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Narrow safety margin in the phyllosphere during thermal extremes

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The thermal limit of ectotherms provides an estimate of vulnerability to climate change. It differs between contrasting microhabitats, consistent with thermal ecology predictions that a species' temperature sensitivity matches the microclimate it experiences. However, observed thermal limits may differ between ectotherms from the same environment, challenging this theory. We resolved this apparent paradox by showing that ectotherm activity generates microclimatic deviations large enough to account for differences in thermal limits between species from the same microhabitat. We studied upper lethal temperature, effect of feeding mode on plant gas exchange, and temperature of attacked leaves in a community of six arthropod species feeding on apple leaves. Thermal limits differed by up to 8 °C among the species. Species that caused an increase in leaf transpiration (+182%), thus cooling the leaf, had a lower thermal limit than those that decreased leaf transpiration (−75%), causing the leaf to warm up. Therefore, cryptic microclimatic variations at the scale of a single leaf determine the thermal limit in this community of herbivores. We investigated the consequences of these changes in plant transpiration induced by plant–insect feedbacks for species vulnerability to thermal extremes. Warming tolerance was similar between species, at ±2 °C, providing little margin for resisting increasingly frequent and intense heat waves. The thermal safety margin (the difference between thermal limit and temperature) was greatly overestimated when air temperature or intact leaf temperature was erroneously used. We conclude that feedback processes define the vulnerability of species in the phyllosphere, and beyond, to thermal extremes.

thermal adaptation | leaf temperature | biophysical ecology | extended phenotype | plant–insect interactions

Climate change erodes biodiversity by causing niche shifts and extinctions (1). There is an urgent need to forecast the ecological impact of climate change accurately to anticipate its consequences for land use, the management of pest and invasive species, and biological conservation. Sophisticated statistical approaches have been developed for predicting the impact of climate change on species distributions with little a priori knowledge about the species concerned (2), but only mechanistic approaches can address the question as to how climate change will affect species (3, 4). Recent approaches have integrated physiological traits, including the thermal tolerance limits of species, with the biophysical modeling of ectotherm body temperature to depict relationships between microhabitat choice and the physiological limits of ectotherms in changing environments (5–7). These studies constitute a major step forward, but they consider physiological limits in terms of coarse-scale climatic variables, largely ignoring microclimate diversity at finer scales (8–11). This is problematic, as patterns in the physiological limits of ectotherms are better explained by environmental gradients than by macroecological processes (12, 13).

Thermal tolerance limit is currently the best available metric for assessing the thermal safety margin available to ectotherms. Macroecological studies on high-temperature tolerance limits in ectotherms have demonstrated only a weak latitudinal trend, with tropical species slightly more tolerant than temperate ectotherms in general (14, 15). Thermal tolerance limits may be phylogenetically constrained, and the relatedness of species may limit opportunities for local adaptation (16, 17). Alternatively, according to thermal ecology theory, thermal tolerance limit is a trait adapted to the microenvironmental conditions experienced by the organism (18). These microclimatic conditions may display a high degree of spatial variability and heterogeneity such that the use of a geographic scale is likely to blur patterns of local adaptation seen at the scale of the microhabitat (19–21). The interspecific variability of upper thermal tolerance limits, particularly at temperate latitudes (14), can be explained by the predictions of thermal ecology theory: The thermal tolerance limits of ectotherms may differ between contrasting microhabitats present in the same local area (12, 19, 22), but they may also differ between species living in the same microhabitat (23). The determination of macroecological patterns, therefore, requires comparative data for the various communities living at each site and in each microhabitat, and such knowledge is not yet available. We investigated the role of fine-scale microclimate variations as a driver of thermal limit diversity in a community of arthropods living on leaves. Even if different species seem to use the same microhabitat (e.g., the leaf surface), they may experience contrasting microclimatic conditions due to the subtle changes in the thermal properties of the leaf microhabitat that they introduce. We focus on thermal extremes because they directly determine survival and because the comparison of their metrics with thermal tolerance limits is straightforward (24).

Significance

The thermal limits of terrestrial ectotherms vary more locally than globally. Local microclimatic variations can explain this pattern, but the underlying mechanisms remain unclear. We show that cryptic microclimatic variations at the scale of a single leaf determine the thermal limit in a community of arthropod herbivores living on the same host plant. Herbivores triggering an increase in transpiration, thereby cooling the leaf, had a lower thermal limit than those decreasing leaf transpiration and causing the leaf to warm up. These subtle mechanisms have major consequences for the safety margin of these herbivores during thermal extremes. Our findings suggest that temperate species may be more vulnerable to heat waves than previously thought.

Author contributions: S.P. and J.C. designed research; S.P. performed research; S.P. and J.C. analyzed data; and S.P. and J.C. wrote the paper.

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See Commentary on page 5220.

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The plant leaf surface, or phyllosphere, hosts a tremendous diversity of communities (25, 26). The phylloclimate is defined as the microclimatic conditions occurring at the phyllosphere (27, 28). Leaves absorb some of the energy from the radiation they intercept, but they also lose energy during evapotranspiration and exchange convective energy with the surrounding air (29–31). Leaf surface temperature may, therefore, deviate from the temperature of the surrounding air by several degrees (28, 32–35). Leaf surface temperature can affect the temperatures experienced by arthropods small enough to be embedded within the leaf boundary layer (36–39). The thermal tolerance limits of ectotherms living within the leaf boundary layer in relation to leaf surface temperature patterns have never before been studied, despite species-specific herbivore-induced modifications to leaf surface temperature (37). However, an analogous situation has been described for ants living in different boundary layers across the vertical gradient of trees (12).

Leaf surface temperature is modulated by leaf ecophysiology, in particular stomatal behavior, which sets leaf transpiration rate (40). All else being equal, lower levels of transpiration (stomata closed) cause the leaf surface to warm up, whereas higher levels of transpiration (stomata open) are associated with a cooling of the leaf surface. Leaf transpiration responds to diverse factors, including temperature and light (41). Leaf transpiration is also affected by biotic stresses. Arthropod herbivores feeding on leaf tissues induce marked changes in leaf ecophysiology (42–44). Some species, such as aphids, increase transpiration by causing the stomata to open, whereas others, such as spider mites, reduce leaf transpiration by causing stomatal closure or dry necrosis (44). Thus, arthropods causing a decrease in leaf transpiration should also cause an increase in leaf surface temperature. According to thermal ecology predictions, these arthropods should have higher thermal limits than species that increase leaf transpiration and cool the leaf surface. We tested this prediction by comparing the thermal limits of herbivore species and the leaf temperature resulting from their feeding on a leaf during extreme thermal events.

We studied a community of six phytophagous arthropod species feeding on the same host plant (apple leaves) to avoid any confounding effects of host-plant species. The influence of each species on leaf photosynthesis rate was used as an indicator of the degree of injury caused by feeding (three of the species considered are tissue piercers, two are phloem feeders, and one is a leaf miner; detailed life histories are in *SI Appendix*, Box 1). The species were studied separately to prevent confounding interspecific interactions. We investigated the link between thermal tolerance limits and leaf temperatures during the early development of populations on leaf surfaces, when the leaves are still photosynthesizing. We described and identified the mechanisms underlying the relationship between leaf transpiration and thermal tolerance limits in three steps. We first obtained a phenomenological description. The thermal tolerance limits of the different species [upper lethal temperature (ULT), defined as the temperature causing 50% mortality in a given group after exposure for 1 h to the experimental temperature (13)] and the gas exchanges in the leaves (photosynthesis, transpiration rate, and stomatal conductance) attacked by each species were measured under optimal conditions. The shape of the relationship between thermal limit and leaf transpiration rate was used to assess the link between the feeding mode of the herbivores and their tolerance of high temperatures. The temperature of attacked leaves was measured for most species under moderate conditions to determine the direct effect of herbivores on their host leaf's temperature. We then performed a mechanistic analysis to determine whether the temperature of the attacked leaf during thermal extremes could account for ULT variations in the arthropod community studied. We modified the "classic" biophysical model of leaf temperature (29) for this purpose, by including ecophysiological parameters corresponding to the effects of each arthropod on the leaf, to predict the temperature of the leaf attacked by each herbivore species under extreme thermal conditions (high air temperature and high levels of solar radiation). Finally, we carried out a vulnerability analysis, in which we used a combination of thermal tolerance limits and leaf temperatures to determine the tolerance of the various species to warming. We explored the feedback loop between herbivores and their plant environment, by determining the extent to which the predicted warming tolerance of each arthropod species was biased if the subtle mechanisms by which herbivores modify their thermal environment were ignored, with cascading effects on the thermal tolerance limit of the species concerned.

Results

Thermal Limits and Plant Gas Exchange. In a dynamic ramping assay reflecting the thermal conditions at the leaf surface in the field when the surrounding temperature is increasing (see *Materials and Methods*), we found that the ULT of the six species differed by up to 8.5 °C (Fig. 1). ULT ranged from 37.4 °C for the rosy apple aphid to 45.9 °C for the two-spotted spider mite. Overall, tissue piercers (spider mites and the lace bug) had a higher ULT than phloem feeders (the two aphid species considered). The leaf miner was intermediate: Its fourth stage had a ULT close to that of phloem feeders, whereas the ULT of its fifth stage was close to that of tissue piercers (Fig. 1). For all species, the logistic dose–response curve fitted survival rate as a function of experimental temperature well ($R^2 > 0.78$ and $P < 0.05$ for all; see detailed statistics in *SI Appendix*, *Supplemental Information S1* and Table S1).

We used an infrared gas analyzer to measure assimilation rate, transpiration rate, and stomatal conductance on leaves attacked by the arthropod species, under optimal conditions for apple leaves (45, 46): irradiance, 1,500 $\mu mol \cdot m^{-2} \cdot s^{-1}$; leaf temperature, 25 °C; water vapor deficit, 1 kPa; and CO_2 concentration in the air, 390 ppm (see *Materials and Methods*). The various herbivore species had different effects on plant gas exchange during early infestation. Phloem feeders increased assimilation rates, whereas tissues piercers impaired photosynthesis little, if at all (ANOVA: $F_{7,112} = 8.26$, $P < 0.001$, Fig. 2). A similar ranking of effects was obtained for stomatal conductance (ANOVA: $F_{7,112} = 40.69$, $P < 0.001$, *SI Appendix*, *Supplemental Information S2*) and leaf transpiration rate (ANOVA: $F_{7,112} = 28.36$, $P < 0.001$, *SI Appendix*, *Supplemental Information S2*). Phloem feeders increased leaf transpiration rate, whereas tissue piercers tended to decrease transpiration rate.

The link between thermal limits and plant responses to herbivory was analyzed by focusing on leaf transpiration rate, because this response variable is the one with the most direct effect on leaf temperature. ULT was correlated with the transpiration rate of attacked leaves under optimal conditions, with a nonlinear trend (Fig. 3; power regression analysis, $y = ax^b$: $a = 44.47$, $b = -0.14$, $R^2 = 0.71$, $F_{1,5} = 12.49$, $P = 0.017$). Species inducing an increase in leaf transpiration rate had a lower ULT than those decreasing leaf transpiration rates. The temperature of leaves attacked by the species inducing the most extreme changes in leaf transpiration matched the expectations (Fig. 3): The two-spotted spider mite caused a decrease in leaf transpiration rate and lived at a surface 8 °C warmer than the air, while the green apple aphid increased leaf transpiration and developed at a leaf temperature only 1 °C above ambient air. Further experimental support, including a fully coherent ranking of all species, was obtained in the highly unnatural environment of the leaf chamber of the LI-6400 (LI-COR Inc.) gas analyzer (*SI Appendix*, *Supplemental Information S3*).

Biophysical Modeling. We used a biophysical model to calculate mean leaf temperature as a function of the environmental

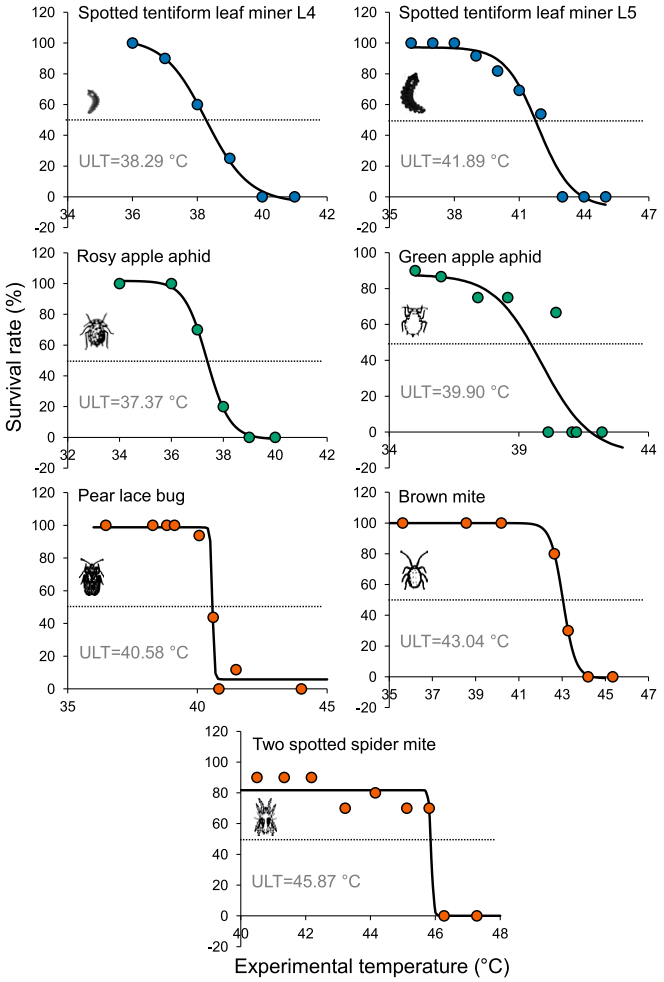


Fig. 1. Determining the ULT of species. The survival rate of each group is shown as a function of experimental temperature. Each dot represents the result for a group (n = 10 to 15 individuals). The curves are logistic dose–response fits. The intersection of the nonlinear regression line and the 50% threshold (horizontal dashed lines) corresponds to the ULT (indicated in gray type). Colors indicate feeding guild: phloem feeder (green), leaf miner (blue), and tissue piercer (orange). Species included spotted tentiform leaf miner, *Phyllonorycter blancardella*; rosy apple aphid, *Dysaphis plantaginea*; green apple aphid, *Aphis pomi*; pear lace bug, *Stephanitis piri*; brown mite, *Bryobia rubrioculus*; and two-spotted spider mite, *Tetranychus urticae*.

conditions and properties of intact and attacked leaves. We then compared the temperatures of leaves attacked in extremely hot conditions with the thermal limits of the arthropod species studied. The biophysical model is based on a leaf heat budget, taking into account transfers of heat between the leaf and its surroundings. It includes the heat gained or lost during the absorption and emission of radiation, convective and conductive transport, and evapotranspiration via stomata (29, 40). The classic version of the leaf heat budget model (29) was used to calculate the mean temperature of intact leaves (*SI Appendix, Supplemental Information S4*). Modified versions of this model were then used to simulate the temperature of leaves attacked by the various arthropods under extreme air temperatures (*SI Appendix, Supplemental Information S4*). The main parameter of the model including the effects of the herbivores considered was stomatal conductance, resulting in changes in leaf transpiration rates. The models were run with environmental parameters set to values corresponding to extreme climatic events (high levels of radiation, low wind speed; see *Materials and Methods*). In particular, the simulations were performed with different air temperatures, corresponding to the 90th, 95th, 99th, and 99.9th percentiles of the hourly air temperature distribution for 2012 near Tours, France (27.4 °C, 29.7 °C, 33.6 °C, and 37 °C, respectively; *SI Appendix, Supplemental Information S5*). These quantiles are often used to describe thermal extremes (24, 47).

Unsurprisingly, the model predicted an increase in the temperature of the attacked leaf with increases in the temperature of the atmosphere, for all species (Fig. 4). Nevertheless, leaf temperature differed among the arthropod species considered, depending on their effect on leaf transpiration rate at a given environmental temperature. Phloem feeders systematically experienced cooler leaf temperatures than tissue piercers, for all surrounding air temperatures considered (Fig. 4*A*). Phloem feeders were predicted to decrease leaf temperature, whereas tissue piercers were expected to increase leaf temperature. These herbivore-induced changes in leaf temperature were linked to effects on gas exchange and latent heat loss (*SI Appendix, Supplemental Information S6*). The leaf miner species again yielded intermediate results, depending on larval stage (Fig. 4*A*). The excess leaf temperature (number of degrees above the temperature of the surrounding air) was systematically smallest for species inducing an increase in transpiration rate (Fig. 4*B*). Overall, the difference in excess temperature between the two most extreme species (two-spotted spider mite versus the rosy apple aphid) was about 4 to 5 °C. Finally, ULT was correlated with the temperature of the attacked leaf at all surrounding air temperatures used in the model (Pearson correlation coefficient between 0.76 and 0.84, $P < 0.05$; *SI Appendix, Supplemental Information S7*). The environmental temperature corresponding to the 99th percentile of the air temperature distribution (i.e., 33.6 °C) was considered a thermal danger to about half the species considered (Fig. 5).

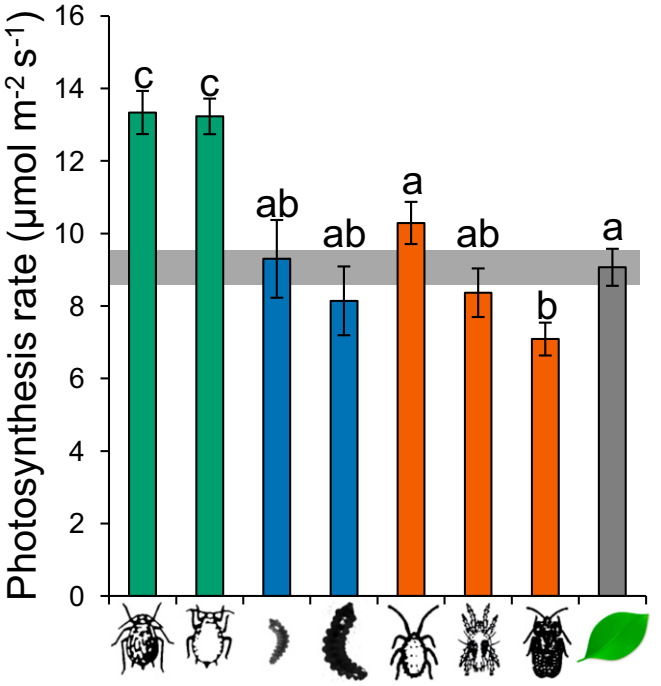


Fig. 2. The effect of arthropod feeding mode on plant performance. The photosynthesis rate (mean ± SEM) of the leaves attacked by each herbivore species is shown, ranked by feeding mode: phloem feeding (green), leaf mining (blue), and tissue piercing (orange). The gray bar and the gray horizontal band represent the mean photosynthesis rates of intact leaves (±SEM). Identical letters indicate a lack of significant difference.

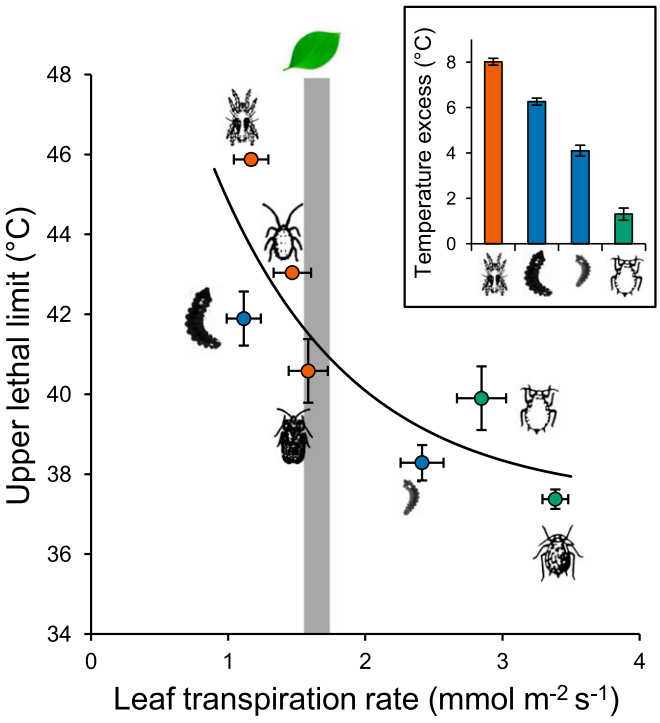


Fig. 3. The thermal tolerance limit of arthropods is related to their effect on leaf transpiration. The ULT (estimated from the nonlinear regression ± 95% confidence interval) is shown as a function of the transpiration rate of attacked leaves (mean ± SEM). The vertical gray bar indicates the mean transpiration rate of intact leaves as a reference. Colors indicate feeding mode (green, phloem feeding; blue, leaf mining; orange, tissue piercing). The regression line is a power function. *Inset* shows the temperature excess (leaf minus air temperatures; mean ± SEM) of leaves attacked by three of the considered species, illustrating the thermal effects of herbivore feeding.

Vulnerability Analysis: Warming Tolerance. We analyzed vulnerability to extreme heat events by calculating the warming tolerance of each species. Warming tolerance is defined as the difference between the temperature experienced and the thermal tolerance limit (48, 49). A positive warming tolerance indicates that the insect can tolerate warming, up to a certain amplitude, before 50% of the population dies. By contrast, a negative warming tolerance indicates that the tolerance threshold has already been exceeded and that further increases in temperature are likely to prove fatal. We calculated three different warming tolerance metrics with various degrees of tightness of coupling between the arthropod and the leaf (13, 49). First, the realized warming tolerance was calculated as the difference between the temperature of the leaf attacked and the ULT for each species. The outputs of the biophysical model at different air temperature values (see above) were used for this calculation. Second, the approximate warming tolerance was calculated with intact leaf temperature and used to quantify the effect of the herbivore-induced changes in gas exchange on warming tolerance. Third, the naive warming tolerance of each species was calculated, based on air temperature, to quantify the error of prediction due to a lack of consideration of the microclimatic component. The warming tolerance metrics were calculated for the environmental temperature corresponding to the 99th percentile of the air temperature distribution (i.e., 33.6 °C).

The realized warming tolerance (i.e., taking the temperature of the leaf attacked into account) differed between species and was generally small. The two spider mite species (tissue piercers) had the highest warming tolerance levels (2 to 3 °C), whereas phloem feeders were either close to the thermal danger threshold or had already crossed it (Fig. 6). The leaf miner was not tolerant to this extreme air temperature event. By contrast, a naive approach, ignoring microclimatic temperatures and instead using surrounding air temperature, consistently overestimated warming tolerance by 4 to 12 °C (Fig. 6). The approximate approach, based on leaf temperature, but without taking into account changes in transpiration rate, overestimated warming

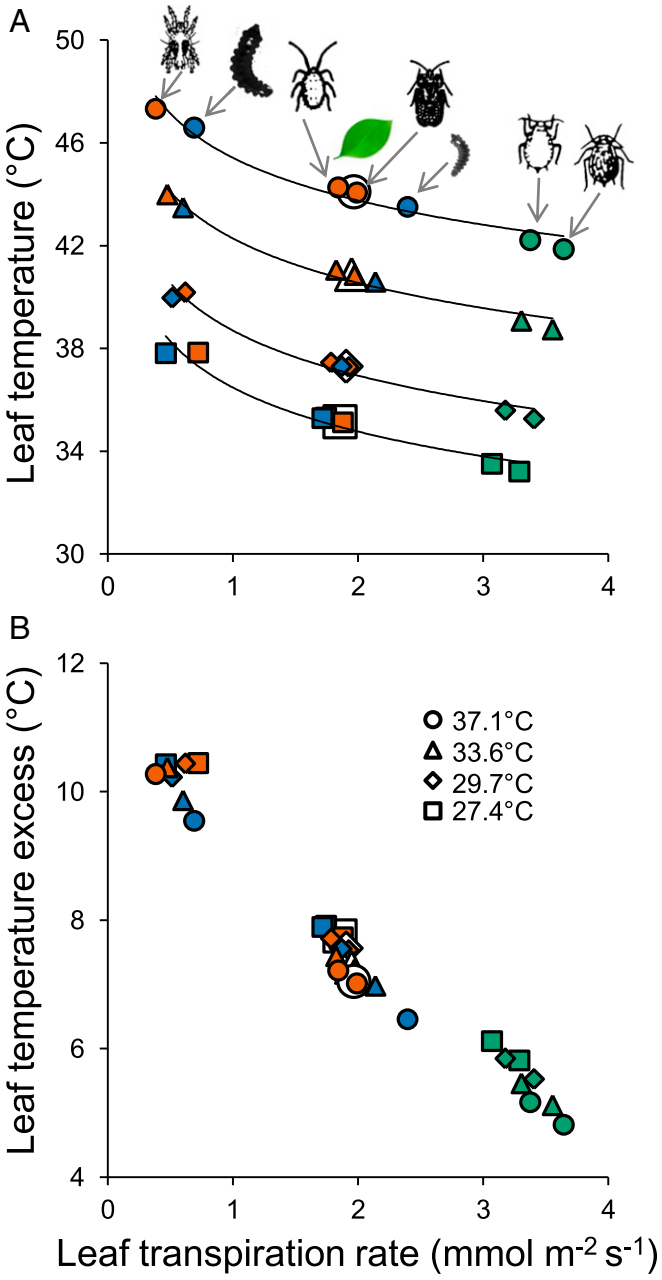


Fig. 4. The temperature of the attacked leaf differs between arthropod species. The simulated attacked leaf temperature (*A*) and the simulated attacked leaf excess temperature relative to the surrounding air (*B*) are shown as a function of the effect of each species on leaf transpiration rate. Model simulations were run at different surrounding air temperatures (□, 27.4 °C; ◇, 29.7 °C; △, 33.6 °C; ○, 37 °C) corresponding to the air temperature extremes for 2012 at the study site. Colors indicate feeding mode (green, phloem feeding; blue, leaf mining; orange, tissue piercing). The large open symbols represent the temperature of the intact leaf. Regression lines are polynomial functions for visual purposes.

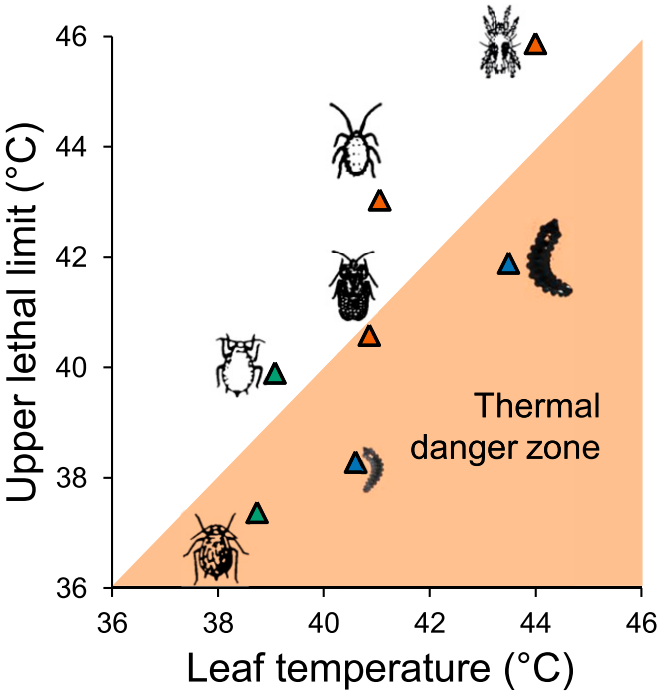


Fig. 5. Leaf temperature during extreme air temperature conditions accounts for thermal limits. The ULT of each species is shown as a function of the simulated attacked-leaf temperature at an air temperature of 33.6 °C, corresponding to the 99th percentile of the air temperature distribution for 2012. Colors indicate feeding mode (green, phloem feeding; blue, leaf mining; orange, tissue piercing). The thermal danger zone (shaded area, delimited by the 1:1 relationship) represents the area of the graph in which the microclimatic temperature exceeds the ULT.

tolerance for spider mites and underestimated it for phloem feeders and the fifth larval stage of the leaf miner (Fig. 6). The warming tolerance of the lace bug was well predicted by intact leaf temperature, because this species has little influence on leaf gas exchange. The amplitude of the bias in warming tolerance prediction was generally linked to herbivore-induced modifications to leaf ecophysiology (*SI Appendix*, *Supplemental Information S8*).

Discussion

Despite the differences in ULT between tissue piercers and phloem feeders, both had realized warming tolerances of the same order of magnitude, ±2 °C, leaving little opportunity to cope with extreme events. This narrow safety margin during extreme heat is much smaller than previously suggested (6, 48, 50). Thermal ecology theory explains the interspecific variability of thermal limits when the subtle processes through which organisms modify their microhabitat are taken into account. This theory can thus be applied to many other systems to determine the thermal safety margin of ectotherms more globally. Other organisms living on the leaf surface, such as phytopathogens, are directly influenced by leaf temperature (51). These fungi and bacteria often modify leaf ecophysiology, including transpiration rate (52). Furthermore, many entomopathogenic bacteria and viruses make use of the leaf surface to infest new insect hosts (53), and their propagation is undoubtedly driven by leaf temperature. This same principle applies to host–parasite relationships. The thermal biology of parasites relative to hosts determines infection risk (54, 55), but parasite species can have markedly different thermal limits (56). Herbivorous arthropods are themselves hosts to various parasites and parasitoids, which are in turn dependent on the thermal dynamics induced by their hosts. Finally, ecosystem engineers generally create new environments that are not necessarily linked to another trophic level (57). Nothing is known about the thermal limits of ecosystem engineers, but we would expect there to be a relationship, at the local scale, between their thermal limits and the thermal environment they create, resulting in small thermal safety margins for these organisms too.

Our biophysical modeling approach has limitations, however, because it focuses exclusively on air temperature as the primary environmental driver of leaf energy budgets (29, 58). Other factors, such as wind, shade, and drought, probably also modulate microclimatic temperatures (*SI Appendix*, *Supplemental Information S9*). In addition, biophysical models predict the mean temperature of a leaf surface (29), but temperature is heterogeneous over the surface of the leaf (33), and arthropods can make use of this heterogeneity for behavioral thermoregulation (36, 37) (*SI Appendix*, *Supplemental Information S9*). Finally, the quantification of thermal extremes may be more complex than simply determining distribution quantiles (24, 47). Our approach was designed to focus on thermal extremes that are challenging the thermal limits of arthropods at the leaf surface. We quantified the thermal safety margin of these herbivores under the worst possible extreme scenario without thermoregulation.

The Thermal Tolerance Thresholds of Herbivores. An understanding of the thermal biology of species is crucial for assessments of the vulnerability of organisms to changing climates (5). The thermal tolerance limits of ectotherms vary locally along thermal gradients, as elegantly demonstrated for ants (12) and frogs (22) across vertical forest gradients and for crabs in the rocky intertidal ecosystem (19). In these examples, thermal tolerance limits varied by 5 to 10 °C. Here, a similar amplitude of variation in thermal limits was measured for a community of herbivorous

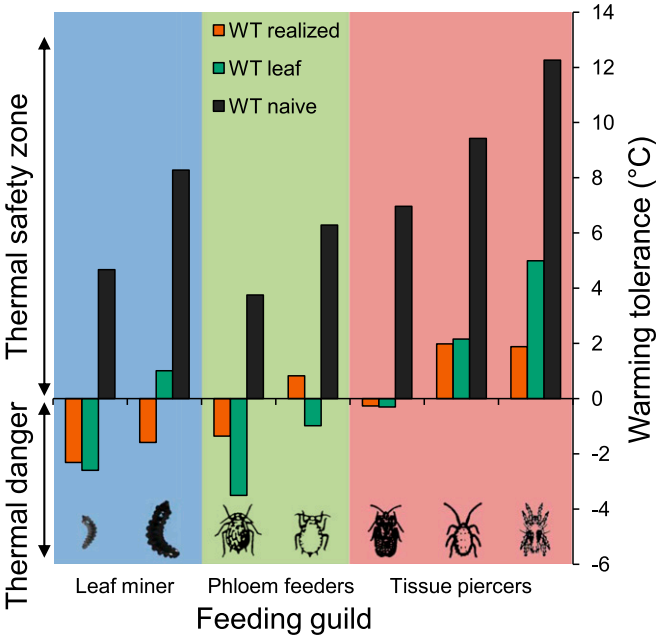


Fig. 6. Thermal safety margin as function of the tightness of coupling between the herbivore and the leaf. The warming tolerance (WT) of each arthropod species was calculated using the surrounding air temperature (black bars, erroneous naive approach), the temperature of intact leaves (green bars, a mostly erroneous approach), and the attacked-leaf temperature (orange bars, the best estimate). Warming tolerance quantifies the amplitude of warming that a species can tolerate before it dies under a given set of conditions. Herbivorous species are arranged according to their feeding guild (background colors: blue, leaf miners; pale green, phloem feeders; pink, tissue piercers); see Fig. 1 for the names of the species.

arthropods inhabiting the same microhabitat, the phyllosphere. The thermal limits of the six species studied here varied by 8.5 °C. Phloem feeders (aphids) were less tolerant to high temperatures than tissue piercers (spider mites), and the leaf miner was intermediate between the two, with variation during development. About 62% of the variability in thermal tolerance limits in these species can be explained by herbivore-induced leaf temperature. Indeed, the changes in transpiration rate generated differences in leaf temperature of 5.26 °C (with a range of 8.5 °C for thermal limits). This variability is similar to the range of critical temperatures reported for arthropods at the same latitude (14, 59) (*SI Appendix*, *Supplemental Information S10*). The microclimate of species at a very fine scale may, therefore, account for much of the variability of critical or lethal temperatures for ectotherms.

Damage and Plant Ecophysiology. Various effects on leaf ecophysiology were observed, depending on feeding mode, consistent with the findings of previous broad-scale studies on the effects of insect-mediated injury on plant gas exchange (44, 60). Tissue piercers reduced transpiration rate (by 75% for the two-spotted spider mite), whereas phloem feeders increased transpiration rates (by 182% for the rosy apple aphid). Tissue piercers, such as mites and bugs, severely damage leaf tissues by piercing mesophyll cells to feed on their contents (61, 62). This activity does not necessarily influence plant gas exchange at low-to-moderate herbivore densities (63). However, at higher densities, decreases in leaf transpiration and rates of photosynthesis are commonly observed after tissue-piercer feeding (62). By contrast, phloem feeders, such as aphids, can induce an increase in stomatal conductance and photosynthesis rate (64, 65). Evapotranspiration may sometimes occur through the injuries caused by the stylet, which must be inserted through the leaf epidermis to reach the phloem (66). The leaf miner is a particular case, with a gradual decrease in leaf transpiration rate from the fourth to fifth larval stage, due to the induction of stomatal closure (13). Thermal limits are known to vary with larval stage in several insects (67, 68), and we suggest that the temporal dynamics of their leaf microclimate can account for much of this developmental variation.

The Thermal Biology of Communities. The subtle effects of each herbivore on gas exchange in its host plant have implications at the community scale. With the exception of the two aphid species, these herbivores are only rarely found together on the same apple tree, although they can coexist in the same orchard. Strong competitive interactions between these herbivores probably prevent them from coexisting on the same leaves at the same time in the growing season, although competition by exclusion alone may be too simplistic to explain herbivore assemblages (69). The two aphid species can be observed on the same apple tree, but on different leaves (70, 71): The rosy apple aphid mostly develops on leaves in the shade, whereas the green apple aphid is found on apical leaves exposed to full sun (72). This suggests niche partitioning consistent with their thermal tolerance limits, but this process has never been studied in detail in these species. The application of thermal adaptation theory to our findings would result in a prediction that the two-spotted spider mite, which has the highest ULT, should exclude the other herbivores under extreme environmental conditions if all are present on the same plant at the same time. However, there are currently no data available to test this prediction. In addition, this ranking of potential competitors may vary across the temperature range, because the thermal optima for development differ between these herbivores: about 30 to 35 °C for the two-spotted spider mite (73, 74) versus ∼28 °C for the green apple aphid (75). Spider mite populations may, therefore, perform less well than aphids at temperatures below 30 °C. Communities of arthropods in the phyllosphere could be used as a system model to link community processes and microclimate mosaics within especially complex microhabitats, particularly given that plant biochemistry can also modulate herbivore interactions (76).

Ectotherms Are More Vulnerable to Thermal Extremes than Previously Thought. We explored the consequences of the subtle mechanism of thermal adaptation in these herbivores on their level of tolerance to extreme heat. The more tolerant species (tissue piercers) already inhabit a warmer microclimate than phloem feeders. We therefore need to integrate both thermal tolerance limits and the effect of warming on the insect microclimate into our analyses (13, 49). Phloem feeders were found to be slightly more vulnerable than tissue piercers, suggesting that particular groups may be more at risk than others under climate change, depending on feeding mode. The large discrepancies between the realized and naive warming tolerances (up to 12 °C) highlight the huge error of prediction that can occur if vulnerability to climate change is investigated without taking the microclimate into account. Even worse, most studies of global change use monthly mean air temperature to calculate these vulnerabilities (11). Unfortunately, such approaches buffer single extreme events sufficient to kill a significant portion of the populations present. Overall, environmental temperatures above the 99th percentile of the distribution for 2012 constituted a thermal danger for half the herbivore species studied (Fig. 5). This result suggests that (*i*) high-resolution sampling of environmental variables is essential to capture these rare extreme events, and (*ii*) a detailed understanding of the microclimate of species is required to determine the extent to which environmental variables are filtered at the scale of the organism. These aspects are particularly crucial for temperate ectotherms (as studied here), which already experience thermal extremes close to those observed in the tropics (47). Moreover, the amplitude of change in these thermal extremes due to climate change is greater in temperate regions than at low latitudes (47). Unlike the forest understory (22, 77), temperate phylloclimates are magnifying these thermal extremes, thereby placing species inhabiting the phyllosphere at greater risk of extinction.

Materials and Methods

Plants and Insect Species. The species were collected in the apple orchard of La Morinière, close to the laboratory (47°09′ N, 0°35′ E; elevation, 95 m above sea level). Each species was collected in a different year because they were not all present simultaneously: two spider mite species (the two-spotted spider mite *Tetranychus urticae* and the brown mite *Bryobia rubrioculus*) in 2011, two aphid species (the green apple aphid *Aphis pomi* and the rosy apple aphid *Dysaphis plantaginea*) and the spotted tentiform leaf miner (*Phyllonorycter blancardella*) in 2012, and the pear lace bug (*Stephanitis piri*) in 2015. All arthropods were subsequently reared on 1- to 2-y-old apple seedlings (*Malus domestica*, Golden cultivar) in a greenhouse in Tours, France (47°21′ N, 0°42′ E). Arthropods from spring generations were used in all experiments. Leaf gas exchange was measured 1 or 2 y after the establishment of the populations on apple seedlings in the greenhouse. Apple seedlings were planted in earthenware pots (11.5 cm in diameter) and watered every 2 d. A nutrient solution was added to the water once weekly (6% nitrogen, 6% P_2O_5, and 6% K_2O, by volume). The daily amplitude of change in conditions was similar throughout the spring and between years (2011–2015) in the greenhouse. In particular, daily air temperature (daily range, 14.5 to 38.5 °C; global mean, 24.4 °C), daily relative humidity (daily range, 29.5 to 95%; global mean, 74%), and radiation load, which was up to 875 W/m^2 at the level of the plants, were similar between years. All measurements (thermal tolerance limits and leaf gas exchange) were made at the same time in the spring of the abovementioned years. For a given species, the thermal limits of different groups of individuals (see below) were measured within the same week, and all individuals experienced very similar daily temperature conditions in the greenhouse during the 2 wk before a given trial (i.e., mean daily air temperature, 25.3 °C; mean daily minimum air temperature, 18.1 °C; and mean daily maximum air temperature, 34.8 °C).

Thermal Tolerance Limits. Thermal tolerance limits were determined by measuring the ULT of the adult stage for all species except the leaf miner, for which tolerance limits were determined at the fourth and fifth larval stages

(this species has five larval stages, which develop within the mined leaf). ULT is defined as the temperature causing 50% mortality in a given group (essentially the LD_{50}) after exposure to the experimental temperature for 1 h (13). Both experimental and modeling studies showed that the daily maximal temperature experienced by these species at the surface of apple leaves or within leaf tissues (leaf miner) lasted no more than about 1 h, at about midday (28, 78, 79). A ramping temperature assay was used to simulate realistic thermal conditions, but see ref. 13 for a discussion on the influence of methodology on thermal limit determination (e.g., time of exposure versus rate of increase in temperature). Field measurements showed that the temperature of apple leaf surfaces and mines exposed to solar radiation changed at a rate of 0.37 °C/min on average (range, 0.11 to 3.35 °C/min) (78). This rate of temperature increase occurs when a surface is exposed to solar radiation in the morning up to noon.

We placed a group of 10 to 15 individuals of a given species in a Petri dish in a climatic chamber (VB 1014-A; Vötsch) and assessed mortality after 1 h of exposure to the experimental temperature. Insects were collected from leaves in the greenhouse in the morning, when air temperature was about 25 °C, and were immediately placed in a Petri dish. Petri dishes (one for each group of insects) were equipped with a fine copper/constantan thermocouple (type T, 0.2 mm in diameter; TC S.A.; connected to a CR1000 station; Campbell Scientific) measuring the temperature inside the dish close to the arthropods. A piece of wet cotton wool was used to generate high humidity within the sealed Petri dish so that organisms did not dry out. After an acclimation period of 15 min at 29 °C, the temperature was ramped up at a rate of 0.32 °C/min until the experimental temperature was reached. The experimental temperature was then maintained for 1 h. Survival was assessed 15 h after treatment. During this 15-h period, the arthropods were kept in the Petri dishes at 25 °C, with a freshly cut apple leaf to prevent deaths due to nutritional stress. The test involved touching the arthropods with a fine needle; those that were alive responded by moving. Possible bias due to thanatosis (individuals pretending to be dead), a particular problem with the lace bug, was overcome by marking the position of individuals in the Petri dish. Individuals were considered to be dead if they did not change position over a period of 30 min. Each group was exposed to a single temperature treatment. In total, 765 individuals were processed.

Leaf Gas Exchange. Gas exchanges were measured with an infrared gas analyzer equipped with a 2 × 3 cm leaf chamber system (LI-6400; LI-COR Inc.) and an external light source (6400-02B; LI-COR Inc.). Assimilation rate, transpiration rate, and stomatal conductance were measured on leaves attacked by the arthropod species, sometimes in a different year for some herbivores. The gas exchanges of intact apple leaves were also measured during each session to ensure that gas exchanges were similar between years. Each session occurred during the same period of the year (May and June) in the greenhouse. Gas exchange was measured under optimal conditions for apple leaves (45, 46): irradiance, 1,500 $\mu mol \cdot m^{-2} \cdot s^{-1}$; leaf temperature, 25 °C; water vapor deficit, 1 kPa; and CO_2 concentration in air, 390 ppm. Leaves were allowed to equilibrate for 20 to 30 min before any measurements were taken, and data were discarded if stomatal conductance was not stable after 45 min. Each session in a given year involved measurements on both attacked and intact leaves. The gas exchanges of intact apple leaves did not differ between sessions. For attacked leaves, the leaf surface was gently brushed with a fine pencil to eliminate any arthropods from the surface so that the gas exchange from the animals did not bias the measurements for the leaf. For the leaf miner, gas exchange in the area of the leaf mine was assessed as previously described (80). Intact portions of leaf around the mine were covered with plant oil to prevent transpiration from intact leaf tissues. Leaves were cut and scanned after measurements. Scans were analyzed with ImageJ software (W. Rasband, NIH) to measure mine areas for the expression of stomatal conductance per unit of transpiring surface.

Different species may be found on leaf cohorts of different ages. The various species overlap (to a large extent) over the leaf age gradient; however, later leaf-miner stages are more frequently found on moderately old leaves, and the green apple aphid is essentially observed on relatively young leaves because it moves to the newly emerging leaves at the top of the shoots. Spider mites and lace bugs can colonize leaves of any age, but their densities result in measurable effects only after several weeks, when the leaves are mature. We therefore sampled gas exchange across a large spectrum of leaf ages (total range, 7 to 100 d; mean leaf age, 36 d for intact leaves, and 40, 36, 34, 56, 52, 41, and 45 d for leaves attacked by the green apple aphid, pear lace bug, brown mite, two-spotted spider mite, spotted tentiform leaf miner fifth and fourth larval stages, and rosy apple aphid, respectively). Mean leaf age was comparable for intact leaves and the leaves attacked by each arthropod species. Herbivore pressure was also standardized for each species according to the level of leaf damage, and not according to the density of the herbivore, because each species has a markedly different population growth rate. Furthermore, similar densities of spider mites and aphids have different effects on leaf ecophysiology, because these species differ considerably in body size, per capita feeding rate, and life span. A single leaf miner causes visible damage to a leaf, whereas the effect of a single spider mite cannot be detected. We therefore measured leaf gas exchange on leaves bearing one to two spotted tentiform leaf miners (focusing on the mined surface only, see method in ref. 80), 10 to 14 brown mite individuals (a leaf can host up to 22 individuals), and 10 to 21 individuals of the two-spotted spider mite. The number of two-spotted spider mites on a single leaf can be much higher, up to several hundreds, but we focused here on the period of population development at the leaf surface before the individuals begin producing silk and living above the leaf surface. In addition, three to 12 pear lace bug adults (a leaf contained up to 15 adults), and 11 to 28 individuals each of the green apple aphid and the rosy apple aphid were used. All these densities correspond to relatively early stages of infestation, and feeding on the plants started several weeks before measurements.

Leaf Temperature Measurements. We measured the temperature of attacked and intact leaves to determine the amplitude of temperature changes induced by the herbivores when feeding on an apple leaf. These measurements were done on key species that showed the most extreme ULTs, namely, the two-spotted spider mite, the spotted tentiform leaf miner, and the green apple aphid. These species were studied separately with a different approach. The temperature of leaves attacked by the two-spotted spider mite ($n = 36$) was measured with a thermal imaging device (B335; FLIR Systems) equipped with a macro lens (10 mm infrared lens; FLIR Systems) as in ref. 36. Leaf temperatures were measured under controlled conditions in a climatic chamber (VB 1014-A; Vötsch): air temperature, 25 °C or 30 °C (we did not observe any difference in leaf temperature excess between these two groups; therefore, we merged them here); relative humidity, 60%; wind speed, 0.3 m/s; and global radiation level, 220 to 240 W/m^2 (see ref. 36 for more details). For the spotted tentiform leaf miner [both L4 ($n = 10$) and L5 ($n = 13$)], the temperature of mines was measured using fine thermocouples as in ref. 45 in the same climatic chamber: air temperature, 25 °C; relative humidity, 65%; wind speed, 0.3 m/s; and global radiation level, 516 to 565 W/m^2 (see ref. 13 for more details). For the green apple aphid, the temperature of attacked leaves was measured in the field, in the same apple orchard as above, using fine thermocouples (copper/constantan, type T, 0.2 mm in diameter; TC S.A.) connected to a weather station (CR1000 equipped with a multiplexer AMT25; Campbell Scientific) set to record temperatures every 10 min. The thermocouples were positioned underneath the surface of five leaves hosting a colony of aphids and five leaves without any aphid on the same apple tree. We extracted the data measured at 1400, 1500, and 1600 hours during 12 cloudless days between June 19 and July 1 in 2012 to report temperatures of attacked leaves when solar radiation was high (mean ± SE, 583 ± 38 W/m^2; range, 147 to 981 W/m^2). Air temperature varied in the range 17.6 to 29.4 °C during that period. All temperature data were merged, since no difference was observed among the time intervals. Finally, we calculated the leaf temperature excess, which is defined as the difference between leaf and air temperatures.

Biophysical Modeling. We used a biophysical model to calculate mean leaf temperature as a function of the environmental conditions and the properties of intact and attacked leaves, for comparison with arthropod thermal limits. The biophysical model is based on a leaf heat budget, with calculation of the heat transfers between the leaf and its surroundings (29, 40). This heat budget model of an intact leaf has been fully validated in various contexts by different groups (28, 30, 32). Modified versions of the classic leaf heat budget model (29) were used to simulate the temperature of leaves attacked by the various arthropods (*SI Appendix, Supplemental Information S4*). For the leaf miner species, we used the biophysical model previously developed for predicting temperatures within leaf mines (13, 45, 78, 79). This model introduces a new term, the heat exchanged between the mine and the adjacent leaf tissues, and considers the change in leaf surface absorbance for incoming radiation and changes in stomatal behavior (*SI Appendix, Supplemental Information S4*). For the other arthropod species, we changed the stomatal conductance parameter in the classic version of the leaf heat budget, except for the two-spotted spider mite, for which the absorbance of the attacked leaf tissues was also modified due to the rapid change in leaf color after spider mite attack (81). For all species, we simulated leaf temperature for the corresponding maximal stomatal conductance. The stomatal responses to temperature, light, and vapor pressure deficit in attacked leaves were considered to be similar to those of intact

leaves (*SI Appendix, Supplemental Information S4*). Stomatal functions reaching a plateau at high temperatures were used, because transpiration rate becomes unresponsive to small changes in temperature and vapor pressure deficit at the extreme end of the range (82). We calculated microclimatic temperatures under constant wind speed (1 m/s) and humidity parameters (relative humidity, 75%). The models do not consider plant water and nutritional limitations but were used to calculate microclimatic temperatures for leaves fully exposed to solar radiation at midday, when the surrounding air temperature reaches the daily maximum. The radiation level was set to 982 W/m^2, corresponding to the 95th percentile of the distribution of hourly global radiation levels for 2012 (*SI Appendix, Supplemental Information S5*). The models were run for different values of air temperature corresponding to the 90th, 95th, 99th, and 99.9th percentiles of the hourly air temperature distribution for 2012 (27.4 °C, 29.7 °C, 33.6 °C, and 37 °C, respectively; *SI Appendix, Supplemental Information S5*). Finally, we compared the temperature of leaves attacked at these air temperatures with the ULT for each species to infer the vulnerability of each species to extreme conditions.

Data Analysis. The ULT of each species was extracted from a logistic regression analysis of survival and temperature. Using TableCurve software (Systat Software), we fitted a logistic dose–response model to data for survival rate as a function of experimental temperature. This nonlinear model contains four parameters, including the LD_{50} value (78, 83). This procedure also estimates the 95% confidence interval of ULT for each species. The influence of each species on leaf gas exchange (assimilation rate, transpiration rate, and stomatal conductance) was then compared using ANOVA, with species as a fixed factor and with the calculation of pairwise probabilities in Fisher's least significant difference test. All the data for leaf gas exchange were normally distributed, with equal variances. The link between ULT and leaf transpiration rate was best described by a power relationship ($y = ax^b$).

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