Functional Ecology

British Ecological Society

Functional Ecology 2012, **26**, 844–853 doi: 10.1111/j.1365-2435.2012.02013.x

PERSPECTIVES

Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms

Sylvain Pincebourde*,[1] and H. Arthur Woods[2]

[1] *Institut de Recherche sur la Biologie de l'Insecte (IRBI, CNRS UMR 7261), Université François Rabelais, 37200, Tours, France; and* [2] *Division of Biological Sciences,University of Montana, Missoula, MT, 59812 USA*

Summary

1. Significant deviations between macro- and microclimates are quite common in different ecosystems. Such deviations have also been observed between leaf and air temperatures. The surface of leaves hosts a huge diversity of organisms. Here, we point out the crucial role of leaf microclimates in the fate of leaf-dwelling organisms in a changing climate.

2. Leaf microclimate, which includes temperature and humidity at the leaf surface, results from the biophysical filtering of local macroclimates by the plants themselves through complex and nonlinear processes. However, because the processes contributing to leaf microclimate are poorly understood, we lack a strong basis for predicting the impacts of global warming on plants and their denizens.

3. We describe two mechanisms that generate climate uncertainty at the leaf surfaces. First, stomatal responses to the environment generate great complexity in the dynamics of leaf temperatures. Secondly, herbivores, by feeding on leaf tissues, modify their leaf microclimates. Little is known about how these modifications affect the ecophysiology of organisms at the leaf surface, an effect called physical feedback of herbivory.

4. Recent findings report a latitudinal gradient in the temperatures of tree leaves, which can be linked to gradients in plant structural traits. We propose two competing hypotheses to describe how the leaf microclimate will change with global warming across latitudes. These hypotheses predict opposite patterns of change in the leaf microclimate.

5. How can we reduce our uncertainty about what will happen at leaf surfaces? Recent advances in stomatal biology give cues regarding the direction and the speed at which plant stomata will influence the evolution of leaf microclimates. In addition, local heterogeneity in microclimatic conditions might help leaf-dwelling organisms to find suitable microhabitats, as long as they can migrate over short distances.

6. The challenges now are to understand whether leaf microclimates will buffer or magnify the amplitude of warming, and to determine how much the outcome will affect ecological processes within new microclimates. Leaf microclimates can provide suitable microhabitats in an unfavourable climate, and conversely, they can bring a species to local extinction in what would seem to be an otherwise favourable climate.

Key-words: boundary layer, global warming, herbivory, humidity, leaf microclimate, plant–insect relationships, stomata, temperature

Introduction: Environmental biophysics of organisms at the leaf surface

Collectively, leaves are among the most important microhabitats in the biosphere. Leaves are, foremost, plant organs for gas exchange and energy capture. The leaf

---

*Correspondence author. E-mail: sylvain.pincebourde@univ-tours.fr system is probably the most important biological unit linking the global climate (e.g. evapotranspiration and carbon dioxide assimilation) and the functioning of ecosystems (e.g. recycling of nutrients). But leaves are also home to an enormous diversity of other organisms, from bacteria to arthropods, spanning several functional groups and trophic levels – symbionts, parasites, herbivores, predators, parasitoids etc. (Preece & Dickinson 1971; Strong, Lawton & Southwood 1984; Juniper & Southwood 1986; Meyer & Leveau 2012). This relationship between the host plant leaf and associated organisms has been extensively studied from evolutionary (e.g. phylogenetic associations between herbivores and host plants) and ecological perspectives (e.g. the nutritional ecology of herbivore insects and plant defences) (Labandeira *et al.* 1994; Lewinsohn, Novotny & Basset 2005; Van Loon, Casas & Pincebourde 2005; Wilf *et al.* 2006). Fewer researchers have attempted to describe and explain how organisms interact with their host plant leaves from the perspective of environmental biophysics. From a purely physical point of view, the leaf surface is a highly characteristic microhabitat, as the abiotic conditions within the leaf boundary layer can differ markedly from those in ambient air (Willmer 1986; Boulard *et al.* 2002). Here, we point out the crucial role of leaf microclimates in the fate of leaf-dwelling organisms in a changing climate.

Significant deviations between macro- and microclimates are quite common in different ecosystems (e.g. Helmuth, Kingsolver & Carrington 2005; Helliker & Richter 2008; Scherrer & Korner 2010, 2011). For example, intertidal microhabitat temperatures for the mussel *Mytilus californianus*, along the west coast of North America, are poorly predicted by macroenvironmental conditions; microhabitat temperatures instead rely on complex interplay among macroenvironment and local factors such as tidal regime and wave splash (Helmuth *et al.* 2006). Likewise, significant deviations have also been observed between temperatures at the leaf surface and in surrounding air (Linacre 1964, 1967; Chelle 2005). The influence of leaf microclimates on organisms depends on organismal body size. Large organisms such as last-instar sphingid caterpillars (Lepidoptera) are more influenced by ambient conditions than by leaf microclimatic conditions (Casey 1976; A.H. Woods, unpublished). By contrast, small arthropods at the leaf surface are more likely to be completely embedded within the leaf boundary layer (Woods 2010). These tiny organisms should experience leaf temperature surface variations rather than ambient air directly. Also, water vapour pressure is higher within the leaf boundary layer compared to ambient (Willmer 1986). Organisms at the leaf surface experience these abiotic conditions within the leaf envelope, but this is only rarely considered in studies looking at the effects of climate variations on leaf-dwelling organisms, with a few notable exceptions. North American pitcher-plant mosquitoes are adapted to variations in their pitcher leaf microclimate, which magnify the daily air temperature increase (Kingsolver 1979), rather than to ambient summer or winter conditions (Bradshaw, Fujiyama & Holzapfel 2000). Moth eggs in an Arizona desert avoid lethally high temperatures by developing on host leaves that transpire away significant heat (Potter, Davidowitz & Woods 2009). Leaf miners modify plant tissues so that they magnify air temperature increases during the day, but buffer thermal extremes to limit overheating (Pincebourde & Casas 2006a). Such links between an organism's thermal requirements and how it uses or manipulates leaf filters probably are widespread.

Adding the leaf microclimate as a factor when studying the response of organisms to climate change cannot be made without adding complexity. Leaf microclimates, which include temperature and humidity at the leaf surface, result from the biophysical filtering of local macroclimates by the plants themselves through complex, nonlinear processes (Nobel 1999). These processes can be integrated into a heat budget, which computes leaf temperature from the characteristics of its physical environment (Gates 1980; Jones 1992; Nobel 1999). Briefly, the balance between radiative energy absorption and heat losses during convection and evapotranspiration drives the leaf-to-air temperature deviation at short time-scales (Schuepp 1993). Most of the knowledge on leaf heat budget balance model was acquired decades ago by micrometeorologists and plant ecophysiologists but has not yet played a central role in studies by ecologists working on climate change (see Woodward, Smith & Emanuel 1995; Hanson *et al.* 2005). Significantly more work on the potential effects of climate change on the leaf energy budget has been performed by agroecologists (Brouder & Volenec 2008). Nevertheless, a mechanistic approach provides a strong background for placing the abiotic environment actually experienced by leaf-dwelling organisms into models of the ecological effects of climate change.

Our understanding of how the leaf system will filter future climates is extremely limited. Here, we explain how this lack of knowledge adds uncertainty to our ability to predict the response to climate change of the leaf microclimate and of organisms living within it. Our aim is to stimulate research in this field such that this uncertainty can be reduced in the future. Also, we do not intend to be exhaustive – our purpose is not to list all parameters that should be addressed when studying leaf microclimates. Rather, we highlight several ways in which understanding key mechanisms better will improve our ability to forecast the impacts of climate change on organisms in the leaf envelope. Most of the microclimate uncertainty at leaf surfaces lies in two parameters: (i) how will stomata respond to fluctuations and climate change? and (ii) how will the leaf microclimate be modified by herbivory in a changing climate? Answering these questions requires understanding the details of how leaves produce microclimates. Thereafter, we discuss the leaf microclimate in a global context, as recent research provides unexpected and surprising behaviour of leaf surface temperature along a latitudinal gradient (Helliker & Richter 2008). Finally, we suggest future directions for research.

The leaf thermostat: stomata

The leaf microclimate depends on interactions among a set of hierarchical factors: season, regional climate, local topography (Sears, Raskin & Angilletta 2011), canopy and plant structure (Campbell & Norman 1998; Sinoquet *et al.* 2001), and, most proximately, the structure and ecophysiology of individual leaves (Nobel 1999). Stomata deserve special attention as they simultaneously regulate leaf budgets for water, CO_2 and heat. The leaf surface temperature depends greatly on the opening level of stomata, suggesting an analogy between stomata and a thermostat. The level of stomatal opening directly and proportionally sets the stomatal conductance for water vapour. Higher conductance directly elevates rate of evapotranspiration, which in turn depresses leaf temperature (Campbell & Norman 1998). For example, modelling of the leaf energy budget shows that a 40-fold increase in stomatal conductance can cause leaf temperature to drop by 15 °C in large leaves under full sun (Campbell & Norman 1998). Leaf temperature of course depends on other abiotic factors, such as radiation level, wind speed, humidity and on plant ecophysiology (e.g. leaf shape and size). Among these factors, however, the stomata represent the only biological system over which the plant exerts short-term control. Indeed, stomatal opening reflects both exogenous (environmental fluctuations) and endogenous (plant ecophysiological status) factors (Damour *et al.* 2010).

Stomatal opening is influenced nonlinearly and interactively by multiple factors (Jarvis 1976; Jones 1999; Hetherington & Woodward 2003), many of which will be altered by climate change. At the level of the phylloclimate (*sensu* Chelle 2005), the effects of irradiance, humidity (vapour pressure deficit), temperature and atmospheric CO_2 have been studied extensively over the past decades. The most typical responses of stomatal conductance to such factors were clearly nonlinear (Jarvis 1976; Morison 1987; Oren *et al.* 1999; Huxman & Monson 2003) (Fig. 1a,b). Jarvis (1976) established the first model integrating the stomatal responses to a change in irradiance, leaf water vapour deficit, leaf temperature, CO_2 and leaf water potential. Although the Jarvis model explained most of the variability in stomatal conductance, it has been criticized for not incorporating the interactive effects of environmental factors on the stomatal response (Damour *et al.* 2010). Such interactive effects do exist, however. For example, increasing leaf temperature tends to lower the amplitude of the stomatal response to increasing leaf water vapour deficit (Mott & Peak 2010). Level of CO_2 also modulates the interactive effects of temperature and water vapour on stomatal conductance (Wilson & Bunce 1997). At the scale of the entire plant, long distance signalling between plant organs leads to interactive effects between below-ground and aerial processes. For example, soil drought influences stomatal conductance by altering the leaf water status (Damour *et al.* 2010). Understanding how stomata will integrate future climate change remains a great challenge, and solving this question necessitates a better understanding of the way signalling cascades interact from whole plants to cells. This sensitivity of stomata to multiple influences defines the first level of climate uncertainty at leaf surfaces.

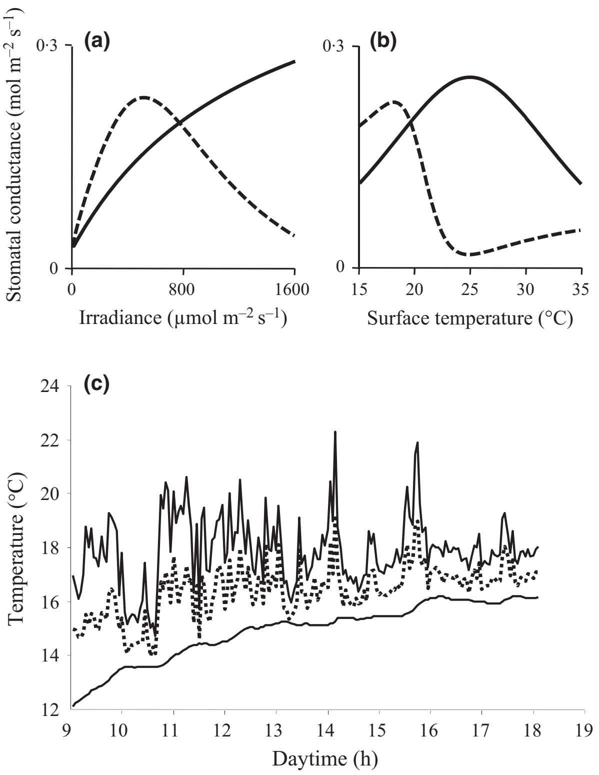

Fig. 1. Linking herbivory, stomatal conductance and microclimatic temperature changes in plant–herbivore relationships. The graphs illustrate the stomatal conductance response to a change in irradiance (a) and surface temperature (b) for intact leaf tissues (solid lines) and tissues attacked by a leaf mining moth larvae (dashed lines). Leaf miner feeding activity leads to stomatal closure at moderate and high irradiance levels and at elevated surface temperature. This stomatal closure contributes to warming the attacked leaf tissues as seen in (c) when plotting the daily temperature dynamics of both attacked (dashed line) and intact (solid line) leaf tissues in full sunlight as well as ambient air temperature (bottom solid line). Redrawn from data in Pincebourde & Casas (2006a) and Pincebourde *et al.* (2007).

A second level of climate uncertainty follows the decoupling in the characteristic time-scales of environmental fluctuations (e.g. within-day) or changes (e.g. years to decades) and of stomatal responses. In general, stomatal responses are not instantaneous. When light and CO_2 levels fluctuate, the stomatal conductance can be above or below the time-averaged stomatal conductance established under corresponding constant conditions, depending on the frequency of the fluctuations (Cardon, Berry & Woodrow 1994). Delays in stomatal responses can cause severe distortions from steady state, especially during high-frequency fluctuations like sun flecks under dynamic cloud cover (Stegemann, Timm & Küppers 1999). These delays could be modulated by the plant itself, as stomata are under control of a circadian clock that tends to anticipate opening at dawn and promote closing well before dusk (Hotta *et al.* 2007). However, the influence of within-day amplitude of variations in light, humidity, temperature or even CO_2 (see De Araujo *et al.* 2008) on stomatal responses has received little attention.

It is well recognized that stomatal conductance and leaf surface temperature are intimately linked to each other. Indeed, thermal imaging is used to infer indirectly the stomatal conductance from leaf surface temperature recordings, at both whole leaf and canopy scales (Jones 1999; Leinonen *et al.* 2006). Recent studies focused on the intraleaf surface thermal heterogeneity reporting that most of the heterogeneity is correlated with heterogeneity in the stomatal opening level (Prytz, Futsaether & Johnsson 2003). A similar correlation was found at the intracanopy scale when distinguishing leaves in the shade from leaves fully exposed to sunlight (Leinonen & Jones 2004). Few studies provide direct quantitative information on the amplitude of leaf surface temperature fluctuations caused by a given variation of stomatal conductance. For example, Jones (1999) found that under typical conditions with stomatal conductance about 200 mmol m^{-2} s^{-1}, the sensitivity of *Phaseolus* leaf surface temperature to a change of 10% in stomatal conductance can be as much as 0·5 °C. The natural intraleaf heterogeneity of stomatal conductance can cause a leaf surface temperature gradient of up to 4–5 °C in *Phaseolus* (Jones 1999). A similar difference (5 °C) was found when comparing *Vicia* leaves from water-stressed (relatively close stomata) and well-watered (open stomata) plants (Leinonen & Jones 2004). Such thermal deviations are of the same order of magnitude than the temperature difference between leaves in the shade and exposed to direct sunlight (e.g. Pincebourde *et al.* 2007). The stomatal responses to environmental factors probably lead to leaf surface temperature variations of lower amplitude compared to diurnal and seasonal temperature fluctuations, but they clearly drive the leaf-to-air temperature deviation significantly for organisms living at the leaf surface.

The integration time of stomata sets their ability to track seasonal variation as well as long-term environmental change (Hetherington & Woodward 2003). Seasonal variation in stomatal conductance (Morecroft & Roberts 1999) clearly integrates across daily leaf microclimates, because leaves in full sun and in shade (i.e. different radiation level and therefore different leaf surface temperature) do not show the same patterns of variation (Morecroft & Roberts 1999). In addition, the recent rise in global CO_2 levels has led to reduced stomatal conductance, from plastic response in stomatal density and pore size (Woodward 1987; Lammertsma *et al.* 2011). Nevertheless, virtually nothing is known whether within-day patterns interfere with the ability of stomata to track long-term environmental change.

These temporal patterns in stomatal response likely determine the patterns of leaf surface temperature. Interestingly, such temporal mechanisms could buffer or amplify the effects of environmental factors on leaf temperature. In this context, stomatal delays are analogous to thermal inertia in their effects on temperature of organisms. For example, slow stomatal closure could buffer the rise in temperature stemming from short but extreme compound events, such as the combination of low wind and high solar load from sun flecks (e.g. a leaf receiving solar radiation for a short time-window in a canopy gap), while ambient air is relatively dry and warm (Vogel 2009). Nevertheless, how such co-occurring 'normal' events can lead to compound extreme events is largely ignored in the plant sciences (see Vogel 2009), despite recent attention in intertidal ecology (Denny *et al.* 2009). Several older studies examined effects of compound events on the body temperature of insects associated with plant canopies (*Colias* butterflies; Kingsolver & Watt 1983) or with small plant-created aqueous habitats (pitcher-plant mosquitoes; Kingsolver 1979). In the context of leaf-associated insects, the limited knowledge on the temporal behaviour of stomata in fluctuating environments makes uncertain what the leaf surface temperature trends will be as climate changes. Future studies should embed empirical and modelling approaches to understand how complex macroenvironments produce various leaf microclimates. These studies must take into account rather complex environmental properties, such as autocorrelation among environmental variables (Kingsolver & Watt 1983) and temporal coincidence of different potential stressors (Pincebourde *et al.* 2012), and should fold the nonlinear stomatal dynamics into mechanistic and quantitative models.

Influence of herbivory on leaf microclimates

Most leaf-associated organisms are active at the leaf surface, and many feed on the leaf tissues by various mechanisms. While some herbivores (e.g. caterpillars) strongly alter the integrity of a leaf by directly consuming plant tissues, thereby impacting leaf shape and size (Heinrich 1971), other herbivores (e.g. aphids and spider mites) suck on sap by piercing the leaf integument or by feeding on plant cells from the inside (e.g. leaf mining and galling insects) (Hering 1951). These feeding strategies alter several parameters of a leaf energy balance, such as stomatal conductance (Raimondo *et al.* 2003; Reddall *et al.* 2004; Aldea *et al.* 2005; Pincebourde *et al.* 2005) and absorbance of solar radiation (Pincebourde & Casas 2006a,b). The formation of galls constitutes a more significant modification of local leaf or stem structure (Stone & Schonrogge 2003). Leaf galls raise the relative humidity around the galling insect (Miller, Ivey & Shedd 2009) and provide a warmer microenvironment to the insect (Layne 1993). To our knowledge, however, little is known about how herbivory affects leaf microclimates and virtually nothing on its feedback to arthropod ecophysiology, an effect also called 'physical feedback of herbivory' (Pincebourde and Casas 2006a,b).

Since the review on the subject by Welter (1989), several remarkable studies have looked at the impact of herbivory or pathogens on gas exchange (photosynthesis, transpiration and stomatal conductance) by leaves. Whether herbivory's effect on stomatal conductance is large or small depends on the type of feeding strategy, but in general, arthropod feeding leads to decreased stomatal conductance and transpiration (Nabity, Zavala & Delucia 2009) (Fig. 1a,b). This suggests that the surface temperature of an attacked leaf is likely to be higher compared to an intact leaf (Fig. 1c), although the temperature increase can be limited to the injured areas of the leaf (Aldea *et al.* 2006) (Fig. 2). However, transpiration rate may be decoupled from stomatal conductance under herbivory as the arthropod feeding activity can damage leaf epidermis and plant cells, thereby establishing new ways for water vapour to escape. Such non-stomatal water loss was shown to become unimportant several days following herbivory by a caterpillar on *Arabidopsis*, probably because the leaves deposited suberin in wounded areas (Tang *et al.* 2006). By contrast, non-stomatal water loss was still significant 6 days after attack in the Japanese beetle and corn earworm caterpillar (Aldea *et al.* 2005). These temporal dynamics, coupled with the spatial heterogeneity over a leaf surface, might increase the amplitude of leaf temperature fluctuations within the time window corresponding to the developmental time of an arthropod.

What we need now are more direct studies of the spatial distribution of stomatal functionality in relation to the location of leaf damage (where 'functional' means that stomata still respond to environmental fluctuations). It is not always clear whether stomata in attacked leaves conserve the same functionality compared to stomata in intact leaves. Although they often may not, this is not the case for leaves attacked by endophytic insects (leaf miners; Raimondo *et al.* 2003; Pincebourde *et al.* 2005). For example, stomata in the leaf tissues mined by lepidopteran leaf miners remain functional but show responses to changes in radiation level, water vapour pressure deficit and temperature that differ from their responses in intact leaf tissues (Pincebourde & Casas 2006a) (Fig. 1a,b). Nevertheless, it is reasonable to think that stomatal functionality would be annihilated in severely attacked leaves. A very low transpiration rate coupled with a change in leaf coloration (darker) likely turns the leaf microclimate into a dryer and hotter microhabitat. Therefore, herbivory likely amplifies the effects of environmental variation on leaf microclimates.

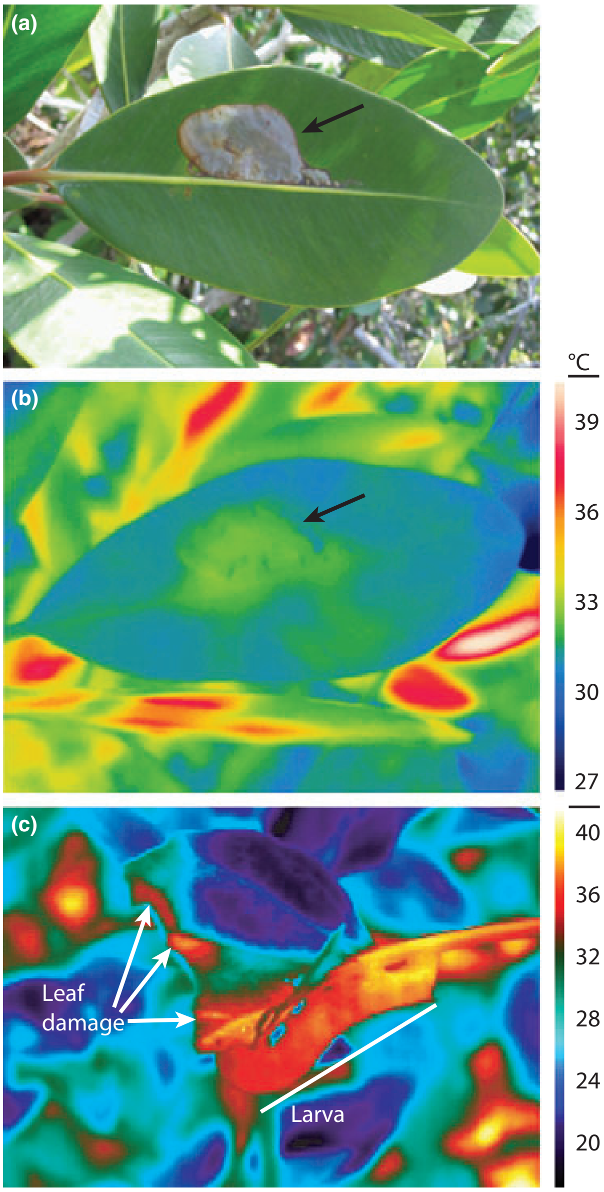

Fig. 2. Effect of herbivory on leaf surface temperature. (a) Picture of damage caused by a leaf miner caterpillar (*Phyllonorycter* sp.) on a leaf of *Cluzia* sp. in a tropical forest (photo Sylvain Pincebourde). (b) The corresponding infrared image (thermography) shows that the damaged leaf area is warmer than the intact leaf surface (32·7 vs. 30·9 °C, respectively) (photo Sylvain Pincebourde). (c) Infrared image (thermography) of a fifth-instar caterpillar of *Manduca sexta* feeding on a leaf of *Datura wrightii*, in southern Arizona, showing that the leaf temperature increase can be limited to the attacked leaf portion (photo H. Arthur Woods).

Leaf microclimates at the global scale

As we explain above, leaf microclimate depends on weather, topography, canopy structure and endogenous factors. Because most of those factors vary with latitude, one can reasonably expect a strong latitudinal gradient in leaf temperatures. However, like most physiological rates, photosynthesis is temperature-dependent (Sage & Kubien 2007). The capacity of a plant to assimilate atmospheric CO_2 is optimal at a given (leaf) temperature within a thermal range, below and above which the rate is severely limited (Sage & Kubien 2007). An interesting hypothesis emerging recently is that plants may evolve mechanisms that keep the temperature of their leaves as close as possible to this optimum across broad latitudinal gradients, resulting in the apparent absence of gradients in leaf temperature. This hypothesis was supported recently by Helliker & Richter (2008). By measuring oxygen isotope ratios of cellulose in 39 tree species, they showed that temperatures of tree canopies during photosynthesis, when averaged over growing seasons, are remarkably constant from subtropical to boreal latitudes. Helliker & Richter (2008) further suggest that the air-to-leaf temperature deviation increases with latitude such that the global average of leaf temperature is around 21 °C at all latitudes (Fig. 3a). Indeed, the same conclusion was obtained by Linacre (1964, 1967) who carried out a meta-analysis on midday leaf and air temperatures from about 60 different species (from tree to grass species), finding that the air-to-leaf temperature deviation decreases with air temperature such that leaf temperature was 28·5°C ± 7·9 °C (mean ± SD) (Fig. 3b). He also demonstrated that there is equality between leaf and air temperatures at around 30 °C. In the analysis, however, Linacre focused on well-watered plants to eliminate the effects of water stress. And, more importantly, he focused on leaves exposed to full sun at midday, which explains the difference in the leaf temperature reported in his study (28·5 °C) and by Helliker & Richter (2008). Leaves in shaded parts of a tree are normally closer to ambient air temperature than leaves under full sun. The canopy averaging of Helliker & Richter (2008) therefore causes the leaf temperature target to be lower than the one reported by Linacre (1964, 1967).

The relationship between air-to-leaf temperature deviation and latitude given by Helliker & Richter (2008) has strong implications for organisms living at the leaf surface. First, in temperate regions, both leaf biophysics and other factors varying with latitude (e.g. canopy structure and daylength) magnify thermal fluctuations from the environment, because leaf temperature is close to ambient air at night but goes well above air temperature during the day. Secondly, at low latitudes, leaf and canopy filters tend to buffer diurnal increases in air temperature such that leaf temperature fluctuation amplitudes are lower than ambient air. Indeed, plants have developed specific strategies to control leaf temperature according to environmental conditions. For example, high transpiration rates and reflective hairs allow tropical leaves, and some desert leaves, to reach lower-than-ambient temperatures (Smith 1978; Potter, Davidowitz & Woods 2009). By contrast, plants at high latitudes have evolved strategies for constraining convective heat loss, for example by growing denser branches (Leuzinger & Korner 2007), thereby promoting high air-to-leaf temperature deviation. Other leaf structural traits that play a role in the leaf heat budget, such as leaf size and shape or leaf mechanical properties, also vary with latitudinal climate (Onoda *et al.* 2011; Peppe *et al.* 2011). Overall, these leaf structural traits are not expected to change much over short time-scales, albeit some were found to be relatively plastic to temperature changes (Royer *et al.* 2009; De Boer *et al.* 2011). The latitudinal gradient in leaf structural traits raises significant questions about how latitude-specific will be the effects of climate change. We summarize and encapsulate the opposing possibilities by laying out two competing hypothesis, the *differential-buffering-ability* hypothesis and the *fluctuation-adapted* hypothesis.

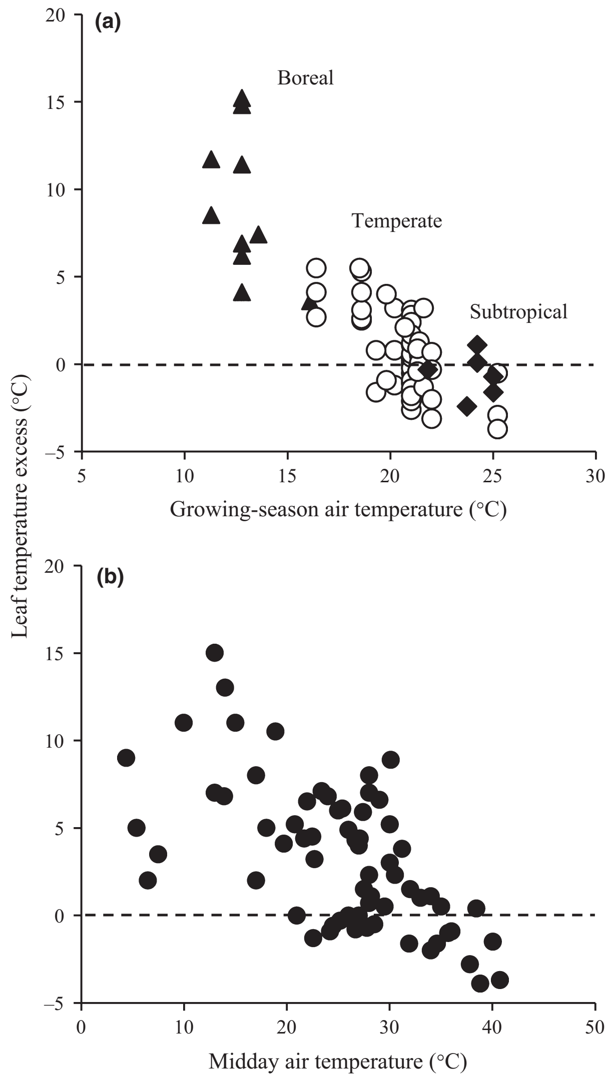

Fig. 3. Global trends in leaf temperature excess via two distinct approaches. (a) Leaf temperature minus ambient growing-season temperature is shown as a function of ambient growing-season temperature for different latitudes (boreal, temperate and subtropical regions) and for 39 tree species. Leaf temperatures correspond to averages over growing season. They were resolved by analysis of the oxygen isotopic ration in the cellulose. Redrawn from data provided in the supplementary materials by Helliker & Richter (2008). (b) Midday leaf temperature minus midday ambient air temperature is shown as a function of the midday ambient air temperature in 70 plant species from different localities and including greenhouses. Data points are instantaneous temperature measurements. Redrawn from data provided by Linacre (1967).

The *differential-buffering-ability* hypothesis states that the amplitude of temperature change at the leaf surface will be negligible in the tropics, at least compared to higher latitudes. Leaves at low latitudes are already adapted to dampen the effects of elevated air temperature. These leaves can therefore buffer future warming, as long as the amplitude of the warming does not exceed their buffering abilities. Indeed, the rate of warming is much lower in tropical regions than at high latitudes (IPCC 2007). By contrast, leaves in temperate and boreal areas are more adapted to magnify environmental fluctuations. The surface temperatures of high-latitude leaves will therefore increase as much as does the ambient air. Leaf-associated organisms will therefore experience warming at the leaf surface only at high latitudes, leading subsequently to accelerated development of insects, for example, as long as the critical temperature threshold is not reached. Further, mortality events might occur once leaf surface temperature goes above this threshold. In general, according to this *differential-buffering-ability* hypothesis, global change is likely to cause important ecological effects at high latitudes, where the leaf microclimate will change the most, whereas the direct effects could be negligible in tropical regions. An important caveat about this hypothesis is that the outcome depends also on climate-driven changes in cloud cover, because solar radiation plays such an important role in leaf heat budgets.

By contrast, the *fluctuation-adapted* hypothesis proposes that climate-driven ecological shifts will be more important at low rather than at high latitudes. Leaves in boreal and temperate latitudes are already adapted to highly fluctuating environments, whereas leaves in the tropics are not. Compared to (sub)tropical leaves, therefore, temperate leaves should be preadapted to cope with even larger temporal fluctuations. Indeed, climate change scenarios predict a higher thermal variance for future climates (IPCC 2007). Even if the amplitude of the temperature change is more pronounced at high latitudes, plants and leaf-dwelling organisms are already adapted to such levels of thermal variance. Indeed, increasing the thermal variance might even have a positive impact on some life-history traits (Niehaus *et al.* 2012) as long as temperature remains within the performance breadth (Neuwald & Valenzuela 2011). By contrast, increasing the temperature variance at low latitude, where organisms live in general near their temperature tolerance threshold (Dillon *et al.* 2010), would cause major thermal stress and temperature-induced mortality events. This hypothesis implies that slower warming in the tropics would have more ecological consequences than at temperate latitudes. The main caveat is that the outcome in terms of survival and distribution will depend on whether sublethal and lethal tolerance levels are reach more frequently or not.

The two hypotheses (*differential-buffering-ability* and *fluctuation-adapted*) make remarkably divergent predictions about latitudinal gradient of ecological impacts in arthropod–plant associations under global warming. The *differential-buffering-ability* hypothesis suggests that plant structure and physiology will further magnify the latitudinal gradient in rising air temperature, with the consequence that mid- and high-latitude arthropod–plant associations will change more than will tropical associations. By contrast, the *fluctuation-adapted* hypothesis focuses on latitudinal gradients in adaptation to variable environments *per se*, with the consequence that low-latitude arthropod–plant associations will change the most, even if the total magnitude of change is smaller. This distinction among hypotheses hinges on the more fundamental observation that predicting how organisms will respond to climate change depends as much on organismal physiology as on how climate changes in terms of average, variance and temporal pattern for example (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Dillon *et al.* 2010; Pincebourde *et al.* 2012).

Future directions: quantifying and reducing the uncertainty

Above, we highlighted two processes leading to climate uncertainty at the leaf surface – stomatal behaviour and effect of herbivory on leaf microclimate. This uncertainty, generated by plant ecophysiological responses to their environments, must be factored into our uncertainty in how macroenvironmental change will be transmitted to the leaf surface, and in how surface changes will affect leaf-dwelling organisms and their communities of endosymbionts. The joint effect of these uncertainties severely challenges our ability to forecast how climate change will affect the distribution and abundance of organisms in the leaf envelope. Also, the complexity of the mechanisms underlying the leaf microclimate functioning (e.g. stomata) adds high uncertainty to what will be the leaf microclimate for its associated organisms in the coming decades. Nevertheless, several recent studies give us ways to start quantifying, and possibly reducing, this level of uncertainty.

A general pattern of acclimation and adaptation of the stomatal system might emerge. Plant species have reduced their maximal level of stomatal conductance in response to increase atmospheric CO_2 over past several decades, owing to a reduction in the size and number of stomata (Lammertsma *et al.* 2011). Modulation in the leaf structure, observed in several plants in Florida during the past century, occurred within a pre-existing range of leaf phenotypes suggesting that rapid acclimation or plasticity is possible (Lammertsma *et al.* 2011). A modelling approach also showed that this reduction in maximal stomatal conductance will continue as atmospheric CO_2 keeps increasing, until the plants reach the limits of their plasticity (De Boer *et al.* 2011). Reduced maximal stomatal conductance not only leads to lower transpiration rates in general but also diminishes the relative importance of short-term stomatal responses to environmental fluctuations. Thus, we can predict an increase in leaf temperature as leaf structures acclimate to changing levels of CO_2. In addition, daily fluctuations in ambient levels of light, temperature and humidity might be expected to alter leaf temperature relatively less in the future compared to today.

Most organisms living at the leaf surface are mobile. As climate changes, they may therefore be able to move from unsuitable to suitable leaf microclimates, as long as such microclimates are available. Indeed, a recent thermal imaging study in alpine landscapes shows that local topography and soil temperature contribute to high thermal heterogeneity of plant surfaces, to the point that microtopography can mimic temperature differences of large latitudinal and elevation gradients (Scherrer & Korner 2010, 2011). Organisms living in such landscapes have therefore the possibility to move within their microhabitat to remain in a suitable thermal environment. Organisms might even be able to find suitable leaf microclimates within a single plant, as plant architecture is complex enough to establish very steep thermal gradients (Pincebourde *et al.* 2007). Such movements of organisms between different parts of a single plant, or between plants in a population, will likely alter the structures of local food webs, via changes in species interaction strengths (Barton & Schmitz 2009).

The challenges now are to understand whether leaf microclimates will buffer or magnify the amplitude of warming and to determine how much the outcome will affect ecological processes within the new microclimate. Meeting these challenges will require mechanistic and quantitative approaches that explicitly incorporate the nonlinearities of the leaf filter, the anticipated changes in local temperature and hydrological cycle, and the thermal requirements and tolerance of leaves and their denizens. Leaf microclimates can provide suitable microhabitats in an unfavorable climate, and conversely, they can bring a species to local extinction in what would seem to be an otherwise favourable climate.

Acknowledgements

Our opinion reported in this article first emerged during discussions at the APS 2010 Meeting ‘Global change and global science: comparative physiology in a changing world’ in Westminster, CO, USA. We are grateful to Kristen Potter, Jérôme Casas, Joel Kingsolver and an anonymous referee for stimulating comments. SP acknowledges support from the ANR (project MicroCliMite, MCM). AW acknowledges support from NSF’s Division of Integrative Organismal Systems (IOS-0844916).

References

Aldea, M., Hamilton, J.G., Resti, J.P., Zangerl, A.R., Berenbaum, M.R. & Delucia, E.H. (2005) Indirect effects of insect herbivory on leaf gas exchange in soybean. *Plant, Cell and Environment*, **28**, 402–411.

Aldea, M., Hamilton, J.G., Resti, J.P., Zangerl, A.R., Berenbaum, M.R., Frank, T.D. & Delucia, E.H. (2006) Comparison of photosynthetic damage from arthropod herbivory and pathogen infection in understory hardwood saplings. *Oecologia*, **149**, 221–232.

Barton, B.T. & Schmitz, O.J. (2009) Experimental warming transforms multiple predator effects in a grassland food web. *Ecology Letters*, **12**, 1317–1325.

Boulard, T., Mermier, M., Fargues, J., Smits, N., Rougier, M. & Roy, J.C. (2002) Tomato leaf boundary layer climate: implications for microbiological whitefly control in greenhouses. *Agricultural and Forest Meteorology*, **110**, 159–176.

Bradshaw, W.E., Fujiyama, S. & Holzapfel, C.M. (2000) Adaptation to the thermal climate of North America by the pitcher-plant mosquito, *Wyeomyia smithii*. *Ecology*, **81**, 1262–1272.

Brouder, S.M. & Volenec, J.J. (2008) Impact of climate change on crop nutrient and water use efficiencies. *Physiologia Plantarum*, **133**, 705–724.

Campbell, G.S. & Norman, J.M. (1998) *An Introduction to Environmental Biophysics*. Springer Verlag, New York.

Cardon, Z., Berry, J. & Woodrow, I. (1994) Dependence of the extent and direction of average stomatal response in *Zea mays* L. and *Phaseolus vulgaris* L. on the frequency of fluctuations in environmental stimuli. *Plant Physiology*, **105**, 1007–1013.

Casey, T.M. (1976) Activity patterns, body temperature and thermal ecology in two desert caterpillars (Lepidoptera: Sphingidae). *Ecology*, **57**, 485–497.

Chelle, M. (2005) Phylloclimate or the climate perceived by individual plant organs: What is it? How to model it? What for? *New Phytologist*, **166**, 781–790.

Damour, G., Simonneau, T., Cochard, H. & Urban, L. (2010) An overview of models of stomatal conductance at the leaf level. *Plant Cell and Environment*, **33**, 1419–1438.

De Araujo, A.C., Kruijt, B., Nobre, A.D., Dolman, A.J., Waterloo, M.J., Moors, E.J. & De Souza, J.S. (2008) Nocturnal accumulation of CO_2 underneath a tropical forest canopy along a topographical gradient. *Ecological Applications*, **18**, 1406–1419.

De Boer, H., Lammertsma, E., Wagner-Cremer, F., Dilcher, D., Wassen, M. & Dekker, S. (2011) Climate forcing due to optimization of maximal leaf conductance in subtropical vegetation under rising CO_2. *Proceedings of the National Academy of Sciences USA*, **108**, 4041–4046.

Denny, M., Hunt, L., Miller, L. & Harley, C. (2009) On the prediction of extreme ecological events. *Ecological Monographs*, **79**, 397–421.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6668–6672.

Dillon, M.E., Wang, G. & Huey, R.B. (2010) Global metabolic impacts of recent climate warming. *Nature*, **467**, 704–706.

Gates, D.M. (1980) *Biophysical ecology*. Springer-Verlag, New York.

Hanson, P.J., Wullschleger, S.D., Norby, R.J., Tschaplinski, T.J. & Gunderson, C.A. (2005) Importance of changing CO_2, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations. *Global Change Biology*, **11**, 1402–1423.

Heinrich, B. (1971) Effect of leaf geometry on feeding behaviour of caterpillar of *Manduca sexta* (Sphingidae). *Animal Behaviour*, **19**, 119–124.

Helliker, B.R. & Richter, S.L. (2008) Subtropical to boreal convergence of tree-leaf temperatures. *Nature*, **454**, 511–515.

Helmuth, B., Kingsolver, J.G. & Carrington, E. (2005) Biophysics, physiological ecology, and climate change: does mechanism matter? *Annual Review of Physiology*, **67**, 177–201.

Helmuth, B., Broitman, B.R., Blanchette, C., Gilman, S.E., Halpin, P., Harley, C.D.G., O’donnell, M.J., Hofmann, G.E., Menge, B. & Strickland, D. (2006) Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecological Monographs*, **76**, 461–479.

Hering, E.M. (1951) *Biology of leaf miners*. Uitgeverij Dr. E. Junk, Gravenhage.

Hetherington, A.M. & Woodward, F.I. (2003) The role of stomata in sensing and driving environmental change. *Nature*, **424**, 901–908.

Hotta, C., Gardner, M., Hubbard, K., Baek, S., Dalchau, N., Suhita, D., Dodd, A. & Webb, A. (2007) Modulation of environmental responses of plants by circadian clocks. *Plant Cell and Environment*, **30**, 333–349.

Huxman, T.E. & Monson, R.K. (2003) Stomatal responses of C3, C3-C4 and C4 *Flaveria* species to light and intercellular CO_2 concentration: implications for the evolution of stomatal behaviour. *Plant, Cell and Environment*, **26**, 313–322.

IPCC (2007) *Climate change 2007: the physical science basis.Conrtibution of working group I to the fourth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge.

Jarvis, P.G. (1976) The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London B*, **273**, 593–610.

Jones, H.G. (1992) *Plants and Microclimate: a Quantitative Approach to Environmental Plant Physiology*. Cambridge University Press, Cambridge.

Jones, H.G. (1999) Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. *Plant, Cell and Environment*, **22**, 1043–1055.

Juniper, B. & Southwood, R. (1986) *Insects and the plant surface*. Edward Arnold, London.

Kingsolver, J.G. (1979) Thermal and hydric aspects of environmental heterogeneity in the pitcher plant mosquito. *Ecological Monographs*, **49**, 357–376.

Kingsolver, J.G. & Watt, W.B. (1983) Thermoregulatory strategies in *Colias* butterflies: thermal stress and the limits to adaptation in temporally varying environments. *The American Naturalist*, **121**, 32–55.

Labandeira, C.C., Dilcher, D.L., Davis, D.R. & Wagner, D.L. (1994) Ninety-seven million years of angiosperm-insect association: paleobiological insights into the meaning of coevolution. *Proceedings of the National Academy of Sciences USA*, **91**, 12278–12282.

Lammertsma, E., De Boer, H., Dekker, S., Dilcher, D., Lotter, A. & Wagner-Cremer, F. (2011) Global CO2 rise leads to reduced maximum stomatal conductance in Florida vegetation. *Proceedings of the National Academy of Sciences USA*, **108**, 4035–4040.

Layne, J.R.J. (1993) Winter microclimate of goldenrod spherical galls and its effects on the gall inhabitant *Eurosta solidaginis* (Diptera: Tephritidae). *Journal of Thermal Biology*, **18**, 125–130.

Leinonen, I. & Jones, H.G. (2004) Combining thermal and visible imagery for estimating canopy temperature and identifying plant stress. *Journal of Experimental Botany.*, **55**, 1423–1431.

Leinonen, I., Grant, O., Tagliavia, C., Chaves, M. & Jones, H. (2006) Estimating stomatal conductance with thermal imagery. *Plant Cell and Environment*, **29**, 1508–1518.

Leuzinger, S. & Korner, C. (2007) Tree species diversity affects canopy leaf temperatures in a mature temperature forest. *Agricultural and Forest Meteorology*, **146**, 29–37.

Lewinsohn, T.M., Novotny, V. & Basset, Y. (2005) Insects on plants: diversity of herbivore assemblages revisited. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 597–620.

Linacre, E.T. (1964) A note on a feature of leaf and air temperatures. *Agricultural Meteorology*, **1**, 66–72.

Linacre, E.T. (1967) Further notes on a feature of leaf and air temperatures. *Theoretical and Applied Climatology*, **15**, 422–436.

Meyer, K.M. & Leveau, J.H.J. (2012) Microbiology of the phyllosphere: a playground for testing ecological concepts. *Oecologia*, **168**, 621–629.

Miller, D.G.I., Ivey, C.T. & Shedd, J.D. (2009) Support for the microenvironment hypothesis for adaptive value of gall induction in the California gall wasp, *Andricus quercuscalifornicus*. *Entomologia Experimentalis et Applicata*, **132**, 126–133.

Morecroft, M.D. & Roberts, J.M. (1999) Photosynthesis and stomatal conductance of mature canopy oak (*Quercus robur*) and Sycamore (*Acer peusoplatanus*) trees throughout the growing season. *Functional Ecology*, **13**, 332–342.

Morison, J.I.L. (1987) Intercellular CO_2 concentration and stomatal response to CO_2. *Stomatal Function* (eds E. Ziegler, G.D. Farquhar & I. R. Cowan). pp. 229–252. Stanford University Press, Stanford.

Mott, K. & Peak, D. (2010) Stomatal responses to humidity and temperature in darkness. *Plant Cell and Environment*, **33**, 1084–1090.

Nabity, P.D., Zavala, J.A. & Delucia, E.H. (2009) Indirect suppression of photosynthesis on individual leaves by arthropod herbivory. *Annals of Botany*, **103**, 655–663.

Neuwald, J. & Valenzuela, N. (2011) The lesser known challenge of climate change: thermal variance and sex-reversal in vertebrates with temperature-dependent sex determination. *PLoS ONE*, **6**, e18117.

Niehaus, A.C., Angilletta, M.J.J., Sears, M.W., Franklin, C.E. & Wilson, R.S. (2012) Predicting the physiological performance of ectotherms in fluctuating thermal environments. *The Journal of Experimental Biology*, **215**, 694–701.

Nobel, P.S. (1999) *Physicochemical & Environmental Plant Physiology*. Academic Press, New York.

Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M.F., Clissold, F.J., Cornelissen, J.H.C., Diaz, S., Dominy, N.J., Elgart, A., Enrico, L., Fine, P. V.A., Howard, J.J., Jalili, A., Kitajima, K., Kurokawa, H., Mcarthur, C., Lucas, P.W., Markesteijn, L., Perez-Harguindeguy, N., Poorter, L., Richards, L., Santiago, L.S., Sosinski, E.E., Van Bael, S.A., Warton, D. I., Wright, I.J., Wright, S.J. & Yamashita, N. (2011) Global patterns of leaf mechanical properties. *Ecology Letters*, **14**, 301–312.

Oren, R., Sperry, J., Katul, G., Pataki, D., Ewers, B., Phillips, N. & Schafer, K. (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell and Environment*, **22**, 1515–1526.

Peppe, D., Royer, D., Cariglino, B., Oliver, S., Newman, S., Leight, E., Enikolopov, G., Fernandez-Burgos, M., Herrera, F., Adams, J., Correa, E., Currano, E., Erickson, J., Hinojosa, L., Hoganson, J., Iglesias, A., Jaramillo, C., Johnson, K., Jordan, G., Kraft, N., Lovelock, E., Lusk, C., Niinemets, U., Penuelas, J., Rapson, G., Wing, S. & Wright, I. (2011) Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. *New Phytologist*, **190**, 724–739.

Pincebourde, S. & Casas, J. (2006a) Multitrophic biophysical budgets: thermal ecology of an intimate herbivore insect-plant interaction. *Ecological Monographs*, **76**, 175–194.

Pincebourde, S. & Casas, J. (2006b) Leaf miner-induced changes in leaf transmittance cause variations in insect respiration rates. *Journal of Insect Physiology*, **52**, 194–201.

Pincebourde, S., Frak, E., Sinoquet, H., Regnard, J.L. & Casas, J. (2005) Herbivory mitigation through increased water use efficiency in a leaf mining moth-apple tree relationship. *Plant, Cell and Environment*, **29**, 2238–2247.

Pincebourde, S., Sinoquet, H., Combes, D. & Casas, J. (2007) Regional climate modulates the canopy mosaic of favourable and risky microclimates for insects. *Journal of Animal Ecology*, **76**, 424–438.

Pincebourde, S., Sanford, E., Casas, J. & Helmuth, B. (2012) Temporal coincidence of environmental stress events modulates predation rates. *Ecology Letters*, in press doi: 10.1111/j.1461-0248.2012.01785.x.

Potter, K., Davidowitz, G. & Woods, H.A. (2009) Insect eggs protected from high temperatures by limited homeothermy of plant leaves. *Journal of Experimental Biology*, **212**, 3448–3454.

Preece, T.F. & Dickinson, C.H. (1971) *Ecology of leaf surface micro-organisms*. Academic Press, London.

Prytz, G., Futsaether, C.M. & Johnsson, A. (2003) Thermography studies of the spatial and temporal variability in stomatal conductance of *Avena* leaves during stable and oscillatory transpiration. *New Phytologist*, **158**, 249–258.

Raimondo, F., Ghirardelli, L.A., Nardini, A. & Salleo, S. (2003) Impact of the leaf miner *Cameraria ohridella* on photosynthesis, water relations and hydraulics of *Aesculus hippocastanum*. *Trees*, **17**, 376–382.

Reddall, A., Sadras, V.O., Wilson, L.J. & Gregg, P.C. (2004) Physiological responses of cotton to two-spotted spider mite damage. *Crop Science*, **44**, 835–846.

Royer, D.L., Meyerson, L.A., Robertson, K.M. & Adams, J.M. (2009) Phenotypic plasticity of leaf shape along a temperature gradient in *Acer rubrum*. *PLoS ONE*, **4**, e7653.

Sage, R.F. & Kubien, D.S. (2007) The temperature response of C3 and C4 photosynthesis. *Plant, Cell and Environment*, **30**, 1086–1106.

Scherrer, D. & Korner, C. (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology*, **16**, 2602–2613.

Scherrer, D. & Korner, C. (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, **38**, 406–416.

Schuepp, P.H. (1993) Leaf boundary layers. *New Phytologist*, **125**, 477–507.

Sears, M.W., Raskin, E. & Angilletta, M.J. (2011) The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology*, **51**, 666–675.

Sinoquet, H., Le Roux, X., Adam, B., Ameglio, T. & Daudet, F.A. (2001) RATP: a model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: application to an isolated tree crown. *Plant, Cell and Environment*, **24**, 395–406.

Smith, W.K. (1978) Temperatures of desert plants - Another perspective on adaptability of leaf size. *Science*, **201**, 614–616.

Stegemann, J., Timm, H.C. & Küppers, M. (1999) Simulation of photosynthetic plasticity in response to highly fluctuating light: an empirical model integrating dynamic photosynthetic induction and capacity. *Trees - Structure and Function*, **14**, 145–160.

Stone, G.N. & Schonrogge, K. (2003) The adaptive significance of insect gall morphology. *Trends in Ecology and Evolution*, **18**, 512–522.

Strong, D.R., Lawton, J.H. & Southwood, R. (1984) *Insects on plants: Community patterns and mechanisms*. Blackwell Scientific Publications, London.

Tang, J.Y., Zielinski, R.E., Zangerl, A.R., Crofts, A.R., Berenbaum, M.R. & Delucia, E.H. (2006) The differential effects of herbivory by first and fourth instars of *Trichoplusia ni* (Lepidoptera: Noctuidae) on photosynthesis in *Arabidopsis thaliana*. *Journal of Experimental Botany*, **57**, 527–536.

Tewksbury, J.J., Huey, R.B. & Deutsch, C.A. (2008) Putting the heat on tropical animals. *Science*, **320**, 1296–1297.

Van Loon, J.J.A., Casas, J. & Pincebourde, S. (2005) Nutritional ecology of insect-plant interactions: persistent handicaps and the need for innovative approaches. *Oikos*, **108**, 194–201.

Vogel, S. (2009) Leaves in the lowest and highest winds: temperature, force and shape. *New Phytologist*, **1**, 3–26.

Welter, S.C. (1989) Arthropod impact on plant gas exchange. *Insect-plant interactions* (ed. E.A. Bernays), pp. 135–150. CRC Press, Boca Raton, FL, USA.

Wilf, P., Labandeira, C.C., Johnson, K.R. & Ellis, B. (2006) Decoupled plant and insect diversity after the end-cretaceous extinction. *Science*, **313**, 1112–1115.

Willmer, P. (1986) Microclimatic effects on insects at the plant surface. *Insects and the plant surface* (eds B. Juniper & R. Southwood), pp. 65–80. Edward Arnold, London.

Wilson, K. & Bunce, J. (1997) Effects of carbon dioxide concentration on the interactive effects of temperature and water vapour on stomatal conductance in soybean. *Plant Cell and Environment*, **20**, 230–238.

Woods, H.A. (2010) Water loss and gas exchange by eggs of *Manduca sexta*: trading off costs and benefits. *Journal of Insect Physiology*, **56**, 480–487.

Woodward, F.I. (1987) Stomatal numbers are sensitive to increases in CO_2 from preindustrial levels. *Nature*, **327**, 617–618.

Woodward, F.I., Smith, T.M. & Emanuel, R. (1995) A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles*, **9**, 471–490.

Received 17 December 2011; accepted 25 April 2012
Handling Editor: Charles Fox