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How Did the Swiss Cheese Plant Get Its Holes?

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ABSTRACT: Adult leaf fenestration in “Swiss cheese” plants (*Monstera* Adans.) is an unusual leaf shape trait lacking a convincing evolutionary explanation. *Monstera* are secondary hemiepiphytes that inhabit the understory of tropical rainforests, where photosynthesis from sunflecks often makes up a large proportion of daily carbon assimilation. Here I present a simple model of leaf-level photosynthesis and whole-plant canopy dynamics in a stochastic light environment. The model demonstrates that leaf fenestration can reduce the variance in plant growth and thereby increase geometric mean fitness. This growth-variance hypothesis also suggests explanations for conspicuous ontogenetic changes in leaf morphology (heteroblasty) in *Monstera*, as well as the absence of leaf fenestration in co-occurring juvenile tree species. The model provides a testable hypothesis of the adaptive significance of a unique leaf shape and illustrates how variance in growth rate could be an important factor shaping plant morphology and physiology.

Keywords: adaptation, leaf fenestration, leaf shape, *Monstera*, sunfleck.

Introduction

Compared to other aspects of leaf morphology such as size, little is known about the adaptive significance of leaf shape variation in terrestrial plants (Nicotra et al. 2011). However, it is generally thought that shape might serve some of the same functions as other aspects of leaf morphology, such as thermoregulation (Parkhurst and Loucks 1972; Givnish and Vermeij 1976), light interception (Horn 1971), and deterring herbivory (Brown and Lawton 1991). Deep lobing, or other shapes that reduce the effective leaf size in hot and dry environments, is the best-studied example. Smaller effective leaf size, approximately the diameter of the largest circle encompassed by the leaf lamina, decreases the boundary layer resistance (Gates 1968). Decreased boundary layer resistance prevents overheating and increased transpiration in hot, sunny environments, selecting for small and deeply lobed leaves (e.g., McDonald et al. 2003). More recently, leaf hydraulic architecture has

emerged as an important determinant of leaf shape (Zwieniecki et al. 2004). Because a large fraction of hydraulic resistance occurs in the leaf (Sack and Holbrook 2006), leaf shape may be important in preventing water stress, especially in hot, sunny conditions.

Many shape variations, like lobing or compound leaves, have evolved independently many times, in some cases convergently in response to similar selective pressures. Unusual shapes that have evolved once or a few times are more difficult to study with comparative methods and thus require alternative approaches. Window-like perforations, termed leaf fenestration, are perplexing and found predominantly in the adult leaves of *Monstera* Adans. (Araceae). Although leaf fenestration in *Monstera* was described by European botanists as early as 1693 (Madison 1977a), few hypotheses for its evolutionary origin exist. After reviewing these hypotheses, I present and analyze a novel model demonstrating that leaf fenestration may reduce variance in canopy growth rate in understory environments where a large fraction of carbon gain comes from brief, intermittent periods of direct light (sunflecks) that are unpredictably distributed in the forest.

Despite the ubiquity of *Monstera* in tropical understories and ornamental settings in the North Atlantic, the adaptive significance of its leaf fenestration has received little attention from biologists. Madison (1977a) refers to a “fanciful interpretation with no basis in reality” put forth by early post-Darwinian author H. W. King (1892), who conjectured that holes allow water to drip through to the ground. Madison (1977a) himself suggested that fenestration, like other forms of leaf dissection, would be advantageous in portions of the canopy with higher irradiance by reducing boundary layer resistance and permitting greater convective leaf cooling. He cited work demonstrating reduced leaf temperature in lacerated leaves of *Musa*. However, this might be an inappropriate comparison, as *Musa* are pioneer species of canopy gaps in full sun, whereas *Monstera* are found in shade (Madison 1977a). Gunawardena and Dengler (2006) reiterate Madison’s thermoregulation argument but also conjecture that fenestration could act akin to mottling in understory herbs, which has been ascribed to camouflage from vertebrate

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herbivores (Givnish 1990). However, the camouflage hypothesis is applicable for plants very near the forest floor, not climbers several meters above. This hypothesis also fails to explain why juvenile leaves of the same species lack fenestration.

The Growth-Variance Hypothesis for Leaf Fenestration

This study explores whether leaf fenestration might serve another function altogether, reducing variance in growth rate and, hence, fitness. I term this the growth-variance hypothesis. In *Monstera* habitat, tropical rainforest understories, sunflecks can contribute >50% of carbon gain, but their distribution is unpredictable in space and time (Chazdon 1988). The patchy distribution of sunflecks may lead to high variance in canopy growth rate. Population genetic theory demonstrates that selection maximizes the geometric mean fitness (Gillespie 1973), which is sensitive to both the arithmetic mean and variance. Consequently, traits, such as leaf shape, that decrease variance in resource acquisition and fitness can lead to higher geometric mean fitness (Frank 2011 and references therein). In the next section, I analyze a model that demonstrates that leaf fenestration and other forms of leaf dissection affect the variance in, but not the mean, canopy growth rate. Assuming that canopy growth rate contributes to fitness, the model predicts that leaf fenestration increases fitness when a large portion of carbon gain depends on stochastic sources of light (sunflecks).

Model

A glossary of symbols used in the model is given in table 1. The amount of ground area (A_{ground}) covered by a given leaf area (A_{leaf}), assuming constant total leaf mass and leaf mass per area, depends on the amount of leaf dissection. For leaves with entire margins, the ratio of leaf to ground area is unity. For dissected leaves, this ratio will be less. The ratio of leaf area to ground is a dimensionless unit ρ :

$$\rho = \frac{A_{\text{leaf}}}{A_{\text{ground}}}, \quad (1)$$

where ρ varies from 0 (completely dissected) to 1 (entire) and is analogous to the leaf area index for a single leaf.

For simplicity, I assume that sunflecks are distributed uniformly throughout space and time at a daily rate λ (sunfleck $\text{m}^{-2} \text{day}^{-1}$). Assuming a constant fleck size, duration, and per area photosynthetic rate (mol $\text{CO}_2 \text{m}^{-2} \text{t}^{-1}$), P_{fleck} (mol $\text{CO}_2 \text{sunfleck}^{-1}$) is the amount of carbon assimilated per fleck. The number of sunflecks intercepted by a single leaf area (including holes) per day (N) is the

product of the ground area covered by a leaf and the daily rate of sunflecks:

$$N = \lambda A_{\text{ground}}. \quad (2)$$

However, more highly dissected leaves will be unable to utilize the fraction of irradiance that falls between the lamina (i.e., into the leaf "holes"). For simplicity, rather than treat holes as discreet units, I assume that holes in leaf lamina are infinitesimally small and uniformly dispersed over the ground area occupied by the leaf. Therefore, the daily carbon assimilation of a leaf (P_{leaf}) is the product of number of sunflecks intercepted, the assimilation per fleck, and the ratio of leaf to ground area:

$$P_{\text{leaf}} = \rho N P_{\text{fleck}}. \quad (3)$$

This assumption is valid if sunflecks are sufficiently large, such that there is not much variation introduced by some falling entirely on lamina or entirely in holes. The assumption is also unaffected if sunflecks are large (on the order of A_{ground}) because more dissected leaves will partially intercept a large sunfleck that would have been missed by a less dissected leaf. By substitution from equations (1) and (2), it is evident that daily carbon assimilation in this model is not dependent on ρ :

$$\begin{aligned} P_{\text{leaf}} &= (\lambda A_{\text{ground}}) P_{\text{fleck}} \frac{A_{\text{leaf}}}{A_{\text{ground}}} \\ &= \lambda P_{\text{fleck}} A_{\text{leaf}}. \end{aligned} \quad (4)$$

If leaf dissection does not alter mean daily carbon assimilation, how can it affect plant growth and fitness? When the light environment is stochastic, and the number of sunflecks incident on a leaf is treated as a random variable, the variance in growth rate is a function of ρ . To arrive at this result, I scale up from leaf-level photosynthesis to whole-plant canopy dynamics in a phase of exponential growth with a stochastic rate of increase dependent on the number of sunflecks.

Let A_t be the whole plant canopy area at time t . The number of leaves in the canopy at t (L) is the canopy area divided by the leaf area:

$$L = \frac{A_t}{A_{\text{leaf}}}. \quad (5)$$

The daily canopy carbon assimilation at time t (P_t) is simply the product of the number of leaves and daily carbon assimilation per leaf defined in equation (4). The relationship between canopy area and daily assimilation is derived by combining equations (4) and (5):

Table 1: Glossary of symbols used in the model

Symbol	Description	Units
A_{ground}	Ground surface area encompassed by leaf perimeter, including holes and dissected areas	$\text{m}^2 \text{ leaf}^{-1}$
A_{leaf}	Area of a single leaf (constant)	$\text{m}^2 \text{ leaf}^{-1}$
A_t	Whole canopy leaf area at time t	m^2
$A_{t, \text{ground}}$	Whole canopy ground area encompassed by leaf perimeter at time t	m^2
L	Number of leaves at a given time	Leaves
LMF	Leaf mass fraction; assimilate dedicated to canopy area growth	
LMA	Leaf mass per area	g m^{-2}
λ	Daily rate of sunfleck occurrence	No. sunflecks $\text{m}^{-2} \text{ day}^{-1}$
N	Number of sunflecks per day	No. sunflecks day^{-1}
P_{diffuse}	Photosynthesis from diffuse light (constant)	$\text{mol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$
P_{fleck}	Photosynthesis per sunfleck (constant)	$\text{mol CO}_2 \text{ sunfleck}^{-1}$
P_{leaf}	Photosynthesis per leaf per day	$\text{mol CO}_2 \text{ leaf}^{-1} \text{ day}^{-1}$
P_t	Whole canopy photosynthesis at time t	$\text{mol CO}_2 \text{ day}^{-1}$
R	Daily maintenance costs per leaf area	$\text{mol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$
ρ	Ratio of leaf area to ground	

$$\begin{aligned}
 P_t &= LP_{\text{leaf}} \\
 &= L\lambda P_{\text{fleck}} A_{\text{leaf}} \\
 &= \left(\frac{A_t}{A_{\text{leaf}}}\right) \lambda P_{\text{fleck}} A_{\text{leaf}} \\
 &= A_t \lambda P_{\text{fleck}}.
 \end{aligned}
 \tag{6}$$

The ground area of the canopy at time t is simply $A_{t, \text{ground}} = LA_{\text{ground}}$. Given constant A_{leaf} and A_{ground} , ρ is constant:

$$\rho = \frac{A_{\text{leaf}} N_{\text{leaf}}}{A_{\text{ground}} N_{\text{leaf}}} = \frac{A_t}{A_{t, \text{ground}}}.
 \tag{7}$$

After substitution,

$$P_t = \rho N P_{\text{fleck}},
 \tag{8}$$

where the number of sunflecks per day N is a Poisson random variable:

$$N \sim \text{Poisson}\left[\frac{A_t \lambda}{\rho}\right].
 \tag{9}$$

I have assumed that the number of light flecks is Poisson distributed because (1) it is an appropriate and widely used model for counts and (2) it is easy to analyze because it has a single parameter. I have not included spatial or temporal heterogeneity in sunfleck rate. However, this should not affect the results qualitatively because the distribution of a Poisson random variable with a nonhomogeneous rate parameter is also Poisson.

Canopy growth is a function of the amount of carbon

assimilated and is thus proportional to canopy area. However, I assume no canopy area dependent regulation of growth in the model (i.e., per area photosynthetic rates are constant). Leaf mass fraction (LMF); assimilate allocated to canopy growth as opposed to roots, stems, or reproductive structures; and leaf mass per area (LMA; $\text{mol CO}_2 \text{ m}^{-2}$) are assumed constant. The daily maintenance costs per canopy area due to factors such as respiration, herbivory, and mechanical damage is R ($\text{mol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$). The P_{diffuse} ($\text{mol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$) is the photosynthetic rate from diffuse light, assumed constant. The change in canopy area in 1 day is

$$A_{t+1} = A_t + A_t \frac{\text{LMF}}{\text{LMA}} [(P_{\text{diffuse}} - R) + P_t].
 \tag{10}$$

Therefore, the difference equation for canopy growth is

$$\Delta A_t = A_{t+1} - A_t = A_t \frac{\text{LMF}}{\text{LMA}} [(P_{\text{diffuse}} - R) + P_t].
 \tag{11}$$

The mean ($\mu_{\Delta A}$) and variance $\sigma_{\Delta A}^2$ in growth rate, derived from standard equations, are

$$\mu_{\Delta A} = E[\Delta A_t] = A_t \frac{\text{LMF}}{\text{LMA}} [(P_{\text{diffuse}} - R) + \lambda P_{\text{fleck}}],
 \tag{12}$$

$$\sigma_{\Delta A}^2 = E[(\Delta A_t)^2] - E[\Delta A_t]^2 = A_t \left(\frac{\text{LMF}}{\text{LMA}}\right)^2 \rho \lambda P_{\text{fleck}}^2.$$

Inspecting the bracketed term of $\mu_{\Delta A}$, there is clearly a deterministic portion of growth (left) governed by diffuse light and maintenance costs, and a stochastic component (right) that depends on intercepting sunflecks. Increased

ρ implies more area to intercept sunflecks but less photosynthesis per sunfleck because of holes in the lamina; thus, there is no effect of ρ on the mean, as expected. However, increased ρ means that a leaf is foraging over a larger area and thus less susceptible to random spatial variation. Hence, the variance in growth does depend on ρ .

What is the fitness consequence of variance in canopy growth rate? Assuming that reproductive success is proportional to biomass, then decreased variance in growth rate will decrease variance in reproductive success by reducing either the variance in size at reproduction or the waiting time until a specific size necessary for reproduction is attained. Higher variance will be especially detrimental if there are diminishing returns of biomass to fitness because individuals with unusually low biomass will not be compensated by individuals with equally unusually high biomass. However, it is not necessary to assume diminishing returns to biomass because there are diminishing returns from absolute to relative fitness (Gillespie 1977; Orr 2007), where relative fitness is absolute divided by mean fitness. This ensures that chance reductions in biomass are more costly than gains from chance increases in biomass.

In this highly stylized model without costs or limitations on selection, leaf fenestration should always evolve. Rather than arbitrarily assigning a cost, I analyze under what conditions the benefits of fenestration are greatest and when they are the smallest. To do so, I first derive the change in geometric mean fitness with change in ρ . Because $\mu_{\Delta A}$ and $\sigma_{\Delta A}^2$ are always directly proportional to canopy area, it follows that the mean and variance of total growth are proportional to these factors. Using the approximation for the geometric mean fitness $G \approx \mu - \sigma^2/2\mu$, it follows from equation (12) that

$$\frac{dG}{d\rho} \propto - \frac{\text{LMF}}{\text{LMA}} \frac{\lambda P_{\text{fleck}}^2}{(P_{\text{diffuse}} - R) + \lambda P_{\text{fleck}}}. \quad (13)$$

Leaf fenestration will be most significant when the growth rate is high. To see this clearly, I assume that the stochastic component of plant growth dominates the deterministic component ($P_{\text{diffuse}} - R = 0$), but the same basic result holds if this assumption is relaxed:

$$\frac{dG}{d\rho} \propto - \frac{\text{LMF}}{\text{LMA}} P_{\text{fleck}}. \quad (14)$$

Thus, the change in fitness with ρ increases with traits that increase growth rate (leaf mass fraction and the photosynthesis per sunfleck) but is inversely proportional to leaf mass per area, a trait that decreases growth rate. The appendix shows representative results from stochastic simulations demonstrating that selection on leaf fenestration (1) increases as growth rate increases and (2) decreases as the

importance of sunflecks decreases, holding growth rate constant.

Discussion

Leaf fenestration in *Monstera* is a unique leaf shape trait without a compelling evolutionary hypothesis. I address this deficiency by modeling a simple, testable hypothesis for the evolution of fenestration in stochastic light environments. As long as reproductive success is a function of canopy growth, leaf fenestration will increase geometric mean fitness by reducing the variance in fitness in stochastic light environments. Figure 1 illustrates a worked example. The crux of this growth-variance hypothesis can be understood by considering the limiting cases of an entire ($\rho = 1$) and an infinitely dissected ($\rho = 0$) leaf. The entire leaf will capture all the light of the sunflecks that

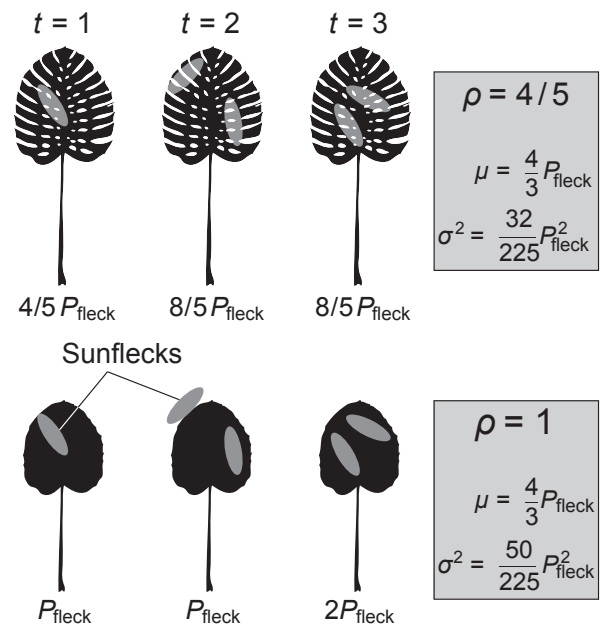


Figure 1: A worked example of the mean and variance in daily leaf photosynthesis for a fenestrated ($\rho = 4/5$; top) and an entire ($\rho = 1$; bottom) leaf. Leaf area (A_{leaf}) is the same for both leaves, but A_{ground} is higher in the fenestrated leaf (above) because of holes. The shape and distribution of sunflecks (translucent gray ellipses) are the same for both leaf shapes. The mean daily leaf photosynthesis is the same in both leaf shapes. The fenestrated leaf (above) intercepts five sunflecks but uses $4/5$ of the light for photosynthesis because of holes. The entire leaf (below) intercepts fewer sunflecks (4) but uses all of the light. Because $5 \times 4/5 = 4$, the average carbon gain is the same. However, the variance is lower among days for the fenestrated leaf because it has only a single day ($t = 1$) when it captures a single sunfleck. Additionally, the variance is proportional to the square of the photosynthesis per sunfleck (see “Discussion” for the significance of this result). Leaf silhouettes are adapted from Madison (1977a, fig. 20).

hit it but may by chance go long periods without any sunflecks. Conversely, an infinitely dissected leaf will capture an infinitesimal portion of every sunfleck. Thus, while the expected amount of carbon gain has not changed, the variance has decreased to 0.

The growth-variance hypothesis is readily falsifiable. A straightforward experiment would be to place grids, similar in size to *Monstera* leaves, of light sensors at the same height and in the same orientation as actual leaves. By allowing some of the grids to have holes, while keeping the total number of sensors constant, one could simulate variation in ρ . After a season, it should be possible to determine whether “fenestrated” grids had lower day-to-day variance in light. If not, the hypothesis should be rejected. In combination with photosynthetic light curves of plants in the field, it would also be possible to model the proportion of carbon gain from diffuse light and sunflecks. It is difficult to say what fraction of carbon gain needs to come from sunflecks before fenestration is important. However, the degree of fenestration may positively correlate with the fraction of carbon from sunflecks across sites. If the hypothesis survives these tests, further modeling and experiments will be needed to investigate whether the effect of fenestration in reducing growth rate variance holds once biological realism is added. I made several potentially unrealistic assumptions for analytical tractability and/or to demonstrate a result without unnecessary detail. In particular, I have only modeled the effect under exponential growth, but self-shading, resource limitation, plant height, and other factors will eventually regulate growth.

If the growth-variance hypothesis is correct, why is leaf fenestration rare? Table 2 summarizes the following arguments regarding ecological scenarios most and least favorable to selection for least fenestration, according to the model. The assumptions of the model are not appropriate for understanding the evolution of leaf dissection or compound leaves in full sun and/or arid environments. I model the number of sunflecks as a Poisson random variable, which is appropriate when they are sufficiently rare. As “sunflecks” become common enough that light becomes indistinguishable from partial to full sun, the spatial and

temporal variance should decrease, excepting diurnal and larger-scale variance (e.g., cloud cover) that affects all plants equally. In those environments, alternative hypotheses have been proposed (Parkhurst and Loucks 1972; Givnish 1978). The growth-variance hypothesis demonstrates one way that leaf dissection may be an environmentally overdetermined trait; that is, it can be adaptive for very different ecological reasons. This may in part explain the difficulty in finding consistent environmental correlates of leaf shape (e.g., Malhado et al. 2010; Warman et al. 2010).

The growth-variance hypothesis may be relevant to other peculiar features of *Monstera* and other aroids. As indicated above, a salient feature of *Monstera* and other climbers is pronounced leaf heteroblasty, the ability of a single genotype to produce qualitatively different morphologies during development (Zotz et al. 2011). After attaching to a host tree, individuals develop as “shingle plants.” Leaves of shingle plants are small relative to those of adult plants, entire (lacking fenestration, lobing, or teeth), and appressed to the surface of the host tree trunk rather than held away. At some point during ontogeny, plants abruptly transition to their fenestrated/dissected form with elongated leaves held away from the tree (Madison 1977a; Ray 1983a, 1983b, 1990; Lee and Richards 1991). A parsimonious hypothesis for the adaptive significance of leaf fenestration should also account for heteroblasty. Lee and Richards (1991) adduce several facts showing that light gradients in the canopy are the primary determinant of leaf morphology in heteroblastic species. For example, leaves of the shingle plant generally resemble extreme shade plants in many micro- and macroscopic features (Lee and Richards 1991). Furthermore, a climber that overgrows its host tree and topples back into the understory may revert to a flagellar form in search of a new host (Madison 1977a; Ray 1983a, 1990, 1992). Under the growth-variance hypothesis, why are juvenile leaves not similarly fenestrated? A tentative explanation comes from considering the vertical light gradient along which the heteroblastic transition occurs. Light in the deepest shade of a tropical rainforest understory is of lower quantity and quality (Lee 1987). Because the quantity and quality of sunflecks are correlated with those of total light (Smith et al. 1992),

Table 2: Three relevant scenarios of selection for leaf fenestration

Light habitat	Growth rate	Relative benefit of leaf fenestration	Explanation
Shade, light flecks important	Slow	Weak	Slow-growing plants (juvenile <i>Monstera</i> , shade-tolerant trees) have lower variance in growth rate
Shade, light flecks important	Fast	High	Fast-growing plants (adult <i>Monstera</i>) have higher variance in growth rate
Open, light flecks irrelevant	Slow or fast	Weak	In open environments, deterministic component of growth dominates

P_{fleck} likely shows a vertical gradient. Furthermore, their horizontal leaf orientation reduces light interception, leading to slower growth (Oberbauer and Noudali 1998). As equation (14) demonstrates, slow growth reduces the contribution of ρ to fitness. If there is some cost to production of fenestrated leaves (e.g., energetic costs of producing relatively expensive mechanical support tissues), perhaps the heteroblastic transition occurs where P_{fleck} is such that the benefits outweigh the costs. *Monstera* species vary with respect to their elevation at reproduction and leaf fenestration ($0.4 > \rho > 1$; calculated from leaf silhouettes in Madison 1977a), and some species are neotenus, never producing fenestrated leaves. Thus, a further prediction of the model is that within *Monstera* and ecologically similar species, these variables should be correlated with the light environment (P_{fleck}). However, there is no reason to expect a general relationship between fenestration and heteroblasty.

Lee and Richards (1991) observed that while climbers were often developmentally heteroblastic, shade-tolerant trees that pass through the same light gradients do not generally exhibit heteroblasty. Why are there no “Swiss trees”? Equation (14) suggests a tentative explanation. The strategy of climbers is to parasitize the support structure of host trees and allocate greater resource fractions to leaves (high LMF). Conversely, shade-tolerant, late-successional trees tend to have the lowest LMF values across all plants (Niinemets 2010). The change in fitness with change in ρ may be highest in climbers and lowest in juvenile trees. All else being equal, fitness of climbers should be most sensitive to changes in leaf dissection, while late-successional trees should tend to be the least sensitive. Differences between LMF in climbers versus trees exemplify a more general prediction of the model that may explain why other tropical shade plants are not fenestrated (table 2). Equation (14) and stochastic simulations (appendix) demonstrate that the fitness benefit of leaf fenestration and functionally analogous traits decreases along a gradient from fast to slow growth strategy (table 2; fig. A1A). The strategy of climbers, which is to outgrow their hosts, may make them especially sensitive to variance in growth rate compared to co-occurring species employing slower growth strategies.

Alternative Hypotheses for Fenestration

Thermoregulation via reduced boundary layer conductance (see “Introduction”) and increased leaf hydraulic conductance are the most plausible alternative hypotheses for leaf fenestration. Givnish and Vermeij (1976) do not address *Monstera* specifically but invoke thermoregulation to explain heteroblasty in confamilial *Philodendron* that reduce the effective size of adult leaves with lobing. In one study, leaf shape had no effect on leaf temperatures of tropical understory climbers (Fetcher 1981), possibly be-

cause irradiance several meters above the forest floor, which is well below full sunlight (e.g., Montgomery and Chazdon 2001), is insufficient to elevate leaf temperature much above air temperature. Similarly, another study of tropical trees found much lower leaf temperatures and vapor pressure deficits in understory compared to canopy leaves (Pearcy 1987). At irradiances found in tropical understories, leaf shape may not be important in thermoregulation. However, brief, intense sunflecks may challenge the hydraulic supply in understory species. Large leaves have reduced major vein density and are more susceptible to water stress because of lower leaf hydraulic conductance (Scoffoni et al. 2011). If large leaves are advantageous in *Monstera* (see below), fenestration may effectively increase major vein density by cutting out lamina between major veins, thereby reducing water stress and stomatal closure during sunflecks. Two lines of evidence from *Monstera* and *Ficus* suggest that hemiepiphytes, despite being connected to the soil by feeder roots, are hydraulically limited and perhaps susceptible to leaf water stress. Stems of *Monstera acuminata* are inversely tapered, increasing in thickness higher in the canopy, indicating that hydraulic demand increases as the plant grows into sunnier, less humid environments (López-Portillo et al. 2000). In *Ficus*, hemiepiphytic species had lower hydraulic conductivity than congeneric trees (Hao et al. 2010).

Both thermoregulation and hydraulic supply hypotheses for leaf fenestration require that large leaf size be advantageous in *Monstera*. Otherwise, small, entire leaves would function as well. Givnish and Vermeij (1976) argued that construction cost efficiencies arise from economies of scale in large leaves. However, more recent theory and evidence indicate that large leaves may be inherently disadvantageous because they require greater biomass allocation to mechanical support tissue (Niklas et al. 2007; Niinemets et al. 2007). Large leaves may improve light interception efficiency by reducing leaf aggregation (Duursma et al. 2012). Detailed empirical measurements of light interception, leaf temperature, and water stress during sunflecks will be necessary to address the significance of large leaves and related hypotheses with respect to leaf fenestration.

Conclusions

The growth-variance hypothesis offers a novel explanation for leaf fenestration in *Monstera* that can be readily falsified with simple experiments. While motivated by the problem of leaf fenestration in *Monstera*, the growth-variance hypothesis is relevant to other tropical shade lianas and hemiepiphytes. The model also applies a well-known result from population genetics—selection depends on both the mean and variance in fitness—to explain the adaptive significance of leaf shape. Compared to its utility in fields

like life-history evolution (e.g., Real and Ellner 1992), the effects of traits on variance in fitness are rarely discussed in the ecophysiological literature. Although the importance of light variability on carbon gain has been previously noted (Ruel and Ayers 1999), this study exemplifies how the principle may be broadly useful in understanding the adaptive significance of other features of plant morphology and physiology.

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APPENDIX

Stochastic Simulations

I simulated whole-plant canopy dynamics using equation (11):

$$\Delta A_t = A_{t+1} - A_t = A_t \frac{\text{LMF}}{\text{LMA}} [(P_{\text{diffuse}} - R) + P_t],$$

where P_t is as defined in equations (8) and (9):

$$P_t = \rho N P_{\text{fleck}}.$$

$$N \sim \text{Poisson} \left[\frac{A_t \lambda}{\rho} \right].$$

For simulations, I iterated the model 100 time steps for 10^5 “individuals” starting from an initial size, A_0 . I calculated the fitness (geometric mean biomass) of plants with $\rho = \{0.4, 0.6, 0.8\}$ relative to entire plants ($\rho = 1$). In the first set of simulations, I varied intrinsic growth rate by changing the value of LMF/LMA (fig. A1A).

The average growth rate of the canopy is $[(P_{\text{diffuse}} - R) + \lambda P_{\text{fleck}}]$, which is a combination of constant (left side) and stochastic (right side) light for photosynthesis. To demonstrate that fenestration becomes more important as a greater fraction of photosynthesis comes from stochastic sources, I kept this sum constant while varying the contribution of constant and stochastic photosynthesis sources (fig. A1B).

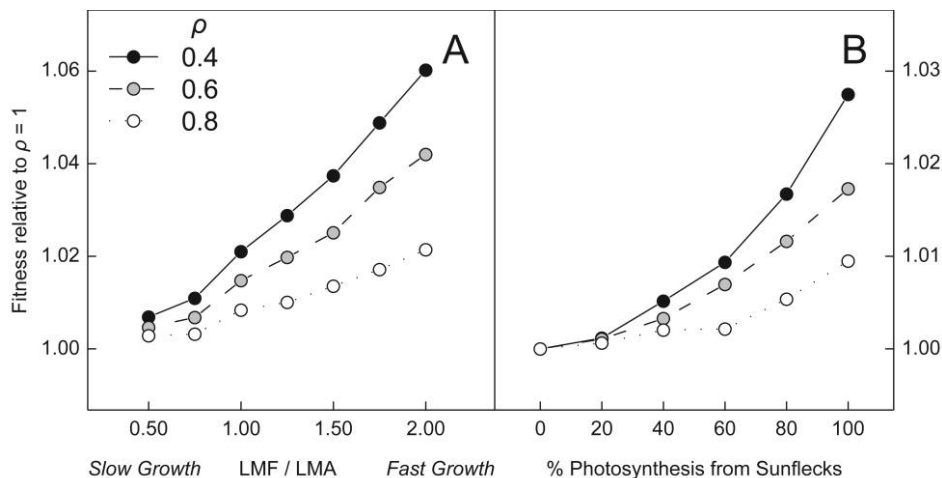


Figure A1: Stochastic simulations of whole-plant canopy growth and fitness. The Y-axis is the relative geometric mean of fitness of fenestrated leaves ($\rho = \{0.4, 0.6, 0.8\}$) relative to entire leaves. A, Faster intrinsic growth rate, which is affected by LMF/LMA, increases the importance of leaf fenestration. Parameters: $A_0 = 10$, $\lambda = 1$, $P_{\text{fleck}} = 0.1$, $P_{\text{diffuse}} - R = -0.9$. B, The proportion of photosynthesis from sunflecks compared to diffuse light affects the benefits of fenestration, holding other factors constant. Parameters: $A_{\text{leaf},0} = 1$, $[(P_{\text{diffuse}} - R) + \lambda P_{\text{fleck}}] = 0.1$. $P_{\text{diffuse}} - R$ (constant) and λP_{fleck} (stochastic) were adjusted so that their sum remained the same while the contribution of each changed from 0% to 100%.

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Swiss cheese plant (*Monstera deliciosa*).