The adaptive function of leaf fenestrations in *Monstera spp.* (Araceae): a look at water, wind, and herbivory

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ABSTRACT

A very important component of biodiversity in tropical forests is the vast variation in leaf morphology among different plant species. Leaf morphology is often a result of adaptations to the specific environmental conditions of a particular ecosystem or habitat. The *Monstera* genus of tropical plants in the Araceae family has very unique morphological leaf characteristics; it has large, deeply incised leaves with holes along the primary veins. There are many hypothesized adaptive functions of these holes, but no direct experimental studies have been completed to determine the functions they actually serve. This study directly tests the functional significance of the holes in *Monstera deliciosa* leaves in Monteverde, Costa Rica for three of the most generally accepted hypotheses: water uptake, wind damage reduction, and herbivory deterrence. The difference between normal *Monstera* leaves and control leaves with no holes were measured in three different treatments, one for each of the hypothesized important factors. *Monstera* leaves with holes were found to have a significantly higher amount of water capture by the roots of the plant than the leaves without holes. Holes in *Monstera* leaves were not found to have a very large impact on the degree of wind damage that a plant endures, and the presence of holes was found to actually increase the level of herbivory on a given leaf. These findings confirm that the holes in *Monstera* leaves are an adaptive function for increasing water uptake efficiency, but contradict the general consensus that the leaves are also adapted to decrease damage from water and herbivory pressures.

RESUMEN

Un componente muy importante de la diversidad en los bosques tropicales es la gran variación en la morfología entre las especies de plantas. La morfología de las hojas es a menudo el resultado de adaptaciones específicas a condiciones ambientales de ecosistemas o hábitats particulares. El género de plantas tropicales *Monstera* en la familia Araceae tienen características morfológicas únicas; es grande, incisa y con huecos a lo largo de las venas primarias. Existen varias hipótesis de las funciones adaptativas de los huecos, pero ningún experimente ha sido completado para determinar las funciones actuales de los mismos. Este estudio prueba directamente la funcionalidad de los huecos en hojas de *Monstera deliciosa* en Monteverde, Costa Rica para las tres hipótesis más aceptadas: captura de agua, reducción del daño por el viento e impedimiento de herbivoría. Las diferencias entre hojas normales y con huecos de *Monstera* se midieron en tres diferentes tratamientos, uno para cada hipótesis. Las hojas de *Monstera* con huecos presentan significativamente una mayor captura de agua por las raíces que las hojas sin huecos. Los huecos en las mismas no demostraron tener un impacto mayor en el daño por viento , y la presencia de huecos en las hojas demostró tener un impacto mayor en el grado de herbivoría en hojas en particular. Estos descubrimientos confirman que los huecos en *Monstera* son una adaptación funcional para aumentar la eficiencia en la captura de agua, pero contradice el consenso general de que las hojas son también adaptaciones para disminuir el daño por agua y herbivoría.

INTRODUCTION

An important and very prevalent component of diversity in tropical forests is the vast range of differences in plant and leaf morphology. Leaves serve a very important function in plants. Specifically, the variety of shapes and sizes of leaves are products of the relative cost and benefit syntheses that determine all naturally selective adaptations (Gutschick 1999). The conditions that morphological characteristics adapt to may be related to precipitation levels, sunlight availability, interactions with animals or other plant species, temperature, nutrient availability, consistency of conditions, or climatic extremes. The evolution of specific morphological characteristics of an individual plant reflects the adaptive response of the plant to its specific habitat.

Leaf size may range from a few millimeters to several meters in size with several different shapes and textures, reflecting the specific abiotic and biotic conditions of their particular niche. (Brown and Lawton 1991). Plants in the understory of a mature seasonal tropical wet forest have specific environmental stressors. Particularly, low light availability low amounts of precipitation, differences in the strength of wind, and predation pressure due to herbivory may affect the leaf morphology of understory rainforest plants (Osborne 2000), Plants that live in the forest floor show stress of water loss much more quickly than canopy plants (McDade *et al.* 1994), and this is likely due to the fact that canopy trees intercept much of the precipitation and not much reaches the forest floor. Several different studies have found that only 75-80% of falling rain actually reaches the forest floor (Leigh 1999). Therefore, understory plants must have adaptations to deal with low water conditions, and plants in such environments with low water conditions were found to have narrower leaves, thicker lamina, and denser leaf tissue (Cunningham *et al.* 1999). Leaf characteristics are further adapted to deal with specific challenges based on its place and role in the forest and its interactions with other species (Press 1999). To deal with herbivory in tropical forests, leaves tend to develop increased toughness, as insects often eat the softest leaves they can find (Marquis 1992). It has also been found that sustained levels of herbivory by insects over time modified plant shape in pinon pine, *Pinus edulis* (Whitham and Mopper 1985), For conditions with limiting nutrient availability plants may allocate biomass to the plant parts that allow for greater uptake efficiency of the limiting nutrient. For example, plants that grow in nitrogen-poor environments produce more shoot material and less root material to levels that allow for a better balance of carbon and nutrients for optimal growth (Chapin *et al.* 1987). Lastly, more studies have found evidence for plants developing morphological adaptations for wind pressure. Trees that live in high wind conditions have adapted over the long term to have smaller leaves, which reduce the amount of surface area to resist the wind (Coutts and Grace 1995). The ability to develop adaptations via natural selection is a crucial aspect of leaf morphology that allows a species to survive for many generations.

Species in the *Monstera* genus (Araceae), are particularly interesting plants to study morphological leaf diversity via adaptations since they have a very unique leaf structure that has not been well studied. In its adult stages, the leaves of *Monstera* vines develop deep incisions from both sides that go very close to the center of the leaf and also develop holes within the leaf, called fenestrations (Zuchowski 2005). These leaf fenestrations, which form by programmed cell death, make *Monstera* distinguishable and

and interesting to study the mechanisms of evolution of particular leaf morphologies. There are several hypotheses on the potential adaptive value of the holes in *Monstera* plants, but no studies have been done to directly test these possible adaptive functions. *Monstera deliciosa*, or the Swiss Cheese Plant, is widespread throughout both coasts of Costa Rica (Zuchowski 2005). *Monstera* is naturally an understory vine in tropical wet and moist forests that has large leaves that lie erect from the trunk of its host tree, with the roots attached to the forest floor at the base of the tree. Because of its position in the understory, *Monstera* experiences a limiting level of water reaching its roots. The holes may serve to increase water capture efficiency because the holes allow for water to pass to the ground closer to the trunk. *Monstera* is also subject to wind damage when found in open areas or on forest edges and the fenestrations may reduce damage from wind by creating an area for wind to pass through. In all places that it is located, these vines are subject to damage from insect herbivory and it has been hypothesized that the holes in *Monstera* leaves deter herbivory by looking like a leaf that has already been eaten or decreasing surface area so that insects have a harder time getting around on the leaves (Donnelly 1997). I examined the function of these leaf fenestrations more closely to find out if they are an adaptive characteristic to help the plant with wind, rain, and/or herbivory by directly measuring the effect the holes have on these three factors. I predicted that the fenestrations in *Monstera* are an adaptive trait that increases the efficiency of water reaching the roots of the plant, helps reduce damage to the plant from wind, and helps deter herbivory.

MATERIALS AND METHODS

Study Site and **Organism**

Monstera deliciosa can be found everywhere in the Monteverde community, and leaves were easily collected from various locations in the Monteverde area at 1450 meters above sea level. The Pacific slope, at the elevation of the study site experiences a dry season every year for 4-6 months and moderate to extremely strong winds during the transition seasons, but the forest is relatively moist the entire year due to clouds passing through its high elevation. The forest is characterized with abundant epiphytes and a very dense understory (Nadkarni and Wheelwright 2000). Several *Monstera* species can be found in this region but *Monstera deliciosa* is especially abundant throughout the community along roadsides and in gardens.

Monstera leaves were then brought into the laboratory at the Estacion Biologia in Monteverde, Costa Rica to conduct all experiments. The study was done in three separate treatments, each one assessing the adaptive function of the fenestrations with respect to water, wind, and herbivory by comparing the differences between *Monstera* leaves with holes and leaves without holes. For the wind and water treatments, trials were completed on regular, mature *Monstera* leaves that were relatively intact and on control leaves that were created to effectively be *Monstera* leaves without the fenestrations. The control leaves were initially made by taking regular *M. deliciosa* leaves and filling in the holes and incisions with leaf material from other *M. deliciosa* leaves via cutting and gluing. The first half of control trials for both the wind and water treatments was completed on this leaf model. Due to the time-consuming nature of this methodology and fragility of the sample leaves, the holes and incisions of the second half of the control leaves were filled in with duct tape. Preliminary trials with the new control model indicated that the differences in data values between the two models were negligible.

Water Treatment

To test the effect of the holes in *M. deliciosa* on water capture efficiency, an artificial tree was created in the lab that *Monstera* vines could be assembled on. The artificial tree was made on a tall two-by-four wooden board that had five long nails, situated directly above each other about 6 inches apart, sticking all the way through it on which leaves could be fixed perpendicular to the "trunk". *M. deliciosa* leaves were gathered from the field and the petioles uniformly cut to 35 centimeters long. A different leaf was stuck on each of the nails so that a complete "plant" was made that was five leaves tall, climbing up the tree. The artificial tree was attached to a laboratory wall and a circular water collecting bin with a 45 cm diameter was placed below the bottom leaf and 20 centimeters away from the base of the board. Eight liters of water were poured out of a watering can from 4-6 inches above the top leaf and collected in the bin at the bottom. The volume of the collected water was measured and recorded. Each plant arrangement of five leaves was repeated for three trials and then the plants would be switched and rearranged from a larger pool of *Monstera* leaves to create new plants. 20 different plant arrangements were created out of 20 *M. deliciosa* leaves for a total of 60 trials. This process was repeated for the control leaves and 10 different plant arrangements were created out of 10 leaves for a total of 30 control trials.

Wind Treatment

To test the difference between leaves with holes and leaves without on the amount of wind damage each receives, the change of the angle between the *Monstera* petiole and the leaf plane was measured before and during the addition of wind pressure. The actual angles were too small to reliably measure with any tool, so trigonometry was needed to calculate the angles in a triangle model. One leaf at a time was stuck on the bottom nail on the artificial tree and a piece of string was fixed to the board at an appropriate distance above so that a triangle could be made with the piece of string as the hypotenuse, the floor between the board and where the string meets the ground as the base, and the board of the tree from the floor to the point where the string was fixed as the back side. The string was pulled taut tangent to the plane of the leaf to the floor. Measurements were taken and recorded for the length of the back side and base side of the triangle before any wind was applied. Wind pressure was applied by placing a *Phantom High Speed Velocity* fan one meter away from the base of the tree and blown directly at the leaf on setting 3, the highest setting, for 30 seconds. The hypotenuse string was pulled to stay in line with the plane of the leaf to its maximum displacement during the 30 seconds. Measurements for the back and base sides of the triangle were taken and recorded for the maximum displacement. This method was repeated for 20 *M. deliciosa* leaves and 15 control leaves.

Herbivory Treatment

To test the effect of *Monstera* fenestrations on herbivory levels, generalist insect herbivores (Orthoptera) were observed to see if they preferentially selected leaf samples with holes or ones without. Ten individuals of the same Orthopteran species were obtained from the Monteverde Butterfly Garden and each was placed in its own container. Each container had two leaf cut-outs from the same young *M. deliciosa* leaf. One of the cut outs in each container was from the interior part of the leaf that had holes in it, and the other was from the outer part of the lobes and had no holes. After two days, measurements of the area of herbivory on each leaf section were taken with clear, plastic grid sheets and the leaves were replaced with new ones. The leaves were changed three times for each grasshopper for a total of 30 herbivory trials.

RESULTS

Water Treatment

More water was collected underneath normal *Monstera deliciosa* leaves that had holes than under leaves with filled in holes (*t test* = -9.658, $P < 0.0001$). The mean volume of water collected in the bin was 1424.5 ± 95.03 mL for normal *Monstera* leaves while the mean volume for collected water for control leaves was almost 12 times less, at 120.167 ± 12.35 mL (Fig. 1).

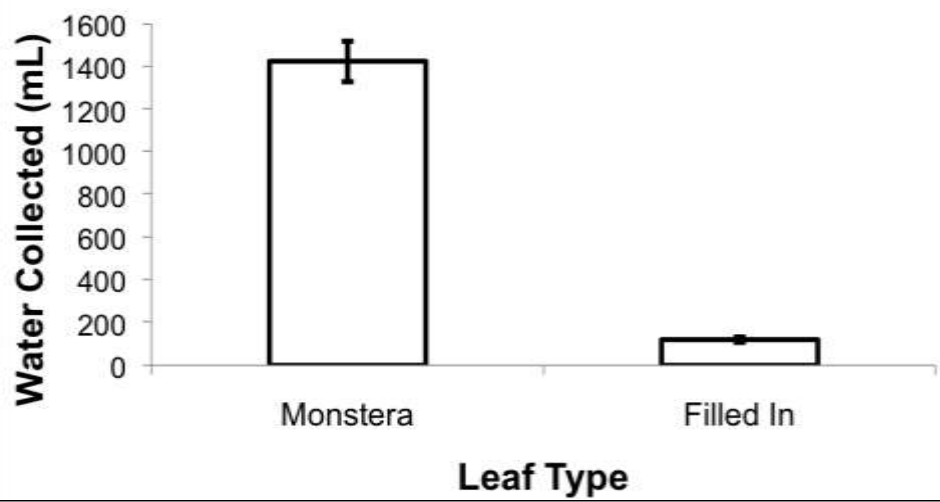

Figure 1: The average volume of water ± SEM collected at the base of an artificially created *Monstera* vine by leaf type (N=60 for *Monstera* and N=30 for Filled In).

Wind Treatment

The change in angle between the petiole and the plane of the leaf blade with and without wind pressure was small for both *M. deliciosa* leaves and the filled in control leaves but was greater for the filled in than for the *M. deliciosa* leaves, though not statistically significant (*t test* = 1.846, *P*=0.0738). The mean angle change for *Monstera* leaves was 1.38 ± 0.14 degrees and the change for the control leaves was only slightly greater at 2.06 ± 0.38 degrees (Fig. 2).

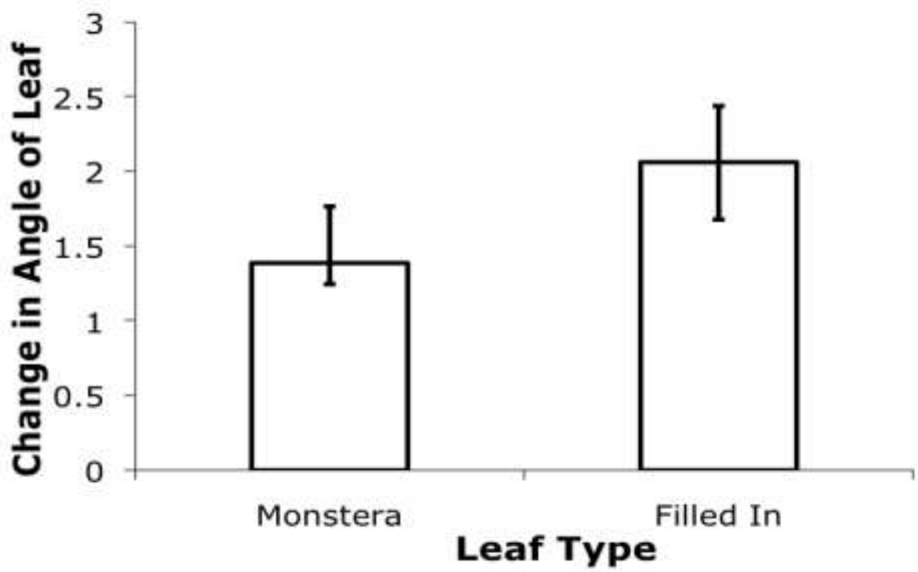

Figure 2: Average change in angle ± SEM between leaf and petiole due to wind pressure by leaf type (N = 20 for *Monstera* and N = 15 for Filled In).

Herbivory Treatment

Herbivory by the generalist Orthopteran was significantly higher for segments of *M. deliciosa* leaves with holes than the *M. deliciosa* leaf segments that were void of holes (*t test* = 4.546, *P* < 0.0001). The Orthopterans ate a mean amount of 13.073±1.99 square millimeters on the segments with holes and ate only about one-fourth of this amount on complete leaf segments at 3.594±0.6 square millimeters (Fig. 3). Herbivory was often disproportionately high on the swollen veins of the leaves if the particular leaf had a vein. As the leaves with holes were taken from the central part of the leaf, most of the leaf segments containing swollen veins were leaf sections with holes.

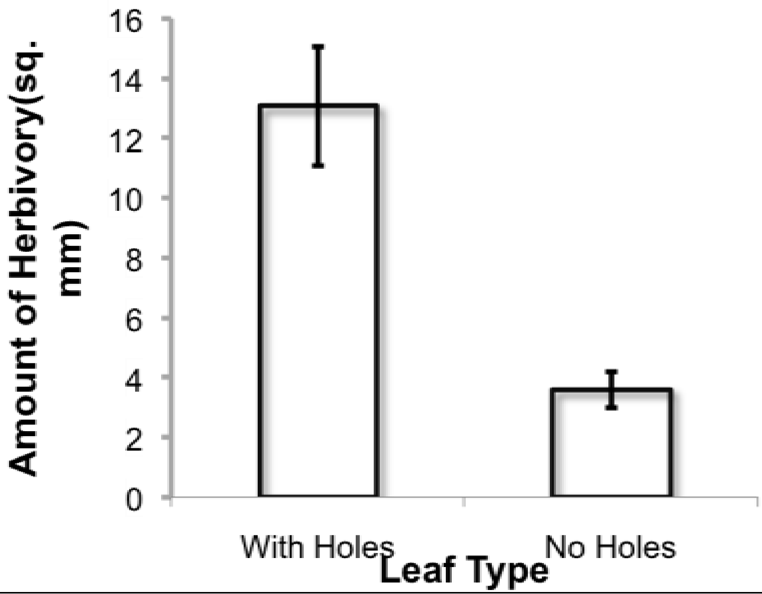

Figure 3: Average area herbivory in square millimeters ± SEM from generalist Orthopteran by leaf type (N = 30 for both *Monstera* and Filled In).

DISCUSSION

The study showed clear patterns of the potential adaptive function of fenestrations in *Monstera* leaves for rainfall, wind damage, and insect herbivory. The primary adaptive function that the holes and incisions in *Monstera* species serve is to increase the amount of water uptake at the root of the vine. This is very important for *Monstera* plants because it is difficult for the roots of *Monstera* to get water without this trait. As previously mentioned, understory plants receive a limited amount of water from precipitation due to the canopy trees intercepting most of this important resource. This is especially prevalent in Monteverde, which has a lot of epiphytes and very dense vegetation in the understory (Nadkani and Wheelwright 2000). Increased density in the understory would inhibit the forest floor from receiving water even more because there are extra tree layers to absorb the precipitation that does make it through the canopy layer. Furthermore, *Monstera* leaves are large, are positioned erect from the host tree, and its roots are situated at the base of the tree in the ground, since *Monstera* begins growing from the ground before it attaches to a host tree. The fenestrations in the *Monstera* genus are an effective adaptation for increasing water uptake efficiency because water is able to drip through the holes and cuts in the side to land closer to the plant roots and are therefore more likely to get absorbed the roots. Without its fenestrations, water would roll all the way off the leaves and land far from the roots, as they did with the control leaves. Since the roots are located close to the host tree, the water is less likely to be absorbed if it lands far away from the tree.

I show that the fenestrated leaves did not develop in the *Monstera* genus as an adaptation to reduce damage from wind. This contradicts a general hypothesis that *Monstera* fenestrations developed to reduce wind damage since wind can easily pass through the holes, creating less wind resistance on the leaf surface. My study was the first to directly test this relationship and the data refute this hypothesized function. There was a trend that indicated leaves were more displaced with the fenestrations filled in than the normal *M. deliciosa* leaves, meaning that the fenestrations may be providing some degree of relief from wind damage. Since the difference was not significant, it cannot be assumed that the fenestrations developed directly as an adaptive strategy for wind in *Monstera*. Understory environments do not usually experience heavy winds (McDade *et al.* 1994), much less the sustained pressure needed to evolve a novel adaptive characteristic. Certain tropical rainforest tree species possess lobed leaves in the windy canopy because they help reduce wind damage, but they do not possess lobed leaves in the understory (Ennos 1977). This study supports that wind is only an ecological factor in edges and canopy areas, where wind pressure is much stronger and more sustained, Therefore wind pressure would have to be much stronger in the Monteverde understory to act as an agent for adaptive characterestics.–Even though *Monstera* is present in disturbed windy areas, most of the plants found in those areas were planted by people and it is not the natural habitat that *Monstera* is adapted to.

My study also does not support the hypothesis that the fenestrations in *Monstera* serve to deter herbivory by appearing unattractive to insect herbivores as a result of being shown to be already heribvorized. My results indicate that the exact opposite is true; generalist herbivores eat a greater area of leaves with fenestrations than without. A leaf that looks like other insects have already eaten it and has holes it in may be attractive to generalists because it indicates that the leaf is definitely palatable, high in nutrition, and soft enough to eat. Herbivores have demonstrated to selectively eat young, tender leaves with higher nutritional quality in both field experiments and lab experiments (Perez-Harguindeguy et al. 2003). This being true, my data indicate the fenestrations in *Monstera* did not adapt in response to herbivory pressure. This is contradictory to a previous study that concluded that fenestrations developed as an anti-herbivory agent to compensate for a low level of secondary compounds measured in *M. deliciosa leaves* (Donelly 1997). However the Donnelly 1997 study failed to directly look at herbivores differentially selecting between leaves with and without holes; too many unsupported assumptions were made. In my study, much of the herbivory was on swollen leaf veins and these happened to only be present on leaves with holes. The Orthopterans may have preferred this plant material over the regular leaf material and herbivory levels may have been biased towards preference for the fenestrated leaves due to this variable. An additional study should eliminate swollen leaf veins as a factor to support the hypothesis that herbivory is higher on fenestrated versus non-fenestrated leaves.

The longstanding and general consensus has been that the adaptive function of the fenestrated leaves in *Monstera* is due to water, wind, and herbivory pressures. This study directly examined how the holes make a difference with respect to these three factors and it indicates that the primary function of *Monstera* fenestrations is actually to increase water uptake efficiency at the roots.

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