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Title: Plasticity and adaptation to high light intensity amplify the advantage of amphistomatous leaves

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**Abstract:** The presence of stomata on both leaf surfaces (amphistomy) increases photosynthesis by reducing the distance for CO2 diffusion between stomata and chloroplasts. Paradoxically, most leaves are hypostomatous (stomata on lower surface), despite the photosynthetic advantage of amphistomy. Across 29 diverse populations of "wild tomatoes", leaves developed under high light intensity benefit more from amphistomy in terms of CO2 assimilated for a given stomatal conductance than plants developed under low light. Furthermore, populations native to open habitats benefit more from amphistomy than those from more closed habitats. Thus, plasticity and adaptation together may explain why amphistomatous leaves are prevalent in sunny, open habitats, including many crops. Contrary to common assumptions, amphistomy can save water because hypostomatous leaves evaporate 10-65% more to achieve the same photosynthetic rate.

**Main Text:** Stomata are microscopic pores on the surfaces of leaves and other photosynthetic organs formed by a pair of guard cells. They are essential for balancing carbon gained per unit water lost and were an essential innovation in vascular plants, permitting them to grow tall on land by enabling access to CO2 for photosynthetic carbon assimilation while preventing hydraulic failure in variable environments (*1*–*3*). Optimal stomatal function depends on both dynamic changes in aperture on the scale of minutes to hours, as well as static anatomy determined by developmental plasticity and constitutive genetic differences (*4*–*6*). Understanding how stomata respond to environmental change over daily, developmental, and evolutionary time is important for studying adaptation (*1*, *7*, *8*), inferring paleoclimate from fossil cuticles (*9*–*11*), predicting responses to climate change (*12*–*15*), and improving crops (*16*). Stomatal function contributes to global carbon and water cycles (*17*) and therefore to predicting future climate (*18*).

Despite extensive theoretical and empirical progress understanding stomata function and anatomy from molecular to ecosystem levels, the adaptive significance of amphistomatous leaves remains an important unsolved problem in leaf structure-function relationships (*19*–*26*). Amphistomatous leaves develop abaxial and adaxial stomata whose aperture can be independently regulated (*27*–*31*) to control gas exchange through each surface. All else being equal, simultaneous gas exchange through stomata on both surfaces increases CO2 supply to chloroplasts by providing a second parallel pathway through leaf intercellular airspaces, enhancing photosynthesis (*20*, *32*). The extent to which amphistomy increases CO2 supply depends on resistance to diffusion in intercellular airspaces. This resistance can be low in thin, porous, amphistomatous leaves (*28*, *33*), but may be more substantial in thick, dense, hypotomatous leaves (*34*). We refer to the intercellular airspace conductance (𝑔ias), the inverse of resistance. Amphistomatous leaves also lose more water through evaporation because of a second boundary layer conductance (*35*), but the additional carbon gain should be enough to offset this cost in most realistic scenarios (*36*).

The paradoxical fact is that, despite the photosynthetic benefit, most leaves are not amphistomatous. Many vertically oriented and/or isobilateral leaves are amphistomatous (*25*). But among dorsiventral leaves, it is primarily herbaceous plants in open, high light habitats that tend to have amphistomatous leaves (*22*, *39*–*44*). Most other leaves, except those from aquatic habitats, are hypostomatous, producing stomata only on the lower, abaxial surface. Even resupinate leaves develop stomata on the lower, albeit adaxial surface (*45*), suggesting that leaf orientation (lower vs. upper) rather than leaf polarity (abaxial vs. adaxial) is causal. Stomatal density ratio, defined as the ratio of upper to total stomatal density, is a quantitative metric of stomatal distribution. The covariation between stomatal density ratio and light habitat is both qualitative and quantitative. A higher proportion of sun leaves are amphistomatous (*39*) and the proportion of stomata on the upper, adaxial surface increases with light (*42*, *43*). Resolving why high light intensity favors amphistomatous dorsivental leaves is an important first step toward understanding variation in stomatal density ratio and leaf structure-function relationships more

generally.

The overarching hypothesis is that leaves with greater stomatal density ratio are more common in open sunny habitats because they increase photosynthesis most in those circumstances. An amphistomatous leaf increases photosynthetic carbon gain compared to an otherwise identical hypostomatous leaf by increasing conductance through the leaf intercellular airspaces and boundary layers. We quantify this benefit as the amphistomy advantage (AA), the log-response ratio of photosynthesis in an amphistomatous leaf compared to an otherwise identical pseudohypostomatous leaf (*20*, *46*). Why would AA be greater in sun than shade? We consider three nonmutually exclusive hypotheses that we classify as ‘acclimation’, ‘plasticity’, and ‘constitutive’ (Fig. 1).

*Acclimation hypothesis*: Photosynthetic induction to high light intensity typically involves increases in total leaf stomatal conductance (increased CO2 supply), the concentration of active Rubisco, and electron transport capacity (increased CO2 demand). If the acclimation hypothesis is correct, we predict that AA2000 > AA150 for all populations regardless of native habitat or growth environment. AA2000 is the AA measured under high light intensity (PPFD = 2000 µmol m−2 s−1); AA150 is the AA measured under low light intensity (PPFD = 150 µmol m−2 s−1).

*Plasticity hypothesis*: Individuals of the same genotype often develop dramatically different leaves in sun and shade conditions (*47*). Plastic responses are likely adaptations to optimize photosynthesis at different light intensities in variable environments (*48*). Plastic changes in leaf anatomy and biochemistry could modulate AA as a byproduct. Thicker or less porous leaves, both of which are associated with high leaf mass per area (LMA), will have lower 𝑔ias; leaves with increased total stomatal density and photosynthetic capacity have greater potential CO2 supply and demand. Under the plasticity hypothesis, we predict that AAsun > AAshade for all populations and light intensities. AAsun is the AA measured on sun leaves; AAshade is the AA measured on shade leaves.

*Constitutive hypothesis*: In environments that are relatively constant or where environmental change cannot be anticipated by a reliable cue, natural selection will favor constitutive expression of optimal phenotypes. We therefore predict genotypes from more sunny, open habitats will have consistently greater AA under all measurement and growth light intensities. For herbaceous plants, light intensity is largely a function of the tree canopy (*49*). Herbs growing in the open will regularly experience high light intensity; herbs growing under a forest canopy will often experience low light intensity.

The primary directional predictions for each hypothesis are summarized in Table 1; detailed predictions for results that would indicate simultaneous support for multiple hypotheses are in Table S3.

We tested these hypotheses by comparing AA among amphistomatous wild tomato species (Table S1; Figure S2; (*50*)) from different native light habitats, grown under simulated sun and shade light treatments, and measured under contrasting light intensities (low and high). We measured AA on 572 individual plants from 29 populations (average of 9.86 replicates per light treatment) using a recently developed method (*46*). With this method, we directly compare the photosynthetic rate of an untreated amphistomatous leaf to that of the same leaf with gas exchange blocked through the adaxial (upper) surface by transparent plastic, which we refer to as ‘pseudohypostomy’. To compare amphi- and pseudohypostomatous leaves at identical whole-leaf stomatal conductance (𝑔sw), we measure 𝐴 over a range of 𝑔sw, inducing stomatal opening and closure by modulating humidity (see supplementary text for further details). We estimated ‘amphistomy advantage’ (AA) *sensu* (*20*), but with modifications previously described in (*46*) and here (Supplementary Materials). The native light intensity was represented by plant area index (PAI m2 m−2), estimated using a global gridded data set derived from the Global Ecosystem Dynamics Investigation [GEDI; (*51*)] and georeferenced accession collection information from the Tomato Genetics Resource Center (Table S1). The growth light intensities were PPFD = 761 µmol m−2 s−1 (sun treatment) and 115 µmol m−2 s−1 (shade treatment) while all other environment conditions were nearly identical (see Materials and Methods). The high and low measurement light intensities were PPFD = 2000 µmol m−2 s−1 (97.8:2.24 red:blue) and PPFD = 150 µmol m−2 s−1 (87.0:13.0 red:blue), respectively.

Consistent with biophysical theory of CO2 diffusion within leaves, AA > 0 for all populations (Fig. 2A). Bayesian phylogenetic mixed effects models that allowed AA to vary between measurement light intensities, growth light intensities, and among populations outperformed simpler models based on information criteria (Table S6). Measured under high light intensity, AA was consistently greater for sun plants. The average AA among populations in the shade treatment was 0.041 (range: 0.007–0.113; 19 of 29 populations significant); however, the same populations grown at high light intensity showed a mean AA of 0.052 (range: 0.020–0.120; 20 of 29 populations significant). Contrary to the predictions of the acclimation hypothesis, AA was greater in all populations under low measurement light intensity for both sun and shade grown plants. The overall average AA of shade and sun grown plants measured under low light intensity was 0.064 (range: 0.022–0.137; 28 of 29 populations significant) and 0.100 (range: 0.049–0.206; 27 of 29 populations significant), respectively. There was a modest tendency for populations from more open habitats (lower PAI) to exhibit greater AA and the slope was significantly different than 0 in 3 of the 4 treatment combinations (Fig. 2B).

The pattern of AA across wild tomatoes strongly supports the plasticity hypothesis, contradicts the acclimation hypothesis, and provides modest support for the constitutive hypothesis. Plastic changes in leaf thickness and/or packing density, summarized by the bulk leaf mass per area (LMA), may mediate the effect of growth light intensity on AA. LMA increased in sun grown plants in all populations by an average of 123% [95% CI: 42.9 to 256%], qualitatively similar to plastic responses in many species (*47*). While LMA is weakly, albeit significantly (Table S5), associated with individual-level AA (Fig. 3), the effect of growth light intensity on AA is still predictive based on model comparison using information criteria (Table S6). However, the direct effect of the sun treatment on AA was weaker when LMA was included in the model (Table S4 vs. Table S5), suggestive of a mediating role. Many anatomical traits underlie LMA (*52*) and future research will be needed to identify which particular traits, such as leaf thickness or mesophyll porosity, are responsible for mediating AA. The fact that the AA of sun plants was greater under low measurement light intensity supports a long-standing hypothesis that resistance to CO2 diffusion is greater in the upper than lower portions of the leaf interior (*53*). At low light intensity, photosynthesis is weighted toward the upper palisade where most light is intercepted. If resistance to CO2 diffusion is high in the upper palisade, amphistomy may, unexpectedly, be particularly beneficial for sun leaves experiencing intermittent shade or cloud cover. Our study is limited in testing this because we could not directly measure the stomatal conductance ratio and intercellular resistance on each surface. Future experiments measuring AA with a dual sided chamber (*31*, *33*) can overcome these limitations.

We conclude that both developmental plasticity and adaptation to open habitats, but not acclimation, may explain the long-standing observation that amphistomatous leaves are more common in sunny habitats, at least among herbaceous plants including crop relatives. This result changes our understanding by showing that high light intensity *per se* does not increase the benefit of amphistomy. Instead, the benefit increases as a byproduct of anatomical and biochemical changes caused by plasticity and adaptation to higher light intensity. To gain more precise understanding of when amphistomy is most beneficial will require further research on its leaf anatomical and biochemical basis.

The magnitude of AA we document across populations is also noteworthy, as it implies that hypostomatous leaves predominant in mesic to wet forests globally are giving up ‘free’ carbon that would require little to no additional water loss. The cost of hypostomy can be quantified as the difference in total 𝑔sw that an amphistomatous leaf would require to achieve the same photosynthetic rate. This cost can be locally approximated on a log-ratio scale as AA/𝜀𝑔 (Supporting Information), where 𝜀𝑔 is the elasticity of 𝐴 to 𝑔sw. For AA = 0.05, the water cost of hypostomy would be 0.5 (64.9%) at low elasticities (𝜀𝑔 = 0.1) and 0.1 (10.5%) at high elasticities (𝜀𝑔 = 0.5). For plants to expend this much extra water implies a large fitness cost of upper stomata in certain ecological contexts. As this is the first quantitative comparison of AA across species, estimates from a broader range of species and more stressful environments will be required to fully understand the ecological causes and consequences of stomatal distributions on leaf surfaces.

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