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Opinion

Plant Thermoregulation: Energetics, Trait–Environment Interactions, and Carbon Economics

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Building a more predictive trait-based ecology requires mechanistic theory based on first principles. We present a general theoretical approach to link traits and climate. We use plant leaves to show how energy budgets (i) provide a foundation for understanding thermoregulation, (ii) explain mechanisms driving trait variation across environmental gradients, and (iii) guide selection on functional traits via carbon economics. Although plants are often considered to be poikilotherms, the data suggest that they are instead limited homeotherms. Leaf functional traits that promote limited homeothermy are adaptive because homeothermy maximizes instantaneous and lifetime carbon gain. This theory provides a process-based foundation for trait–climate analyses and shows that future studies should consider plant (not only air) temperatures.

Trends

Plants are generally considered to be poikilotherms that do not thermoregulate. However, empirical data show that plants are actually limited homeotherms that do thermoregulate.

Plant thermoregulation and limited homeothermy decouples physiological functioning from climatic variation to promote metabolic homeostasis and maximize carbon assimilation and fitness.

Energy budgets and carbon economics provide a mechanistic theory for understanding and predicting these relationships. Specifically, theory suggests that thermoregulation evolved via natural selection on traits to maximize lifetime carbon gain, growth, production, and fitness across climate gradients.

Future studies need to consider plant tissue (and not only air) temperatures.

Plant Thermoregulation: Implications for Plant Functioning

Many plants can thermoregulate to maintain relatively stable tissue temperatures in the face of variable environmental temperatures [1–5]. Some use variation in leaf functional traits to passively thermoregulate and avoid unfavorable temperature extremes [6–8]. Others create metabolic heat to actively thermoregulate and attract pollinators or increase growth rates [9]. Despite this diverse and scattered literature, the implications of thermoregulation have been difficult to implement. Many studies in physiology, ecology, and climate science still regard plants as poikilotherms – with temperatures that are determined solely by the environment [4]. As a result, it is commonly assumed that plant temperatures are equal to the ambient air temperature [10].

We focus hereon an important outcome of thermoregulation that has potential to unite trait-based ecology: limited homeothermy. Because it weakens the links between climate and plant performance [4,11,12], limited homeothermy has implications for how we model trait-climate interactions, plant growth rates, vegetation dynamics, and the carbon budgets of ecosystems. Using the example of plant leaves, we explore how the interplay of morphology and physiology leads to limited homeothermy.

The Limited Leaf Homeothermy Hypothesis

The limited leaf homeothermy hypothesis (cf. [4]) posits that specific suites of leaf traits have evolved via natural selection to buffer variation in environmental temperature and maintain leaf temperatures within a narrower range of variation around metabolic optima. It predicts that leaf

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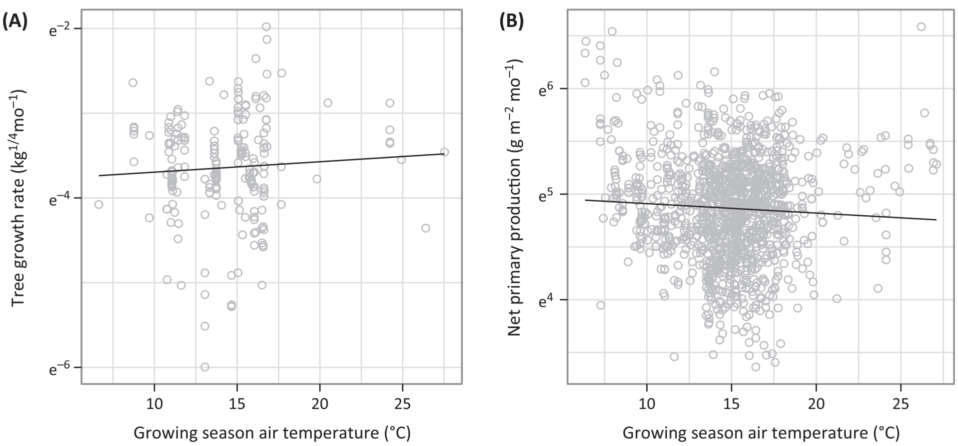

Trends in Ecology & Evolution

Figure 1. Global Invariance of Plant Growth and Forest Production across Air Temperature Gradients. (A) Mass-corrected monthly (mo^{-1}) tree growth rate does not vary with air temperature (P = 0.365, r^2 = 0.004). Figure redrawn from [19]. (B) Monthly net primary production varies marginally with air temperature (P = 0.048), but none of the variation is explained by air temperature (r^2 = 0.003). Figure redrawn from [20].

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temperatures are controlled passively via coordinated shifts in climate, functional traits, and leaf physiology. The hypothesis assumes that limited homeothermy is advantageous because it allows, in the face of wide variation in ambient air temperatures, the continuous use of a common set of photosynthetic and respiration enzymes with relatively narrow thermal tolerance ranges, and/or stabilizing metabolic reaction rates to maintain positive carbon balance. The end result is a maximization of net carbon assimilation, growth, production, and fitness across climate gradients (Figure 1). If correct, this photosynthesis-weighted view of leaf homeothermy will reshape our understanding of plant–climate interactions, with profound implications for studies in plant and ecosystem ecology that commonly use air temperature as a proxy for plant temperature [10].

Leaf Energetics Unifies Our View of Thermoregulation and Trait–Climate Interactions

Although leaf energy balance and photosynthesis are deeply interwoven, they are often considered in isolation (cf. [13]). This separation reflects a logistical legacy because measuring photosynthesis via modern field methods necessarily removes a leaf from its natural environment, and measuring the natural energy balance of a leaf precludes measurements of photosynthesis. However, plants are photoautotrophic, sessile organisms. The solar radiation they use to synthesize chemical energy also affects the temperatures of their leaves.

Although it has been known for more than a century that temperature influences physiological and metabolic rates [14], predicting how climate affects organismal performance is more complicated, given the decoupling of plant and air temperatures. Temperature has strong and well-documented effects on tissue-level rates of metabolism [15] and physiology [16]. Even so, recent studies have shown that tissue-level results do not scale up to individuals and ecosystems. For example, air temperature is a poor predictor of plant growth and production after controlling for standing biomass, plant age, and growing season length (Figure 1) [17–20]. Clearly, our understanding of how climate influences plant physiology and performance remains incomplete, and a more mechanistic approach is needed [21,22].

The trait-based approach, heralded as a new paradigm in ecology [13,23], shows considerable promise. The approach posits that functional traits mediate organism–environment interactions,