on the same column groups mean significant difference under different IAA levels.

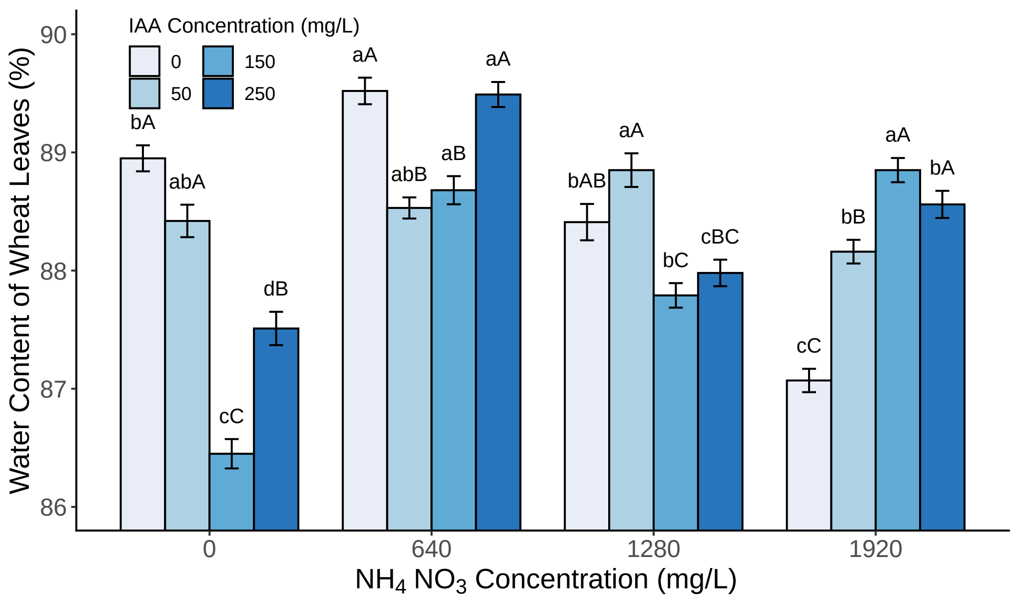

Fig. 2. Water content (%) in the leaves of *Triticum aestivum* treated with different combinations of NH_4NO_3 and IAA. Columns in the same color with different lowercase letters differ significantly under different N levels. The same capital letters on the same column groups mean no significant difference under different IAA levels.

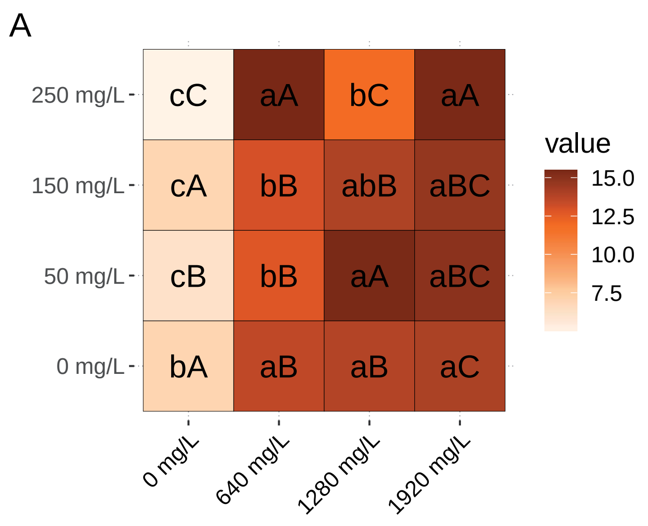

Fig. 3. Content of Chlorophyll a+b (A; mol/L) and Carotenoid (B; mol/L) in wheat leaves. Vertical axes represent the IAA levels and horizontal axes were the NH_4NO_3 levels. Means (± SE) with different lowercase letters in a line differ significantly under different N levels; different capital letters in the same column mean significant difference under different IAA levels within each figure.

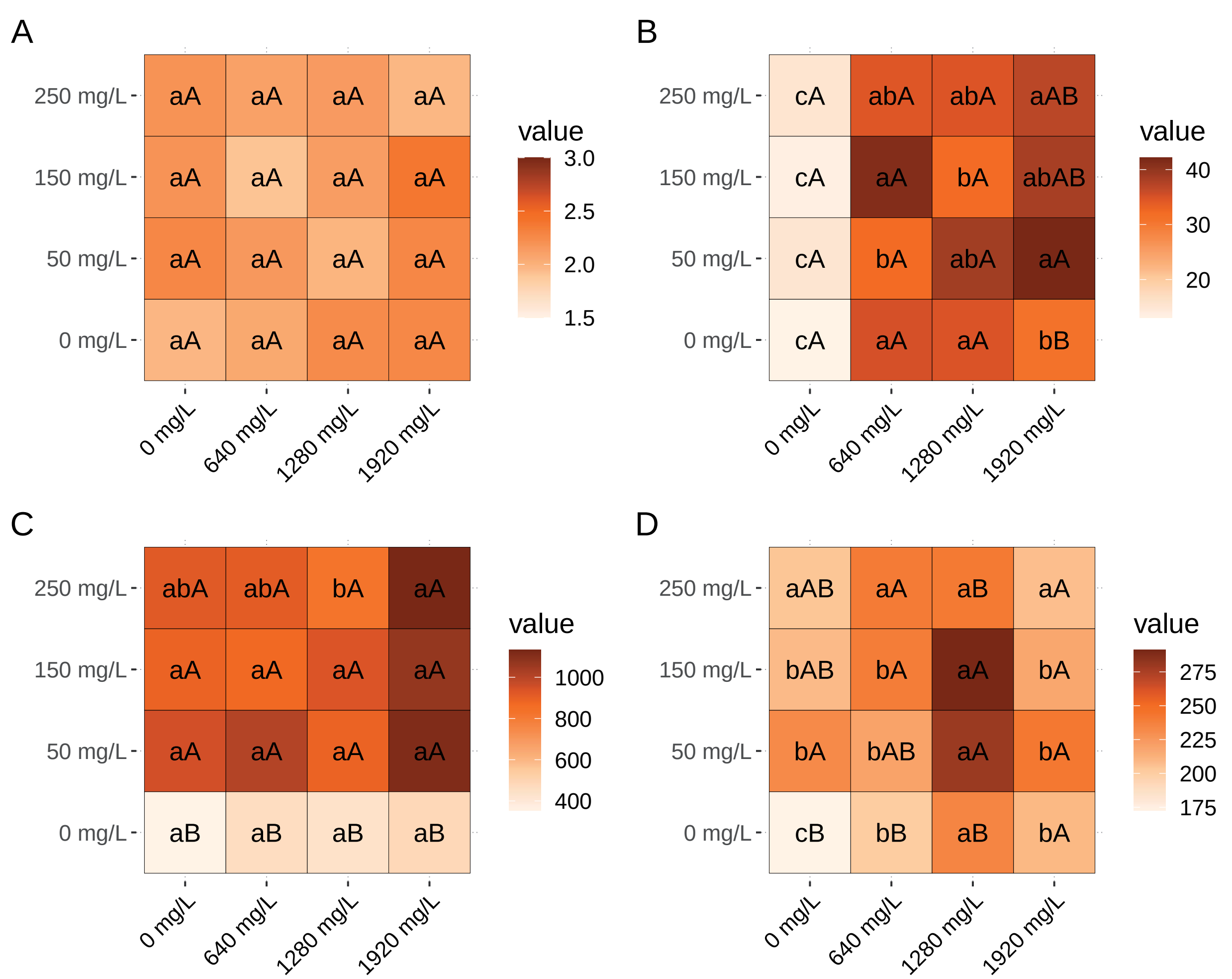

Fig. 4. Content or activity of detoxification enzymes of wheat. A: SOD (U/mg FW); B: PPO (ΔOD410/min/g FW); C: POD (ΔOD470/min/g FW); D: CAT (ΔOD405/min/g FW). Vertical axes represent the IAA levels and horizontal axes were the NH_4NO_3 levels. Values are means (± SE). Means (± SE) with different lowercase letters in a row differ significantly under different N levels; different capital letters in the same column mean significant difference under different IAA levels within each figure.

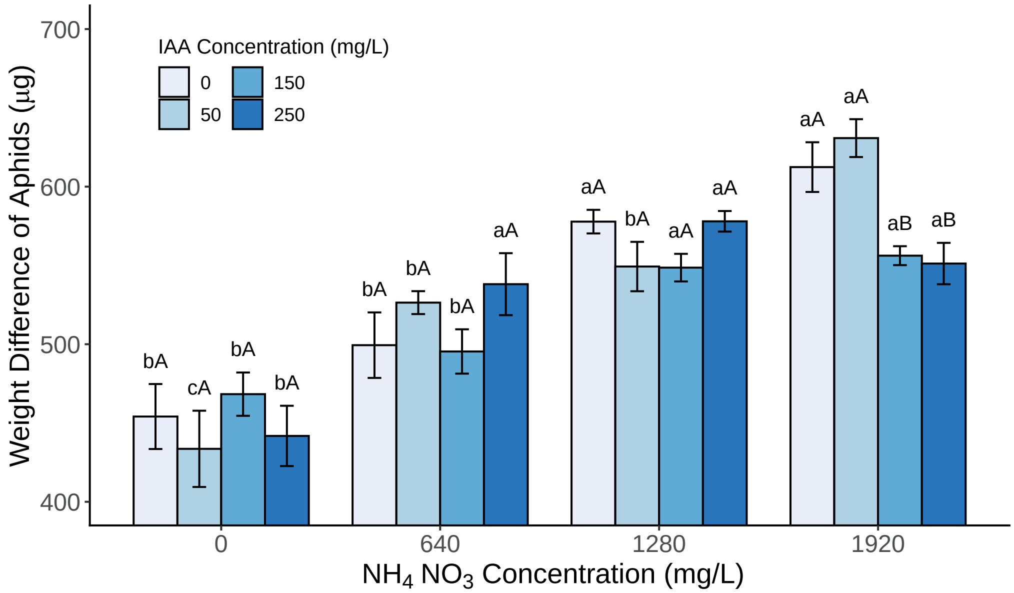

Fig. 5. Weight differences of *Sitobion avenae* reared on *Triticum aestivum* plants. Means (± SE) with different lowercase letters differ significantly under different N levels; different capital letter mean significant difference under different IAA levels within each figure.

did not show any main effect, while the two factors showed significant interactive effects ($F = 23.65$; df = 9, 144; $P < 0.001$). Both N and IAA had the main effect on carotenoid levels ($F = 110.7$; df = 3, 144; $P < 0.001$; $F = 6.595$; df = 3, 144; $P < 0.001$) and their interaction was significant ($F = 3.868$; df = 9, 144; $P < 0.001$). Specifically, wheat had greatest levels of chlorophyll a and b with 640 mg/L (or 1920 mg/L) NH_4NO_3 and 250 mg/L IAA but lowest when 0 mg/L NH_4NO_3 and 250 mg/L IAA was applied ($P < 0.001$; $P < 0.001$). Carotenoid levels were greatest when 1920 mg/L NH_4NO_3 and 250 mg/L (or 150 mg/L) IAA were applied but significantly lower without NH_4NO_3 (all $P < 0.001$).

When examining secondary metabolites in wheat (Fig. 4), neither N nor IAA had any main effect on the SOD activity from leaves ($F = 0.8459$; df = 3, 144; $P = 0.471$; $F = 0.153$; df = 3, 144; $P = 0.927$) but N showed main effects on the activity of PPO ($F = 77.37$; df = 3, 144; $P < 0.001$), POD ($F = 9.065$; df = 3, 144; $P < 0.001$) and CAT ($F = 23.64$; df = 3, 144; $P < 0.001$). Only the interactive effects of PPO ($F = 2.016$; df = 9, 144; $P = 0.041$) and CAT ($F = 2.465$; df = 9, 144; $P = 0.012$) activity were significantly influenced. Specifically, N increased PPO activity significantly (all $P < 0.05$) when compared with groups without N application.

3.2 Effect of NH_4NO_3 and IAA on aphids

The results illustrated that NH_4NO_3 had the greatest effect ($F = 65.04$; df = 3, 144; $P < 0.001$) on body weight differences between aphids and the interactive effect of the two factors was significant ($F = 3.254$; df = 9, 144; $P = 0.001$) but the main effect of IAA ($F = 1.330$; df = 3, 144; $P = 0.267$) was not. Body weight of *S. avenae* was greatest when 1920 mg/L NH_4NO_3 and 50 mg/L IAA was applied and lowest in 0 mg/L N treatments ($P < 0.001$) (Fig. 5).

For the secondary metabolites in aphids (Fig. 6), N showed main effects on all the parameters measured ($P = 0.005$ for AKP; all $P < 0.001$ for other variables), while IAA only had main effects on the amount of trehalose ($F = 8.756$; df = 3, 144; $P < 0.001$) and SOD activity ($F = 8.19$; df = 3, 144; $P < 0.001$). The interactive effects of N and IAA significantly influenced the amount of trehalose ($F = 9.56$; df = 9, 144; $P < 0.001$) and the activity of SOD ($F = 2.218$; df = 9, 144; $P = 0.024$) and POD ($F = 2.946$; df = 9, 144; $P = 0.003$). Regarding the activity of the metabolic enzymes, N had significant effects on trehalase ($F = 11.74$; df = 3, 144; $P < 0.001$), sucrase ($F = 10.87$; df = 3, 144; $P < 0.001$) and amylase ($F = 15.69$; df = 3, 144; $P < 0.001$), whereas the main effect of IAA and the interactive effect between N and IAA was not significant. Trehalase activity in aphids was lowest when 1280 mg/L NH_4NO_3 and 250 mg/L IAA was applied and highest when no N was applied to the wheat ($P < 0.001$). From all the treatment groups, the group containing 1280 mg/L NH_4NO_3 and 0 mg/L (or 250 mg/L) IAA showed the highest levels of trehalose, whereas it was lowest when 0 mg/L $NH_4NO_3$was applied (all $P < 0.001$). For detoxification metabolites, the activity of SOD in aphids was highest when N and IAA were both 0 and relatively low from treatments with high levels of IAA and N. The AKP activity of aphids was maximal when 1920 mg/L N and 150 mg/L IAA was applied. CAT activity in aphids was least when

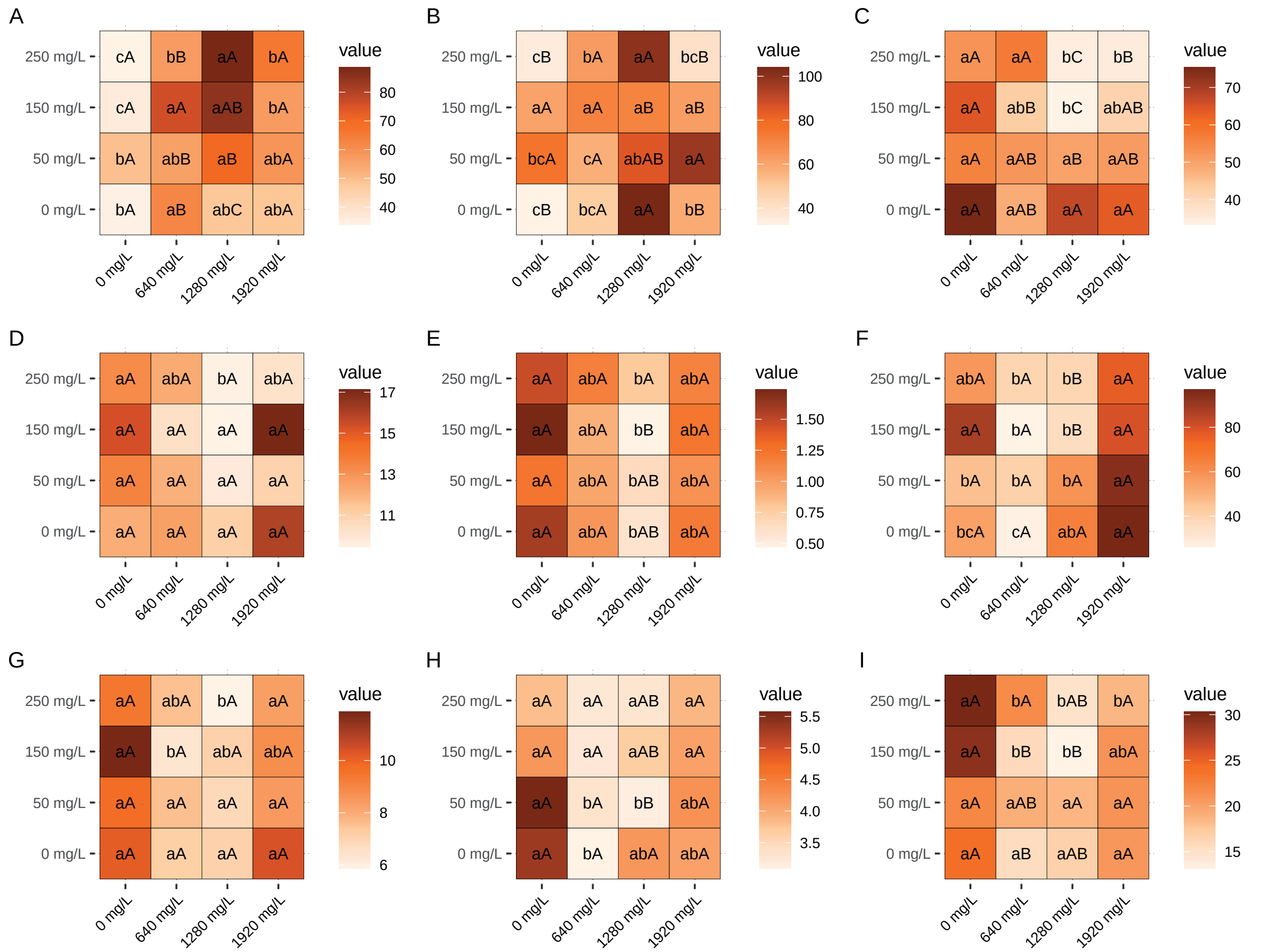

Fig. 6. Concentration of total protein (mg/mL; A), trehalose (mmoL/L; B), superoxide dismutases (SOD; U/mgpr; C), alkaline phosphatase (AKP; U/gpr; D), catalase (CAT; ΔOD405/min/mg pr; E) and peroxidase (POD; ΔOD470/min/g pr; F) and activity of trehalase (mmoL/L/mg pr/min; G), sucrase (mmoL/L/mg pr/min; H), and amylase (mg/mL/mg pr/min; I) of aphids. Vertical axes represent the IAA levels and horizontal axes were the NH_4NO_3 levels. Means (± SE) with different lowercase letters in the same row differ significantly under different N levels; different capital letters in a column mean significant difference under different IAA levels within each figure.

1280 mg/L N and 150 mg/L IAA was used and highest with 0 mg/L NH_4NO_3 ($P < 0.001$). POD activity was maximal when 1920 mg/L N and 0 mg/L IAA was applied and lowest with 640 mg/L NH_4NO_3 and 150 mg/L IAA ($P < 0.001$).

3.3 Effect of NH_4NO_3 and IAA on parasitoids

Nitrogen showed main effects on the secondary metabolites, including the amount of trehalose ($F = 13.17$; df = 3, 64; $P < 0.001$) and the activity of SOD ($F = 11.83$; df = 3, 64; $P < 0.001$), AKP ($F = 3.444$; df = 3, 64; $P = 0.022$), trehalase ($F = 5.11$; df = 3, 64; $P = 0.003$) and sucrase ($F = 5.657$; df = 3, 64; $P = 0.002$). Conversely, IAA did not show main effects on the activity of AKP ($F = 0.85$; df = 3, 64; $P = 0.471$). The interaction of N and IAA significantly affected the body length of *A. asychis* and the metabolic enzymes, trehalase and sucrase (all $P < 0.05$). The body-length was the highest from three treatments (treatments 6, 8 and 15), and no application of both factors led to the smallest parasitoids. Although parasitoids from seedlings in treatments 6 and 8 were in the same size, they showed significant differences in the content of trehalose ($P < 0.001$), total protein ($P = 0.005$), SOD ($P = 0.019$) and trehalase ($P = 0.006$) (Fig. 8). Specifically, the concentration of trehalose in parasitoids was highest when 640 mg/L NH_4NO_3 and 50 mg/L IAA was used but lowest when none was applied ($P < 0.001$). Regarding SOD, treatment 6 showed low activity compared to other treatments ($P < 0.001$).

3.4 Correlation of different parameters among the three trophic levels

Correlation analysis of aphid parameters showed that DW was positively correlated with the amount of trehalose ($R =$

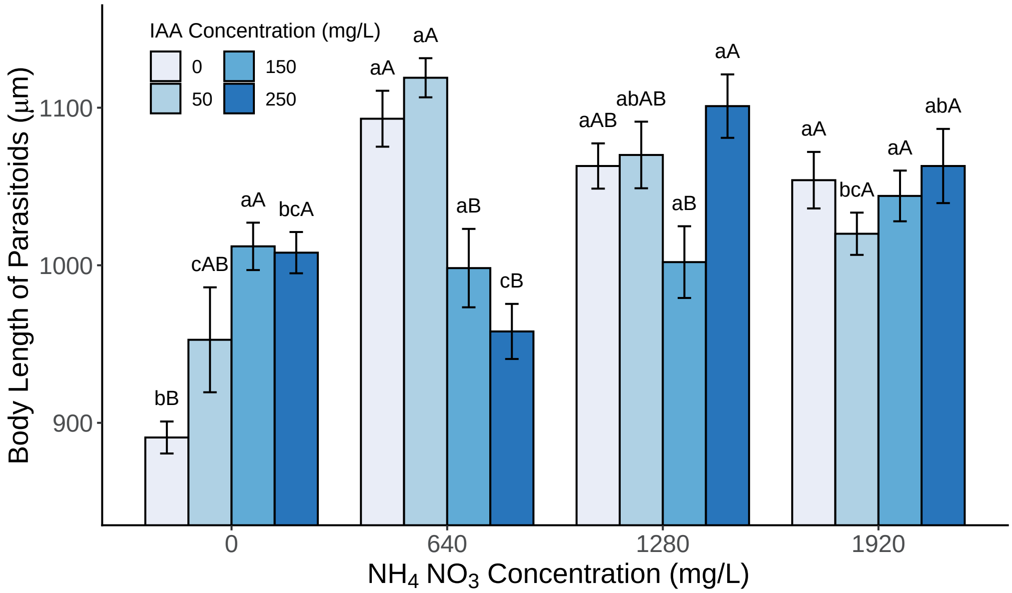

Fig. 7. Body length of *Aphelinus asychis* fed with *Sitobion avenae* reared on *Triticum aestivum* plants. The same lowercase letters on column in the same color mean no significant difference under different N levels. Different capital letters on the same column groups mean significant difference under different IAA levels.

0.554; N = 16; P = 0.026) and total protein (R = 0.444; N = 16; P = 0.085) but negatively correlated with CAT (R = –0.524; N = 16; P = 0.037) and amylase (R = –0.485; N = 16; P = 0.057) activity. Trehalose content was negatively correlated with the activity of CAT (R = –0.640; N = 16; P = 0.008), amylase (R = –0.454; N = 16; P = 0.077) and trehalase (R = –0.476; N = 16; P = 0.062), while trehalase activity showed a positive correlation with CAT (R = 0.835; N = 16; P < 0.001), amylase (R = 0.809; N = 16; P < 0.001), sucrase (R = 0.665; N = 16; P = 0.005) and SOD activity (R = 0.589; N = 16; P = 0.016).

Correlation analysis of indices between tritrophic interactions showed that DW of aphids had a positive correlation with leaf area (R = 0.513; N = 16; P = 0.042), chlorophyll (R = 0.806; N = 16; P < 0.001), carotenoid (R = 0.771; N = 16; P < 0.001) and PPO (R = 0.785; N = 16; P = 0.001) of wheat seedlings. Furthermore, total protein of aphids showed positive correlations with leaf area (R = 0.852; N = 16; P < 0.001), chlorophyll (R = 0.607; N = 16; P = 0.013), carotenoid (R = 0.683; N = 16; P = 0.004), PPO (R = 0.697; N = 16; P = 0.003) and CAT (R = 0.691; N = 16; P = 0.003) of wheat. The amount of trehalose of aphids were also positively correlated with leaf area (R = 0.463; N = 16; P = 0.071), PPO (R = 0.473; N = 16; P = 0.064) and CAT (R = 0.661; N = 16; P = 0.005), while SOD activity from the pests was negatively correlated with the above indexes (R = -0.790; N = 16; P < 0.001; R = -0.548; N = 16; P = 0.028; R = –0.485; N = 16; P = 0.057) in wheat plants. Moreover, activities of AKP and CAT in aphids were also negatively correlated with leaf area (R = –0.489; N = 16; P = 0.054; R = –0.645; N = 16; P = 0.007) and POD activity showed a negative correlation with water content (R = –0.533; N = 16; P = 0.034). Similarly, the activity of the metabolic enzyme trehalase in aphids was also negatively correlated with water content in wheat (R = –0.587; N = 16; P = 0.017). Leaf area of wheat negatively affected the activity of trehalase (R = –0.673; N = 16; P = 0.004), amylase (R = –0.567; N = 16; P = 0.022) and sucrase (R = –0.577; N = 16; P = 0.019). Meanwhile, chlorophyll levels, carotenoid content, PPO and CAT activity of wheat all negatively influenced these metabolic enzymes (All P < 0.05).

Interestingly, correlation analysis of factors between aphids and parasitoids showed that body-length of parasitoids was positively correlated with DW (R = 0.654; N = 16; P = 0.006) and trehalose (R = 0.458; N = 16; P = 0.074) of aphids. Conversely, body-length (R = –0.479; N = 16; P = 0.061), AKP activity (R = –0.679; N = 16; P = 0.004) and trehalose amount (R = –0.566; N = 16; P = 0.022) of parasitoids were negatively correlated with sucrase activity in aphids while sucrase of parasitoids was positively correlated with sucrase of aphids (R = 0.568; N = 16; P = 0.022). AKP activity in parasitoids had a negative correlation with SOD of aphids (R = –0.502; N = 16; P = 0.048).

Regarding the correlation between wheat plants and parasitoids, there was a low positive correlation between body length and leaf area (R = 0.394; N = 16; P = 0.131), chlorophyll content (R = 0.406; N = 16; P = 0.118) and PPO activity (R = 0.489; N = 16; P = 0.055). For detoxification metabolites in parasitoids, AKP activity was positively correlated with the PPO activity in wheat leaves (R = 0.405;

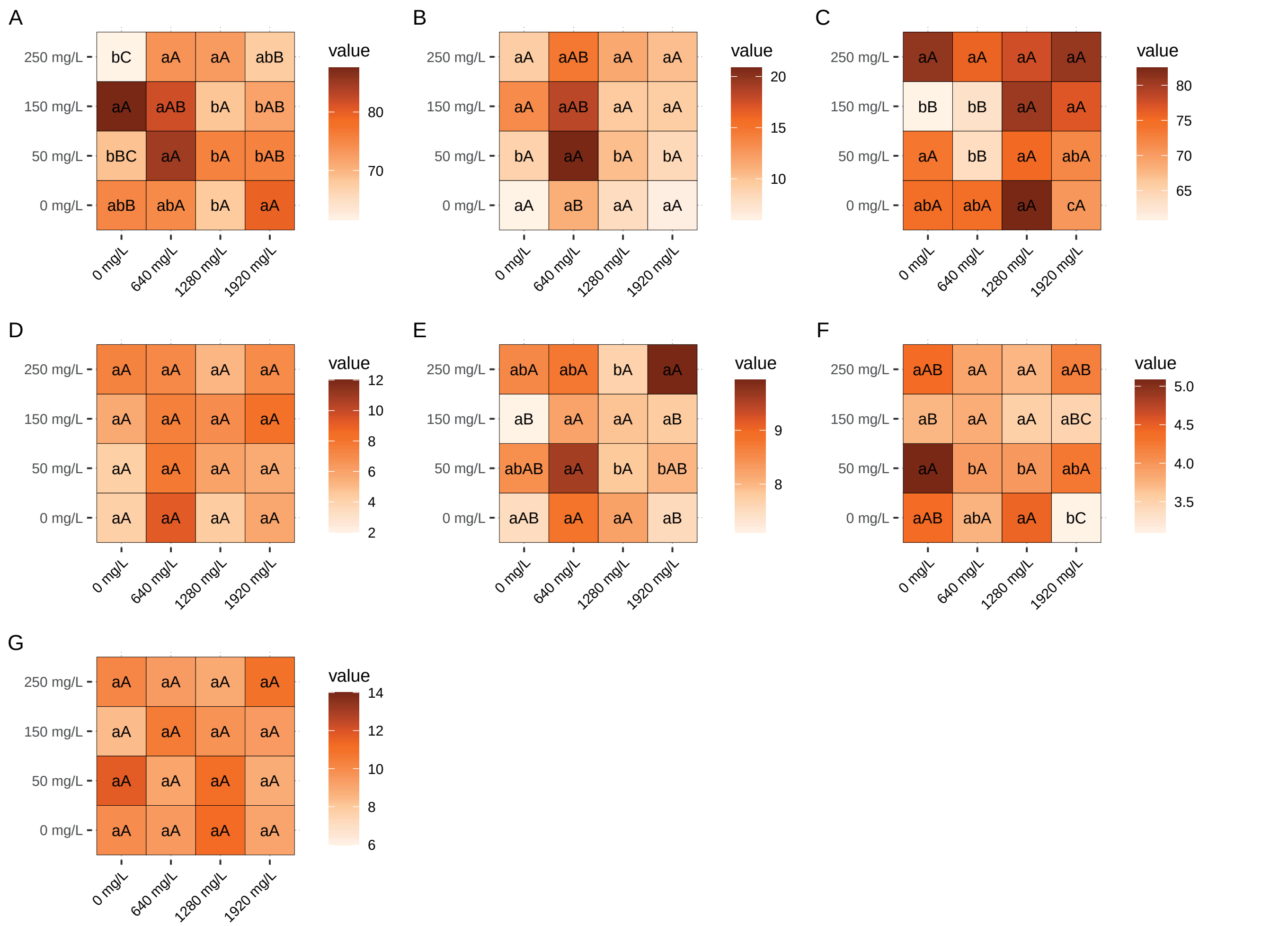

Fig. 8. Concentration of total protein (mg/mL; A), trehalose (mmoL/L; B), superoxide dismutases (SOD; U/mgpr; C), alkaline phosphatase (AKP; U/gpr; D), and activity of trehalase (mmoL/L/mg pr/min; E), sucrase (mmoL/L/mg pr/min; F) and amylase (mg/mL/mg pr/min; G) of parasitoids. Vertical axes represent the IAA levels and horizontal axes were the NH_4NO_3 levels. Means (± SE) with different lowercase letters in the same row differ significantly under different N levels; different capital letters in a column mean significant difference under different IAA levels within each figure.

N = 16; P = 0.119). Furthermore, the activity of sucrase in parasitoids was negatively correlated with chlorophyll (R = –0.485; N = 16; P = 0.057) and carotenoid content (R = –0.480; N = 16; P = 0.060).

4 Discussion

This research revealed the fitness, detoxification metabolism and tritrophic interactions among the three tropic levels were influenced by nitrogen fertilization and the application of PGRs. Specifically, both nitrogen and IAA had independent main effects on leaf area, water content, photosynthetic pigments and secondary metabolites of wheat. The interactive effect between the two factors was also statistically significant. Leaf area of wheat seedlings first increased, then decreased with greater concentrations of NH_4NO_3 or IAA. Growth of wheat seedlings was likewise promoted with the appropriate concentration of NH_4NO_3 or IAA while high or low nitrogen and PGR concentrations were inhibitive to growth (Galloway et al. 2003; 2004; Ladha et al. 2005; Galloway & Cowling 2002; Vessey 2003; Drizou et al. 2018). The application of 1280 mg/L NH_4NO_3 and 150 mg/L IAA to wheat led to lower water content, which could enhance the nutritional value of wheat. Increased chlorophyll and carotenoids and more secondary metabolic substances infer more resistance to herbivores. Consequently, 1280 mg/L NH_4NO_3 and 150 mg/L IAA could be assumed as the most suitable concentrations for the growth of wheat seedlings.

Regarding the secondary metabolites, a higher content of nitrogen (1280, 1920 mg/L NH_4NO_3) also significantly increased the content of photosynthetic pigments, CAT and PPO in wheat. It has been reported that the production of PPO reduces the performance of some chewing herbivores while their role in host resistance to aphids is still controversial (Constabel & Barbehenn 2008). The activity of PPO in wheat leaves increased SOD activity in aphids and consequently the AKP activity in parasitoids increased, indicating the application of N influenced secondary metabolites in wheat plants and two higher trophic levels. Similarly, different concentrations of IAA improved the activity of POD in wheat leaves, which catalyzes the rigidification of the cell walls thereby creating physical barriers preventing insects with piercing/sucking mouth parts from feeding and preventing pathogen invasion (Almagro et al. 2009; Liu et al. 2010). Furthermore, some other PGRs, including methyl jasmonate (MeJA) and salicylic acid (SA), have been reported to increase the activity of POD in wheat seedlings (Howe & Jander 2008; Vlot et al. 2009; Cao & Liu 2014; Jaouannet et al. 2014). However, the relationship between aphid invasions and the activity of POD is not fully clear.

DW of aphids feeding on wheat seedlings cultivated under different concentrations of Hoagland's solution increased with greater nitrogen content. DW was the highest when *S. avenae* fed on wheat treated with 1920 mg/L NH_4NO_3 and 0 mg/L IAA or 50 mg/L IAA. Although the same DW was produced, trehalose in the two aphid populations was significantly different, most likely caused by fluctuations in PPO and CAT activity in plants. In addition, aphids without nitrogen (or with too much nitrogen) showed higher activity of SOD, AKP, CAT, and POD, indicating that the anti-stress physiology of aphids feeding on wheat with 0 or 1920 mg/L NH_4NO_3 compared to other conditions (Hottiger et al. 1987; Gadd et al. 1987; Dreyer et al. 1985). Similarly, *Hippodamia variagata* (Goeze) showed slower prey consumption rates and altered foraging behavior on *Aphis gossypii* Glover feeding on higher N fertilized cucumber plants (Hosseini et al. 2018). The activity of sucrase and amylase was relatively higher when 0 mg/L NH_4NO_3 was used, meaning more nutrition was taken in by aphids feeding on wheat lacking nitrogen.

The research presented here indicated that IAA alone did not significantly reduce DW of aphids under the same concentration of nitrogen or affect their detoxification ability (AKP, CAT, POD) and nutritional enzymes. Other studies also observed no significant effect of PGRs on aphid abundance (Prado & Frank 2013). However, IAA inhibited parasitoid growth and decreased body-length when 150 and 250 mg/L IAA was added to Hoagland's solution (640 mg/L NH_4NO_3). Studies on *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) and *Aphidius colemani* (Viereck) (Hymenoptera: Braconidae) also showed that PGRs negatively influenced parasitoid fitness and reduced parasitism rates, suggesting PGRs might have negative long-term effects on biological control (Prado & Frank 2013; Li et al. 2016). For instance, parasitoid size and development could be reduced via direct or indirect PGR toxicity, such as paclobutrazol (Honeyborne 1969; Couty et al. 2001).

Interestingly, although DW of aphids had positive correlations with leaf area, chlorophyll, carotenoid and PPO of wheat seedlings, wheat grown under the best growth conditions did not produce the largest aphids. Wheat grown with 1920 mg/L NH_4NO_3 and 0 mg/L IAA had lower water content than wheat grown with 1280 mg/L NH_4NO_3 and 150 mg/L IAA, which could result in higher nutritional concentrations. Although wheat grown with 1280 mg/L NH_4NO_3 and 150 mg/L IAA had larger leaf area and greater photosynthetic activity, more secondary metabolites were produced. Activity of POD and CAT in wheat grown with 1280 mg/L NH_4NO_3 and 150 mg/L IAA was higher than that in wheat grown with 1920 mg/L NH_4NO_3 and 0 mg/L IAA. These secondary metabolites are toxic to herbivores with piercing and sucking mouthparts.

Furthermore, not only the largest aphids, but also medium-weighted aphids, produced the largest sized parasitoids. Aphids feeding on wheat grown with 1280 mg/L NH_4NO_3 and 250 mg/L IAA had more total protein and trehalose than 1920 mg/L NH_4NO_3 and 0 mg/L IAA treatment groups. This could indicate that aphids feeding on wheat grown with 1280 mg/L NH_4NO_3 and 250 mg/L IAA provided enhanced nutritional content for immature parasitoids. These results concur with research published by Chesnais et al. (2016), reporting that plant suitability was reduced by excessive N input and aphid performance was consequently negatively affected. However, the application of IAA with N also altered the influence of N in our research, indicating bottom-up effects could impact the third trophic level (Han et al. 2015, 2019). Body-length of parasitoids had a non-significant but positive correlation with trehalose content of aphids. Activity of SOD, AKP and POD in aphids feeding on wheat grown with 1280 mg/L NH_4NO_3 and 250 mg/L IAA was lower compared to those in aphids feeding on wheat grown with 1920 mg/L NH_4NO_3 and 0 mg/L IAA. This indicates that aphids feeding on wheat applied with 1280 mg/L NH_4NO_3 and 250 mg/L IAA contained less reactive oxygen species (ROS), phosphate monoester (Funk 2001) and less hydrogen peroxide (H_2O_2), which might be toxic to nucleic acids, proteins and membrane lipids (Mittler 2002; Matés & Sánchez-Jiménez 1999; Gao et al. 2013). It has also been reported that better host embryo growth could adversely influence the development of parasitoid eggs (Pizzol et al. 2012; Thiery & Desneux 2018; Guo et al. 2019; Li et al. 2019; Zang et al. 2021) and larger or stronger aphids also influenced parasitoid growth due to higher activities of secondary metabolites from our assays, resulting in smaller female parasitoids. These conditions could therefore be preferential for development of immature parasitoids and medium-sized aphids of enhanced nutritional value for predators and parasitoids (Zhang 1991).

In practice, for artificial regulation, wheat seedlings grown with 1280 mg/L NH_4NO_3 and 150 (250) mg/L IAA would have larger leaf area, are of greater nutritional value, enhanced photosynthetic activity, greater resistance to herbivores and produce large-size *A. asychis*. Under certain conditions, the application of 1280 mg/L NH_4NO_3 and 150 (250) mg/L IAA is beneficial to wheat growth in the field or under greenhouse conditions. Furthermore, in a banker plant system, our results indicated that to meet the demand for transportation, space limitation or time constraints, different conditions should be applied for wheat production. For example, 1280 mg/L NH_4NO_3 and 250 mg/L IAA produces the greatest leaf area and largest *A. asychis*, while 640 mg/L NH_4NO_3 and 50 (or 0) mg/L IAA is a more economical way to produce large-sized *A. asychis*. Application of 1920 mg/L NH_4NO_3 and 0 mg/L IAA could control leaf area of wheat seedlings (the least leaf area) and produce large-sized *A. asychis*. Meanwhile, 640 mg/L NH_4NO_3 and 250 mg/L IAA would control the size of parasitoids and while these are promising recommendations, other important ecological indices such as fecundity, parasitism rates, eclosion rates, sex ratio or even functional responses must be examined prior to application (Frank 2010; Ohta & Honda 2010).

In summary, our research demonstrated that both nitrogen and IAA had significant effects on tritrophic interactions. Thus, the manipulation of growth conditions of wheat had a tritrophic effect on aphids and parasitoids and should therefore be considered when implementing different IPM options. According to Zhu et al. (2020), nitrogen fertilizer could enhance pest impact by *Cyrtorhinus lividipennis* Reuter through mediated controlling effects. The effects of plant defenses and insect nutrition for parasitoid production needs further investigation. The effects of other elements such as K, P, Ca, Mg, or even trace elements, should also be investigated. In addition to IAA, other important PGRs such as gibberellic acid, paclobutrazol and abscisic acid could be applied to plants in future studies. Understanding all the effects of these variables on the *T. aestivum – S. avenae*–*A. asychis* system will lead to enhanced pest management approaches in the future.

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Author Contributions: KZ, TX and ND designed the assay; KZ and ND conducted the experiments; ND, SW and KZ analyzed the data; ND, KZ, TX, JRS and JDH wrote the manuscript; YFC made the figures; all authors revised the manuscript.

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