INVITED REVIEW

Trait Multi-Functionality in Plant Stress Response

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Synopsis Plants often experience multiple stresses in a given day or season, and it is self-evident that given functional traits can provide tolerances of multiple stresses. Yet, the multiple functions of individual traits are rarely explicitly considered in ecology and evolution due to a lack of a quantitative framework. We present a theory for considering the combined importance of the several functions that a single trait can contribute to alleviating multiple stresses. We derive five inter-related general predictions: (1) that trait multifunctionality is overall highly beneficial to fitness; (2) that species possessing multifunctional traits should increase in abundance and in niche breadth; (3) that traits are typically optimized for multiple functions and thus can be far from optimal for individual functions; (4) that the relative importance of each function of a multifunctional trait depends on the environment; and (5) that traits will be often "co-opted" for additional functions during evolution and community assembly. We demonstrate how the theory can be applied quantitatively by examining the multiple functions of leaf trichomes (hairs) using heuristic model simulations, substantiating the general principles. We identify avenues for further development and applications of the theory of trait multifunctionality in ecology and evolution.

Introduction

Plants are adapted to a sessile life, and thus endure fluctuating environmental conditions across days and seasons, including extremes in light, temperature, and water availability, and threats by herbivores, pathogens, and fire. If one defines "environmental stress" as a condition reducing fitness in the absence of adaptation (Hoffmann and Hercus 2000; Del Giudice et al. 2018), plants would generally experience multiple stresses each day, were it not for their adaptations. Adaptation to avoid, reduce, or mitigate stress can be atomized in terms of measures of organism structure and function, referred to as "functional traits," which may be discrete (i.e., present/absent) and/or may vary continuously across species (Ackerly et al. 2000; Ackerly and Monson 2003; Violle et al. 2007). Most studies focus on single roles of given traits (Caruso et al. 2019). Yet, plant stresses are often combined (Grubb 1998; Laanisto and Niinemets 2015), and a given functional trait can provide tolerances of multiple stresses (Table 1;

Gutschick 1999; Givnish 1987; Hoof et al. 2008; Pasquet-Kok et al. 2010; Pivovaroff et al. 2014; Tsujii et al. 2016; Medeiros et al. 2019; Farina et al. 2019; Rosell 2019). No framework has existed to explain why traits have multiple functions, or to quantify the relative importance of each trait function in given environmental contexts.

Here, we present a theory for considering the combined importance of a given trait in alleviating multiple stresses. We then apply the general theory quantitatively using model simulations examining a common plant trait, leaf trichomes (hairs), substantiating the general principles. We identify avenues for further development and refinement of the theory and applications of the theory of trait multifunctionality in ecology, evolution, and genetics.

Basic derivation of the multifunctional impact of given traits on plant fitness

A functional trait may influence any component of fitness—e.g., growth, survival, or fecundity—though

Table 1 Examples of multifunctional traits or structures

	Putative functions	References
Plant structures or structural traits		
Leaf trichome density	Reflection of excess irradiance, leaf wettability, leaf water uptake, boundary layer thickness (and thus, water use efficiency, and control of leaf temperature), protection from herbivory	Ehleringer et al. (1976), Baldocchi et al. (1983), Press (1999), Dalin et al. (2008), (Kenzo et al., 2008), Agrawal et al. (2009), Aryal and Neuner (2010), Fernandez et al. (2014), Bickford (2016), and Tsujii et al. (2016)
Leaf mass per area (LMA)	Higher LMA confers increased leaf lifespan due to mechanical protection, resistance to herbivory, conservative resource use, higher photosynthetic rate per leaf area; lower LMA contributes to greater light capture, and faster growth	Wright et al. (2004), Poorter et al. (2008), and Onoda et al. (2011)
Leaf size	Smaller leaf size reduces overheating under high temperatures (via thinner boundary layer), and/or provides drought tolerance via denser leaf major veins; larger leaves may achieve greater photosynthetic rates in warmer/wetter conditions, larger leaves may have greater light capture per mass invested, and may cast shade on competing plants	Givnish (2008), Scoffoni et al. (2011), Sack et al. (2012), and Wright et al. (2017)
Plant height, and tree growth form	Greater height confers the ability to escape shade, enhanced propagule dispersal, and deeper roots to access nutrients and the water table; short stature confers reduced wind exposure, shorter hydraulic pathlength and corresponds to smaller vessels and potentially greater drought tolerance	Moles et al. (2009), Thomson et al. (2011), and Boyce et al. (2017)
Xylem	Water transport, storage and support, with relative functions depending on allocation to different cell types, i.e., the transport function contributed by the conduits, the water storage by tracheids, and support by tracheids and fibers	Pratt et al. (2008) and Plavcova et al. (2019)
Leaf vein bundle sheath	Sugar loading and unloading from the phloem, water storage, nutrient transport, filtering the transpiration stream, photosynthetic reactions in C_4 species	Griffiths et al. (2013) and Sack and Scoffoni (2013)
Leaf bundle sheath extensions	Light capture, water storage, water transport	Sack and Scoffoni (2013)
Wood density	High wood density corresponds to smaller vessels and potentially increased drought tolerance, as well as mechanical protection and potentially greater resistance of herbivory	Poorter et al. (2008), Zanne et al. (2010), and Reich (2014)
Chemical composition traits		
Leaf nitrogen concentration	Higher N contributes to higher photosynthetic rate, and lower N to reduced palatability to herbivores	Grubb (1998) and Reich (2014)
Leaf silicon concentration	High Si concentration may contribute to generalized abiotic stress tolerance and resistance to herbivory	Cooke et al. (2016) and Deshmukh et al. (2017)
Plant physiological traits		
Transpiration rate	A special case of multifunctionality arising as a side-effect. Transpiration in plants is widely recognized to occur as a consequence of opening stomata for carbon assimilation, because the moist leaf interior is exposed to the desiccating outside air. Thus, transpiration rate is considered to mainly incur costs, in necessitating the construction of roots and transport tissue. However, multiple benefits have accrued to transpiration: Higher transpiration rate may enable leaf cooling and reduce overheating, may increase nutrient transport through soil to leaves, and from roots to leaves.	Gates (1968), Tanner and Beevers (1990, 2001), and Cramer et al. (2009)
C_4 photosynthesis	Tolerance of high temperatures, mild or moderate drought, soil salinity, and low CO_2.	Sage (2004)
Plant volatile emission rates and composition	Plant volatile compounds may act as signals for plant cross-talk, reduce overheating, attract pollinators, deter herbivores directly or by attracting the enemies of herbivores, act in pathogen defense, and contribute to ozone quenching	Pichersky and Gershenzon (2002) and Holopainen (2004)

Traits may be discrete (i.e., present/absent in different species) and/or may very continuously, with the value contributing to variation in function. Putative functions are listed non-exhaustively with references; in some cases multiple functions have been demonstrated in given or different species, and in other cases, controversies have developed over whether one or another function exists or is important.

the specific components of fitness, and their importance, may vary across different species ([Orr 2009](#)). Further, the influence of a trait on any component of fitness would vary according to the environment. We assume that a quantitative trait with a value T influences fitness through a number (J) of functions (f_j) of T and the environment (a vector of environmental variables, $\mathbf{e}$), and also through direct construction and/or metabolic costs that scale with T by a proportionality factor, c (which itself may depend on the f_j and $\mathbf{e}$). Thus,

$$F = g(f_1(T, \mathbf{e}), f_2(T, \mathbf{e}), \ldots, f_J(T, \mathbf{e}), \mathbf{e}) - T \\ \cdot c(f_1(T, \mathbf{e}), f_2(T, \mathbf{e}), \ldots, f_J(T, \mathbf{e}), \mathbf{e}) , \quad (1)$$

where $g()$ is a generic mathematical function describing how the f_j and the environment interact to influence F independent of the trait's costs.

To quantify the dependence of fitness on a trait's multiple functions, one can estimate the effect of an infinitesimal change in T on fitness, which is the sum of the functions' marginal influences (m_j), minus the trait's marginal cost ([Fig. 1](#)):

$$\frac{dF}{dT} = \sum_{j=1}^{J} \frac{\partial g}{\partial f_j} \frac{\partial f_j}{\partial T} - c - T \sum_{j=1}^{J} \frac{\partial c}{\partial f_j} \frac{\partial f_j}{\partial T}$$

$$= \sum_{j=1}^{J} m_j(T, \mathbf{e}) - C(T, \mathbf{e}) , \quad (2)$$

where C $(= c + T \sum_{j=1}^{J} \frac{\partial c}{\partial f_j} \frac{\partial f_j}{\partial T})$ is the marginal cost of the trait; if c does not depend on the functions directly, then C simply equals the unit marginal cost, c.

When natural selection has optimized the value of T, then $dF/dT = 0$, analogous to the equimarginality principle, which holds that profit is maximized when the marginal product of inputs equals their marginal cost (e.g., [Bloom et al. 1985](#)):
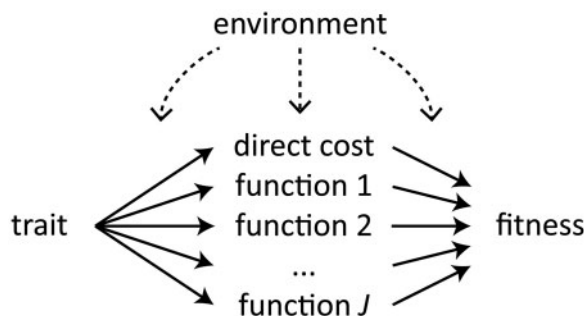

Fig. 1 Multifunctional traits influence fitness through a set of distinct effects (functions), including the direct cost of the trait itself. The dependence of each function on the trait, the functions themselves and the effects of each function on fitness, may each be directly influenced by environmental conditions.

$$\sum_{j=1}^{J} m_j(T, \mathbf{e}) = C \ \left(\text{optimum}\right) . \quad (3)$$

[Equation (3)](#) extends the equimarginality principle to the case where an input (the trait) generates a product (fitness) via multiple "revenue streams" (the trait's multiple functions). The marginal influence of a given function need not be positive: a function may switch from beneficial to detrimental depending on the environmental context. This framework accounts for the array of costs associated with multifunctionality, and accounting for these costs systematically should ensure that simply adding functions to a trait does not artificially inflate the magnitude of F. Given economies of scale with respect to the multiple functions of traits, such that the costs are not always proportional to the benefits, additional functions will tend to increase F.

A finite trait shift (say, from T_1 to T_2) causes a finite change in fitness ($\delta F = F(T_2) - F(T_1)$), which can be deconvolved into *partial influences* (p_j) from each of the trait's multiple functions: i.e., the portions of δF that can be attributed to each function. The partial influences cannot be calculated unambiguously unless $g()$ is linear (in which case they are independent and separable), but one estimate of p_j is the definite integral of m_j over the trait shift:

$$p_j(T_1, \ T_2, \ \mathbf{e}) = \int_{T_1}^{T_2} m_j(T, \mathbf{e}) dT . \quad (4)$$

The partial influences can also be expressed as fractions of the total influence ([Buckley and Diaz-Espejo 2015](#); [Rodriguez-Dominguez et al. 2016](#)), by dividing each by δF to give the *relative influence* (r_j) of function j:

$$r_j = \frac{p_j(T_1, \ T_2, \ \mathbf{e})}{\delta F(T_1, \ T_2, \ \mathbf{e})} , \quad (5)$$

where $\delta T = T_2 - T_1$. The relative influences add to one. If $r_j = 0.75$, for instance, then T impacts fitness mostly (75%) via function j, and the other functions mediate only 25% of the trait's total influence on fitness.

Five predictions of trait multifunctionality

Several key principles emerge from this theory. First, trait multifunctionality should be extremely common. [Equation (1)](#) shows that adopting new beneficial functions for an existing trait enhances fitness without necessarily increasing the trait's cost proportionally. Note that some traits might require

modification to confer an additional function, and this should occur with an economy of scale with respect to cost. For example, leaf trichomes can prevent herbivory by interfering with insect access to the lamina tissue, regardless of the trichome color (Dalin et al. 2008), but if bright in color, they can also reflect excess sunlight, and thus, cost-effective, bright trichomes would be expected (Ehleringer et al. 1976).

Second, species with multi-functional stress tolerance traits should have a wide niche breadth, being favored in any environment that includes at least one of the multiple stresses that the trait mitigates, and being excluded only in environments in which the trait has a net detriment. For example, leaf trichomes may contribute positively to fitness in environments with excess light, herbivores, or both, but would reduce fitness in shady environments lacking herbivores.

Third, from Equation (3), because traits should be optimized for multiple rather than single functions, traits should take values far from their optima with respect to single functions.

Fourth, from Equation (5), a trait's multiple functions can shift in relative importance depending on the environment.

Fifth, the fitness benefit of trait multi-functionality over the evolutionary history of a lineage or a given species explains why traits should frequently be "co-opted" for additional functions, i.e., switch from one role to another (also known as "exaptation"; Gould and Vrba 1982). Indeed, exaptations have been frequently described in biology, with feathers originating before they were used in flight, and metabolism networks shifting in function (Barve and Wagner 2013). Numerous examples occurred in the history of plant life (Table 2). Traits may evolve a new function *de novo* when an environmental stress is relieved, due to climate change or the invasion of a new environment without the stress, given the evolution of a second benefit by slightly shifting the trait would outweigh the trait's cost. Additionally, traits may take on a new function by "pre-adaptation," when a species with a multi-functional trait invades a new environment in which the original stress is absent but the trait mitigates a new stress (Ackerly 2004). Over time, the trait may shift to optimize the new function, and lose effectiveness or relevance for the original function.

Illustrating the benefits of trait multi-functionality quantitatively: the importance of leaf hairstyle

To demonstrate these concepts, we consider leaf trichomes (hairs), an often charismatic trait present in typically >50% of species of diverse ecosystems (Johnson 1975). Trichomes are diverse in structure and density and can provide a range of functions depending on the species, influencing light relations, gas exchange, water uptake, water repellency and protection from herbivory, and thereby contribute critically to environmental tolerances and

Table 2 Examples of trait co-optation hypothesized in the literature

Trait	Context for shift in trait function	Original function(s)	New function	References
Plant cell wall	Algae to land plants	Reduction of volume shrinkage during dehydration stress in algae	Structural support on land	de Vries and Archibald (2018)
Stomata	From the sporophytes of bryophytes to across vascular plants	Aiding the dehydration of spores in the sporophyte	Control of water loss and carbon gain	Duckett et al. (2009), Field et al. (2015), and Brodribb et al. (2020)
High vein density	from C_3 to C_4 species	Increasing the water supply and enabling greater stomatal opening and rates of photosynthetic carbon gain	A component of Kranz anatomy, with Calvin cycle reactions confined to the leaf vein bundle sheaths, an anatomical mechanism enabling the C_4 carbon concentrating mechanism	Sage (2004) and Christin et al. (2013)
Small vessels	In lineages that radiated out of the tropics into the temperate zone	Tolerance of aridity	Tolerance of freeze–thaw embolism	Zanne et al. (2014)
Leaf trichomes (hairs)	In milkweeds	Tolerance of aridity	Tolerance of herbivory	Agrawal et al. (2009)
Urushiol	In species of the Anacardiaceae (e.g., poison ivy)	Reduction of microbe infection and growth	Deterrence of disturbance by humans	Mohan et al. (2006) and Jang et al. (2018)

productivity in crop and non-crop species (Table 1). Research to clarify the roles of leaf trichome density has been hampered by lack of an integrative approach, and thus, leaf trichomes are generally ignored in current models of leaf and plant optical properties, gas exchange, productivity and water use, and trait-based ecological distributions. Yet, characterizing the linkage between structure and function can inform the design of crops with

improved tolerances (e.g., of drought or herbivory), water use efficiency, and productivity (Baldocchi et al. 1983; Peter et al. 1995; Dalin et al. 2008), with potential applications in food security and sustainability, even mitigating regional climate change, e.g., by promoting leaf cooling (Doughty et al. 2011).

We tested the five general principles derived from trait multifunctionality theory with a modeling analysis. We focus on three of the known functions of
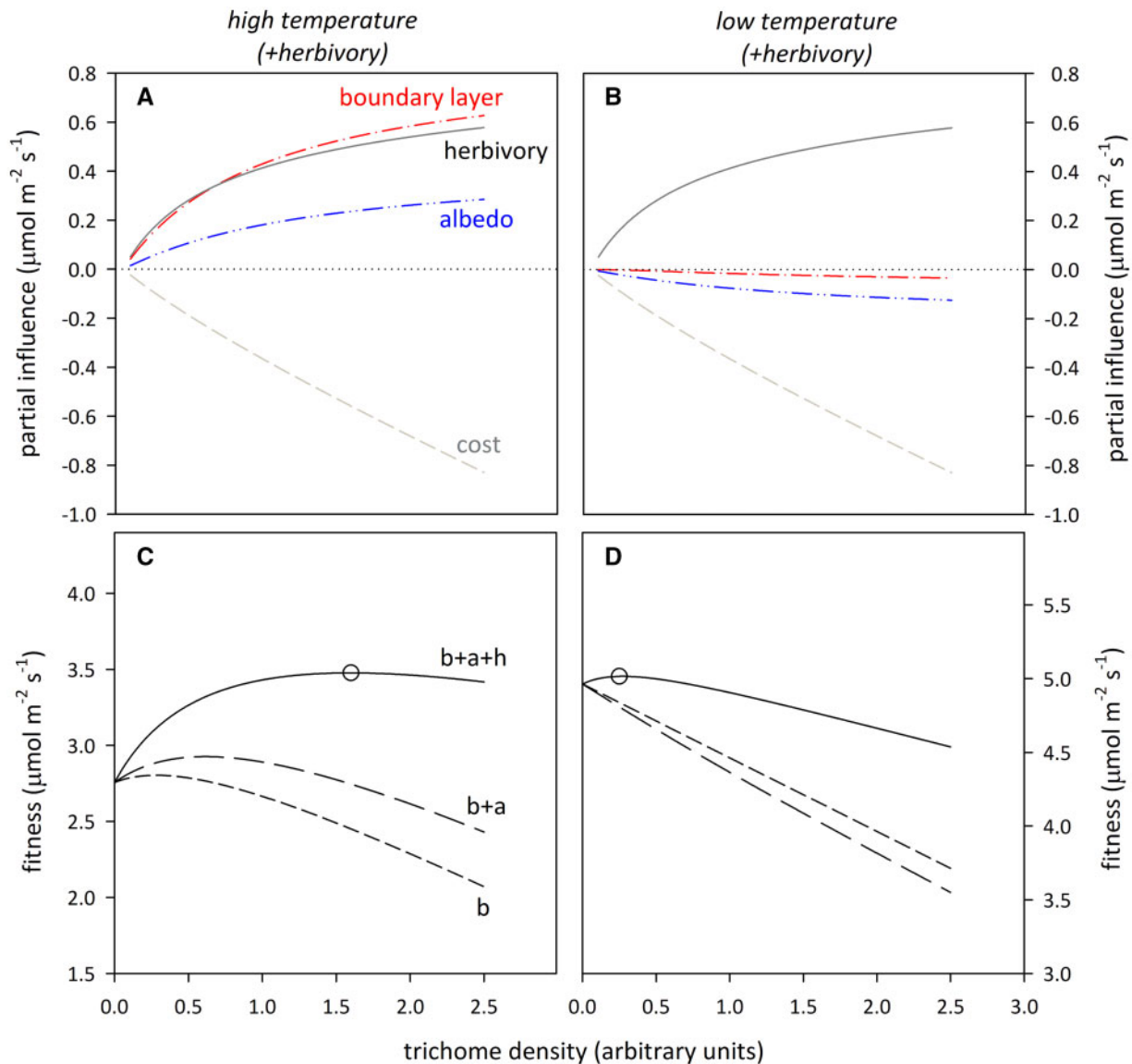

Fig. 2 The fitness advantage of multifunctionality in any given environmental combination. Quantitative partitioning of changes in fitness (mean photosynthetic rate over the leaf's lifespan) caused by increases in a quantitative trait (leaf trichomes, i.e., hairs, in this example), relative to a value of zero for that trait (no trichomes in this case), into contributions ("partial influences"; **A** and **B**) from each of multiple functions and the direct cost of the trait shift, in two environmental conditions (A: 35°C; B: 15°C). In warmer conditions, all three functions of leaf trichomes are beneficial, such that accumulating more functions always improves fitness (**C**: short-dashed line = fitness including only the boundary layer function [b], long-dash = with the albedo function added [b + a], solid line = further adding the herbivory function [b + a + h]). Thus, the optimal value of trichome density (open circle in C) is high. By contrast, in cooler conditions, only the herbivory function is beneficial, so the boundary layer and albedo functions are detrimental (B) and the optimal trichome density is lower (**D**). Note that the partial effects have the same dimensions as the measure of fitness, which in this case is a photosynthetic rate and hence a flux (CO_2 uptake per unit time, per unit leaf area).
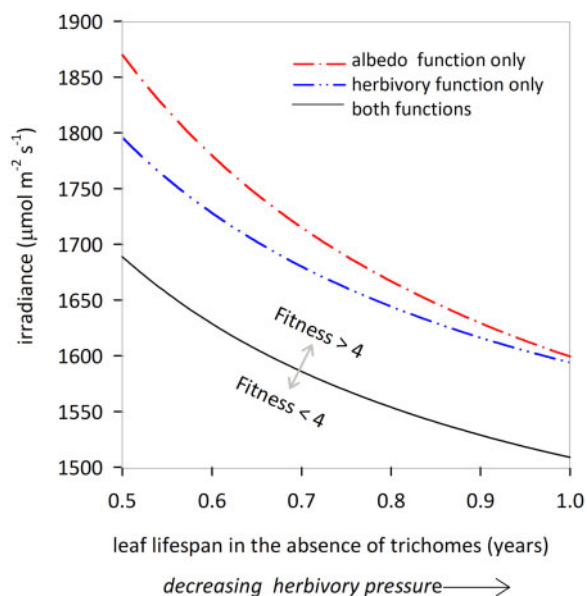
Fig. 3 Multifunctional traits lead to greater fitness across a wider niche breath. In a niche space made up of combinations of high and low irradiance and high and low levels of herbivory (represented here by leaf lifespan in the absence of trichomes), when trichomes confer multiple functions (i.e., reflection of excess irradiance and protection from herbivory), they enable the occupation of a greater niche space, here denoted by the area of the graph above each line (which indicates the conditions for which fitness reaches some threshold above which a species can persist; we used a threshold of 4 μmol m^{-2} s^{-1} here for illustrative purposes). The viable niche space is larger when both functions are included (solid line) than when either function by itself is included (dash-dot lines).
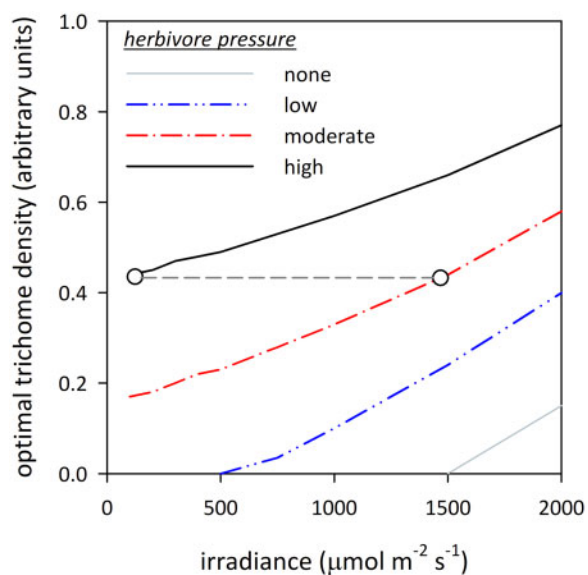

Fig. 4 Traits are optimized according to multiple functions, leading to spurious sub-optimality with respect to single functions. In this example, the optimal value of leaf trichome density increases with both light intensity (irradiance, x-axis) and herbivore pressure (different lines). However, if the herbivore function is not recognized and one compares two populations with different herbivore pressures (e.g., the two open symbols connected with a dashed horizontal line), one may spuriously infer that trichome density is suboptimal with respect to its function for reflecting excess light, or conversely that light intensity is irrelevant to the adaptive significance of leaf trichomes.

leaf trichomes: deterring herbivory, which increases the mean functional lifespan of leaves; increasing leaf boundary layer resistance, which reduces the exchange of water vapor, CO_2, and sensible heat between the leaf and atmosphere; and increasing albedo (reflectance of visible light). The latter two functions may be beneficial in some circumstances and detrimental in others. In the Appendix, we provide heuristic expressions for these functions, and a biophysical model of leaf gas exchange and energy balance, enabling the estimation of how leaf trichomes would influence fitness by impacting the net carbon balance of a leaf over its lifespan.

First, we confirmed a fitness advantage of trait multifunctionality over single functionality in environments with combined stresses, i.e., under very high irradiance (hence high temperature) and herbivory (Fig. 2A, C). In a low-temperature environment, two of the trait's functions are detrimental (Fig. 2B), yet the optimal trichome density is still positive (Fig. 2D) due to the benefit of the herbivory function.

Second, we confirmed that a species with multifunctional stress tolerance traits should increase in abundance across environments. Across a landscape of combinations of high and low irradiance and herbivory, in which one assumes a threshold fitness necessary for persistence, trichome multifunctionality enabled a species to occupy a larger area of niche space (Fig. 3).

Third, we confirmed that the optimal trait value for a multifunctional trait differed from the value which would be calculated with respect to a single function. The optimal value of leaf trichome density varies with irradiance, and, independently, increases with herbivore pressure (Fig. 4).

Fourth, we confirmed that trait functions shift in relative importance depending on the environment, with the importance of trichomes for mitigating high temperatures or herbivory increasing under the appropriate conditions (Fig. 5).

Finally, we confirmed that leaf trichomes should switch in their major function during evolution, i.e., show trait co-optation or exaptation (Table 2 and Fig. 6). In our simulation, a species is initially adapted to an environment not favorable for leaf trichomes (low temperature, high irradiance, and lacking herbivores). When a herbivore enters the environment, creating a fitness benefit for leaf
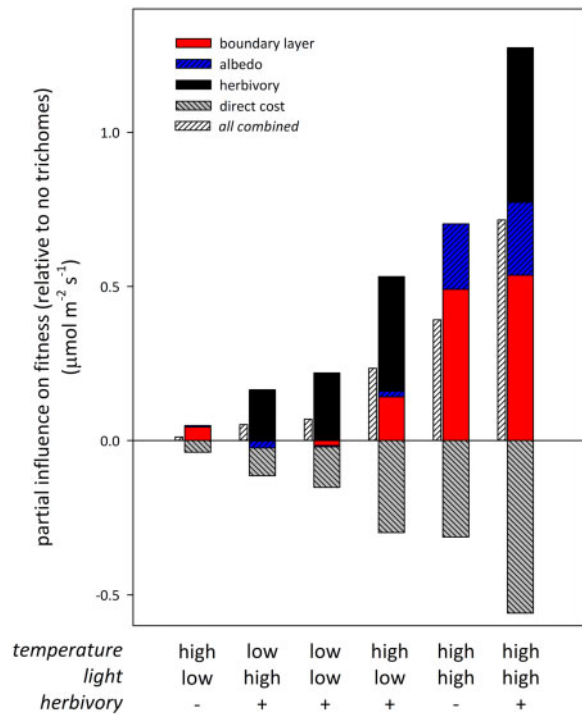
Fig. 5 Quantitative importance of given function depends on environment. The contributions of each of a trait's multiple functions (partial influences, indicated by the wide shaded bars) to the overall net benefit of the trait (indicated by the narrow hashed bars; "all combined") depend on environmental conditions. Partial influences were calculated for every combination of three binary environmental conditions (high and low temperature [35°C and 15°C, respectively] and light [1500 and 500 μmol m^{-2} s^{-1}, respectively] and presence or absence of herbivory [minimum leaf lifespan 0.5 or 1.0 years, respectively]), at the optimum level of leaf trichome density; results are shown for the six combinations for which trichomes were predicted to be beneficial, ordered by increasing total fitness benefit.

trichomes, there is selection for the development of trichomes. Later, the environment warms, enhancing the benefit of leaf trichomes. Eventually, the herbivore pressure recedes, yet the trichomes are retained, due to their benefit associated with reflecting excess light in a hot environment. Thus, hairy leaves initially evolved to mitigate herbivory, but were later co-opted to mitigate heat stress.

These simulations show how trait multifunctionality can be considered quantitatively in a synthetic modeling approach, and supported the general principles of trait multi-functionality.

Outlook: the complex network of trait multifunctionality

Given the importance of trait multifunctionality, tests and debates focused on the importance of singular trait functions may miss their overall important contribution. Indeed, across populations of

given species, or different species, traits may not align with environmental gradients as expected from consideration of tolerance of single stresses (Fig. 4; Fletcher et al. 2018; Rosas et al. 2019).

Recognition of trait multifunctionality requires a network conceptualization of trait–function relationships, especially when considering other important complexities in trait-based ecology. Suites (or "constellations," or networks) of correlated traits have been recognized to contribute in ensemble to stress tolerance. For example, "economics" traits, frequently inter-correlated, contribute to tolerance of resource scarcity by reducing overall demand for resources (e.g., high leaf mass per area, high wood density, high foliar nutrient concentrations [Sack et al. 2003; Wright et al. 2004; Reich 2014]). Flooding tolerance depends on aerial roots as well as aerenchyma (Yamauchi et al. 2018). Such complexities can be addressed by considering nested functions for the traits in Equation (1). Further, multiple independent traits may contribute in combination, or alternatively, to a single higher level function, i.e., "many-to-one mapping" (Wainwright et al. 2005; Wainwright 2007); for example, leaf thickness and leaf toughness may both contribute to tolerance of resource scarcity by increasing leaf longevity (Onoda et al. 2011). On the other hand, there is also the possibility of trade-offs among traits, which could affect the net fitness benefit of a trait in a given environment (Del Giudice et al. 2018). For example, a greater leaf osmotic concentration may provide drought tolerance, but may constrain maximum stomatal opening when water is available (Henry et al. 2019). Notably, such trade-offs, and the costs of traits, may be reduced when trait expression can be shifted across plant ontogenetic (developmental) stages, and across environments; some traits, such as leaf trichomes, are inducible in some species in the environments in which they provide a benefit. Thus, a complete model of the influence of traits on fitness would consider the influence of the trait's expression throughout growth in a given environment.

Given trait multifunctionality, we need a new generation of approaches to resolve the underlying basis for species variation in performance across environments and distributions across habitats and climates. Experiments are needed to examine the multiple functions of given traits for given species across a range of environments. Further, improved process-based models are needed to scale up from traits to predicting plant performance, stress tolerance, and fitness, in a range of environments (e.g., Buckley and Roberts 2006; Marks and Lechowicz 2006). As shown here for leaf trichomes, such models will
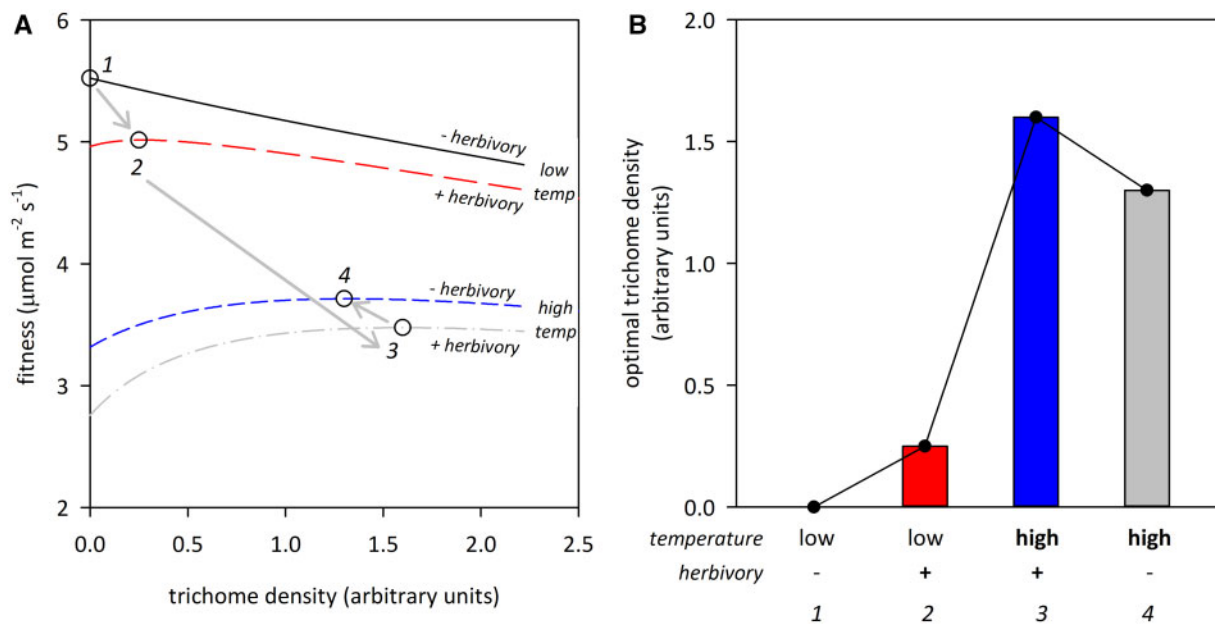
Fig. 6 Trait co-optation for additional function. A multifunctional trait may evolve because of the beneficial effects of one function, but be retained even if those benefits disappear, if, in the intervening period, conditions arise that produce a benefit via another function. In this example, the environment is initially cool and thus not favorable for leaf trichomes, due to the absence of stresses favoring the trait (point labeled "1" in panel **A**, and left-most point in panel **B**), but then an herbivore enters the environment, creating a fitness benefit of leaf trichomes (point "2"). Later, the environment changes again—becoming warmer, which further enhances the benefit of leaf trichomes (point "3"). Eventually, the herbivore pressure recedes, but the trichomes are retained because of their benefit associated with reflecting excess light in a hot environment (point "4"). Thus, in this example, trichomes initially evolved to mitigate herbivory, but were later co-opted to mitigate heat stress.

highlight the pivotal complexities of trait multifunctionality, with networks relating multiple traits directly and indirectly to multiple functions, and vice versa. Further, while this approach has been developed with a focus on plants, the framework is general enough to investigate trait multifunctionality in other organismal systems too.

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Appendix

Here we provide a model for the net carbon balance of a leaf over its lifespan, as a proxy for fitness (F), and heuristic expressions for three putative functions of leaf trichomes (hairs) to permit quantitative exploration of trait multifunctionality. We focus on three known functions of leaf trichomes: deterring herbivory, which increases the mean functional lifespan of leaves; increasing leaf boundary layer resistance, which reduces the exchange of water vapor, CO_2, and sensible heat between the leaf and atmosphere; and increasing albedo (reflectance of visible light). The latter two functions may be beneficial in some circumstances and detrimental in others. For example, increased boundary layer resistance can reduce water stress and improve water use efficiency (photosynthetic CO_2 gain per unit of water vapor loss). However, it also reduces heat exchange with the atmosphere, which may be beneficial (e.g., in cold environments) or detrimental (e.g., in hot environments). Likewise, high albedo can prevent damaging light stress by reflecting excess light, but in light-limited environments (e.g., shaded positions in a plant canopy), it would merely suppress light capture for photosynthesis.

For simplicity, we estimate carbon balance based on leaf gas exchange at a single point in time, meant to be indicative of average conditions over the leaf's lifespan. We define

carbon balance as photosynthesis (net CO_2 assimilation rate, A) minus three costs: the cost of acquiring and transporting water to leaves to replace evaporative vapor losses (assumed to be proportional to the evaporation [transpiration] rate E by a factor χ), the cost of the trichomes themselves (assumed proportional to leaf trichome density [H, arbitrary units] by a factor c), amortized over the leaf lifespan (τ_l), and the cost of other leaf tissues (L), also amortized over the leaf lifespan (τ_{leaf}):

$$F(H, \mathbf{e}) = A(H, \mathbf{e}) - \chi(\mathbf{e}) \cdot E(H, \mathbf{e}) - \frac{cH + L}{\tau_{leaf}(H, \mathbf{e})} \quad . \quad (6)$$

Biophysical models for A and E are given below, after the derivation of expressions for the multiple functions of leaf trichomes. The dependences of A and E on H arise from multiple functions of leaf trichomes. For example, albedo (ρ) affects photosynthesis directly via light capture and indirectly via effects of light on leaf temperature. Boundary layer resistance (r_b) affects the substrate concentration ($[CO_2]$) for photosynthesis by restricting CO_2 diffusion into the leaf, and also affects the activity of photosynthetic and respiratory enzymes via leaf temperature. r_b directly affects the rate of water vapor diffusion out of the leaf, but also indirectly affects the vapor gradient from leaf to air, because the vapor concentration in the leaf airspaces depends on leaf temperature. Water use efficiency (carbon gain per unit water loss) is thus indirectly influenced by both ρ and r_b. Deterrence of herbivory affects carbon balance by increasing the average leaf lifespan.

For the sake of demonstration, we describe the herbivory deterrence function, f_h—that is, the effect of leaf trichomes on leaf lifespan via herbivory deterrence—as follows:

$$f_h(H, \mathbf{e}) = \frac{\tau_{leaf}(H, \mathbf{e})}{\tau_{leaf}(0, \mathbf{e})}$$
$$= 1 + \frac{H}{H + \beta_h} \cdot \left(\frac{\tau_{leaf,max}(\mathbf{e})}{\tau_{leaf}(0, \mathbf{e})} - 1 \right) , \quad (7)$$

where β_h is an empirical parameter representing the trichome density at which the herbivory deterrence effect is one-half of its maximum, $\tau_{leaf, max}$ is the maximum leaf lifespan in the absence of herbivory, and $\tau_{leaf}(0)$ is the minimum leaf lifespan in the presence of unmitigated herbivory. τ_{leaf} is shown as depending on the environment ($\mathbf{e}$) to capture the effect of herbivore presence itself on $\tau_{leaf}(0)$; in the simulations shown in the main text, we adjusted $\tau_{leaf}(0)$ upward or downward to denote decreased or increased herbivore pressure, respectively. Thus, $f_h = 1$ in the absence of trichomes ($H = 0$), and f_h increases with H in saturating fashion, toward an asymptote of $\tau_{leaf, max}/\tau_{leaf}(0)$.

Boundary layer resistance affects the total resistances for H_2O and CO_2 diffusion between the leaf airspaces and the atmosphere (r_{tw} and r_{tc}, respectively), and defines the resistance for sensible heat exchange with the atmosphere (r_h). r_{tw} and r_{tc} are also affected by the resistance through stomatal pores in the leaf epidermis. We suppose that leaf trichomes of length l_h increase boundary layer resistance in saturating fashion, by adding a resistance that asymptotically approaches the diffusive resistance of a perfectly still air of thickness l_h, or l_h/D_{wa} (where D_{wa} is the binary diffusivity of water vapor in air). Thus, the function of trichomes with respect to boundary layer resistance, f_b, is

$$f_b(H, \mathbf{e}) = \frac{r_{bw}(H, \mathbf{e})}{r_{bw}(0, \mathbf{e})} = \frac{r_{bw}(0, \mathbf{e}) + \frac{H}{H + \beta_b} \cdot \frac{l_h}{D_{wa}}}{r_{bw}(0, \mathbf{e})}, \quad (8)$$

β_b is an empirical factor that captures the efficacy of leaf trichomes in reducing advective transport, and probably depends on trichome shape; β_b would be smaller for shapes that were more effective in reducing transport. Note that f_b is independent of the diffusing species (CO_2, H_2O, or heat). $r_{bw}(0, \mathbf{e})$ depends on the environment chiefly due to the effect of wind speed, as

$$r_{bw}(0, \mathbf{e}) = 0.004 \cdot \frac{R_{gas} T_{air,K}}{D_{wa} P_{atm}} \sqrt{\frac{d_l}{v_w}}, \quad (9)$$

where R_{gas} is the ideal gas constant (8.31446 Pa m^3 mol^{-1} K^{-1}), $T_{air, K}$ is the air temperature in kelvins, P_{atm} is the atmospheric pressure in pascals, d_l is the downwind leaf width in meters, and v_w is the wind speed in m s^{-1} (Nobel 2009). Equation (9) gives r_{bw} in units of m^2 s mol^{-1} (the term 0.004 implicitly has units of s m^{-1}). The diffusivities for heat, water vapor, and CO_2 differ, such that, for a flat plane, r_h equals $1.08 \cdot r_{bw}$, and the boundary layer resistance for CO_2, r_{bc}, equals $1.37 \cdot r_{bw}$. These ratios are smaller than the ratio of the respective molecular diffusivities, because transport through a boundary layer is partly by advection, which is unaffected by diffusivity. (By contrast, the ratio of the stomatal resistances to CO_2 [r_{sc}] and H_2O [r_{sw}] equals the ratio of D_{wa} to the molecular diffusivity of CO_2 [1.6], because transport through stomata is entirely by diffusion; Cowan 1977.) The relative contributions of diffusion and advection to transport through the trichome layer are unknown and may vary with trichome morphology and density; for simplicity in this heuristic exercise, Equation (8) assumes diffusion predominates.

Finally, we suppose that leaf trichomes increase albedo (ρ) in saturating fashion, approaching unity for infinitely dense trichomes:

$$f_a(H) = \frac{\rho(H)}{\rho(0)} = \frac{\rho(0) + (1 - \rho(0)) \cdot \frac{H}{H + \beta_a}}{\rho(0)}$$
$$= 1 + \frac{H}{H + \beta_a} \cdot \left(\frac{1}{\rho(0)} - 1 \right), \quad (10)$$

where $\rho(0)$ is the minimum albedo (i.e., the value in the absence of leaf trichomes). To compute the effects of boundary layer resistance and albedo on photosynthesis and transpiration, we use a biophysical model for A and E given by Von Caemmerer and Farquhar (1981). Photosynthesis can be limited either by carboxylation of ribulose-1,5-bisphosphate (RuBP) in the Calvin cycle, or by regeneration of RuBP. Under carboxylation-limited conditions, A is given by

$$A_v = V_{cmax} \cdot \left(\frac{c_i - \Gamma^*}{c_i + K_c \left(1 + \frac{O}{K_o}\right)} \right) - R_d, \quad (11)$$

where V_{cmax} is the maximum velocity of RuBP carboxylation by the enzyme Rubisco, c_i is the concentration of CO_2 in the intercellular airspaces, Γ^* is the photorespiratory CO_2 compensation point, K_c and K_o are the Michaelis constants for RuBP carboxylation and oxygenation, respectively, O is the oxygen concentration, and R_d is the rate of non-photorespiratory CO_2 release. Under regeneration-limited conditions, A is given by

$$A_j = \frac{1}{4} J \cdot \left(\frac{c_i - \Gamma^*}{c_i + 2\Gamma^*} \right) - R_d, \quad (12)$$

where J is the potential rate of electron transport through the photosynthetic electron transport chain, given by

$$J = \left(\frac{1}{2\theta_J} \right) \left(J_{max} + \phi i - \sqrt{(J_{max} + \phi i)^2 - 4\theta_J J_{max} \phi i} \right) \tag{13}$$

where $\theta_j \leq 1$ is a dimensionless empirical parameter, J_{max} is the maximum potential electron transport rate, i is the absorbed photosynthetic photon flux, and ϕ is the effective quantum yield (Farquhar and Wong 1984). Note that the albedo effect of trichomes operates via i, which equals $i_o \cdot (1 - \rho(H))$, where i_o is the incident photosynthetic photon flux.

Photosynthesis is also limited by CO_2 diffusion across the boundary layer and through the stomatal pores, such that

$$A_s = \frac{c_a - c_i}{1.37 r_{bw}(H) + 1.6 r_{sw}}, \quad (14)$$

where c_a is the ambient CO_2 concentration (outside the boundary layer) and r_{sw} is the stomatal resistance to water vapor. To eliminate c_i from these equations, one can combine

Equations (10) and (13) to produce a quadratic expression for c_i under carboxylation-limited conditions, and then apply that expression to Equation (10) to compute A under carboxylation-limited conditions (A_v). This is repeated using Equations (11) and (13) to compute A under regeneration-limited conditions (A_j), and finally the actual assimilation rate is calculated as the hyperbolic minimum of A_v and A_j:

$$A = \left(\frac{1}{2\theta_A}\right)\left(A_v + A_j - \sqrt{\left(A_v + A_j\right)^2 - 4\theta_A A_v A_j}\right) \tag{15}$$

where $\theta_A \leq 1$ is a dimensionless empirical parameter describing the degree of colimitation. Transpiration rate is given by

$$E = \frac{w_{sat}(T_{leaf}) - w_{air}}{r_{bw}(H) + r_{sw}} , \tag{16}$$

where w_{sat} is the saturated water vapor mole fraction, which depends on leaf temperature (T_{leaf}) and is an estimate of the water vapor mole fraction in the leaf intercellular airspaces, and w_{air} is the ambient water vapor mole fraction. Equation (16) assumes cuticular transpiration is negligible, and the leaf is amphistomatous. The dependence of w_{sat} on T is given by

$$w_{sat}(T) = \left(\frac{0.006112}{P_{atm}}\right)\exp\left(\frac{17.62 \cdot T}{243.12 + T}\right) , \tag{17}$$

(World Meteorological Organization 2008), where T is in degrees C. T_{leaf} can be estimated from energy balance.

The expressions above for A and E depend on leaf temperature [several parameters in Equations (10)–(12) are temperature-dependent], and T_{leaf} in turn depends on E. Resolving this system thus requires a model for leaf energy balance. At steady state, and ignoring chemical energy storage, thermal energy balance for a leaf implies

$$0 = Q(H) + \epsilon_{air}\sigma T_{air,K}^4 - \epsilon_{leaf}\sigma T_{leaf,K}^4 \\ - \frac{c_{pa}}{r_h(H)}\left(T_{leaf,K} - T_{air,K}\right) - \lambda E , \tag{18}$$

where Q is the absorbed shortwave radiation ($\approx 0.3173 \cdot i_o/(1-\rho)$; Buckley et al. 2014), $T_{air,K}$ and $T_{leaf,K}$ are air and leaf temperatures, respectively, in kelvins, ε_{air} and ε_{leaf} are the longwave emissivities of the atmosphere and leaf, respectively ($\varepsilon_{air} = 0.642(w_{air} \cdot P_{atm}/T_{air,K})^{1/7}$; Brutsaert 1975), σ is the Stefan–Boltzmann constant, c_{pa} is the molar heat capacity of air, and λ is the latent heat of vaporization.

Equation (17) assumes that the leaf in question is atop a canopy exposed to the atmosphere, and that lower leaves leaf have a similar temperature as the target leaf, so that net infrared emission occurs only from the upper leaf surface. Solving for $T_{leaf,K}$ requires eliminating the term in the 4th power of T_{leaf}, and the implicit dependence of E on T_{leaf} via w_{sat}. $T_{leaf,K}^4$ can be eliminated by the following approximation:

$$T_{leaf,K}^4 \approx T_{air,K}^4 + 4T_{air,K}^3\delta_T , \tag{19}$$

which arises from expanding $\left(T_{air,K} + \delta_T\right)^4$, where $\delta_T = T_{leaf,K} - T_{air,K}$, and omitting terms with 2nd- or higher powers of δ_T (e.g., Jones 1992). To eliminate the dependence of $w_{sat}(T_{leaf})$ on T_{leaf}, this term can be approximated by linear extrapolation, as

$$w_{sat}(T_{leaf}) \approx w_{sat}(T_{air}) + s\delta_T , \tag{20}$$

where s is the derivative of w_{sat} with respect to T, evaluated at T_{air} ($s = w_{sat}(T_{air}) \cdot 17.62 \cdot 243.12/(243.12 + T_{air})^2$). Then Equation (15) can be written as

$$E = \frac{w_{sat}(T_{air}) - w_{air}}{r_{bw}(H) + r_{sw}} + \frac{s\delta_T}{r_{bw}(H) + r_{sw}} . \tag{21}$$

Applying Equations (18) and (20) to Equation (17) gives δ_T as

$$\delta_T = \frac{Q(H) + (\epsilon_{air} - \epsilon_{leaf})\sigma T_{air,K}^4 - \lambda\frac{w_{sat}(T_{air}) - w_{air}}{r_{bw}(H) + r_{sw}}}{4\epsilon_{leaf}T_{air,K}^3 + \frac{c_{pa}}{r_h(H)} + \frac{\lambda s}{r_{bw}(H) + r_{sw}}} , \tag{22}$$

T_{leaf} is then calculated as $T_{air} + \delta_T$.

The values of temperature-dependent photosynthetic parameters (V_{cmax}, J_{max}, Γ_*, K_c, K_o, R_d, θ_j, and ϕ) were adjusted for leaf temperature (Bernacchi et al. 2001, 2003). For V_{cmax}, J_{max}, and R_d, values at 25°C were assumed to be proportional to i_o (Field 1983; Farquhar 1989), such that $V_{cmax}(25°C) = \{50\,\mu mol\ m^{-2}\ s^{-1}\} \cdot (i_o/1500\,\mu mol\ m^{-2}\ s^{-1})$, $J_{max}(25°C) = 2.1 \cdot V_{cmax}(25°C)$ (Wullschleger 1993), and $R_d(25°C) = 0.0089 \cdot V_{cmax}(25°C)$ (dePury and Farquhar 1997). Stomatal conductance ($1/r_{sw}$) was also assumed to scale with $V_{cmax}(25°C)$, such that $r_{sw} = \{7\ m^2\ s^1\ mol^{-1}\} \cdot (50\,\mu mol\ m^{-2}\ s^{-1}/V_{cmax}(25°C))$.

We applied the model described above using parameter values given in Table A1, and varied three input parameters during simulations: air temperature (T_{air}), incident photosynthetic photon flux (i_o), and $\tau_l(0)$, the latter adjusted to represent changes in baseline herbivory pressure.

Table A1 Mathematical symbols used in this Appendix

Description	Symbol	Units	Value if fixed
Net CO_2 assimilation rate	A	µmol m^{-2} s^{-1}	
A under RuBP regeneration-limited conditions	A_j	µmol m^{-2} s^{-1}	
A under RuBP carboxylation-limited conditions	A_v	µmol m^{-2} s^{-1}	
Michaelis constant for albedo function	β_a	–	1
Michaelis constant for boundary layer function	β_b	–	1
Michaelis constant for herbivory deterrence function	β_h	–	1
Unit cost of leaf trichomes	c	µmol m^{-2}	0.25
Ambient CO_2 mole fraction	c_a	µmol mol^{-1}	400
intercellular CO_2 mole fraction	c_i	µmol mol^{-1}	
unit carbon cost of water uptake and transport	χ	µmol mol^{-1}	1500
molar heat capacity of air	c_{pa}	J mol^{-1} K^{-1}	29.2
downwind leaf width	d_l	m	0.025
binary diffusivity of water vapor in air	D_{wa}	m^2 s^{-1}	2.55·10^{-5}
leaf transpiration rate	E	mol m^{-2} s^{-1}	
longwave emissivity of atmosphere	ε_{air}	–	
longwave emissivity of leaf	ε_{leaf}	–	0.98
fitness (carbon balance)	F	µmol m^{-2} s^{-1}	
albedo function of leaf trichomes	f_a	–	
boundary layer function of leaf trichomes	f_b	–	
herbivory deterrence function of leaf trichomes	f_h	–	
effective quantum yield of electrons	ϕ	–	0.3
photorespiratory CO_2 compensation point	Γ_*	µmol mol^{-1}	
leaf trichome density	H	–	
absorbed photosynthetic photon flux	i	µmol m^{-2} s^{-1}	
incident photosynthetic photon flux	i_o	µmol m^{-2} s^{-1}	500 or 1500
potential electron transport rate	J	µmol m^{-2} s^{-1}	
maximum potential electron transport rate	J_{max}	µmol m^{-2} s^{-1}	
Michaelis constant for RuBP carboxylation	K_c	µmol mol^{-1}	
Michaelis constant for RuBP oxygenation	K_o	µmol mol^{-1}	
carbon cost of leaf tissues other than trichomes	L	µmol m^{-2}	0.56
leaf trichome height	l_h	m	2.5·10^{-4}
latent heat of vaporization	λ	J mol^{-1}	44000
ambient oxygen concentration	O	µmol mol^{-1}	210000
atmospheric pressure	P_{atm}	Pa	101325
absorbed shortwave radiation	Q	J m^{-2} s^{-1}	
curvature parameter for photosynthesis	θ_A	–	
curvature parameter for electron transport rate	θ_J	–	
leaf boundary layer conductance to water vapor	r_{bw}	m^2 s^1 mol^{-1}	
rate of non-photorespiratory CO_2 release	R_d	µmol m^{-2} s^{-1}	
ideal gas constant	R_{gas}	Pa m^3 mol^{-1} K^{-1}	8.31446
stomatal resistance to water vapor	r_{sw}	m^2 s^1 mol^{-1}	
leaf albedo (shortwave reflectivity)	ρ	–	
derivative of w_{sat} with respect to temperature	s	mol mol^{-1} K^{-1}	
Stefan-Boltzmann constant	σ	J m^{-2} s^{-1} K^{-4}	5.67·10^{-8}

(continued)

Table A1 Continued

Description	Symbol	Units	Value if fixed
air temperature	T_{air}	°C	15 or 35
air temperature in kelvins	$T_{air,\ K}$	K	
leaf temperature	T_{leaf}	°C	
leaf temperature in kelvins	$T_{leaf,\ K}$	K	
leaf lifespan	τ_{leaf}	years	
leaf lifespan in the absence of leaf trichomes	$\tau_{leaf}(0)$	years	0.5 or 1
maximum leaf lifespan	$\tau_{leaf,\ max}$	years	1
ambient water vapor mole fraction	w_{air}	mol mol^{-1}	0
saturated water vapor mole fraction	w_{sat}	mol mol^{-1}	
RuBP carboxylation capacity	V_{cmax}	µmol m^{-2} s^{-1}	
wind speed	v_{w}	m s^{-1}	10