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Early eclosion of overwintering cotton bollworm moths from warming temperatures accentuates yield loss in wheat

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ABSTRACT

Understanding and predicting the impact of climate change on population demography, biotic interactions and ecosystem service is central to ecology. Long-term time series analysis of insect populations is crucial for analyzing the effect of climate change on plant–insect interactions in agro-ecological systems; yet such data are often lacking. Here, based on field experiments and the long-term time series of the overwintering adult cotton bollworm *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) collected since 1975, we investigate the dynamic trend of *H. armigera*, as well as its driving forces and effects on the recruitment of *H. armigera* and crop yield. Results illustrated a shift to early eclosion of diapausing pupae due to global warming, extending the duration and abundance of adults in the overwintering generation. This then led to more larvae recruited in the first generation, and consequently damages the wheat at early growing stages. Our results suggest that the asynchronous effects of rising global surface temperature on the relative growth rate of spring crops and insect pests could intensify in the future, causing accentuated crop yield loss. To mitigate the adverse herbivore-mediated effect on crop yield in a warming climate, efficient cultivation measures and pest management are necessary, such as planting precocious crops with short growth period and timely control of insect pests.

1. Introduction

Understanding and predicting the impacts of anthropogenic climate change on population demography, biotic interactions and ecosystem services is fundamental in current ecology (Jamieson et al., 2012). The climate can influence plants and insects through a variety of physiological and phenological processes, including metabolism, reproduction, growth, development and migration behavior (Durant et al., 2007). The impacts of climate change, however, include both direct effects on plant and insect demography and indirect effects through cross-trophic interactions (Brown et al., 1998; Coley, 1998; Massad and Dyer, 2010). Knowing the potential response of insects to climate change and the effect of climate change on plant-insect interactions helps us to better formulate pest management strategies or tactics (Ladányi and Horváth, 2010; Jamieson et al., 2012). To this end, long-term time series of insect populations plus field experiments are crucial for elucidating the effect of climate change on plant-insect interactions in agroecological systems, and yet such data is often lacking.

Climate change poses one of the most serious challenges to the sustainability of agroecological systems (Zilberman et al., 2002). Effects of climate change on plant/pest populations rely on the integral of climate and other related factors such as soil moisture (Fuhrer, 2003). Temperature is identified as the dominant abiotic factor affecting herbivorous insects (Bale et al., 2002); it has a direct effect on ontogenetic development, survival, and reproduction of insects, as well as an indirect effect on generation time and population growth rate (Forster et al., 2011). Warm temperatures often have a positive effect on the abundance of insect populations.

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For example, warm temperatures and low annual precipitation favor the outbreak of mountain pine beetle (*Dendroctonus ponderosae*) in the southern Rocky Mountains (Chapman et al., 2012). Warm temperatures halved the reproductive time of the Spruce beetle (*Dentroctonus rufipennis*) (Berg et al., 2006a). Warm temperatures combined with the occurrence of dry summers have triggered the outbreak of *Ips typographus*, one of the most destructive pests of European spruce forests (Marini et al., 2012). The overwintering mortality of adult *Nezara viridula*and *Halyomorpha halys* can be reduced by 15% with 1 °C rise of temperature (Kiritani, 2006). Warm temperatures can also have a positive effect on the productive potential of crops, leading to an extended growing season and thus an increase in crop yield (Shaver et al., 2000; Veteli et al., 2002; Fang et al., 2003, 2004; Peng et al., 2011). However, the indirect herbivore-mediated effect on plants under warming temperatures is poorly studied in agroecological systems.

Besides affecting insect abundance and crop yield, temperature can also affect the traits of interacting species, such as the timing of different life stages in insects and plants (Taylor, 1986; Roberts et al., 2015; Wheeler et al., 2015). Analyses of the consequences of temperature-driven shifts in phenology—the timing of life cycle events, such as the oviposition, hatching, pupation and emergence of insects, and the sprouting, flowering, fruiting of plants, can trace their conceptual origins to the match/mismatch hypothesis (Parmesan and Yohe, 2003; Root et al., 2003). The concept of match/mismatch stems from fisheries biology to understand why the survival of cod and other commercial fish species at their early stages is critical (Durant et al., 2007). The match/mismatch hypothesis (MMH) seeks to explain the recruitment variation in a population by the synchronous phenology of the focal species and its resource (Cushing, 1969). As the response of the timing or duration of ontogeny (plants and insects) to temperature changes can be diverse (Yang and Rudolf, 2010), species interactions as a result can change, decouple or even strengthen over the entire span of their life cycles (Richardson et al., 2013). Studies on the effect of global warming on the phenology of plants and insects has increased dramatically since the 1980s, but only few were examining the effect in agricultural systems (Jamieson et al., 2012). The knowledge gap of how the interactions between insect pests and crops respond to global warming through matching/mismatching phenology needs to be filled.

The adult moth of the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), is one of the most damaging crop pests in Asia (Ge et al., 2005), America (Gujar and Kalia, 2005; Tay et al., 2013), Africa and Europe (Nibouche et al., 1998), characterized by its polyphagy, high mobility, high fecundity, and facultative diapause (Wu and Guo, 2005). It can have four generations per year in northern China (Ge et al., 2005), with the wheat, *Triticum aestivum* as the host crop for the first-generation (G1) larvae, while other three targeting major crops such as corn, cotton, peanut and bean (Wu and Guo 2005). For instance, the outbreak of its second and third generations (G2 and G3 hereafter) in the early 1990s caused a drastic decline of cotton yield in northern China (Wu and Guo, 2005), showing its peak in 1992 (Ouyang et al., 2014).

Since 1997 transgenic cotton with a gene from the bacterium *Bacillus thuringiensis* (Bt) has been widely planted to combat *H. armigera* outbreaks in China. Large-scale cultivation of Bt cotton has contributed more to the reduction of ovular and larval densities in G2 and G3 bollworms than climatic variations (Wu et al., 2008). A Bt cotton diet can further weaken the cold-hardiness of larval in the overwintering generation (G0), consequently reducing the density of G1 bollworms of the following year (Ouyang et al., 2011). However, weakening density dependence from climate change and agricultural intensification can trigger pest outbreaks, highlighting the importance of exogenous factors to safeguarding the population regulating mechanism of negative density dependence (Ouyang et al., 2014). It is therefore of both theoretical and practical value to elaborate regulators of population dynamics for *H. armigera* and the effects of indirect herbivore-mediated interactions on crop yields in a warming environment.

Here, we investigate how changes in abundance and timing of the life stages of G0 *H. armigera* from global warming can influence wheat biomass. Based on a long-term time series of G0 *H. armigera* moth collected since 1975, plus a controlled experiment, we explore the temporal trends in *H. armigera* population dynamics, and their causes and consequences. Our aim is to sequentially address four interrelated issues: (1) detect long-term temporal trends of the G0 cotton bollworm moth; (2) analyze the temporal trends of the local climate; (3) determine the cause of early eclosion in G0 moths; (4) quantify the effect of early eclosion in G0 moths on wheat biomass loss.

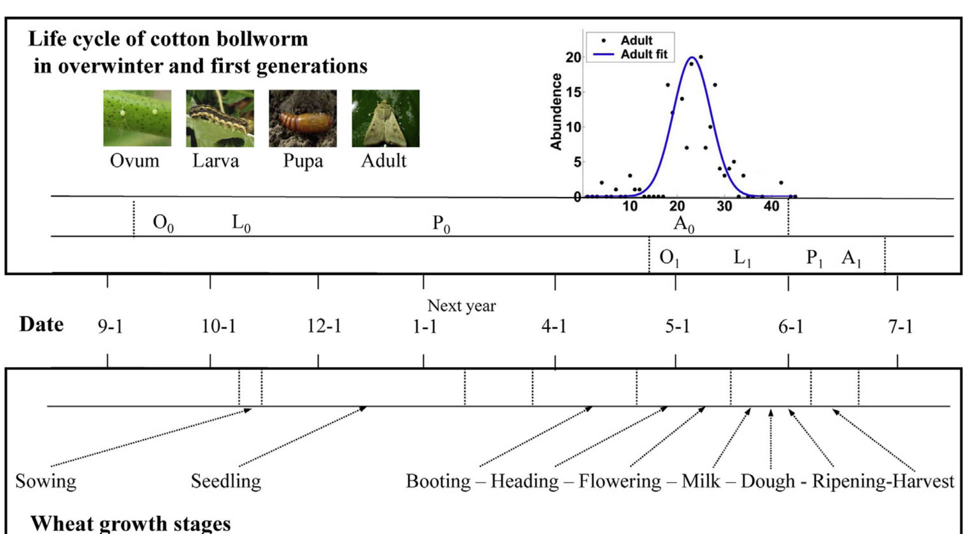

Fig. 1. Life cycle of cotton bollworm and wheat growth stages. Life history of cotton bollworm in overwinter and first generations (upper) and wheat growth stages (under) in Northern China. O_0, L_0, P_0 and A_0 were the oviposition, larva, pupa and adult in overwinter generation. O_1, L_1, P_1 and A_1 were the oviposition, larva, pupa and adult in first generation.