

Different effects of climate change on the population dynamics of insects

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Received: 30 September 2012 / Accepted: 20 December 2012 / Published online: 23 January 2013
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Abstract Climate change affects the pattern of population dynamics of insects in different ways. Global warming not only leads to greater over-winter survival, earlier appearance in spring, an increase in the number of generations in a year, lengthening of the reproductive season, etc., but also affects their biotic associations as a result of changes in interspecific interactions. Changes in the density of insects in response to unusually hot summers provide us with useful indications of the potential effects of global warming. Different insect guilds respond differently to hot summers, which sometimes result in an increase in density and sometimes a decrease. These effects may occur immediately or be delayed by 1 or 2 years. As long as the regime remains unchanged, the affected population can recover sooner or later. Even a single-year change in climate, however, if it allows predators to outbreak, may be strong enough to cause a regime shift. Most insects are susceptible to heat stress between 28 and 32 °C, global warming could have a more profound impact on the population dynamics and biodiversity of arthropods than has previously been predicted.

Keywords Heat stress · Winter mortality · Range expansion · Reproductive interference · Resilience

Introduction

The Intergovernmental Panel on Climate Change (IPCC) (2001) concluded that most of the warming observed over

the last 50 years is attributable to human activities. The global mean surface temperature is predicted to increase by 1.4–5.8 °C from 1990 to 2100. The IPCC suggested that if temperatures rise by approximately 2 °C over the next 100 years, its negative effects would begin to extend to most regions of the world. Climate change will occur from 10 to 1000 times as fast as the dramatic climatic changes that accompanied the end of the last glacial period and caused global warming of some 5 °C over the last 10000 years or so (Ehrlich 1989). Because of the time lag between changes in atmospheric composition and climate, the cumulative effects of the past human activity will take many decades to be fully realized (IPCC 2001), even if greenhouse gas emissions were reduced immediately.

A growing body of information suggests that insects are both directly and indirectly responding to the current changes in climate. Effects of global warming on arthropods have been reviewed and discussed in many papers (Cammell and Knight 1992; Bale et al. 2002; Cannon 1998; Kareiva et al. 1993; Kiritani 1988, 1991, 1999, 2001, 2006, 2007; Kiritani and Yukawa 2010; Kocsis and Hufnagel 2011; Harrington and Stork 1995; Harrington et al. 1999, 2001; Heong et al. 1995; Ladányi and Horváth 2010; McCarty 2001; Walther et al. 2002; Morimoto et al. 1998; Parmesan 1996; Parmesan and Yohe 2003; Porter et al. 1991; Sutherst 2000; Yamamura and Kiritani 1998; Yamamura and Yokozawa 2002; Yamamura et al. 2006).

A key prerequisite for predicting the effects of increased temperature is to describe how environmental change affects directly and indirectly the dynamics of insect populations. Global warming could affect insects indirectly through changes in the quantity of plants and vegetation (Kiritani 2007) and changes in quality, for example C/N ratio (Sionit 1983; Scriber and Slansky 1981; Lincoln et al. 1984; Bezemer and Jones 1998; Coviella and Trumble

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1998; Stiling and Cornelissen 2007), and affect the pattern of population dynamics of arthropods in a variety of ways, including a shift in distribution range, reduction in winter mortality, earlier occurrence in spring, lengthening of the reproductive season, and an increase in the number of generations in a year. Differences in the pattern of response to temperature changes could disrupt synchronization in phenology between insects and host plants or natural enemies (Bale et al. 2002; Cammell and Knight 1992; Hill et al. 2011; Harrington and Stork 1995; Kiritani 2001; Kiritani and Yukawa 2010; Parmesan and Yohe 2003).

Insect resistance to upper lethal temperatures is much less variable among species than that to lower lethal temperatures. Therefore, high temperature is often a major factor in determining the geographic distribution and abundance of insects (Addo-Bediako et al. 2000; Bowler and Terblanche 2008; Bradshaw and Holzapfel 2008; Ikemoto et al. 2012; Zani et al. 2005). Most insects are susceptible to heat stress between 28 and 32 °C, which is lower than commonly believed (Kiritani 2012a). Heat stress may cause unavoidable deleterious effects on all arthropods.

Ecosystems are generally resilient to some extent to changes in climate. A resilient ecosystem can withstand a drought or an unusually hot summer and may not seem to be affected by modest or slow climate changes. However, this resilience has limits. When a change exceeds those limits, the ecosystem undergoes a major change, often shifting to a fundamentally different ecosystem type. This kind of threshold response is common in ecosystems, in which extreme events, for example heat waves and droughts, often induce an irreversible transition of the ecosystem to a new state (Ehrlich et al. 1980; Holling 2004; National Academy of Sciences 2008).

In this article, first, I elucidate that how important is to understand various effects of climate change on a particular species, the southern green stink bug *Nezara viridula*. Second, different effects of high temperatures on the abundance of arthropods and the time lag in the appearance of the effects have been examined across different taxa. Finally, I emphasized the need for field-based long-term monitoring of arthropod population dynamics and the identification of heat-stress syndromes.

Effects of global warming on *Nezara*

Nezara viridula Linnaeus (Hemiptera: Pentatomidae), and its congeneric species the Oriental green stink bug, *N. antennata* Scott (Hemiptera: Pentatomidae), have been studied for more than 50 years and provide us with ongoing data regarding effects of climate change not only on the species themselves, but also on its biotic associates in the community (Kiritani 2011; Kiritani and Hokyo 1970).

N. viridula has a worldwide distribution, occurring throughout the tropics and subtropics and has 3 generations without aestivation, whereas *N. antennata* is native to Asia, is found all over Japan and has two generations with aestivation. *N. viridula* is 2–3 times more fecund and more susceptible to low temperatures than *N. antennata*. Interspecific mating is frequently observed in areas they coexist (Kiritani 1965, 2011; Kiritani and Hokyo 1970).

Range expansion

A major effect of climate change is acceleration of species range shifts. Northward range expansion by some species may disrupt the original biological community through interspecific interaction, e.g. reproductive interference between native and invader. The northern range limit of *N. viridula*, coincided with the 5 °C isotherm of mean monthly temperature for January (MMTJ) (Kiritani et al. 1963). The northward shift of the 5 °C isotherm because of global warming has been providing *N. viridula* with warm winter temperatures and enabling it to overwinter successfully since 2000 in the northern parts of Shikoku and Kyushu, and southwestern parts of Honshu, Japan (Yukawa et al. 2007, 2009). This range expansion has been associated with loss of a native congener, *N. antennata*, as a result of through interspecific mating with *N. viridula*. Currently, most areas previously occupied by *N. antennata* are now either occupied by *N. viridula* only or by a mixture of the two species (Kiritani and Hokyo 1970; Yukawa et al. 2007, 2009). In areas dominated by *N. viridula*, all of the *N. antennata* mated with *N. viridula* (Kiritani et al. 1963). What was happening in the 1960s is now occurring in all regions newly invaded by *N. viridula* as a result of global warming (Yukawa et al. 2007, 2009; Tougou et al. 2009). Consequently, the southern range of *N. antennata* is contracting, not as a result of climatic changes but as a result of a biological factor, reproductive interference.

The time of spring activity and winter mortality

The MMTJ is important in determining not only the distribution range, but also winter mortality and the start of reproduction in spring. In 1964 when the MMTJ was 0.67 °C higher than the 30-year mean, the phenology, e.g. date of 50 % mating, started 2 weeks earlier than the mean date of 1962–1965 (Kiritani and Hokyo 1970).

Theoretically, it is hypothesized that winter survival of insects will be improved by an increase of winter temperature, but actual evidence for this is rather scarce. A regression $Y = -16.45X + 147.08$ ($R^2 = 0.6127$, $P < 0.0001$) between winter mortality of *N. viridula* adults (Y) and MMTJ (X) was obtained. This indicated that every 1 °C rise around $X = 4$ °C would reduce the winter mortality by

approximately 16.5 % for *N. viridula*. (Kiritani et al. 1966b; Kiritani 1971, 2006).

Populations of *N. viridula* that survived the winter had a higher female sex ratio the body size of both sexes was larger than for the population before hibernation. The average percentage of females was 51.8 % before hibernation (autumn) and 61.6 % after hibernation (spring) during 1961–1967. This occurs partly because females are larger than males and survive the winter in greater numbers. Mean winter mortality during the 6 years was 51.9 and 67.7 % for females and males, respectively (Kiritani et al. 1966b; Kiritani and Hokyo 1970). It seems that the individuals most likely to survive during periods of stress are also the individuals most likely to make the greatest contribution to the next generation in the absence of such stress (Zani et al. 2005).

Number of generations per year and voltinism

Insects and spiders are poikilothermic animals. Generally, the number of generations per year is an important characteristic that affects the abundance of multivoltine species (Kiritani 1997; Yamamura 2004). Yamamura and Kiritani (1998) proposed an analytical method for estimation of the potential increase in the number of generations (ΔN) under global warming in temperate zones.

$$\Delta N = (\Delta T / K)[206.7 + 12.46(m - T_0)]$$

The formula contained four independent variables; ΔT is the increase in the annual mean temperature because of global warming when the annual mean temperature is m (°C). T_0 and K refer to the lower threshold temperature for development and thermal constant, respectively. This showed that the greater is ΔT or m , or the lower is T_0 or K , then the greater is ΔN .

Using the mean values of T_0 and K for *N. viridula* and its egg parasitoids, the number of increased generations was estimated when temperatures increased by 2 °C in areas with a current mean annual temperature of 15 °C. *N. viridula* will have one additional generation. Egg parasitoids will produce 2 more generations and may become more efficient biological control agents against *N. viridula* under global warming. However, the net outcome of such interactions during this era of climate change is as yet largely unknown (Kiritani 2007).

Effects of unusual climate

Immediate and direct effects

The year 1998 was the warmest year since instrumental records began throughout the world (Houghton et al. 2001).

The highest mean annual temperature in Japan was also recorded. Pheromone trap catches of the common cutworm male *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) in 1998 was the largest among the past 14 years in Kagoshima Prefecture, where the mean annual temperature was 2.1 °C higher than normal years (Yamaguchi et al. 2001).

Outbreaks of *S. litura* have frequently been observed in various places in Japan in unusually warm and dry years (Kiritani 2001). Abundances of *S. litura* were compared between years with different weather conditions during 1985–2011 (Table 1). High (14<) and low (5>) occurrences of *S. litura* are defined as the number of prefectures that issued warnings about *S. litura*. The deviation of annual mean temperature from the mean of annual temperatures during 1981–2010 was 0.56 °C warmer in the high outbreak years than in the years of low occurrence, but no difference was found in the amount of precipitation. The underlying mechanism has never been clarified, but the activity of a linyphiid spider *Ummeliata insecticeps* (Boesenberg and Strand) (Arachnida: Linyphiidae), an important specific predator of hatchlings, seemed to be strongly suppressed under high-temperature conditions, thereby enabling *S. litura* to escape from natural enemies (Nakasuji et al. 1973).

The highest summer temperature during the last 113 years in Japan was recorded during the summer (June to August) of 2010. In that year, catches of the horn beetle, *Trypoxylus dichotomus* Linnaeus (Coleoptera: Scarabaeidae), and two species of stag beetle, *Macrodercas recta* Motschulsky and *Prosopocoilus inclinatus* (Motschulsky) (Coleoptera: Lucanidae), were the smallest recorded during the 6 years from 2007 to 2012, and the beetles were 30 % less abundant on average, probably because of the extremely high temperature. Populations recovered in 2011 with a mean rate of increase of 68.3 % (Table 2) (Kiritani 2012c).

The hot summer in 2010 negatively affected not only sapwood feeding beetles, but also a variety of ground beetles including *Synuchus cycloderus* Bates, *Carabus lewisianus* Breuning (Coleoptera: Carabidae), *Eusilpha japonica* (Motschulsky) (Coleoptera: Silphidae), and *Agelosus carinatus* (Sharp) (Coleoptera: Staphylinidae) (Table 2). However, the ground beetles decreased in the following spring, 1 year later than the sapwood-feeders.

Stink bugs infesting rice and fruit

Changes in climate and/or land use can also enable previously harmless species to become harmful. Infestations of rice and fruit by stink bugs became nationwide problems in the early 1970s in Japan. Ten species of rice bug and three of fruit bug have been recognized to be of economic importance (Kiritani 2007).

Table 1 Comparison of weather conditions between years with high and low occurrences of *Spodoptera litura* during 1985–2011

No. of years with low or high occurrence	Deviation from annual mean temperature (°C), mean \pm SD	Deviation from annual mean precipitation (cm), mean \pm SD	No. of prefectures issuing warnings, mean \pm SD
Low: 7 years	0.04 \pm 0.29	103.6 \pm 9.6	1.6 \pm 1.9
High: 6 years	0.59 \pm 0.17	104.8 \pm 17.0	18.5 \pm 3.8

High (14<) and low (5>) occurrences of prefectures that issued warnings against *S. litura*

Table 2 Number of sapwood-feeding and overwintered ground beetles before, during and after the 2010 hot summer

	2009 (a)	2010 (b)	2011 (c)	% reduced
Sapwood feeding beetles				$-100(b - a)/a$
<i>Trypoxylus dichotomus</i> (Scarabaeidae)	64	40	66	38
<i>Macrodorcas recta</i> (Lucanidae)	57	45	73	21
<i>Prosopocoilus inclinatus</i> (Lucanidae)	54	35	61	35
Ground beetles				$-100(c - b)/b$
<i>Synuchus cycloderus</i> (Carabidae)	–	117	100	15
<i>Eusilpha japonica</i> (Silphidae)	–	38	27	29
<i>Agelosus carinatus</i> (Staphylinidae)	–	426	261	39
<i>Carabus lewisianus</i> (Carabidae)	–	429	129	70

Sapwood-feeding beetles were caught at fixed light sources. Ground beetles were caught in 52 pit-fall traps in a coppice

Table 3 Relationship between the number of prefectures (Y) that issued warnings against rice and fruit bugs, and the deviation from the 30-year mean temperature during 1985–2011

Pest insects	Time lag (year)	Regression	R^2 and P
Fruit bugs: major 3 species	Current year	$Y = -1.28X_0 + 14.25$	0.0020 and 0.8391
	1 year before	$Y = -2.58X_1 + 14.45$	0.0101 and 0.6487
	2 years before	$Y = 12.16X_2 + 12.02$	0.2582 and 0.0253
Rice bugs: major 10 species including <i>Nezara</i>	Current year	$Y = -0.57X_0 + 14.78$	0.0005 and 0.9198
	1 year before	$Y = 6.21X_1 + 13.51$	0.0743 and 0.2153
	2 years before	$Y = 11.75X_2 + 12.82$	0.2493 and 0.0153

X_0 , X_1 and X_2 are temperatures, respectively, in the current year, 1 year before, and 2 years before

The outbreaks of rice bugs were triggered by an increase of fallow paddy fields because of restrictions of rice cropping since 1970. To make the abundance of fruit bugs and rice bugs comparable, we used the total number of prefectures that issued warnings against these pest bugs (Table 3).

After the Second World War, 42 % of 24.5 million ha of Japanese forest were replaced with plantations of the Japanese cedar (*sugi*), *Cryptomeria japonica* D. Don and the Japanese cypress (*hinoki*), *Chamaecyparis obtusa* Siebold and Zuccarini (Cupressaceae) (Japan FAO Association 1997). The first nationwide outbreaks of fruit-infesting bugs were observed in 1973 and 1975 (Umeya 1976). *Plautia crossota* (Dallas), *Halyomorpha halys* Stål and *Glaucias subpunctatus* (Walker) (Pentatomidae) are dominant species of fruit bugs that cause damage to a range of fruit trees.

However, to complete their life cycle, they require pine cones, which had become widely available on the coniferous trees that had been planted in the 1950s. Dry and hot summers contribute to masting in the following year together with good pine cone production; this resulted in an abundance of fruit bugs in the third year. Thus, there is strong circumstantial evidence that land-use changes have been responsible for the abundance of both rice and fruit bugs during the last 40 years (Kiritani 2007).

To examine whether or not there is a time-lag between annual mean temperature (X) and the frequency of warnings (Y), regression lines between Y and X_0 in the current year, and 1 (X_1) and 2 years (X_2) before were calculated for rice bugs and fruit bugs (Table 3). As we hypothesized for fruit bugs, there was a good correlation between Y and the temperature 2 years before. The number of warnings issued against rice bugs was also correlated with the temperature

2 years before, but exact causes remain to be understood (Table 3).

Heat stress

A total of 119 species were examined to determine the temperature (hereafter, “heat stress temperature”) at which they suffered a physiological disadvantage or heat stress (Kiritani 2012a). Heat stress affected most of these species at temperatures ranging from 28 to 32 °C. The mean values of T_0 and the heat stress temperatures were not different among Coleoptera, Hemiptera, Lepidoptera, and Hymenoptera. T_0 was approximately 10 °C for all of the orders in Japan, and they suffered heat stress at temperatures ranging from 29 to 31 °C (Kiritani 2012a).

Hemiptera has a relatively wide range of T_0 ranging from 5.3 for aphids to 13.1 °C for Heteroptera. The heat stress temperatures, however, varied only slightly, from 29.8 to 30.8 °C (Table 4). Thus, global warming and heat stress would be expected to have a more profound effect on the population dynamics and biodiversity of arthropods than we have previously predicted (Kiritani 2012a).

Musolin et al. (2009) demonstrated experimentally that an elevation of temperature by 2.5 °C would cause deleterious heat stress on the generations of *N. viridula* developing during the summer. Life tables recorded in the 1960s for *N. viridula* demonstrated that natural populations regularly suffered heat stress during the summer, despite its subtropical origin. All of the traits related to reproduction were poorly realized in the 2nd generation, which occurs during the summer (Table 5) (Kiritani 2011).

Heat stress affected not only the 2nd generation but also the reproductive performance of 1st-generation females, whose oviposition occurred during mid July to mid August. A mark–recapture method showed that at least 3000 females invaded the experimental fields but only 10 % of the females participated in the egg laying (Kiritani et al. 1966a; Kiritani 2011).

It has been claimed that tropical insects are relatively sensitive to temperature changes and are currently living very close to their optimum temperature (Deutsch et al. 2008). Species living in environments that are already close to their physiological optima have small thermal safety margins, and thus even a little warming is likely to reduce their performance (Deutsch et al. 2008; Hoffmann 2010; Tobin et al. 2008; Wang et al. 2009).

Heat stress syndromes because of global warming may become apparent not only for *N. viridula*, but also for many other insect taxa. A congeneric species of *N. viridula*, *N. antennata* may be able to avoid heat stress by aestivation (Noda 1984). Whether heat stress will cause *N. viridula* to lose its greater reproductive advantage over *N. antennata* is a

Table 4 Comparison of the lower development threshold (T_0) of Hemiptera taxa, and the mean temperature (°C) at which they suffer from heat stress (Kiritani 2012a)

Taxonomic group	No. of species examined	T_0 (°C), mean \pm SD	Heat stress (°C), mean \pm SD
Aphididae	19 (8) ^a	5.3 \pm 2.6	29.8 \pm 3.6
Cicadellidae	31 (13)	11.2 \pm 2.6	30.2 \pm 2.0
Delphacidae			
Psyllidae, etc.			
Heteroptera	41 (17)	13.1 \pm 2.1	30.8 \pm 2.2

^a Numeral in the parentheses is for heat stress

Table 5 Summary of 14 life tables developed for *Nezara viridula* during 1961–1963 (Kiritani and Hokyo 1970; Kiritani 2011)

Generation	1st	2nd	3rd
No. of eggs used	7,845	37,822	9,912
Duration of nymphs (days)	43.7	27.6	50
Daily survival of nymphs	0.962	0.912	0.946
Female fresh weight (mg) ^b	154	97.4	102.1
Longevity (females, days)	18.4	20.1	<10 months
Preoviposition period	3 weeks	4 weeks	8–9 weeks ^a
Sterile females (%)	20.6	31.8	1.0 ^a
No. eggs/fertile female	181.3	84.3	128.1 ^a

^a After overwintering

^b At the time of emergence

significant ecological issue (Kiritani 2011). Experimental elimination of the symbiont of Japanese *N. viridula* resulted in severe nymphal mortality and emergence of few adults (Tada et al. 2011). Extreme temperatures can reduce endosymbiont populations that are susceptible to high temperatures (Hance et al. 2007). This may be another kind of heat stress to be taken into consideration.

Stability and resilience

The population density of any organism is regulated by density-dependent processes resulting in fluctuations around an equilibrium density. The equilibrium density is also determined by density-independent processes. However, the population density fluctuates substantially and may shift to a regime with a new equilibrium density via a variety of driving factors. Driving factors that can cause such regime shifts include climate change, the introduction of natural enemies to control alien invasive species, resurgence because of pesticide use, cultural practices, land-use change, etc. The time span required for regime

Table 6 Summary of effects of high temperatures on the abundance of arthropods and the time lag in the appearance of the effects

Species/guild	Voltinism	Increase or decrease	No time lag	One year later	Two years later	Changes caused by hot weather	Source
<i>Spodoptera litura</i>	Multi	Increase	X			Escape from linphiid spiders	Nakasuji et al. (1973)
Sapwood feeding beetles	Uni	Decrease	X			Heat stress	This work
Ground beetles	Uni	Decrease		X		Heat stress	This work
<i>Libellula</i> (a dragon fly)	Uni	Decrease		X	X	Increase of predators	Fukui (2010)
Fruit bugs	1–2	Increase			X	Increase in food resource	Kiritani (2007)
Rice bugs	Multi	Increase			X	Unknown	Kiritani (2007)

shift ranges from 1 year to a decade depending on life history traits, distribution range, and the kind and intensity of driving factors (Kiritani 2012b).

Many major disturbances do not lead to regime change. Even 97.5 % mortality of *N. viridula* adults in the 1962/63 winter did not prevent them from recovering to pre-mortality level after only 2 years (several generations) (Kiritani and Hokyo 1970). As mentioned previously, the effects of the 2010 hot summer on sapwood-feeding beetles was transitory and they recovered in the following year (Table 2). As long as the regime remains unchanged and the intensity of driving factor(s) does not overwhelm the regulatory mechanisms in the population, the affected population can recover.

Even a single-year change in climate, however, if it allows predators to outbreak, may be strong enough to cause an irreversible regime shift. During the hot summer of 1998, the invasive crayfish that originated from the USA, *Procambarus clarkii* Girard (Decapoda: Cambaridae), had a population outbreak in a pond (Okegaya-numa in Iwata city, Shizuoka, 7.4 ha in area, 0.6 m in depth) inhabited by an endangered dragonfly, *Libellula angelina* Selys (Odonata: Libellulidae) (Fukui 2010). The equilibrium population density of *L. angelina* was 690 during 1991–1997 but it declined to as low as 135 during 1999–2010 after the outbreak of the predaceous crayfish. This suggests that unexpected catastrophes may occur when the effect of climate change disrupts the mechanisms regulating the population.

All the foregoing accounts regarding different response times to high temperatures, depending on the different driving factors are summarized in Table 6.

Conclusion

Bioclimatic models, for example CLIMEX (Sutherst 2000), have proved useful for investigating the potential effect of climate on insect populations. However, caution should be exercised when applying the models:

1. biotic interactions may not remain the same over time (adaptation can, and is likely to, occur);
2. the genetic and phenotypic composition of populations may change over time and space; and
3. most species have some limitation in dispersal (Olfert et al. 2011).

We now have to add the fact that environments are changing, and the rate of change is unprecedented, and sometimes changes are accompanied by a time lag or a regime shift. Priorities for future research into the effects of climatic changes on arthropods can be identified as including field-based long-term monitoring of arthropod population dynamics and identification of heat-stress syndromes.

Acknowledgments I thank Professor J. Yukawa, Kyushu University, and Professor D. Andow, Minnesota University, for their valuable comments on an earlier version of this manuscript. I acknowledge Drs S. Miyai, T. Kidokoro, and N. Morimoto for providing me with information. I also thank two anonymous referees for their helpful comments.

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