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Tritrophic interaction influenced by warming and tillage: A field study on winter wheat, aphids and parasitoids

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ABSTRACT

Global warming is expected to affect tritrophic interactions between plants, herbivores, and their natural enemies. Tillage, as a pervasive anthropogenic perturbation, also affects agricultural pests and their natural enemies in cropland systems. The effect of warming combined with tillage on tritrophic interactions is poorly known. A field experiment using infrared warming devices was conducted in conventional and no-tillage wheat fields in Northern China to examine the effects of warming and tillage on tritrophic interactions between winter wheat plants, aphids, and parasitoids. The results show that warming increased plant biomass and advanced plant phenology from re-greening to maturity by 6–11 days. No effects of tillage on plant phenology or biomass were found. Warming significantly increased the numbers of the aphid *Sitobion avenae* in 2010, when the parasitoid was scarce. Populations of *S. avenae* were 57.2% larger in warmed than in control plots. In 2011, aphid populations did not differ between warmed and control plots, but parasitoids were abundant, with approximately three times as many in warmed plots than in control ones. The rate of parasitism was also significantly increased in the warmed plots. Tillage had no significant effects on aphid and parasitoid populations in both years. These results indicate that the temperature-induced acceleration of winter wheat phenology resulted in increased aphid abundance. Warming strengthens the bottom-up and top-down effects. The response of parasitoids to warming varied according to their yearly population fluctuations, highlighting the need for a greater basic understanding of parasitoids and conservation of natural enemies.

1. Introduction

Assessing the effect of climate change on each level of tritrophic and trophic interactions is important to efforts designed to gain a deeper understanding of the status of an ecological community in light of a changing climate (Sentis et al., 2013). Global temperatures have increased by approximately 0.74 °C in the last century and further warming is predicted to occur in the next few decades (IPCC, 2007). The increase in temperatures directly affects the survival, development, reproduction, and movement of individual insects, and thus the potential distribution and abundance of species (Cammell and Knight, 1992; Bale et al., 2002). Moreover, climate warming also indirectly modifies food webs and community structure, such as shifting the body-size distributions toward dominance of small- over large-bodied species (Brose et al., 2012).

In a cropland system, both temperature and farming activities could affect the dynamics of a food web. Climate warming could result in higher dispersal rates of ectothermic organisms between local habitats (Brose et al., 2012). Tillage disturbs the soil surface and may affect organisms adversely as they disperse. Whether warming and tillage would have interaction effects on organisms remains unclear. No-tillage (NT) management has been promoted as a way to increase soil organic carbon storage in cropland and reduce CO_2 emissions (Cole et al., 1997). Burton and Krenzer (1985) has found that wheat and sorghum grown using reduced or NT techniques have fewer aphids than conventionally tilled fields in the Great Plains of USA. The primary mechanism involved is thought to be the way incident light reflects from crop residue, which reduces the landing rate of airborne dispersing airborne aphids.

Plants can react to warmer conditions by adjusting their phenology (Sherry et al., 2007; Hovenden et al., 2008). Insect pests are expected to become more abundant as temperatures increase in regions at middle to high latitudes (Fuhrer, 2003). Natural enemies of insect pests may increase their foraging, consumption and growth rates because their metabolism is accelerated by warming (Brown et al., 2004). Clear evidence exists related to the effects

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of warming on the single species level. However, the effects of increased temperatures at the community level are currently less obvious (Gillespie et al., 2012). Warming can also alter the relative importance of bottom-up and top-down effects in ecological communities (Hoekman, 2010). Some theoretical and empirical studies suggest that the top-down effects of predators will be strengthened by warming (Hoekman, 2010; Kratina et al., 2012; Shurin et al., 2012). Warming can also enhance host susceptibility to parasites and enhance the proliferation of a parasite's infective stage, thus increasing top-down effects of parasites (Traill et al., 2010).

Most studies on climatic change have focused on the individual level (mainly individual performances and spatial distribution) and few studies have investigated interactions between abiotic factors and their consequences related to trophic interactions and food web dynamics. However, in recent decades an increasing number of studies have addressed the effects of temperature and other abiotic factors on trophic interactions and food chain dynamics (Bezemer et al., 1998; Greig et al., 2012). For example, warming and nitrogen increased host availability and size, leading to changes in parasitoid feeding behavior, such as parasitoids focusing on more abundant and larger hosts (de Sassi et al., 2012).

Parasitoids occupy a third trophic level and are expected to be highly susceptible to changes in environmental conditions (Hance et al., 2007). Plant-aphid-parasitoid interactions in the context of climate change have not been well studied. A modeling study of plant–aphid–parasitoid under climate change predicted that the responses of both aphids and parasitoids to combined effects of warming and elevated CO_2 will unexpectedly remain the same as current condition (Hoover and Newman, 2004). Temperature variance may not only influence the intra-guild interactions (Gillespie et al., 2012), but may also influence the indirect interaction between aphids and parasitoids (Bannerman et al., 2011).

In the present study, we assessed the effects of warming on the tritrophic relationship of winter wheat plants, aphids, and parasitoids in both conventional tillage (CT) and NT systems. We use infrared heaters to mimic climate warming (Harte et al., 1995; Wan et al., 2002). The specific objectives were to evaluate changes in: (1) wheat plant characteristics, (2) aphid species and abundance, and (3) parasitoid species and abundance.

2. Methods

2.1. Study site

The field experiment was conducted in 2010 and 2011 at Yucheng Experimental Station of the Chinese Academy of Sciences, Shandong Province, China (116°36′ E, 36°57′ N, elevation 20 m). The site is in a temperate, seasonal, semi-humid monsoon climate, where the mean annual temperature is 13.1 °C. The annual temperature in North China where our site is located increased by 1.5 °C between 1951 and 2009 (Zhang et al., 2011). The mean annual precipitation is 582 mm and is concentrated in the summer months. Winter wheat and summer maize double-cropping is predominant in this site.

2.2. Experimental design and treatments

We used a split-plot design with tillage system (i.e., CT or NT) in the main plots and warming (i.e., with or without warming treatment) in the subplots. There were six randomly arranged wheat fields, comprising three CT and three NT fields, each 7 m × 20 m. In each field, two 2 m × 2 m warmed plots and two 2 m × 2 m control plots were spaced 5 m apart along the long side of each field. The warming treatment involved suspending a 165 cm × 15 cm MSR-2420 infrared radiator (Kalglo Electronics, Inc., Bethlehem, PA, USA) 3 m above each plot, consistently heating both during the day and at night. Warming treatment began in February 2010. For control plots (ambient temperatures), 'dummy' heaters of the same shape, size, and installation were used to mimic the shading effect of the warming equipment. The experiment was based on a long-term conservation tillage experiment field initiated in 2003. For the CT system, after maize harvest, standing maize stubble was cut to about 10 cm tall, and other maize residues were removed. A rotary tiller (10–15 cm depth) was used to incorporate standing stubble of maize into the soil prior to the planting of winter wheat. For the NT system, maize residues were chopped into pieces (5 cm length) by hand and retained on the soil surface.

Soil temperatures at 5 cm deep and soil moisture at 0–10 cm deep were monitored by thermocouples and soil moisture sensors, respectively, connected to a datalogger. Two pairs of thermocouples and sensors were positioned 1 m apart in each plot; they were arranged symmetrically and vertically to the infrared heater or "dummy". Temperature and moisture measurements were taken every 10 min.

The phenology of winter wheat was observed from re-greening to harvest. The date was recorded when 50% of the winter wheat in the experiment plots had changed developmental stages. Above-ground biomass was measured in two groups of 20 randomly sampled plants in each plot; plants were dried at 70 °C for 48 h to a constant weight and then weighed in each group. Air-dried grain yield in each 2 m × 2 m plot was also evaluated.

To sample aphids and parasitoids, 20 tillers of wheat were randomly selected from each plot and inspected visually during the wheat milk-ripening period, which is the period when critical aphid damage typically occurs (Liu et al., 1986). In each campaign, we also selected five tillers from each plot and took them to the laboratory for aphid and parasitoid species identification. Samples were taken place once every 5–7 days from late April to early June in both 2010 and 2011.

2.3. Data analysis

Numbers of aphids and parasitoids per 100 tillers were $\log_{10}(x+1)$ transformed, and the rates of parasitism were arcsine-square root transformed to achieve normal distributions. The effects of warming and tillage on plant biomass as well as on aphid and parasitoid populations were analyzed using split-plot ANOVA with tillage as the whole-plot factor, warming as the sub-plot factor. In other words, warming was nested into tillage treatment. A split-plot ANOVA was performed for each tritrophic level. The effects of treatments on peak aphid populations and the rate of parasitism were analyzed by one-way ANOVA, followed by post hoc comparisons using the least significant difference test. The aphid species composition (%) was compared between warmed and control plots using a Chi-square test. All statistical analyses were performed using the SPSS statistical package (version 18.0, SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Treatment effects of warming on microclimate and plants

The microclimate data from February 2010 to July 2011 showed that in CT and NT plots, respectively, warming resulted in an average increase in soil temperature (5 cm depth) of 1.6 ± 0.2 and 1.1 ± 0.1 °C and a decrease by 3.8% and 1.9% in gravimetric soil water content (% volume) at 0–10 cm, respectively.

Continuous warming shortened the winter wheat growing season by decreasing the time from re-greening to maturity by 6 and 11 days in 2010 and 2011, respectively. Other phenological stages changed by 2 days (only re-greening advanced by 2 d) or less, or not at all. Above-ground biomass at maturity was 10.0–19.6% greater in warmed plots than control plots. However, warming had no significant effects on winter wheat yield in either 2010 or 2011 (Table 1). Tillage had no significant effect on plant phenology, biomass and wheat yield.

Table 1
Grain yield in four temperature–tillage treatments of winter wheat and increase in above-ground biomass with temperature, relative to the control, for each tillage system in 2010 and 2011.

Treatment[a]	Yield[b] (Mg ha^{-1})		Increase in above-ground biomass (%)	
	2010	2011	2010	2011
CT0	6.3 ± 0.2	6.6 ± 0.2	–	–
CT1	6.4 ± 0.1	6.6 ± 0.6	13.4	16.8
NT0	6.0 ± 0.3	6.7 ± 0.2	–	–
NT1	5.8 ± 0.2	6.2 ± 0.4	10	19.6

[a] CT0, conventional tillage with no warming; CT1, conventional tillage with warming; NT0, no tillage with no warming; NT1, no tillage with warming.

[b] Yields did not differ significantly ($P < 0.05$) among treatments within a year.

3.2. Aphid populations

In 2010, warming significantly increased the number of aphids, whereas tillage and its interaction with warming had no significant effects (Fig. 1A; Table 2). The predominant species was *Sitobion avenae* F. (99.2%), with *Rhopalosiphum padi* L. present in much smaller numbers. The mean number of aphids in warmed plots was 57.2% higher than that in control plots. Aphid populations grew consistently and peaked on the same day in each treatment in 2010. The peak values were significantly different among treatments. More detailed analysis showed that, in NT, aphid peak value increased significantly due to warming, while in CT, the warming effect was not significant (Fig. 1C).

In 2011, aphid numbers remained much lower than in 2010 and no significant effects of warming or tillage on the number of aphids were observed (Fig. 1B; Table 2). Aphid populations in each treatment peaked on the same day in 2011, and peak values were not significantly different among treatments (Fig. 1D). However, warming significantly changed the composition of aphid species in the peak period; warming enhanced the numbers of *S. avenae* and decreased those of *R. padi*. In warmed plots, the proportion of *S. avenae* (88.4%) was significantly greater than in control plots (48.6%) ($x^2 = 245.35$, $P < 0.001$).

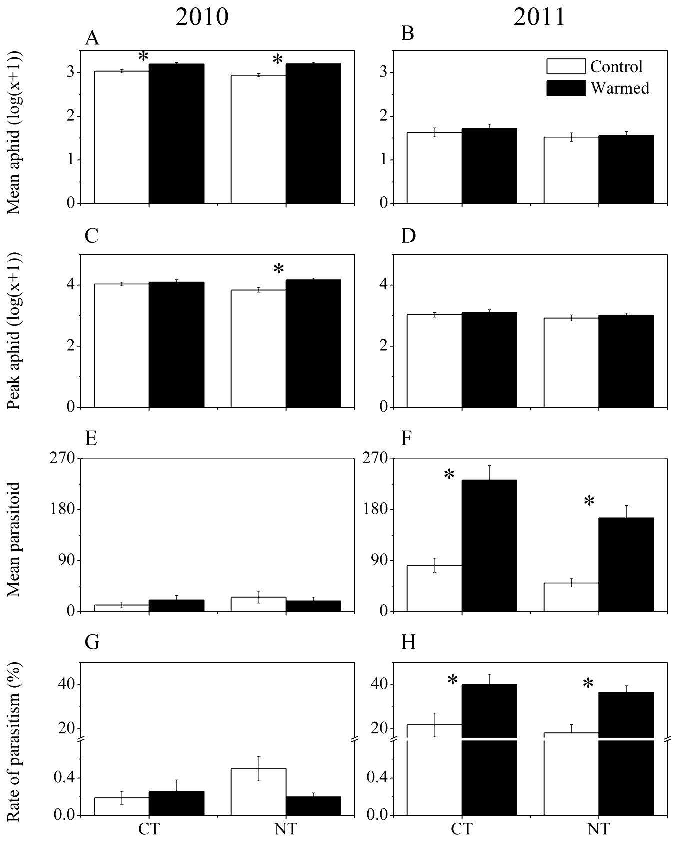

Fig. 1. Mean numbers of aphids and parasitoids per 100 tillers of winter wheat (log ($x+1$)) and rates of parasitism in each treatment in 2010 and 2011. Asterisk means significantly different between warmed and ambient plots (one-way ANOVA, $P < 0.05$). CT0, conventional tillage with no warming; CT1, conventional tillage with warming; NT0, no tillage with no warming; NT1, no tillage with warming.

3.3. Parasitoid responses

In both years, *Aphidius avenae* Haliday was the dominant parasitoid species. In 2010, parasitoid numbers were extremely low (Fig. 1E), and were not affected by warming or tillage (Table 2). The rates of parasitism were similar among treatments, all of them were lower than 1% (Fig. 1G). In 2011, warming significantly increased the numbers of parasitoids and the rate of parasitism (Fig. 1F and H; Table 2). The mean number of parasitoids and the rate of parasitism were approximately 3 and 1.9 times higher in warmed plots than in control plots (Fig. 1F and H), respectively. In both 2010 and 2011, tillage had no significant effect on parasitoid numbers and the rate of parasitism, but the interaction effect of tillage and date on parasitoid populations was significant (Table 2).

4. Discussion

Study of the reaction of tritrophic interactions to global change factors is much needed and will help researchers to predict and manage the consequences of global change at the ecosystem level (Landsberg and Stafford Smith, 1992; Harrington et al., 2001; Hance et al., 2007). An increasing body of evidence exists related to the effects of abiotic factors on tritrophic interactions between plants, herbivores, and their parasitoids. Climate-mediated bottom-up effects can significantly alter food-web structure through both density- and trait-mediated effects (de Sassi et al., 2012). Here we artificially increased temperatures to simulate global warming in two different tillage systems (CT and NT), and investigated the plant-aphid-parasitoid responses. Warming advanced the phenology of winter wheat; the time from re-greening to maturity decreased by 6–11 days, which is consistent with another field study that observed a rise in temperature resulted in advanced wheat growth phenology (White et al., 2011). Warming resulted in increased above-ground biomass in winter wheat. Other in situ infrared heating experiments in grasslands have observed similar biomass increases as in our study (Wan et al., 2009). This can be explained by plant photosynthetic overcompensation (Wan et al., 2009). Although the biomass increased, wheat yield was not significantly affected by warming. The biomass increases were mainly caused by an increase in tiller numbers, which did not contribute to yield (Hou et al., 2012). Warming merely advanced the reproductive period, rather than shortening it, so that the yield remained unchanged in the warming treatment. Tillage has been found to affect wheat yield in divergent directions, by increasing, maintaining or decreasing yield (Dao and Nguyen, 1989; Carr et al., 2003; Kumudini et al., 2008). Our result showed that the yield was not significantly affected by tillage; this was also be indirectly confirmed by the similar phenology and biomass between the NT and CT systems. However, the NT system experienced less change in soil temperature and moisture than the CT system. That may have occurred because the mulch covering on the soil surface of NT insulated the soil from increased temperatures. This may also be related to the fact NT soil experienced less disturbance than CT soil. No significant interaction effect of warming and tillage on wheat plants was observed.

Bottom-up effect occurs through resource availability at the base of the food web, such that increased productivity at lower

Table 2
Results of Split-plot ANOVA for aphids (per 100 tillers), parasitoids (per 100 tillers), and rate of parasitism (%) with warming (W), tillage system (T), and sampling date (Date) as factors, significance ($P < 0.05$) were bolded.

Year	Source	df	Aphids		Parasitoids		Rate of parasitism	
			F	Sig.	*F*	Sig.	*F*	Sig.
2010	W	1	44.043	**0.000**	0.065	0.799	0.748	0.390
	T	1	1.080	0.357	0.238	0.651	0.066	0.810
	Date	3	587.506	**0.000**	34.013	**0.000**	8.701	**0.000**
	W × T	1	2.634	0.109	0.159	0.691	1.722	0.193
	W × Date	3	0.149	0.930	1.231	0.304	2.194	0.096
	T × Date	3	0.240	0.868	5.732	**0.001**	3.949	**0.011**
	W × T × Date	3	1.329	0.271	1.235	0.303	0.676	0.569
2011	W	1	0.220	0.641	124.768	**0.000**	11.907	**0.001**
	T	1	0.634	0.509	2.705	0.242	0.157	0.730
	Date	3	65.247	**0.000**	8.512	**0.000**	149.819	**0.000**
	W × T	1	0.058	0.810	0.042	0.839	0.017	0.897
	W × Date	3	0.065	0.978	7.014	**0.001**	1.912	0.141
	T × Date	3	0.208	0.891	3.292	**0.029**	0.577	0.633
	W × T × Date	3	0.947	0.426	1.487	0.230	1.195	0.322

trophic levels results in increased productivity at higher trophic levels (Hoekman, 2010). Warming strengthened the bottom-up effect in the present study. Wheat phenology and biomass were positively affected by warming and the aphid numbers increased when their parasitoids were absent. Similar evidence has also been found in other plant-aphid systems. For example, an average 2.8 °C rise in temperature over the summer season markedly advanced the phenology of both the host plant *Dryas octopetala* and the aphid *Acyrthosiphon svalbardicum*, and population densities of the aphid were significantly higher when grown at warmer temperatures (Strathdee et al., 1993).

An advance in plant phenology generally indicates a plant species matures earlier in the growing season after which food availability would decrease for herbivores. A model study predicted that an increase in temperature would result in a lower maximum number of aphids and total number of aphid days because the immigrations of aphids would not be altered by the changes in temperature (Skirvin et al., 1997). However, many studies have indicated that animals may adjust their behavior in response to global warming, such as earlier occurrences of spring events (Parmesan and Yohe, 2003). Warming also affected the competition between the two aphid species studied here *S. avenae* and *R. padi*. These two species have different feeding locations. *S. avenae* feeds on ears and upper leaves (Watt, 1979), whereas *R. padi* prefers the stems and lower leaves of the plant (Leather and Dixon, 1981; Qureshi and Michaud, 2005). Although the aphid species occupy different niches, some evidence indicates that they compete (Gianoli, 2000). Warming advanced the emergence of wheat ears, which benefits *S. avenae* correspondingly; thus the proportion of *R. padi* declined. Previous studies on NT effects indicated that agricultural manipulations that differed in disturbance and fertility regimes did not result in bottom-up control of the soybean aphid (Costamagna and Landis, 2006). Our results also showed a similar trend; that is, tillage had no bottom-up effect on aphids. This suggests that manipulation of tillage does not change the quality of winter wheat plants sufficiently to cause significant bottom-up effects on cereal aphid numbers.

The general role of natural enemies in reducing and regulating populations of pests has been extensively reviewed, and their effects may vary considerably under different climatic conditions (Cammell and Knight, 1992). Warming is documented to enhance the top-down effect of predators by raising predator metabolic rates and concomitant processes relating to cooler temperatures (Brown et al., 2004). But the response of parasitoids to warming is difficult to predict and no general consensus exists on their effects, because it depends on the response of the host species. Rare weather events could have a great impact on parasitoid dynamics (Hassell et al., 1993). Both high temperature spikes and low temperatures have negative effects on parasitoids by increasing mortality (Hance et al., 2007; Roux et al., 2010). In our experiment, the response of parasitoids to warming seemed to vary according to their yearly abundance. The severe cold in the spring of 2010 may be responsible for the extreme low numbers of parasitoids in that year. In the presence of parasitoids, warming significantly increased the rate of parasitism, and as a result similar numbers of aphid were found in both the warmed and control plots. It has been suggested that warming would benefit parasitoids and enhance the top-down effect of parasitoids. The effects of temperature on predators (mainly ladybirds) have also been investigated, and their numbers were not affected by warming or tillage, which can be partly explained by frequent movement of predators among plots. Several reports have shown that reduced tillage usually encourages predators, such as carabid and staphylinid beetles (Andersen, 1999, 2003; Nash et al., 2008). In the present study, NT had a neutral effect on parasitoid population. The interaction of tillage and date had a significant effect on parasitoid numbers. This suggests that the response of parasitoids to tillage may become more evident over a long period of time. The potential effects of tillage on parasitoid populations deserve further study.

5. Conclusion

Our results provided direct evidence of increased aphid abundance resulting from higher temperatures in wheat fields. Warming could speed winter wheat development from re-greening to maturity and result in a larger aphid population. In the presence of the parasitoid, warming could increase parasitoid abundance, thereby counterbalancing the potential increase in aphid populations and ultimately resulting in similar aphid densities in warmed and control conditions.

Current models will need further refinement to account for the effects of bottom-up and top-down on the food web. Changes in aphid abundance can be predicted by considering yearly fluctuations in parasitoid populations and aphid–parasitoid interactions. The results of this study highlight the need for having a better fundamental understanding of parasitoids and the conservation of natural enemies.

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