Research Article

Received: 10 January 2018 Revised: 6 July 2018 Accepted article published: 12 July 2018 Published online in Wiley Online Library: 3 September 2018

(wileyonlinelibrary.com) DOI 10.1002/ps.5140

Elevated temperature reduces wheat grain yield by increasing pests and decreasing soil mutualists

Baoliang Tian,[a] Zhenzhen Yu,[a] Yingchun Pei,[a] Zhen Zhang,[a] Evan Siemann,[b] Shiqiang Wan[a] and Jianqing Ding[a*]

Abstract

BACKGROUND: Climate warming is known to affect species' phenology, abundance, and their interactions with other species. Understanding how cultivated plants, their associated community members (including pest insects, natural enemies, soil microbes), and their interactions respond to warming to influence crop yields is critical to current and future food security. We conducted a two-year field study on the effects of elevated temperature on winter wheat growth and grain quality, insect pests, natural enemies, ground arthropods, weeds, and arbuscular mycorrhizal fungi (AMF).

RESULTS: Elevated temperature shortened the period of wheat growth, decreased grain yield, and reduced grain quality by increasing fiber and decreasing wet gluten, protein, total soluble sugars, and starch. Elevated temperature also increased aphid abundance while decreasing AMF colonization rates. Structural equation modeling indicated that the direct negative effect of warming on wheat yield was augmented by indirect negative effects via increased aphid and weed abundances along with decreased AMF colonization.

CONCLUSION: Climate change can potentially affect crop production and quality both directly and indirectly by modifying interactions with aboveground and belowground organisms. Future studies on the effects of climate change on crops should consider the responses of aboveground and belowground biotic community members and their interactions with crop plants.

Supporting information may be found in the online version of this article.

Keywords: AMF; aphid; biological interactions; biotic community; quality; warming

1 INTRODUCTION

Climate change significantly affects the environment, ecosystems and agriculture. Climate warming is known to affect species phenology,[1] distribution,[2] and abundance[3] as well as their interactions with other species.[4] Knowledge of these responses at the community level may help to further understand the effects of climate warming on species and their associated community members.[5] Such studies have recently been reported for marine and stream food webs,[6,7] and soil symbiotic fungi.[8] However, little is known about such effects on crop communities even though this is critical for managing agricultural ecosystems to ensure current and future food supplies.

Crop growth is known to be influenced by aboveground herbivorous insects[9] and their natural enemies (predators and parasitoids),[10] as well as belowground biota such as mycorrhizal fungi.[11] These aboveground and belowground crop community members affect each other,[12] potentially influencing crop yield[13] and quality,[14] and disrupting the stability of the agricultural ecosystem.[15] Many studies have shown that climate warming could affect crop phenology,[16] yields,[17] insect pests,[18] and soil microbes.[8] However, to date, there is no consensus regarding how warming directly affects yield *versus* indirectly affecting yield via pests and mutualists. Some studies have indicated that the response of a crop yield to climate warming is positive, while some others suggest it is negative.[19] One of the reasons for these seemingly conflicting conclusions may be that previous studies have typically included only one community member and excluded others in their experiments. Thus, their results on warming effects were solely at the species level, rather than the community level, neglecting potential interactions with other members of the community that could have strongly influenced the focal species' response. To understand the responses of crop species to climate warming at the community level, the study must simultaneously include the crop plant as well as associated aboveground and belowground community members. Such studies of crops, however, have not yet been conducted.

As one of the most important crops providing vegetal protein in human food, wheat (*Triticum aestivum* L.) plays a critical role in global food security. Indeed, the effects of climate warming on

* *Correspondence to: J Ding, College of Life Sciences, Henan University, Jin Ming Avenue, Kaifeng, Henan 475004, China. E-mail: jding@henu.edu.cn*

a *College of Life Sciences, Henan University, Kaifeng, China*

b *Biosciences Department, Rice University, Houston, TX, USA*

wheat have received much attention, although the results have been inconsistent. Chen *et al.*[20] reported that climate warming might not affect the yield of irrigated wheat, while You *et al.*[21] showed that in non-irrigated regions increasing temperature by 1 °C could decrease wheat yield by as much as 10%. With respect to grain quality, Viswanathan and Khanna-Chopra found that the grain nitrogen content of wheat increased under heat stress.[22] However, Tian *et al.* found that warming reduced grain nitrogen content.[23] The inconsistent effects of warming on wheat may reflect differences in indirect effects via the wheat associated community.

Similar to the earlier contradictory results in the responses of wheat to warming, findings on the warming effects on arbuscular mycorrhizal fungi (AMF) and wheat pest insects have also been inconsistent. AMF are common mutualistic symbionts that can colonize the roots of over 80% of terrestrial plants and increase nutrient and water uptake as well as help to provide resistance to pest insects and diseases.[24] They are considered an important link between aboveground and belowground processes and play an important role in crop responses to climate change.[25] Some studies on plants other than wheat show an increase in AMF colonization in response to increased temperature[26] while others have found that increased temperature can have a negative effect on AMF.[25] These studies demonstrate that warming does not always lead to predictable or significant changes in AMF.[27] Another study that examined the benefits of AMF colonization in wheat over two growing seasons found that AMF colonization rates and wheat growth and yield increases compared to AMF-free plants were smaller in the hotter, drier year compared to the cooler one.[28] Similar conclusions can also be applied to insects, where most studies have shown that increased temperature tends to have positive effects on their abundance. Changing of temperature may also impact insect geographical ranges, overwintering areas, growth rates, number of generations per season, crop–pest synchronization, dispersal and migration, and availability of host plants and refugia which all may influence pest impacts on crops including wheat.[29–31] For instance, aphid populations on wheat increase with warming[32,33] and wheat yield losses from the *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) increase in warmer years.[34] But herbivores may vary in their responses to changes in temperatures. The proportional abundances of the aphids *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae) and *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) on wheat decreased while that of *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae) increased with extreme high temperature event frequency.[35] In addition, climate warming may affect insect distribution and populations indirectly (through hosts, predators, and competitors).[29] For example, warming significantly increased the numbers of the aphid *Sitobion avenae* on wheat in a year when natural enemies were rare,[30] but when parasitoids were common, warming increased the abundance of parasitoids but the aphids were not affected.[31] Therefore, it may be necessary to assess the impact of warming on crops from a community level perspective that incorporates species interactions in order to accurately predict the net effect of warming on wheat yield and quality.

In this study, we examined the effects of elevated temperature on wheat and its associated community members including aboveground herbivorous insects, aboveground natural enemies (predators and parasitoids), ground dwelling arthropods, weeds, and AMF in a two-year field experiment. Specifically, we asked the following questions: (i) How does elevated temperature affect wheat growth, yield, and grain quality? (ii) How do aboveground herbivorous insects, aboveground natural enemies, ground dwelling arthropods, weeds, and belowground AMF respond to elevated temperature? (iii) What are the contributions of indirect effects via these aboveground and belowground community members to wheat responses to warming?

2 MATERIALS AND METHODS

2.1 Study site

We conducted the experiment in sandy soil farmland at Henan University, Kaifeng, Henan Province, China (E: 114.23, N: 34.52, altitude 73 m). Kaifeng has a warm temperate continental monsoon climate with cold, dry winters and windy, dry springs. Mean annual precipitation is 670 mm, with the majority (~86%) occurring from March to October. Mean annual temperatures over the past 40 years were 14 °C with minimum monthly average of −4 °C and maximum monthly average of 32 °C (http://www.nmc.gov.cn/). Each year, we weeded and fertilized (75 g/m^2 of 15-15-15 synthetic fertilizer before sowing) the experimental field then rotary tilled it.

2.2 Study species

We used wheat (*Triticum aestivum*) cultivar Zhoumai 22 for the experiment. It was developed from the hybridized combination of Zhoumai 12, Wenmai 6 and Zhoumai 13 by the Zhoukou academy of agricultural sciences in Henan Province in 2007. It is cold-tolerant and disease-resistant. It is widely grown in the Yellow and Huaihe River basins in China with over 3.3 million hectares in cultivation.[36]

2.3 Experimental design

We conducted a two-year field warming experiment from 2015 to 2017. We established 12 test plots (3 m × 4 m) that were spaced at least 1 m apart. We warmed six plots with MSR-2420 infrared heaters (Kalglo Electronics, Bethlehem, PA, USA), suspended 2.05 m above the ground and set at a radiation output of 2000 W. In each of six control plots, we used a dummy heater of the same shape and size as the infrared heaters to control for shading effects. We ran the heaters continuously each year from sowing (October 8, 2015 and October 8, 2016) until we manually harvested the wheat (May 30, 2016 and May 21, 2017).

2.4 Measurement protocols

2.4.1 Physical environment

We measured soil and air temperatures with alcohol thermometers installed 10 cm belowground and aboveground in three locations in each plot. We recorded temperatures at 10:00–11:00 a.m. once a week. We measured soil moisture at 10 cm depth every seven days with a TDR300 soil moisture probe (Spectrum Technologies, Plainfield, IL, USA) at three locations in each plot.

2.4.2 Plant growth, yield and grain quality

We observed wheat phenology stages from sowing to harvest. We recorded the date of a phenological stage as when 50% of plants in a plot had changed developmental stage.[31,37] We measured the height of 25 randomly chosen wheat plants in each plot in five locations every seven days from emergence to harvest.

At harvest, we counted the number of valid tillers (having an ear) on five plants in each of five (year one) or six areas (year two) in each plot. We counted the number of valid tillers (i.e. number of

Table 1. The effects of warming treatment on maximum wheat height, straw produced, valid tillers per plant, valid tillers per square meter, kernels per ear and thousand kernel weight (TKW) in two growing seasons [year one (2015–2016) and year two (2016–2017)] in a mixed model analysis of variance (ANOVA)

	Treatment		Year		Treatment × year	
Variable	$F_{1,10}$	P	$F_{1,10}$	P	$F_{1,10}$	P
Yield	**6.90**	**0.0253**	**297.03**	**<0.0001**	0.19	0.6713
Height	**11.26**	**0.0073**	**22.7**	**0.0008**	**5.11**	**0.0474**
Straw	0.11	0.7508	**137.25**	**<0.0001**	4.85	0.0522
Tillers/m^2	<0.01	0.9526	**64.67**	**<0.0001**	3.61	0.0867
TKW	1.64	0.2105	**214.10**	**<0.0001**	1.41	0.2500
Tillers/plant	3.75	0.0815	3.63	0.0891	1.03	0.3369
Kernels/ear	2.72	0.1304	3.93	0.0756	0.21	0.6544

Note: significant results are shown in bold typeface.

ears) in three subplots in every plot (50 cm × 50 cm in year one; 100 cm × 100 cm in year two). Then, we removed all the ears from the plants in each subplot to calculate dry ear mass. We removed 500 kernels from the ears in each subplot and weighed them to estimate thousand kernel weight (TKW). We clipped, dried, and weighed five plants in each subplot at ground level to measure straw mass (i.e. all aboveground mass except for the ears). In year one, to estimate yield, we removed the ears from each entire plot, threshed and dried them, then winnowed and weighed the grain. In year two, we used the ears from the three 1 m^2 subplots to estimate yield. We used TKW, number of ears, and yield to estimate the average number of kernels per ear.

We measured wet gluten content, zeleny, and protein content in wheat grains by near infrared transmission (NIT) using 1241 Grain Analyzer (Foss Tecator AB, Höganäs, Sweden) following published methods.[38] We analyzed total soluble sugar, starch, and fiber content with an ultraviolet and visible spectrophotometer (UVS) (Thermo Scientific GENESYS 10S, Waltham, MA, USA) using established methods.[39]

2.4.3 *Pest insects, natural enemies, ground arthropods and weeds*

We estimated foliage arthropods and natural enemies by visually surveying the arthropods on ten plants in each of the five locations in every plot (monthly from March to May in year one, approximately weekly from March to May in year two). We identified them to the narrowest taxon possible (without removing them from the plant). In year two only, we estimated ground arthropods by pitfall traps in the same five locations in every plot. The pitfall traps consisted of a double-layer plastic cup (10 cm in diameter and 12 cm in height) containing 0.1% detergent solution which filled one-third of the cup. We placed pitfall traps with their rims flush with the ground. We left the lids off them for a 24-h period each week from March to May and brought the captured arthropods back to the laboratory for identification. Before harvest, we counted the number of individuals of each weed species in each plot.

2.4.4 *AMF colonization*

We estimated the percentage of wheat root AMF colonization following established methods.[40] In brief, we cleared roots in 2.5% potassium hydroxide (KOH), stained fungal structures with 0.05% Trypan blue, mounted 30 1 cm fine root segments for each plot, and counted the presence of hyphae at 300 grid-line intersections at 200× microscope magnification.[41]

2.5 Data analyses

To examine the effect of elevated temperature on wheat and its aboveground and belowground communities, we performed mixed analysis of variance (ANOVA, proc mixed, SAS 9.4) following a common approach. The models included treatment (control *versus* warming), experiment year (year one *versus* year two), and their interaction as fixed effects. Some models included plot nested within treatment as a random effect (to control for the measurement of variables at multiple times or in multiple subplots within plots). For variables measured multiple times in a year, we also included terms for sampling date (nested in year) and its interaction with warming treatment. Ground arthropods were only measured in a single year of the experiment and, as a consequence, these models did not include year as a predictor. We used partial difference tests to evaluate differences among treatment means for significant factors with more than two levels. All data met the assumptions of ANOVA.

We used structural equation modeling (SEM, Proc Calis, SAS 9.4, covariance matrix, maximum likelihood estimation) with year one data to identify causal linkages from increased temperature (average soil temperature) to potential explanatory variables (AMF colonization, average aphid abundance, weed abundance) and then to yield. We checked the bivariate relationships between variables for linearity. We reported paths as standardized coefficients for significant links ($P < 0.05$) and calculated strengths of indirect effects as the products of the direct path coefficients.

3 RESULTS

On average, experimental warming increased air temperature by 0.86 °C (Supporting Information Fig. S1a) and soil temperature by 1.50 °C at 10 cm depth (Fig. S1b) over the two growing seasons compared to the control plots. It was warmer in the second year of the experiment (air +3.85 °C; soil +0.89 °C). Soil moisture was lower in the second year (−1.6% *v*/*v*; Fig. S1c) but was unaffected by experimental warming ($P = 0.4998$).

3.1 The effect of elevated temperature on wheat biomass, grain quality and phenology

Wheat yield was 40% lower in the second year and experimental warming decreased yield on average by 10% over the course of the experiment (Table 1). There was no difference in warming effects between the two years (Table 1, Fig. 1).

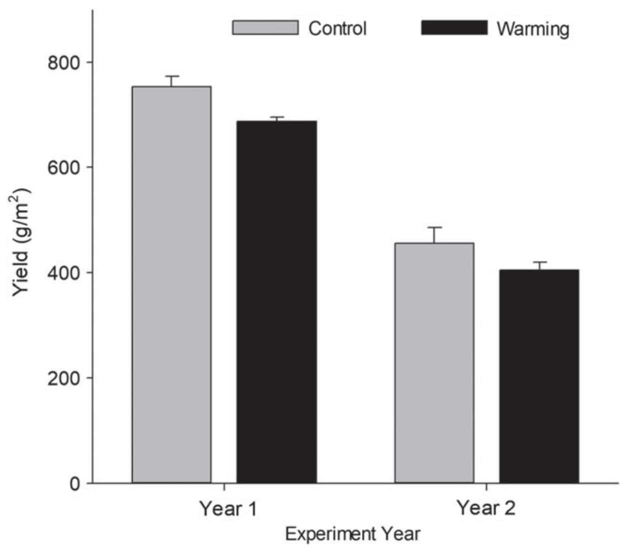

Figure 1. Effects of warming treatment on wheat grain yield. Gray bars = control plots, black bars = warming treatment plots. Year one indicates 2015–2016. Year two indicates 2015–2016. Data are means + standard error.

At their maximum height, wheat plants were shorter in control plots in the first year (60.6 cm) than in the other three treatment combinations (range 67.0 to 69.9 cm; Table 1, Fig. 2(a)). Compared to the first year, the biomass of straw produced was 33% lower, the number of valid tillers per square meter was 37% lower, and average kernel weight was 19% lower (TKW: 46.6 *versus* 37.6 g) in the second year but they were not affected by treatment as a main effect or in interaction with year (Table 1, Fig. 2(b)–(d)). The numbers of valid tillers per plant and kernels per ear did not depend on treatment, year or their interaction (Table 1; Fig. 2(e) and (f)).

Experimental warming decreased kernel contents of wet gluten (20.7% to 17.7%; Fig. 3(a); Table 2), zeleny (20.9 to 16.0 mL; Fig. 3(b); Table 2), protein (10.2% to 8.5%; Fig. 3(c); Table 2), total soluble sugars (8.4% to 7.3%; Fig. 3(d); Table 2), and starch (55.4% to 45.7%; Fig. 3(e); Table 2) but increased the fiber content (22.1% to 32.0%; Fig. 3(f); Table 2). Wet gluten, zeleny, protein, and total soluble sugars were higher, and starch and fiber lower, in the first year (Fig. 3) but the effects of warming did not vary between years (Table 2).

3.2 The effect of elevated temperature on the wheat associated community

The number of aphids per wheat stem was lower in control plots in year one than warm plots in year one, control plots in year two, or warm plots in year two ('treatment × year', Fig .4(a); Table 3). The aphids of *Schizaphis graminum* were more abundant than the aphids of *R. padi* or *Sitobion avenae*, especially earlier in the growing season (Fig. 5). Other aboveground herbivores were rarely sampled (taxa shown in Table S1). The number of natural enemies per stem (taxa shown in Table S1, Fig. 4(b)), The abundances of weeds (taxa are in Table S2, Fig. 4(c)) were higher in year two but they did not depend on warming treatment or the interaction of year and warming (Table 3). AMF colonization was lower in warming plots than in control plots (13.8% *versus* 10.1%) and in year two than in year one (Fig. 4(d)). These effects were additive (Table 3). The numbers of ground dwelling arthropods within functional groups were unaffected by experimental warming (Fig. 6).

The relationships between aphids, natural enemies, and plant phenology were changed by warming in year two. Aphid populations peaked ∼1 week earlier in warming plots but plant phenology advanced more rapidly with warming (12 days) so that aphids were abundant in later stages of wheat development in warming plots (Fig. 7). The effects of warming on population dynamics varied among coccinellid and aphid species (Fig. 6).

3.3 Elevated temperature effects on linkages between biological factors and wheat yield

The SEM indicated that the decrease of wheat yield with warming in year one was associated with higher abundances of aphids and weeds that increased their negative impacts on yield and lower AMF colonization that reduced their positive impact on yield (Fig. 8). There was a direct negative effect of warming (strength −0.490) which was stronger than the indirect effects mediated through aphids ($+0.487 \times -0.137 = -0.07$), weeds ($0.373 \times -0.307 = -0.11$), and AMF ($-0.319 \times +0.113 = -0.04$).

4 DISCUSSION

In this study we examined the effect of elevated temperature on wheat growth, grain production, and grain quality as well as the associated aboveground and belowground biotic communities. We found that elevated temperature advanced plant phenology, decreased wheat yield, and decreased grain quality (decreased wet gluten, zeleny, protein, total soluble sugar, and starch and increased fiber). We also found elevated temperature increased the abundance of aphids but decreased AMF colonization rates on wheat roots. Changes in these pest insects and root mutualists may negatively impact wheat grain yield and quality.

The responses of wheat growth to elevated temperature have received considerable attention, with some results showing that the wheat yield will be decreased under warming conditions[42] but other studies finding increases[43] or a mix of outcomes.[44] They all indicated, however, that growing season length and the duration of key phenological phases are major factors determining grain yield.[45] In our study, changes in the plant growth time, such as shortening of the tillering stage would result in reduction of production. Moreover, if elevated temperatures happen during the time from heading stage to maturing stage, the heat stress can decrease post-heading duration and grain yield, because there is also a significant positive correlation of post-heading duration with tillers and grain number density.[46,47] Elevated temperature may also impact grain quality, such as wet gluten, nitrogen, and soluble sugar,[23] because leaf expansion, photosynthesis and grain filling are key temperature dependent physiological processes.[48] In our warming experiment, the days from heading stage to maturing stage were consistently reduced as much as 4.5 days on average for the two growing seasons. This is a likely reason for the observed decline in grain quality, in the wet gluten, zeleny, protein, total soluble sugars and starch contents.

Previous studies on the effects of warming on insect pests reported that elevated temperature could increase their winter survival, which would likely increase population density in the following spring,[49] as higher temperatures may lengthen the suitable periods for growth and reproduction after diapause.[50] Studies also suggest that warming may directly increase aphid population growth and their net reproductive rate[51] which may be especially important in areas that are too cold for aphid overwintering and populations depend on migration. In this study, we observed overwintering adult aphids even in the coldest month,

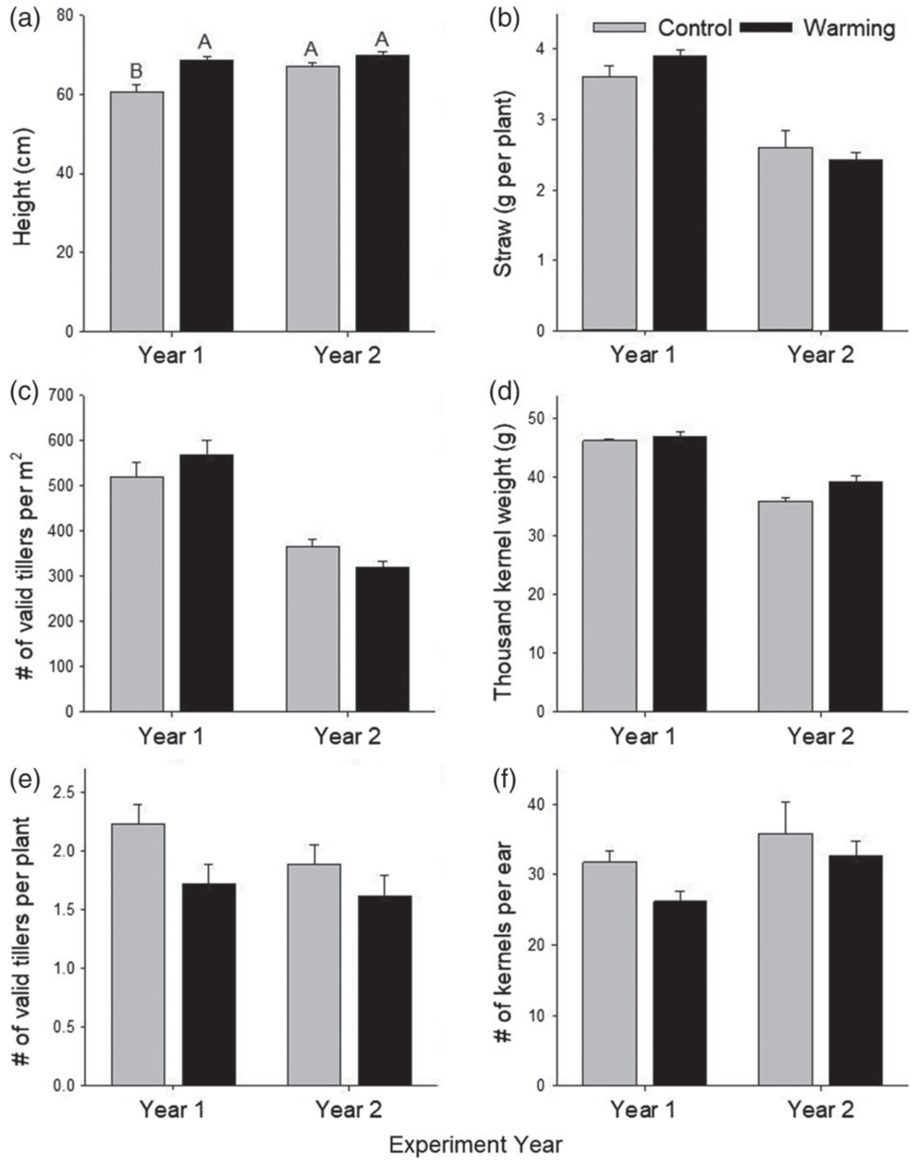

Figure 2. Effects of warming treatment on wheat growth. (a) Plant height, (b) straw weight, (c) number of valid tillers per square meter, (d) thousand kernel weight (TKW), (e) number of valid tillers per plant, and (f) number of kernels per ear in the control (gray bars) and warming (black bars) plots. Year one indicates 2015–2016. Year two indicates 2015–2016. Data are means + standard error. Means with the same letter were not significantly different in *post hoc* tests.

suggesting warming may increase aphid survival in winter and then likely increase the populations in spring. Wheat aphids feed preferentially on the leaf or ear, especially the rachis and base of the spikelet, which is especially damaging to yield.[52,53] In our study, the number of aphids per stem in warming plots was significantly higher than in control plots with the abundances of aphids exceeding published economic injury thresholds.[53] This would suggest that the increase of aphid abundance with warming may cause yield loss as was indicated by the SEM analysis.

The timing of aphid population peaks and plant phenological stages may also play a critical role in the impacts on wheat yield because the economic threshold for aphids on wheat increases rapidly with phenological stage. In one study in Sweden, the economic injury threshold was one aphid per tiller at heading, four aphids per tiller at flowering, and seven aphids per tiller at maturing.[52] In our study, the more rapid shift of plant phenology relative to aphid population peaks had the potential to limit the impacts of increased aphid population abundances. However, in a crop system where plant phenology advances less rapidly than peak pest numbers, the combination of higher pest abundances at earlier, more vulnerable phenological stages could magnify pest-mediated yield losses from warming.

Natural enemies play a key role in regulating pest insect populations and protecting crops. In our study system, the surveyed natural enemies were coccinellid beetles, syrphid flies, spiders, lacewings, and aphidiid wasps. We found no significant effects from elevated temperature on these natural enemy populations, which differed from the effect warming had on the aphids. These contrasting effects on pest insects and natural enemies indicated that elevated temperature had few effects on high trophic levels, which is consistent with previous studies.[54] There is a slight indication in our results that coccinellid populations may have required a longer time to increase after aphid population increases in warming plots (Fig. 5). This may have contributed to the higher numbers

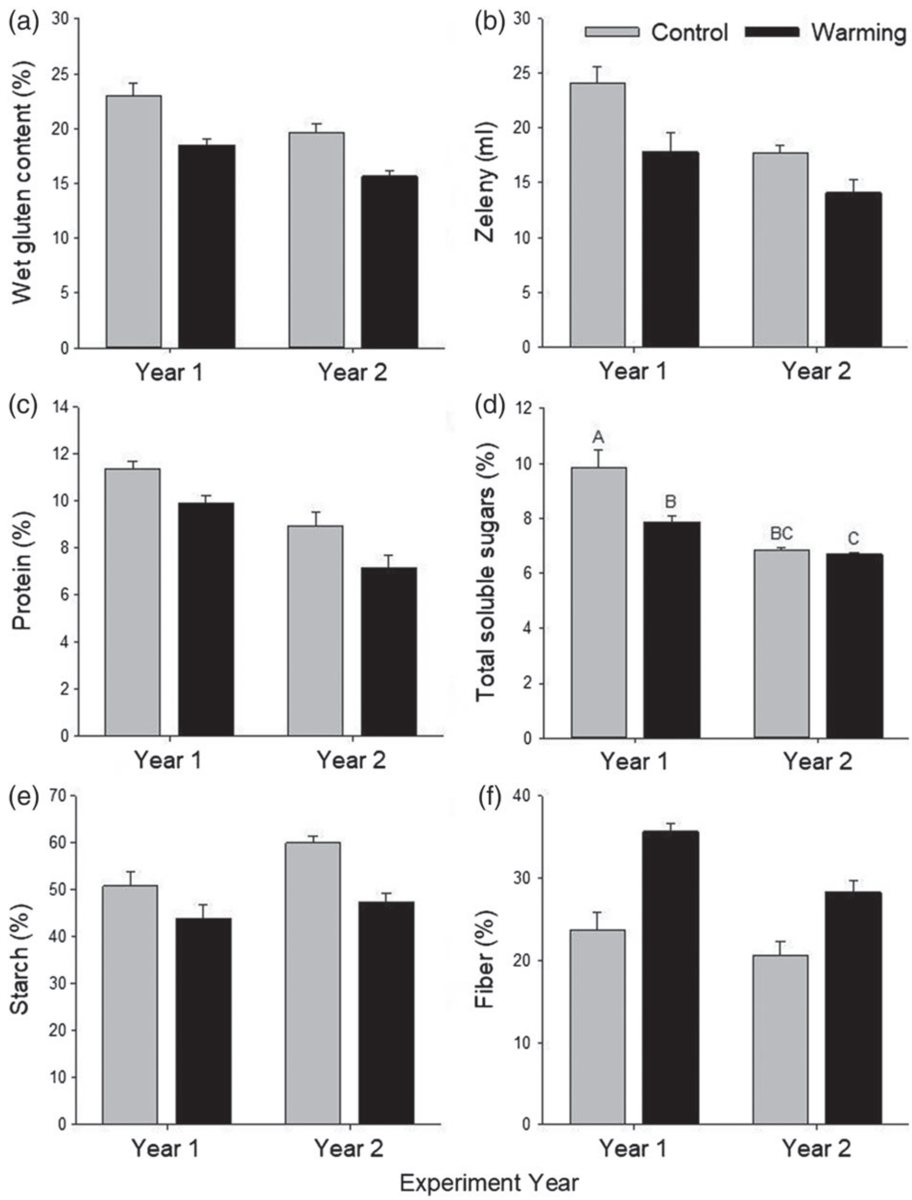

Figure 3. Effects of warming treatment on grain quality. (a) Wet gluten content, (b) zeleny content, (c) protein content, (d) total soluble sugars content, (e) starch content, and (f) fiber content for wheat in the control (gray bars) and warming treatment (black bars) plots. Year one indicates 2015–2016. Year two indicates 2015–2016. Data are means + standard error. Means with the same letter were not significantly different in *post hoc* tests.

Table 2. The effects of warming treatment on the content of wet gluten, zeleny, protein, total soluble sugars, starch, and fiber in wheat grain in two growing seasons [year one (2015–2016) and year two (2016–2017)] in analysis of variance (ANOVA)

	Treatment		Year		Treatment × year	
Variable	$F_{1,10}$	P	$F_{1,10}$	P	$F_{1,10}$	P
Wet gluten	**14.16**	**0.0037**	**26.34**	**0.0004**	0.08	0.7822
Zeleny	**13.00**	**0.0048**	**13.42**	**0.0044**	0.87	0.3716
Protein	**11.17**	**0.0075**	**45.31**	**<0.0001**	0.14	0.7125
Total soluble sugars	**8.54**	**0.0153**	**42.72**	**<0.0001**	**8.29**	**0.0164**
Starch	**13.76**	**0.0040**	**8.88**	**0.0138**	1.68	0.2241
Fiber	**35.48**	**0.0001**	**10.16**	**0.0097**	1.61	0.2330

Note: significant results are shown in bold typeface.

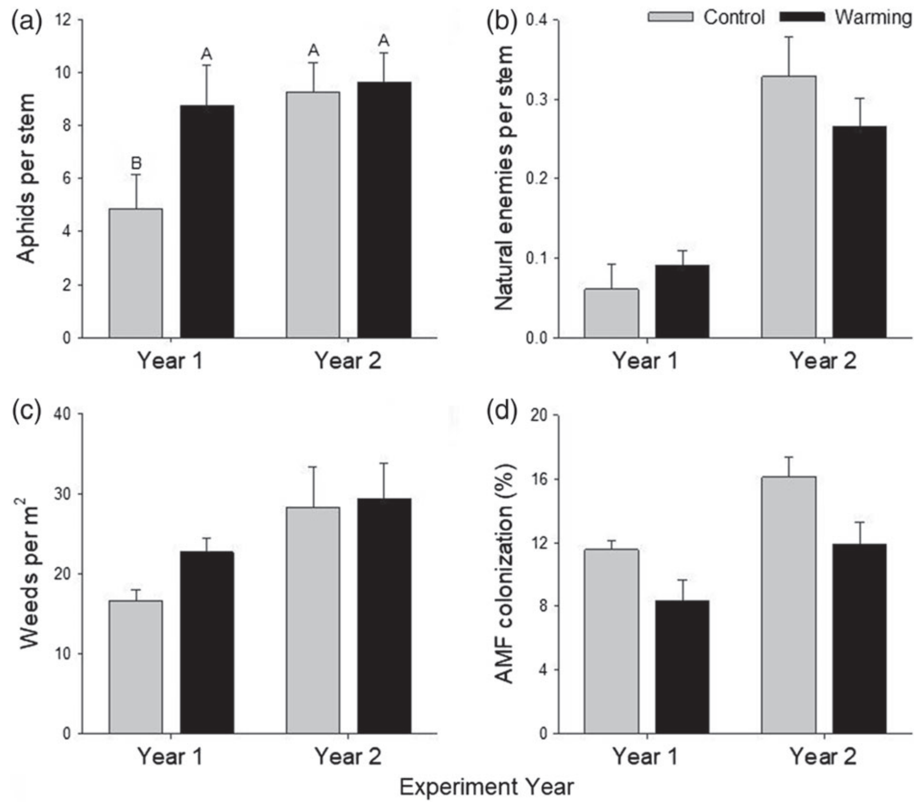

Figure 4. Effects of warming treatment on wheat associated biotic community. (a) Aphid abundance, (b) natural enemy abundance, (c) weed abundance, and (d) wheat root arbuscular mycorrhizal fungi (AMF) colonization in the control (gray bars) and warming treatment (black bars) plots. Year one indicates 2015–2016. Year two indicates 2015–2016. Data are means + standard error. Means with the same letter were not significantly different in *post hoc* tests.

Table 3. The effects of warming treatment on the populations of aphids per stem, natural enemies per stem, weeds per square meter, and arbuscular mycorrhizal fungi (AMF) colonization percent in wheat field in two growing seasons [year one (2015–2016) and year two (2016–2017)] in mixed model analysis of variance (ANOVA)

		Aphids		Natural enemies			Weeds		AMF	
Variable	df	*F*	*P*	*F*	*P*	df	*F*	*P*	*F*	*P*
Treatment	1,10	**6.01**	**0.0341**	0.08	0.7783	1,10	0.94	0.3560	**9.88**	**0.0105**
Year	1110	**11.92**	**0.0008**	**52.76**	**<0.0001**	1,10	**7.66**	**0.0199**	**11.8**	**0.0064**
Treatment × year	1110	**5.26**	**0.0237**	1.95	0.1652	1,10	0.57	0.4673	0.20	0.6634
Day(year)	10 110	**38.27**	**<0.0001**	**21.57**	**<0.0001**					
Treatment × day(year)	10 110	0.60	0.8120	**2.94**	**0.0027**					

Note: significant results are shown in bold typeface.

of aphids observed in those plots. In situations where populations of natural enemies respond positively and rapidly to increases in pest populations due to a warming environment, they may be able to limit the magnitude of pest increases and subsequent yield reductions.[55]

Previous studies have also demonstrated that global warming can affect the growth, phenology, and geographical distribution of weeds.[56] Our study found that there was no difference in weed density between warming and control plots, though the number of weeds in year two was significantly higher than in year one. These results suggest that the effect of elevated temperature on weed populations may be slow. Multi-year experiments may show the effects of warming on the weed seed bank, which can significantly affect weed populations. The composition of the weed community might also be affected as some species became more abundant and others less abundant as a result of warming (Table S2) and they are unlikely to have identical *per capita* effects on wheat. In addition, there was also no significant difference in the composition of the ground arthropod communities between the warming and control treatments in our study. It is likely that a long-term warming experiment may provide a more rigorous test of the responses and impacts of warming mediated through interactions with members of the community that respond differently to changing temperatures.

AMF are associated with most species of terrestrial plants and play an important role in plant nutrition and defense.[24] It has been reported that wheat grain yield and quality are positively correlated with root AMF colonization rate, as AMF increase plant growth by increasing uptake of soil nutrients.[28,57] However, to date, there have been few studies on the effects of climate change on

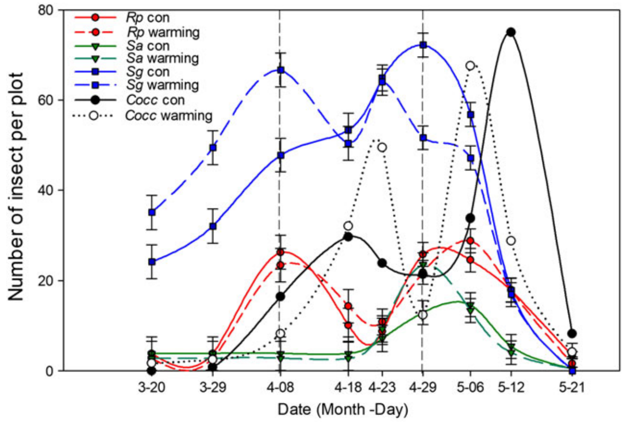

Figure 5. Population dynamics of aphids and natural enemies in warming and control plots in year two (2016–2017). Red lines with circles = the average number of *Rhopalosiphum padi* per plot. Green lines with triangles = the average number of *Sitobion avenae* per plot. Blue lines with diamonds = the average number of *Schizaphis graminum* per plot. Black lines with circles = the average number of coccinellids per plot. Dashed line = in control plots, Solid line = warming treatment plots. Data are means ± standard error.

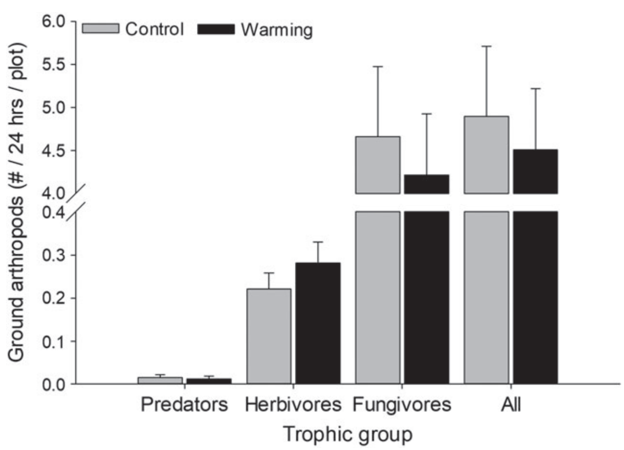

Figure 6. Effects of warming treatment on numbers of ground dwelling arthropods (fungivores, herbivores, predators, all) caught per 24 h of pitfall trap sampling in year two (2016–2017). Gray bars = control plots, black bars = warming treatment plots. Data are means + standard error.

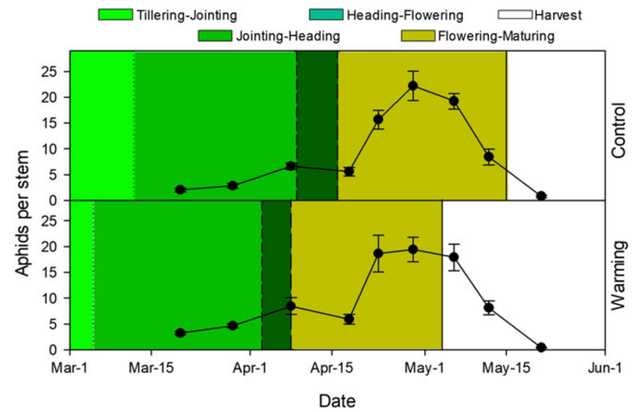

Figure 7. Effects of warming treatment on wheat phenological phase and aphid population dynamics. Lines with errors indicate the number of aphids per stem (means ± standard error) in year two (2016–2017). Different color squares indicate the phenological phases.

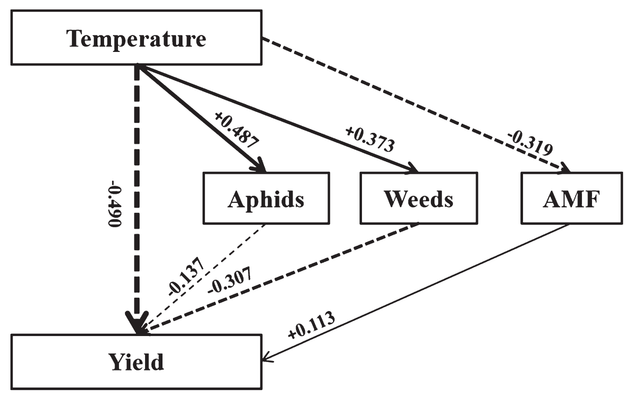

Figure 8. Effect of elevated temperature on aphids, weeds, arbuscular mycorrhizal fungi (AMF) and yield. The results of structural equation modeling (SEM) showing the direct effect of varying soil temperature, and indirect effects via aphid abundance, AMF colonization, and weed abundance, on wheat yield in year one. Positive effects are shown with solid arrows and negative effects are shown with dashed arrows. The width of arrows and the numbers next to arrows indicate the strength of the effect as a standardized regression coefficient. All paths shown were significant at $P < 0.05$.

AMF in wheat (but see Zhu *et al.*[28] showing that AMF benefits were lower in a drier, hotter year). In this study, we found that elevated temperature decreased AMF root colonization by 25% and our SEM model indicated that the AMF reduction negatively affected grain yield. To the best of our knowledge, this is the first study to report that warming affects AMF colonization which in turn indirectly reduces wheat grain yield or quality.

Our findings may provide new insights into how crop communities respond to climate change. In the past few years, field and experimental studies have shown that both crop species and their associated communities can respond strongly to climate warming.[58,59] Furthermore, it has also been demonstrated that plant performance, in general, is sensitive to interactions with their aboveground and belowground communities including herbivores, natural enemies, pathogens, and mutualists.[60] For wheat, how aboveground and belowground interactions are impacted by climate change, and how these changes in species interactions in turn affect grain yield and quality remains largely unknown. In this study, we found that many of the wheat community members, including aboveground insect pests, belowground AMF, and possibly weeds, could be affected by elevated temperature, and then indirectly influence wheat growth, grain yield, and grain quality. Further field and laboratory studies are needed to understand how these aboveground and belowground biological factors affect each other, to directly or indirectly determine wheat responses to climate change.

In summary, this study shows that wheat phenology and growth could be directly affected by climate warming, such that plant height increased but grain yield and quality decreased. Furthermore, climate warming may indirectly affect grain yield by increasing wheat pest insects, such as aphids, and decreasing AMF colonization. Our study is the first to report the response of the wheat associated community to warming for both aboveground and belowground compartments. Our results provide empirical evidence showing that wheat, foliar insects, and soil microbes could simultaneously respond to warming conditions, suggesting that climate change could both directly and indirectly affect crop production and quality. We recommend that future studies on the effects of climate change on agricultural crops consider the interactions between the aboveground and belowground biota and their influence on the target crop.[55]

ACKNOWLEDGEMENTS

The authors gratefully acknowledge help in the field survey from Jianyi Li, Jianing Hu, Xi Wang, Shanshan Shuai, Yannan Li, and Xiao Sun. This work was funded by the National Key R&D Program (2017YFD0200600) and Henan Province Postdoctoral Science Foundation.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

REFERENCES

1 Liu Y, Mu J, Niklas KJ, Li G and Sun S, Global warming reduces plant reproductive output for temperate multi-inflorescence species on the Tibetan plateau. *New Phytol* **195**:427–436 (2012).
2 Valladares F, Matesanz S, Guilhaumon F, Araujo MB, Balaguer L, Benito-Garzon M *et al.*, The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecol Lett* **17**:1351–1364 (2014).
3 Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T *et al.*, An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat Clim Change* **3**:78–82 (2013).
4 Lu X, Siemann E, Shao X, Wei H and Ding J, Climate warming affects biological invasions by shifting interactions of plants and herbivores. *Global Change Biol* **19**:2339–2347 (2013).
5 Chakraborty S, Pangga IB and Roper MM, Climate change and multitrophic interactions in soil: the primacy of plants and functional domains. *Global Change Biol* **18**:2111–2125 (2012).
6 Alava JJ, Cheung WWL, Ross PS and Sumaila UR, Climate change-contaminant interactions in marine food webs: Toward a conceptual framework. *Global Change Biol* **23**:3984–4001 (2017).
7 Clark MS, Sommer U, Sihra JK, Thorne MAS, Morley SA, King M *et al.*, Biodiversity in marine invertebrate responses to acute warming revealed by a comparative multi-omics approach. *Global Change Biol* **23**:318–330 (2017).
8 Treseder KK, Marusenko Y, Romero-Olivares AL and Maltz MR, Experimental warming alters potential function of the fungal community in boreal forest. *Global Change Biol* **22**:3395–3404 (2016).
9 Hare JD, Ecological role of volatiles produced by plants in response to damage by herbivorous insects. *Annu Rev Entomol* **56**:161–180 (2011).
10 Chailleux A, Mohl EK, Teixeira Alves M, Messelink GJ and Desneux N, Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems. *Pest Manage Sci* **70**:1769–1779 (2014).
11 van der Heijden MGA, Sd B, Luckerhoff L, van RSP L and Schlaeppi K, A widespread plant-fungal-bacterial symbiosis promotes plant biodiversity, plant nutrition and seedling recruitment. *ISME J* **10**:389–399 (2016).
12 Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH and Wall DH, Ecological linkages between aboveground and belowground biota. *Science* **304**:1629–1633 (2004).
13 Bender SF and van der Heijden MGA, Soil biota enhance agricultural sustainability by improving crop yield, nutrient uptake and reducing nitrogen leaching losses. *J Appl Ecol* **52**:228–239 (2015).
14 Das A, Patel DP, Lal R, Kumar M, Ramkrushna GI, Layek J *et al.*, Impact of fodder grasses and organic amendments on productivity and soil and crop quality in a subtropical region of eastern Himalayas, India. *Agric Ecosyst Environ* **216**:274–282 (2016).
15 Bender SF, Wagg C and van der Heijden MGA, An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. *Trends Ecol Evol* **31**:440–452 (2016).
16 Leong M, Ponisio LC, Kremen C, Thorp RW and Roderick GK, Temporal dynamics influenced by global change: bee community phenology in urban, agricultural, and natural landscapes. *Global Change Biol* **22**:1046–1053 (2016).
17 Cai C, Yin X, He S, Jiang W, Si C, Struik PC *et al.*, Responses of wheat and rice to factorial combinations of ambient and elevated CO_2 and temperature in FACE experiments. *Global Change Biol* **22**:856–874 (2016).
18 Dangles O, Herrera M, Mazoyer C and Silvain JF, Temperature-dependent shifts in herbivore performance and interactions drive nonlinear changes in crop damages. *Global Change Biol* **19**:1056–1063 (2013).
19 Tao F, Xiao D, Zhang S, Zhang Z and Rötter RP, Wheat yield benefited from increases in minimum temperature in the Huang-Huai-Hai Plain of China in the past three decades. *Agric For Meteorol* **239**:1–14 (2017).
20 Chen C, Zhou GS and Pang YM, Impacts of climate change on maize and winter wheat yields in China from 1961 to 2010 based on provincial data. *J Agric Sci* **153**:825–836 (2015).
21 You L, Rosegrant MW, Wood S and Sun D, Impact of growing season temperature on wheat productivity in China. *Agric For Meteorol* **149**:1009–1014 (2009).
22 Viswanathan C and Khanna-Chopra R, Effect of heat stress on grain growth, starch synthesis and protein synthesis in grains of wheat (*Triticum aestivum* L.) varieties differing in grain weight stability. *J Agron Crop Sci* **186**:1–7 (2001).
23 Tian Y, Zheng C, Chen J, Chen C, Deng A, Song Z *et al.*, Climatic warming increases winter wheat yield but reduces grain nitrogen concentration in East China. *PLoS One* **9**:e95108 (2014).
24 Smith SE and Read DJ, *Mycorrhizal Symbiosis*, 3rd edn. Academic Press, San Diego, CA (2008).
25 Wilson H, Johnson BR, Bohannan B, Pfeifer-Meister L, Mueller R and Bridgham SD, Experimental warming decreases arbuscular mycorrhizal fungal colonization in prairie plants along a Mediterranean climate gradient. *PeerJ* **4**:e2083 (2016).
26 Compant S, Van Der Heijden MGA and Sessitsch A, Climate change effects on beneficial plant–microorganism interactions. *FEMS Microbiol Ecol* **73**:197–214 (2010).
27 Shi G, Yao B, Liu Y, Jiang S, Wang W, Pan J *et al.*, The phylogenetic structure of AMF communities shifts in response to gradient warming with and without winter grazing on the Qinghai-Tibet Plateau. *Appl Soil Ecol* **121**:31–40 (2017).
28 Zhu Y, Lv GC, Chen YL, Gong XF, Peng YN, Wang ZY *et al.*, Inoculation of arbuscular mycorrhizal fungi with plastic mulching in rainfed wheat: a promising farming strategy. *Field Crops Res* **204**:229–241 (2017).
29 Hulle M, Coeur d'Acier A, Bankhead-Dronnet S and Harrington R, Aphids in the face of global changes. *C R Biol* **333**:497–503 (2010).
30 Lopes T, Hatt S, Xu Q, Chen J, Liu Y and Francis F, Wheat (*Triticum aestivum* L.)-based intercropping systems for biological pest control. *Pest Manag Sci* **72**:2193–2202 (2016).
31 Dong Z, Hou R, Ouyang Z and Zhang R, Tritrophic interaction influenced by warming and tillage: a field study on winter wheat, aphids and parasitoids. *Agric Ecosyst Environ* **181**:144–148 (2013).
32 CRJ C, The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biol* **4**:785–796 (1998).
33 Diffenbaugh NS, Pal JS, Trapp RJ and Giorgi F, Fine-scale processes regulate the response of extreme events to global climate change. *Proc Natl Acad Sci USA* **102**:15774–15778 (2005).
34 Ouyang F, Hui C, Men X, Zhang Y, Fan L, Shi P *et al.*, Early eclosion of overwintering cotton bollworm moths from warming temperatures accentuates yield loss in wheat. *Agric Ecosyst Environ* **217**:89–98 (2016).
35 Ma G, Rudolf VHW and Ma CS, Extreme temperature events alter demographic rates, relative fitness, and community structure. *Global Change Biol* **21**:1794–1808 (2015).
36 Wang C, Yin G, Xia X, He Z, Zhang P, Yao Z *et al.*, Molecular mapping of a new temperature-sensitive gene LrZH22 for leaf rust resistance in Chinese wheat cultivar Zhoumai 22. *Mol Breed* **36**:18 (2016).
37 Hou X, Li R, Jia Z, Han Q, Wang W and Yang B, Effects of rotational tillage practices on soil properties, winter wheat yields and water-use efficiency in semi-arid areas of north-west China. *Field Crops Res* **129**:7–13 (2012).
38 Baslar M and Ertugay MF, Determination of protein and gluten quality-related parameters of wheat flour using near-infrared reflectance spectroscopy (NIRS). *Turk J Agric For* **35**:139–144 (2011).
39 Elleuch M, Besbes S, Roiseux O, Blecker C and Attia H, Quality characteristics of sesame seeds and by-products. *Food Chem* **103**:641–650 (2007).

40 Giovannetti M, Sbrana C and Logi C, Early processes involved in host recognition by arbuscular mycorrhizal fungi. *New Phytol* **127**:703–709 (1994).
41 Hildermann I, Messmer M, Dubois D, Boller T, Wiemken A and Maeder P, Nutrient use efficiency and arbuscular mycorrhizal root colonisation of winter wheat cultivars in different farming systems of the DOK long-term trial. *J Sci Food Agric* **90**:2027–2038 (2010).
42 Lizana XC and Calderini DF, Yield and grain quality of wheat in response to increased temperatures at key periods for grain number and grain weight determination: considerations for the climatic change scenarios of Chile. *J Agric Sci* **151**:209–221 (2013).
43 Fang S, Cammarano D, Zhou G, Tan K and Ren S, Effects of increased day and night temperature with supplemental infrared heating on winter wheat growth in North China. *Eur J Agron* **64**:67–77 (2015).
44 Asseng S, Cammarano D, Basso B, Chung U, Alderman PD, Sonder K *et al.*, Hot spots of wheat yield decline with rising temperatures. *Global Change Biol* **23**:2464–2472 (2017).
45 Sadras VO and Monzon JP, Modelled wheat phenology captures rising temperature trends: Shortened time to flowering and maturity in Australia and Argentina. *Field Crops Res* **99**:136–146 (2006).
46 Talukder ASMHM, McDonald GK and Gill GS, Effect of short-term heat stress prior to flowering and early grain set on the grain yield of wheat. *Field Crops Res* **160**:54–63 (2014).
47 Dias de Oliveira EA, Siddique KHM, Bramley H, Stefanova K and Palta JA, Response of wheat restricted-tillering and vigorous growth traits to variables of climate change. *Global Change Biol* **21**:857–873 (2015).
48 Tian Y, Chen J, Chen C, Deng A, Song Z, Zheng C *et al.*, Warming impacts on winter wheat phenophase and grain yield under field conditions in Yangtze Delta Plain, China. *Field Crops Res* **134**:193–199 (2012).
49 Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK *et al.*, Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biol* **8**:1–16 (2002).
50 Takeda K, Musolin DL and Fujisaki K, Dissecting insect responses to climate warming: overwintering and post-diapause performance in the southern green stink bug, *Nezara viridula*, under simulated climate-change conditions. *Physiol Entomol* **35**:343–353 (2010).
51 Barton BT and Ives AR, Direct and indirect effects of warming on aphids, their predators, and ant mutualists. *Ecology* **95**:1479–1484 (2014).
52 Chen CY, Chiu MC and Kuo MH, Effect of warming with temperature oscillations on a low-latitude aphid, *Aphis craccivora*. *Bull Entomol Res* **103**:406–413 (2013).
53 Larsson H, A crop loss model and economic thresholds for the grain aphid, *Sitobion avenae* (F.), in winter wheat in southern Sweden. *Crop Prot* **24**:397–405 (2005).
54 Aguilar-Fenollosa E and Jacas JA, Can we forecast the effects of climate change on entomophagous biological control agents? *Pest Manag Sci* **70**:853–859 (2014).
55 Gustafson DI, Climate change: a crop protection challenge for the twenty-first century. *Pest Manag Sci* **67**:691–696 (2011).
56 Jabran K and Dogan MN, High carbon dioxide concentration and elevated temperature impact the growth of weeds but do not change the efficacy of glyphosate. *Pest Manag Sci* **3**:766–771 (2017).
57 Pellegrino E, Oepik M, Bonari E and Ercoli L, Responses of wheat to arbuscular mycorrhizal fungi: a meta-analysis of field studies from 1975 to 2013. *Soil Biol Biochem* **84**:210–217 (2015).
58 Blois JL, Zarnetske PL, Fitzpatrick MC and Finnegan S, Climate change and the past, present, and future of biotic interactions. *Science* **341**:499–504 (2013).
59 Schleuning M, Fruend J, Schweiger O, Welk E, Albrecht J, Albrecht M *et al.*, Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nat Commun* **7**:13965 (2016).
60 Van der Putten WH, Macel M and Visser ME, Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philos Trans R Soc Lond B Biol Sci* **365**:2025–2034 (2010).