Consequences of Climate Warming and Altered Precipitation Patterns for Plant-Insect and Multitrophic Interactions[1]

Mary A. Jamieson*, Amy M. Trowbridge, Kenneth F. Raffa, and Richard L. Lindroth

Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706 (M.A.J., K.F.R., R.L.L.); and Yellowstone Ecological Research Center, Bozeman, Montana 59718 (A.M.T.)

Understanding and predicting the impacts of anthropogenically driven climate change on species interactions and ecosystem processes is a critical scientific and societal challenge. Climate change has important ecological consequences for species interactions that occur across multiple trophic levels. In this Update, we broadly examine recent literature focused on disentangling the direct and indirect effects of temperature and water availability on plants, phytophagous insects, and the natural enemies of these insects, with special attention given to forest ecosystems. We highlight the role of temperature in shaping plant and insect metabolism, growth, development, and phenology. Additionally, we address the complexity involved in determining climate-mediated effects on plant-insect and multitrophic level interactions as well as the roles of plant ecophysiological processes in driving both bottom-up and top-down controls. Climate warming may exacerbate plant susceptibility to attack by some insect groups, particularly under reduced water availability. Despite considerable growth in research investigating the effects of climate change on plants and insects, we lack a mechanistic understanding of how temperature and precipitation influence species interactions, particularly with respect to plant defense traits and insect outbreaks. Moreover, a systematic literature review reveals that research efforts to date are highly overrepresented by plant studies and suggests a need for greater attention to plant-insect and multitrophic level interactions. Understanding the role of climatic variability and change on such interactions will provide further insight into links between abiotic and biotic drivers of community- and ecosystem-level processes.

Anthropogenic activities have led to rapid and unprecedented increases in atmospheric carbon dioxide (CO_2) and other greenhouse gases, which in turn have resulted in numerous observable climatic changes, such as elevated temperature, increased frequency and severity of extreme weather events (e.g. heat waves and droughts), and altered precipitation patterns (e.g. decreased snow cover) (National Research Council, 2010). Species are responding to these climate change factors, as demonstrated by shifts in phenology (the timing of key biological and life history events), biogeographic ranges, and ecological interactions (Bale et al., 2002; Parmesan and Yohe, 2003; Hegland et al., 2009; Robinson et al., 2012). In this Update, we review and discuss the consequences of climate change on plant-insect and multitrophic interactions. Specifically, we address the direct and indirect effects of climate warming and altered precipitation patterns on plants, phytophagous insects, and higher trophic level organisms. We focus on these two components of climate change, firstly, because temperature is the abiotic factor that most directly influences insects (Bale et al., 2002), and secondly, because water availability plays a prominent role in mediating plant-insect interactions (Mattson and Haack, 1987; Huberty and Denno, 2004). Moreover, heat and drought are often interconnected climatic stressors. While other global change drivers, such as elevated CO_2 and ozone, also have significant consequences for plant-insect and multitrophic interactions, those effects are beyond the scope of this Update and have been have been recently reviewed elsewhere (e.g. Lindroth, 2010; Robinson et al., 2012).

Over the last century, average global surface air temperatures have increased by 0.81°C, and climate models project an additional 1.1°C to 6.4°C increase by the end of the 21st century, with stronger warming trends in terrestrial habitats and at higher latitudes (see National Research Council, 2010 and references therein for observed and predicted patterns discussed here). In addition to elevated mean temperatures, climate models predict an increase in the frequency and intensity of extreme warming events, such as heat waves. Beyond these global warming trends, climate change patterns demonstrate strong seasonal and regional signals. For example, mean winter temperatures in the Midwest and northern Great Plains of the United States have increased by 4°C over the past 30 years. Compared with temperature, observations for precipitation are more variable, demonstrating mean annual increases as well as decreases at regional scales

and across seasons. In general, climate model predictions for changes in precipitation are more uncertain than for temperature. However, some specific projections related to precipitation are considered to be robust, including expected increases in the total area of land affected by drought, the number of dry days annually, and the risk of drought in snowmelt dominated ecosystems. Globally, the land area affected by drought has doubled since 1970, according to historical Palmer Drought Index data. Decreased snowpack is also a well-established consequence of global climate change, and many mid- to high-latitude regions are experiencing earlier snowmelt compared with historical averages: up to 20 d earlier in the western United States. Early snowmelt, coupled with warmer summer temperatures, is predicted to decrease summer water availability in regions dominated by snowmelt (e.g. the U.S. Intermountain Region).

The effects of climate change on plants and insects can be direct, resulting from modifications in climate-sensitive plant and insect traits, or indirect, resulting from climate-induced changes in their reciprocal partners and/or higher trophic level organisms, such as predators,

parasitoids, or pathogens of insects (Fig. 1). We consider both direct and indirect effects here because they can be difficult to disentangle and because their interactions can be important. The composite effect of climate change on plants and insects reflects some combination of individual direct and indirect effects on interacting species. Thus, in some cases, it is not appropriate to disassociate these effects. In this Update, we address (1) direct and herbivore-mediated effects on plants, (2) direct and plant-mediated effects on herbivores, and (3) effects on higher trophic-level organisms and multitrophic-level species interactions. Additionally, we review the state of scientific research on these topics, highlighting areas of research poorly represented in the literature and discuss the implications of climate change effects on species interactions for large-scale environmental change and ecosystem feedbacks. In addition to limiting this Update to climate warming and altered precipitation, we restrict our discussion to natural systems, with special attention to forest ecosystems.

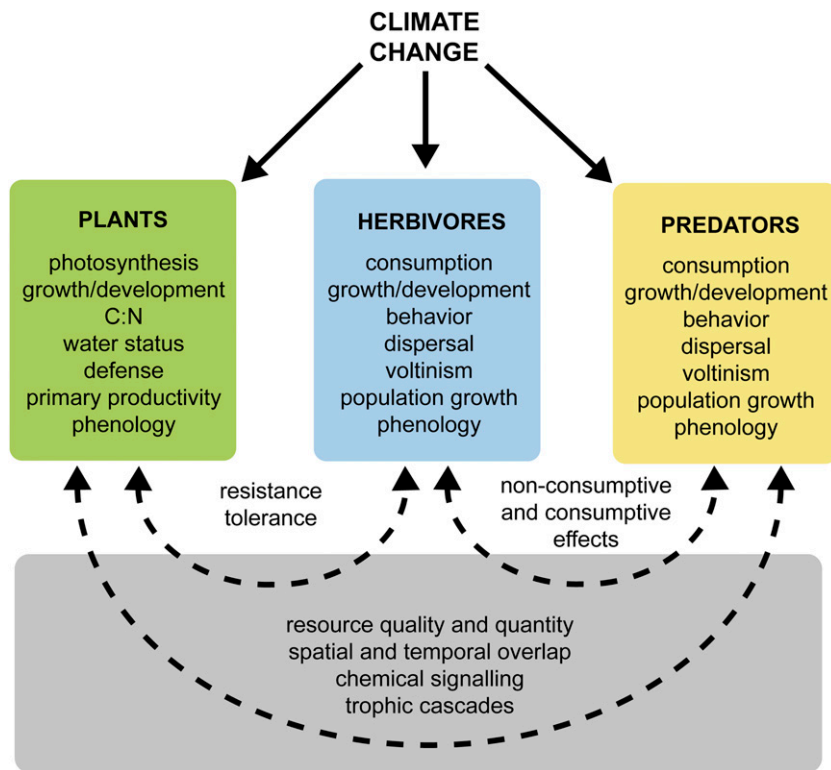This Update article is not an exhaustive review. Rather, it aims to provide a broad, hierarchical overview,

Figure 1. Key traits and processes underlying the response of plants, insect herbivores, and higher trophic level organisms to climate change. Solid arrows represent direct effects of climate change on species traits (in boxes). Dashed arrows represent indirect effects resulting from altered trophic interactions (traits along arrows). The gray box highlights indirect effects that can influence species interactions between and across trophic levels. At the organismal level, direct effects are driven by modifications in climate-sensitive metabolic and physiological processes. At the population level, altered mortality and reproduction due to climate change can affect population growth and drive evolutionary change. At the community level, shifts in spatial and temporal distributions of interacting species may alter resource availability and quality for consumers and top-down controls on plant productivity. In turn, these direct and indirect effects may lead to cascading and feedback effects on ecosystem level traits, including carbon sequestration and net ecosystem production.

which highlights some of the observed and potential ecological consequences of climate warming and altered precipitation patterns on plant-insect and multitrophic species interactions. Consistent with the intended purpose of Update articles to provide a topical summary that is accessible to a broad audience, including students and researchers, we present an introduction to key traits and processes important for understanding plant-insect and multitrophic interactions with respect to climate change. Our primary goal is to identify major pathways and feedbacks by which trophic interactions can mediate plant and insect responses to climate warming and altered precipitation, namely, increased drought frequency and/or intensity.

DIRECT AND HERBIVORE-MEDIATED CLIMATE CHANGE EFFECTS ON PLANTS

The principal effects of climate warming on plants include modification of physiological processes, growth, development, reproduction/mortality, and phenology (Fig. 1). For example, temperature is a key factor controlling plant phenology, and elevated temperatures are expected to advance important phenological stages. In trees, the critical springtime period of budbreak and leaf expansion is cued by both photoperiod and temperature (van Asch and Visser, 2007). Genetically determined differences in budbreak phenology among tree species (i.e. early and late developers) are linked to photoperiod. Within species, however, budbreak is temperature dependent. Upon receiving sufficient winter chilling, buds shift from a dormant phase to a developmental phase, and maturation is strongly temperature dependent thereafter. Timing of budbreak is not only a critical developmental trait for plants, but also an important trait influencing food availability and quality for a number of phytophagous insects.

The major physiological processes (e.g. respiration and photosynthesis) influencing plant growth are also temperature sensitive, but differentially so, both among species and plant functional groups (Tjoelker et al., 1999; Hanson et al., 2005; Rennenberg et al., 2006; Wang et al., 2012). Net photosynthesis (primary production) typically peaks within the range of normally experienced temperatures (Kirschbaum, 2000; Berggren et al., 2009), which as described in the following section, is a key difference with respect to insect herbivores. By increasing net photosynthesis and extending the growing season, warmer temperatures tend to accelerate plant growth. At middle to high latitudes, plant growth rates generally increase with temperature (Norby and Luo, 2004). Likewise, a meta-analysis of plant response to experimental warming revealed that productivity increased with temperature, especially in high latitude sites (Rustad et al., 2001). Growth enhancement may be reduced, however, if respiration increases more strongly than does photosynthesis, in particular under conditions of heat and drought stress (Rennenberg et al., 2006; Berggren et al., 2009). Moreover, the net effect of temperature-induced changes in growth also depends on physiological acclimation, such as temperature acclimation of leaf respiration, which varies among species and functional groups (Tjoelker et al., 1999; Hanson et al., 2005; Rennenberg et al., 2006).

Thus, climate warming may result in positive, negative, or potentially no effect on forest productivity, depending on individual species responses under different climate change scenarios as well as interacting climate change factors (Kirschbaum, 2000). In particular, the effects of warming may differ depending on water availability. Warming during dry periods exacerbates drought stress, insect defoliation, and climate-driven vegetation mortality (Carnicer et al., 2011; McDowell et al., 2011). Moreover, temperature and precipitation can interact in complex ways. For example, reduced snow cover arising from both winter drought and warm temperatures can result in root freezing during intermittent cold events and subsequent tree mortality due to water stress during summer (Hennon et al., 2012). Both the magnitude and timing of changes in temperature and precipitation regimes are critical for plant growth, reproduction, mortality, and the suitability of plants as food resources for phytophagous insects.

Temperature influences not only the quantity but also the quality of primary production. In trees, the period of leaf flush and expansion is marked by declining foliar nitrogen (protein) and water, concomitant with increasing tannins, terpenoids, and physical toughness (Hunter and Lechowicz, 1992; Nealis and Nault, 2005). Thus, warming-accelerated leaf maturation may contract periods of high-quality foliar tissue availability for herbivores. Temperature also affects foliar quality independent of effects on leaf development rates. A meta-analysis by Zvereva and Kozlov (2006) revealed that both sugar and starch levels tend to decline under elevated temperatures, while tissue nitrogen concentrations are unaffected, on average, demonstrating that the nutritional quality of plant tissues for phytophagous insects will likely change with climate warming. Similarly, water availability influences plant quality for herbivores and can differentially affect insect feeding guilds (Huberty and Denno, 2004). Drought tends to elevate levels of sugars and nitrogen in foliage of woody plants (Mattson and Haack, 1987; Koricheva et al., 1998b). Because warming climates will increase the frequency and intensity of drought events, studies evaluating the interactive effects of temperature and water limitation represent a critical area of future research.

Surprisingly little is known about the impacts of elevated temperature on concentrations of secondary metabolites in plants (Bidart-Bouzat and Imeh-Nathaniel, 2008). According to the growth-differentiation balance hypothesis (Herms and Mattson, 1992), if resources (e.g. light and nutrients) are not limiting, warming-accelerated photosynthesis should contribute to growth rather than defense, and levels of C-based secondary compounds should decline. Indeed, levels of phenolic constituents (e.g. flavonoids and tannins) generally do decline with warming, but levels of terpenoids typically increase

(Zvereva and Kozlov, 2006; Bidart-Bouzat and Imeh-Nathaniel, 2008). In studies that have assessed the effects of elevated temperature on plant secondary chemistry, results suggest that the effects may be species and/or context specific. For example, Kuokkanen et al. (2001) reported that elevated temperatures decreased levels of flavonol glycosides and phenolics but did not affect levels of tannins in silver birch (*Betula pendula*), whereas Sallas et al. (2003) found that warming did not affect phenolics but did increase concentrations of terpenoids in both spruce (*Picea abies*) and pine (*Pinus sylvestris*). Water availability and drought stress can also influence levels of plant secondary metabolites, such as cyanogenic glycosides, glucosinolates, and terpenoids, although changes in these allelochemicals also vary among species and in different contexts (Mattson and Haack, 1987; Llusia and Penuelas, 1998; Gutbrodt et al., 2011). Such variation in phytochemical response to temperature and water availability makes it difficult to predict how future climate change scenarios will alter plant resistance across species and ecosystems.

The direct effects of climate change will influence not only plant resistance to insect attack, but also plant tolerance to insect damage. However, very little research has addressed the effects of climate change for plant tolerance traits (e.g. compensatory growth). Extensive springtime defoliation of deciduous trees, such as aspen (*Populus tremuloides*), reduces subsequent growth rates (Stevens et al., 2007), but climate change may alter plant tolerance and performance. For example, Huttunen et al. (2007) reported that silver birch trees have a high capacity to tolerate defoliation and that under the combination of warmer temperatures and elevated CO_2, defoliated trees grew better than undefoliated controls. Because elevated temperatures both increase net primary production and extend the growing season, warming may improve the ability of plants to compensate for defoliation. Alternatively, if warming exacerbates drought conditions, plants may be less tolerant of herbivory. Moreover, the direct and indirect effects of climate change on insects may affect the type of damage plants experience via community shifts in dominant herbivore species or insect feeding guilds as well as changes in the levels of damage, which could lead to herbivore-mediated indirect climate change effects on plant tolerance.

DIRECT AND PLANT-MEDIATED CLIMATE CHANGE EFFECTS ON HERBIVORES

Temperature regulates the metabolism and physiology of insects; thus, climate warming can directly affect the development, growth, reproduction, overwinter survival, behavior, and phenology of phytophagous insects (Fig. 1). Insect metabolic rates are highly sensitive to temperature, roughly doubling with an increase of 10°C across the full range of regularly experienced temperatures (Bale et al., 2002; Berggren et al., 2009). Accelerated metabolism leads to higher consumption, growth, and development rates. Faster development, in turn, may lead to population increases via reduced generation time and decreased

exposure to natural enemies. Moreover, warmer late-winter and early-spring temperatures tend to enhance insect survival (Bale et al., 2002). Already, warming-induced population outbreaks have been shown to arise from a combination of accelerated development and reduced overwintering mortality. For example, recent outbreaks of spruce beetles (*Dendroctonus rufipennis*) and mountain pine beetles (*Dendroctonus ponderosae*) in western North America have been linked with altered life cycles, in particular changes in voltinism (number of annual broods), related to climate warming (Logan et al., 2003; Powell and Bentz, 2009). In some cases, once populations increased in response to initial high temperatures and low precipitation, positive feedbacks between insect density and host selection behavior continued to drive the outbreak cycle, even after initial abiotic releasers returned to normal. Because both recent climate history and predictive climate models indicate future increases in climatic variability as well as elevated temperatures, the likelihood of surpassing critical insect herbivore population thresholds will increase in coming decades (Raffa et al., 2008).

Similar to plants, insect phenology is cued primarily by photoperiod and temperature (van Asch and Visser, 2007). For phytophagous insects at middle to high latitudes that overwinter in diapause, late-season photoperiod is the major cue for onset of diapause, whereas early-season temperature is the primary cue for initiation of development (e.g. eclosion). As a consequence, one of the main effects of climate warming is earlier emergence and development of these insects. Climate warming during the last several decades, which is below projected future rates of change, has already contributed to phenological advances in many insect species (Bale et al., 2002; Parmesan and Yohe, 2003). Because insect metabolism is more sensitive than plant metabolism to temperature increases, insect development (and consumption) may respond more strongly and/or rapidly than plant development (and growth) to climate warming (Bale et al., 2002; Berggren et al., 2009; O'Connor, 2009). The disruption of phenological synchrony between insects and their host plants is regarded as one of the most important potential consequences of climate change for plant-insect interactions (Bale et al., 2002; Parmesan and Yohe, 2003). This is especially true for early spring emerging insects, including some outbreak species such as forest tent caterpillar (*Malacosoma disstria*) and spruce budworm (*Choristoneura fumiferana*), whose fitness is tightly linked to phenological synchrony with their host plant (Parry et al., 1998; Thomson, 2009). Because foliar quality declines with maturation (i.e. nitrogen and water decrease, while tannins, lignin, and physical toughness increase), larvae that emerge and feed synchronously with early phases of leaf flush and expansion often have higher fitness than those that feed in later phases (Parry et al., 1998; Jones and Despland, 2006).

Climate warming and drought may also indirectly influence phytophagous insects via changes in food quality, including nutritional and defensive traits that

occur independently of phenology. As previously described, warming tends to reduce levels of phenolics but increase levels of terpenoids in plant foliage (Zvereva and Kozlov, 2006; Bidart-Bouzat and Imeh-Nathaniel, 2008). Likewise, drought can also increase and/or decrease terpenoids (e.g. Mattson and Haack, 1987; Llusia and Penuelas, 1998), glucosinolates (e.g. Gutbrodt et al., 2011), and other groups of defense compounds. Thus, warming and decreased water availability may alter the dynamics of plant-insect interactions that are influenced by levels of foliar chemical constituents; for example, phenolic glycosides affect gypsy moths (*Lymantria dispar*) feeding on aspen (Donaldson and Lindroth, 2007), terpenoids affect spruce budworms on Douglas fir (*Pseudotsuga menziesii*; Nealis and Nault, 2005), and glucosinolates affect cotton leafworms (*Spodoperta littoralis*) on garlic mustard (*Alliaria petiolata*; Gutbrodt et al., 2011). The consequences of warming and drought stress on host plant quality will likely influence the performance of herbivorous insects, although the magnitude and direction of responses will vary among specialists versus generalists, feeding guilds, and insect species (Koricheva et al., 1998a; Huberty and Denno, 2004; Gutbrodt et al., 2011). Furthermore, the direct and plant-mediated effects of climate change on insect growth and development will alter exposure to and defense against natural enemies (predators, parasitoids, and pathogens). Compared with plants and insect herbivores, these natural enemies may exhibit differential rates (e.g. growth, consumption, and development) of change in response to climate warming and altered precipitation regimes.

CLIMATE CHANGE AND MULTITROPHIC LEVEL SPECIES INTERACTIONS

Despite the large body of literature describing the effects of climate warming on plant and insect physiological processes, performance, and phenology, research on climate change effects on higher trophic level organisms and multitrophic interactions is sparse (see following section). This lack of information is due in part to the difficulty and logistical challenges of assessing mechanisms underlying multicomponent indirect effects as well as the influence of external controls, such as temperature, on interactive effects across trophic levels. Nevertheless, phytophagous insects are regulated by a suite of top-down (e.g. natural enemies) and bottom-up (e.g. host plant availability and quality) controls. Both forces interact to affect insect behavior, performance, and population dynamics (Berryman, 1996; Kidd and Jervis, 1997; Awmack and Leather, 2002). Moreover, climate-mediated effects on higher trophic level organisms can influence plant performance and ecosystem productivity via trophic cascades; for example, the direct negative effects of parasitoids and other predators on herbivores can lead to indirect positive effects on plants.

Natural enemies (e.g. predators, parasitoids, and pathogens) exert significant control over the population densities of insect herbivores and outbreak species (Berryman, 1996; Kidd and Jervis, 1997; Kapari et al., 2006). Climate change may have important direct and indirect effects on the performance, phenology, behavior, and fitness of these higher trophic level organisms (Fig. 1). For example, elevated temperatures may increase parasitoid vital rates, such as metabolic and developmental rates (Hance et al., 2007), similar to phytophagous insects, potentially resulting in a greater number of generations per year. Also, temperature and water availability can influence entomopathogens, such as the fungal pathogen *Entomophaga maimaiga*, which is an important biotic agent regulating gypsy moth populations (Siegert et al., 2009). At higher trophic levels, rates of change and magnitude of response may differ compared with host insect species due to variation in plasticity of traits, such as voltinism, or differences in thermal preference-performance relationships (Hance et al., 2007). For example, Barton (2010) showed a decrease in spatial overlap between predatory spiders and grasshopper prey as a result of differential responses to warming, which allowed herbivorous grasshoppers to increase feeding time.

Food availability and quality for higher trophic level organisms is dependent on host insect response to climate change, which in turn may be affected by host plant response. Thus, elevated temperatures and altered precipitation regimes could disrupt multitrophic interactions, potentially releasing herbivore populations in systems where tripartite phenological synchronies become disassociated. Additionally, climate-induced changes in host plant nutritional and defensive chemistry can alter insect herbivore developmental rates and elemental tissue composition (e.g. nitrogen or toxins), thereby affecting the availability and quality of food resources for parasitoids and other predators (Mattson and Haack, 1987; Berryman, 1996; Ode, 2006). Moreover, in some cases, the nutritional ecology of insect herbivores is mediated by their associations with microbial symbionts, and the relative abundance of symbiotic species can be influenced by temperature (Six and Bentz, 2007).

Parasitoids and predators rely on unique blends of damage-induced plant volatile organic compounds (VOCs) to efficiently locate their host insects. These compounds are considered to be indirect plant defenses, and emissions of VOCs often increase in response to a number of biotic and abiotic stressors (Holopainen and Gershenzon, 2010). In response to damage caused by insects, plants can up-regulate the synthesis of secondary metabolites and/or elicit release of VOCs, which is considered one form of induced plant resistance. Such induced defenses can alter future herbivory, and potentially subsequent outbreaks, via direct and indirect effects on insect herbivore and/or natural enemy populations. Under elevated temperatures, plant volatile compounds can also experience higher levels of biosynthesis and larger emission rates (Niinemets et al., 2004; Holopainen and Gershenzon, 2010). However, the effects of climate warming on the quantity and quality of VOC production and emissions (i.e. plant

chemical signaling) depends on the combined effects of abiotic and biotic factors, including (1) interactions among climate change factors (e.g. water availability), (2) plant traits (e.g. carbon assimilation rates), and (3) herbivore attack (e.g. type and amount of damage). Thus, while emission rates are expected to increase under climate warming, drought, for example, may reduce emissions through ecophysiological controls (Llusia and Penuelas, 1998; Yuan et al., 2009). Ultimately, climate-induced changes in VOC production and emissions may influence parasitoid and predator recruitment as well as top-down controls on herbivore population densities.

Generalist and specialist insect herbivores have adapted mechanisms to metabolize, detoxify, and, in some cases, sequester defense compounds found in plant tissues (Nishida, 2002; Schoonhoven et al., 2005). The energetic costs associated with processing these secondary compounds can reduce resources available for other biological functions, including reproduction, growth, and immune response (Awmack and Leather, 2002; Nishida, 2002; Schoonhoven et al., 2005). Thus, the direct effects of climate change on plants may lead to indirect effects on insect herbivores as well as higher trophic levels. In particular, insect herbivores that sequester plant compounds for their own protection against natural enemies (Nishida, 2002) may be affected by such indirect effects. For these species, host plant chemistry can affect the levels of defenses sequestered (e.g. Jamieson and Bowers, 2012), which can influence palatability to predators (e.g. Camara, 1997) and susceptibility to parasitism (e.g. Smilanich et al., 2009). For higher trophic level organisms, indirect effects of climate change may become attenuated or amplified through the food chain, making multitrophic species interactions even more complex and less tractable than plant-insect interactions. Few studies have synthesized the effects of temperature and water availability on multitrophic interactions from both bottom-up and top-down perspectives.

STATE OF THE FIELD: RESEARCH BIASES AND GAPS

To review research progress, biases, and gaps in knowledge, we conducted a series of Web of Knowledge searches to identify and characterize patterns in the number of studies published on the topics discussed in this Update (Fig. 2). Scientific literature examining the effects of climate warming on plants and insects has increased exponentially since the 1980s, with approximately 20,000 publications to date (not exclusive to natural or forest ecosystems). Because searches that retrieve more than 5,000 results yield approximate rather than the actual number of publications, we choose to limit our search by focusing on the effects of climate warming on plant, insect, and natural enemy development, growth, or phenology (see Fig. 2 for methods). We selected these search terms (i.e. development, growth, or phenology) because they

are relevant traits for species across trophic levels. The most significant finding of our literature search was the strong bias toward research on plants, which accounted for more than 85% of all publications identified using our search terms.

Although research investigating climate-warming effects on plants and insects first emerged in the field of agricultural ecology, growth in publications does not appear to be driven by agroecology, as only a small fraction (<20%) of the studies identified were based in agricultural systems. Increases in publication rates have occurred primarily in the last decade, ranging from a 6- to 9-fold increase across trophic levels (Fig. 2A). The number of studies on insects (all taxonomic and functional groups) pales in comparison to the number on plants, which is a notable difference considering insects represent a greater contribution to biodiversity (more than 3 times the number of species) compared with plants. Moreover, in spite of the well-established ecological and economic importance of insect herbivores, research specifically recognizing this functional group represents a small subset of the cumulative number of studies on insects (241 of the 935). Overall, research on plants, alone, is nearly 10 times greater than on plant-insect interactions, which in turn is approximately 10 times greater than on higher trophic level organisms and/or multitrophic interactions (Fig. 2B).

Despite overall growth in research examining biotic effects of climate warming, there is a gap in knowledge regarding the consequences of climate change for species interactions across trophic levels, including plant-insect and multitrophic level interactions. Considering the importance of top-down controls for plant and insect performance and population dynamics as well as ecosystem productivity, it is important to understand how climate change may affect these types of species interactions. In particular, we propose that research on plant defense strategies (i.e. both resistance and tolerance traits) and the role of these traits in mediating plant-insect and multitrophic level interactions should be a priority area of future studies, especially given the potential for insect pest and outbreak species to drive large-scale ecological and environmental change in response to climate change.

LARGE-SCALE ENVIRONMENTAL RESPONSE AND ECOSYSTEM FEEDBACKS

Some phytophagous insect pests will likely increase in abundance due to accelerated development, increased reproduction, and decreased overwinter mortality with climate warming, which may lead to higher levels of host plant damage. As indicated in the preceding text, however, individual plant and insect species may respond differently. For example, Roy et al. (2004) reported variable responses of herbivores and plant pathogens in response to warming, which led to differing damage patterns among host plant species. Complex interactions between the changing thermal environment and the
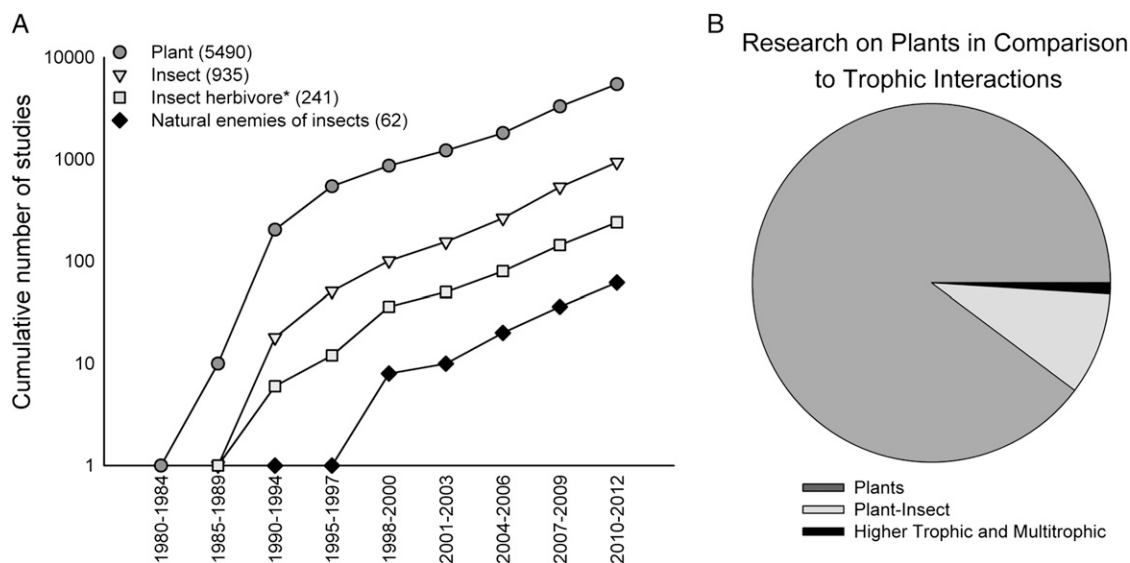
Figure 2. Overview of literature examining effects of climate warming on plants, insects, and higher trophic level organisms. A, Cumulative number of studies (log scale) from 1980 to 2012 located using Web of Knowledge. Common topic and boolean search terms included ("climate change" or "global change") and (temperature or warming) and (growth or development or phenology). Unique search terms for individual trophic categories (graphed lines) included (1) plant (not insect), (2) insect, (3) insect and (herbiv* or outbreak), (4) insect and (parasit* or predator* or tritrophic or multitrophic). B, Comparison of studies on (1) plants, (2) plant-insect interactions, and (3) higher trophic or multitrophic level interactions. Search terms were the same as those used in A, excluding the section representing plant-insect interactions, which involved search terms insect and plant. All searches were conducted August 15, 2012 using Web of Knowledge at the University of Wisconsin.

ecology of individual species may result in future scenarios where host plants are exposed to novel pests, a situation that often favors outbreaks and large-scale environmental change (Roy et al., 2004). Although plants have evolved defenses against insect herbivores, some insects, in particular some outbreak species, have similarly evolved strategies that overwhelm these plant defenses. For example, well-timed simultaneous emergence of herbivores, such as mountain pine beetles (*Dendroctonus ponderosae*), can facilitate mass attacks needed to weaken host plant defenses, while also avoiding exposure of susceptible insect stages to cold temperatures (e.g. adaptive seasonality; Powell and Logan, 2005).

Climate change, in particular increased drought frequency, can influence plant damage by insect herbivores, via changes in plant water status and physiology (McDowell et al., 2011). For example, drought stress has been shown to reduce tree resistance to bark beetle infestation in spruce and pine (Cobb et al., 1997; Berg et al., 2006) and increase insect defoliation on a large-scale community-wide level in temperate forest ecosystems (e.g. Carnicer et al., 2011). The fundamental mechanisms underlying plant susceptibility to insect attack and mortality during drought, however, remain poorly understood (McDowell et al., 2011). A number of hypotheses have emerged to explain how drought induces broadscale vegetation mortality, including that water stress causes plants to become carbon deficient due to metabolic limitations, reducing tolerance and resistance to pest damage (McDowell et al., 2011). Even when water

is not limiting, rising temperatures can affect plant water status by increasing the vapor pressure deficit and decreasing stomatal conductance (Kirschbaum, 2000; Hanson et al., 2005; Adams et al., 2009), which may ultimately decrease labile carbon storage, secondary metabolism, and plant resistance. Likewise, interactions between precipitation and temperature can increase plant susceptibility to insect attack, such as when temperature increases drought stress or when lack of snow cover extends root dormancy and decreases or delays early-season resin flow in trees (Raffa et al., 2008).

Climate-plant-insect relationships have important implications for biogeochemical cycling, biosphere-atmosphere interactions, and global carbon, water, and energy budgets (Adams et al., 2009; McDowell et al., 2011). Globally, a number of woody plant species have experienced extensive die-offs as a result of drought, warmer temperatures, and/or the presence of insect pests and pathogens (Logan et al., 2003; Carnicer et al., 2011; McDowell et al., 2011). Moreover, a number of studies indicate that the frequency and severity of outbreaks by some forest pests will intensify in response to predicted climate change (Logan et al., 2003; Hicke et al., 2006). Forest ecosystems support interactions that occur across trophic levels, and predicted global environmental change may amplify pest outbreaks and associated natural disturbances, which can lead to large-scale community shifts, environmental change, and ecosystem feedbacks (Raffa et al., 2008). For example, climate-released outbreaks of mountain pine

beetle can reduce carbon sequestration and alter other ecosystem processes (Kurz et al., 2008; McDowell et al., 2011), both of which can increase the likelihood of subsequent outbreaks. Research investigating the consequences and feedbacks of climatic variability on plant-insect interactions at multiple levels of ecological organization, from community dynamics to ecosystem functioning, is needed to better predict large-scale environmental responses to climate change.

CONCLUSION

In general, we have discussed climate warming and altered precipitation patterns from a broad perspective in this Update. Predicting how these climate factors will change in the future and interact to influence ecological interactions is complex and requires more precise approaches. For example, future studies should attempt to resolve the relative influence of seasonal changes (e.g. summer versus winter) within a local and regional context, as temperature and water availability act at these temporal and spatial scales to influence the physiology, growth, development, and phenology of organisms and ecological interactions among species. Likewise, researchers should consider local and regional climate projections, rather than global change predictions, when developing hypotheses and making climate-based predictions. For instance, while some northern latitudes are expected to experience greater annual precipitation, summer water availability may decrease in snowmelt-dominated systems. Moreover, such changes in precipitation may be more important for plants compared with phytophagous insects or their natural enemies. Examination of the historic role of climate variability on the physiology and life history strategies of organisms as well as the ecology of species interactions can help elucidate mechanisms underlying species' responses to future climate change.

In addition to elevated temperature and altered precipitation patterns, a number of other human-caused global environmental change factors, including increased ambient CO_2 and ozone levels, nitrogen inputs, biological invasions, land-use change, and habitat fragmentation, will also play important roles in shaping plant-insect and multitrophic interactions. Disentangling the complex interactions among these global environmental changes represents one of the greatest challenges for ecologists. A number of approaches exist for tackling this challenge, such as manipulative field or laboratory-based experiments, simulation or theoretical modeling, and examination of response patterns through correlative and/or observational studies. Of course, each method has unique strengths and limitations. For example, manipulative warming experiments may underestimate phenological response to climate change (Wolkovich et al., 2012) and necessarily exclude some variables to assure adequate replication. Nevertheless, these experiments provide the greatest power for determining mechanisms (e.g. metabolic and physiological processes) underlying

species' responses. Observational studies, in contrast, are well suited for detecting broad patterns and multifaceted relationships but are prone to spurious correlations or can miss important drivers, especially in systems in which critical thresholds separate regimes with inherently different dynamics (Raffa et al., 2008). These different research strategies are complementary, and system-specific combinations of approaches will be needed to improve our understanding of how climate change will affect species interactions in environments of the future.

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