Effects of Sun vs Shade and Leaf Age on Leaf Morphology, Herbivory, and Physical Defenses in the Swiss Cheese Plant (*Monstera adansonii*)

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ABSTRACT

One important structural defense of plants is calcium oxalate crystals or raphides. In this project, I studied one species in the plant family Araceae, *Monstera adansonii,* a widely distributed plant in the tropics, that is known to contain raphides. Plants of this species were sampled in sun or shade locations. For each plant three leaves were sampled, the first fully expanded leaf on a plant (leaf 1) and two more leaves below it, leaf 3 and leaf 5. For each leaf, I measured: leaf area, number of fenestrations (naturally occurring holes in the leaf), amount of herbivory, and density of raphides. I compared these measures on leaves of different ages from sun versus shade plants. Results showed that: 1) older leaves were significantly larger than younger leaves ($P < 0.001$), but there was no effect of light environment ($P = 0.199$); 2) density of raphides was not significantly affected by sun ($P = 0.147$) and density of raphides decreased with leaf age ($P = 0.0097$), 3) the number of fenestrations was significantly higher in plants in the sun ($P = 0.01$), but did not differ with leaf age ($P = 0.702$); 4) herbivory was not affected by sun exposure ($P = 0.29$) but was marginally significantly affected by raphide density ($P = 0.06$); There was a significant interaction between raphide density and light exposure on herbivory, in that in the shade there was a negative relationship where herbivory decreased as raphides increased, but in the sun, a positive relationship where herbivory increases as raphides increase ($P = 0.04$).

INTRODUCTION

During a plant's lifetime, it is besieged by an abundance of biotic and abiotic stressors. Biotic stressors consist of issues such as herbivory and competition from other plants, whereas abiotic stressors are issues such as getting enough sunlight and water. Plants and insects have both evolved and coexisted alongside one another for around 350 million years (Mithöfer 2012). Theory suggests that herbivores and plants are involved in a 'coevolutionary arms race' in which over time, selection has favored plants to evolve more defensive traits (Kariñho-Betancourt et al. 2015) and herbivorous insects have evolved to respond to these defensive traits.

Plant defenses may be chemical defenses or structural (physical) defenses and these defenses can either be already existing in the plant (constitutive) or can be induced after an attack (inducible). Inducible defenses are triggered by pests but can also be induced by environmental factors (Roberts et al. 2006). Examples of chemical defenses are cyanogenic glycosides, glucosinolates, alkaloids, and terpenoids. Examples of structural defenses are waxy leaves, thorns, prickles, trichomes, and thickened cell walls (Mithöfer 2012). There are also structural defenses that are located inside the leaf such as calcium oxalate crystals.

Calcium oxalate crystals, also known as raphides, are structural defenses that have been recorded in most terrestrial plant families (Hanley et al. 2007) and can be found in a variety of plant tissues such as leaves, stems, roots, seeds, flowers, and fruits (Konno et al. 2014). Calcium oxalate crystals grow in aggregate bundles and can be described as pointy, needle-like structures that are visible under a microscope (Prychid et al. 1999). Calcium oxalate crystals are able to inflict damage on both invertebrate and vertebrate herbivores and have been studied for their anti-herbivore defenses (Hanley et al. 2007). These crystals are comprised of calcium and oxalic acid, a common organic acid found in many plants (Franceschi et al. 2005).

Plants in the family Araceae are commonly found in the Neotropics and are typically non-woody perennial herbs whose inflorescences have spadix-shaped structures (Ahmed 2011). One important structural defense in many species in the Araceae family are raphides, which have been found to increase in frequency with calcium presence (Webb 1999). Many parts of the plant contain raphides, but they are most abundant in the leaves (Keating 2004) and may be an important defense against herbivores (Horner 1972). Raphides can be harmful to herbivores through ingestion (Baumgardt 1982) and studies have shown that the mortality rate of insect herbivores can be as high as 86% when ingesting leaves with raphides present (Konno et al. 2014). Depending on the size of the herbivore and its vulnerability to toxins found in plants, raphides can be poisonous and even lethal (Ward 1997).

Monstera adansonii (Araceae), the focal species of this study, is found in the Neotropics and is widely distributed throughout South America and Central America. This species is considered a hemi-epiphyte and is typically noted for its tree-climbing adaptations (Andrade et al. 1998). Also known as the Swiss cheese plant, *M. adansonii* is known to contain raphides. *M. adansonii* was first documented in western literature by Charles Plumier and was later cited by Carl Linnaeus in 1753 (Madison 1977). It was noted for its root dimorphism, leaf structure, and spathe and spadix inflorescence (Madison 1977). *Monstera adansonii* is a shade-tolerant species and reaches its maximum size when growing on trees (Andrade et al. 1998).

Since new leaves the plant produces are typically softer and therefore more vulnerable to herbivory, many plant species allocate resources to protecting these new leaves (Coley 1983). When studying leaf age in saplings in Panama, Coley (1983) discovered that although young leaves are easier for herbivores to consume, they contain two to three times the concentration of phenolics, a class of chemical compounds in plants (Coley 1983). Furthermore, these new leaves lack the ability to regulate calcium, resulting in a higher display of raphides (Prychid 2008). These results suggest that there may be higher amounts of calcium oxalate crystals in younger leaves of *M. adansonii*. The goals of this study were to examine how the environment in which *M. adansonii* plants grow (sun versus shade) and the age of leaves affects 1) raphide content, 2) the number of fenestrations (holes in a leaf), 3) leaf size, and 4) levels of herbivory.

BACKGROUND

1. *Study species*

Monstera adansonii is a common houseplant that is sought after by plant enthusiasts due to its unique foliage and adaptations to low light. It is in the Araceae family, also known as the aroid family which includes 114 genera and 3,700 species worldwide (Boyce et al. 2019). Most commonly, aroids are recognized as herbaceous monocotyledonous epiphytes or semi-epiphytes that are found primarily in the New World Tropics (Ortiz et al. 2021). Species in the Araceae family are known for their prominent morphological diversity (Henriquez et al. 2014). The smallest Araceae species is also the world's smallest known angiosperm (*Wolffia*), and the largest species produces the largest unbranched inflorescence in the world (*Amorphophallus titanum*) (Laurent 2016). Since the tropics hold the highest amount of biodiversity in terrestrial ecosystems (Perfecto et al. 2008), plants in these regions face high levels of competition. The majority of species in the Araceae, including *M. adansonii,* contain calcium oxalate crystals, also known as raphides (Barabé et al. 2004).

2. *Structural defenses*

Structural defenses are an important adaptation that plants use to help evade herbivory and other environmental stressors. Some of these defenses include calcium oxalate crystals (raphides), trichomes, spines, thorns, prickles (spinescence), and hardened or tough waxy leaves (sclerophylly). Calcium oxalate crystals are said to be specifically produced by the plant for defense against herbivores, but not all research agrees (Coté et al. 2012). Thorns and prickles, for example, are significantly more likely to be avoided especially amongst vertebrates (Milewski et al. 1990). Thorns in particular can be especially deadly due to an adaptation in some plants that display thorns, where they introduce fungi and other bacteria into the host when pricked (Halpern et al. 2007). Sclerophylly is also known as a mechanical defense because it is a non-metal toughness or hardness that can add to the strength and resilience of the plant. For plants that exhibit tissue toughness, it can be a combination of a strong cell wall and waxy leaves (Lucas et al. 2000).

3. *Calcium oxalate crystals or Raphides*

   Like many monocot species, plants in the Araceae family contain calcium oxalate crystals, with most research focusing on their concentration in plant leaves (Prychid 2008). Calcium oxalate crystals are needle-like structures formed in bundles that can be found in a variety of organs in plants including leaves, stems, flowers, and roots (Konyar 2014), and are insoluble crystalline salts of oxalic acid and calcium. They are formed inside crystal cells, which are cells that are found in many plant organs that may be specialized for idioblasts depending on the species (Franceschi et al. 1980). Crystal idioblasts are cells that are specialized for the production of these crystals (Franceschi et al 2005). Calcium oxalate crystals are often formed from environmentally derived calcium and biologically synthesized oxalate (Franceschi et al. 2005). There are many hypotheses about why calcium oxalate crystals are produced by plants, but the proposed functions of these crystals are for calcium regulation, plant protection, tissue support, and light gathering and reflection (Nakata 2003). The development of calcium oxalate crystals is largely dependent on environmental factors during plant growth, especially in early plant development. Some of these environmental factors are sunlight, plant location, and access to essential minerals (White et al. 2003). Due to this, most species have a uniform distribution of calcium oxalate crystals within mature plant tissues (Prychid 2008).

The occurrence of raphides in plants can be affected by several different factors. One study discovered that the leaves of plants grown in soils with a higher calcium content yielded more calcium oxalate crystals in their leaves (Molano-Flores 2001). This study also found that plants in areas with higher herbivory had higher raphide concentrations (Molano-Flores 2001). Another study in 2009 examined another species in Araceae, *Dieffenbachia sequine*, but found that there was not sufficient evidence to support the hypothesis that raphides deter herbivory (Coté 2009).

4. *Sun vs shade environments*

Previous research indicates that there is a greater rate of herbivory on plants in shaded areas compared to sunny areas (Maiorana 1981). One possibility for this could be that herbivores (specifically invertebrates) prefer shaded areas away from direct sunlight and predation (Maiorana 1981). Another possibility that was discussed in Maiorana (1981) was that plants in the sun are more toxic than plants in the shade. However, in the research cited in Maiorana (1981), it was found that there was no significant difference between herbivory in sun and shade leaves.

METHODS

Field site

Monteverde, Costa Rica, is known for its striking biodiversity and its unique climate. Home to over 2,500 species of plants, 100 species of mammals, 400 species of birds, and 1200 species of reptiles and amphibians, this Cloud Forest ecosystem supports 2.5% of all biodiversity on Earth (Peters 2022). Monteverde is a high-elevation premontane tropical wet forest (4,364 feet) located in the Tilarán Mountain Range (FIGURE 1). Monteverde is categorized as a Cloud Forest, consisting of low clouds, daily precipitation, and high humidity due to its proximity to the Caribbean and Pacific Oceans. Due to this climate, Monteverde holds a great deal of biodiversity (Kappelle et al. 2004). On an individual tree, many different species of epiphytes and semi-epiphytes grow on the trunk and branches, such as orchids, bromeliads, ferns, lichens, and aroids (Jacobi, personal observation). All sampling research for this project was conducted at the CIEE-Monteverde in the San Luis of Monteverde, Costa Rica. The study site is considered a premontane tropical wet forest, and field collection took place during the Dry Season from March-May. The experimental design and data collection were undertaken as part of a semester-abroad study supervised by Dr. Miguel Chaves in April and May 2022.

Sample collection for measurement of leaf area, fenestration number, and herbivory

To measure leaf area, quantify the number of fenestrations in a leaf, and measure the amount of insect herbivory, samples of *Monstera adansonii* were collected from individual plants located in either sunny areas (FIGURE 2) (N = 32 plants) or shaded areas (N = 32 plants). I defined a "sun" area as an area that is close to a road or path that has been cleared of above vegetation and defined a "shade" area as an area that was in the forest and off trail, with tree cover overhead from the emergent and canopy layers above (FIGURE 3).

From each individual plant, three leaves were collected, starting with the newest, fully expanded leaf, which was called leaf 1. The third leaf (Leaf 3) and the fifth leaf (Leaf 5) below Leaf 1 were also collected in order to investigate the effects of leaf age on the dependent variables. In addition, disks were punched from each leaf to estimate raphide density (see below). Leaves were collected over a span of 10 days, from April 22, 2022, to May 2, 2022.

Samples were processed on the same day that they were collected to assure all samples were processed while still fresh.

To measure the leaf area and count the number of fenestrations per leaf, I took a photograph of the leaf on a scaled piece of paper (FIGURE 4). Using an application called "LeafByte" (Getman-Pickering et al. 2019), I manually measured the area of the leaf and counted the number of fenestrations (FIGURE 4). "LeafByte" (Getman-Pickering et al. 2019) was also used to measure the leaf area lost to herbivory. For the measure of herbivory, each leaf was examined for possible herbivore damage. When the damage was hypothesized to be due to herbivory, the total leaf area was estimated by reconstructing the original leaf boundary and using that to calculate the area lost to herbivory, while also excluding fenestrations from the data. In cases where the original leaf outline could not be reconstructed (e.g., the entire apex of a leaf was removed), that leaf was not included in the analysis.

Measurement of leaf raphide content

To determine the leaf raphide content (Chaves-Fallas 2021), a hole puncher was used to remove a disk with an area of 0.44 cm^2 from the base of the leaf on the left side. These disks were removed on the same day that the leaf was collected. The leaf disk was finely cut into multiple sections using a razor blade to increase the surface area that might release raphides. These sliced leaf sections were then added to a 1.5 mL Eppendorf tube containing 0.5ml of a 7:3 ethanol-water solution (FIGURE 5). The sample was broken up by vortexing the sample for 60 seconds and 20 µl of the sample was placed on a slide. Each slide was examined under the low power objective of a dissecting microscope (10X) and all the raphides in the sample were counted using a tally counter. Leaf raphide content is illustrated as raphides per field of view on slides (FIGURE 6).

Statistical analyses

All statistical analyses were conducted in the statistical programming language R version 4.0.0. (R Development Core Team 2020), with details of each analysis described below. In each analysis, leaf age was coded as a continuous variable.

Leaf area

I analyzed the effect of light and leaf age on leaf area with a linear mixed effect model (lme4 package: lmer) including plant ID as a random effect to account for multiple measures on the same individual plants. I included sun exposure (sun or shade) and leaf age (leaf number 1, 3, or 5) as main effects and their interaction. When interactions were not significant, I removed them from the model and interpret only the main effects.

Raphide density

I analyzed the effect of light and leaf age on raphide density with a linear mixed effect model (lme4 package: lmer) including plant ID as a random effect to account for multiple measures on the same individual plants. I included sun exposure (sun or shade) and leaf age (leaf number 1, 3, or 5) as main effects and their interaction. When interactions were not significant, I removed them from the model and interpret only the main effects.

Fenestrations

I analyzed the effect of light and leaf age on number of leaf fenestrations with a generalized linear mixed effect model (lme4 package: glmer) including plant ID as a random effect to account for multiple measures on the same individual plants. I included sun exposure (sun or shade) and leaf age (leaf number 1, 3, or 5) as main effects and their interaction. I specified a Poisson distribution for the number of fenestrations per leaf. When interactions were not significant, I removed them from the model and interpret only the main effects.

Herbivory

To determine if herbivory varied between sun and shade or with raphide density, I used a generalized linear mixed effect model (lme4 package: glmer) including plant ID as a random effect to account for multiple measures on the same individual plants. Given that leaf age was also related to raphide density, I chose to include leaf age as another random effect and focus on the main effect of raphides as they are deterrent to herbivores. I included sun exposure (sun or shade) and raphide as main effects and their interaction. I specified a binomial distribution for the probability of herbivory (either 0 or 1).

RESULTS

Leaf area

I found that leaf area increases with leaf age (leaf number) but found no significant effect of light exposure (LMM; light level coefficient = 5.239e-02 ± 4.033e-2, t = 1.299, P = 0.199). Leaf age (leaf number) significantly affected leaf size wherein older leaves were significantly larger than younger leaves (FIGURE 7, LMM; leaf age coefficient = 3.266e-2 ± 5.56e-3, t = 5.869, P = < 0.001).

Raphide density

Individual plants in the sun and shade varied substantially in raphides (FIGURE 8). Although the mean density of raphides, on average, was higher in the sun (FIGURE 9, Mean in sun = 43.93, SE = 3.93, mean in shade = 30.51, SE = 1.70), I found no significant effect of sun exposure on raphides (FIGURE 9, LMM; light level coefficient = 0.0943 ± 0.064, t = 1.468, P = 0.147). However, I found a significant negative relationship between raphide density and leaf number, indicating that raphides declined with leaf age (FIGURE 8 LMM; leaf age coefficient = -0.026 ± 0.009, t = -2.626, P = 0.0097).

Fenestrations

I found that leaves growing in the sun had 36% more fenestrations than leaves growing in the shade (FIGURE 10, GLMM; light level coefficient = 0.409 ± 0.159, z = 2.562, P = 0.01). However, there was no relationship between leaf age and the number of fenestrations in leaves (GLMM; leaf age coefficient = 0.0072 ± 0.019, z = 0.382, P = 0.702).

Herbivory

I found no main effect of sun exposure on the probability of leaf herbivory (P = 0.29) or a main effect of leaf age on herbivory (P = 0.15). However, a marginally significant relationship was found between raphide density and the probability of herbivory (P = 0.06); I also found that there was a significant interaction between raphide density and sun exposure (FIGURE 9, GLMM; raphide density and light level coefficient = 0.037 ± 0.018, z = 2.05, P = 0.04), wherein the probability of herbivory on leaves growing in the shade decreases as raphides increase. Compared to leaves in the shade, leaves growing in the sun have an increased probability of herbivory as raphides increase, signifying a positive correlation, whereas leaves growing in the shade have a decreased probability of herbivory as raphide density increase, signifying a negative correlation (FIGURE 11).

DISCUSSION

Overall, my results showed that growing in the sun versus the shade only significantly affected the number of fenestrations, which were higher in the sun, but had no direct effect on leaf size, raphide density, or herbivory. My results also showed that leaf age significantly affected the size of leaves, wherein older leaves were significantly larger than younger leaves. Leaf age also significantly affected raphide density, with older leaves displaying more raphides than younger leaves. However, the age of the leaves had no effect on the number of fenestrations present or the amount of herbivory. When examining the interaction between light level and raphide density, my results show a positive correlation in the sun, where, as raphides increase, so does the probability of herbivory. In the shade, I found a negative interaction, where, as raphides increase, the probability of herbivory decreases significantly. Thus, the environment in which a plant grows can be important in determining how raphides influence herbivory.

Effects of light exposure and leaf age on leaf area

The main results of my study showed that there was significance in that leaf area increases with leaf age, meaning that older leaves were significantly larger than younger leaves, but there was no significance in leaf size to light exposure. Although many leaves across different plant families increase in size with maturation, previous studies have indicated that there would be a greater difference in the size of the leaves in different light levels, specifically that the leaves grown in the shade would be larger on average than the ones in the sun, since they likely develop an adaptation to growing larger leaves in the shade to take need more surface area for sunlight to increase the rate of photosynthesis (Sims et al. 1992). More specifically, the plant expands its leaf to make more room for chloroplast cells (Bielczynski et al. 2017).

Effects of light exposure and leaf age on raphide density

Overall, my results showed that growth in different light exposure environments did not significantly affect raphide density. However, there was a weak negative relationship between raphide density and leaf age, signifying that as a leaf matures, it decreases in raphide concentration.

Previous studies have indicated that there is a higher content of raphides in harsher locations due to increased sun exposure, wind, and herbivory (Kadam et al. 2022) (Webb et al. 1999). In another study researching the growth of raphides in different levels of sun exposure in *A. muelleri* (Araceae), it was discovered that plants exposed to sunlight were on average 3x higher in raphide density than in shaded plants (Chairiya et al. 2012). Although in my research there was no significance of raphide density in the sun or shade, it can be concluded that raphide density can be influenced by both environmental conditions and species-dependent factors. Although prior research indicates that due to new leaves being softer and therefore more vulnerable to herbivory, the young leaves of plants are more likely to contain defenses than mature leaves (Coley 1983). Furthermore, new leaves are not able to regulate calcium intake as successfully as mature leaves, therefore new leaves may result in a higher display of raphides (Prychid 2008). This research supports my findings in that the new leaves of a plant contain a higher density of raphides than mature leaves.

Effects of light exposure and leaf age on fenestrations

The main results of my study showed that there was no significant relationship between the age of the leaf and the number of fenestrations. However, my results show that leaves grown in the sun had significantly more fenestrations (36%) than the leaves grown in the shade.

Previous studies, along with my study, have found that fenestrations develop as a response to environmental factors such as increased light levels. Fenestrations in leaves are first visible at the beginning of a leaf's development as newly, unfurled leaves and although the size of the fenestrations may change as the leaf matures, the overall number of fenestrations on a leaf remains the same (Gunawardena et al. 2004). Prior research indicates that understory plants are less likely to have as many fenestrations as those grown in an area with direct sunlight across the same species (Muir 2012). Due to the lack of light reaching the understory layer of the rainforest, these plants rely on sunflecks, which are brief, intermittent periods of intense light, as their only source of light exposure. Due to this, plants in the understory have adapted to produce fewer fenestrations for the purpose of increasing the surface area to attain as much light as possible (Muir 2012). This suggests that *M. adansonii* do not gain or lose their fenestrations over time, and that number of fenestrations is more influenced by environmental factors than leaf age.

Effects of light exposure, leaf age, and raphide density on herbivory

Overall, my results showed that there was no significant effect of sun exposure or leaf age on the probability of leaf herbivory, yet there was a marginally significant effect of raphide density on herbivory. My results indicate that there was a significant interaction between raphide density and sun exposure. These findings indicate that for leaves grown in the shade, there is a negative relationship between raphide density and herbivory – as raphides increase, herbivory decreases. For leaves in the sun, there is a positive relationship between raphide density and herbivory – as raphides increase, herbivory also increases.

Although there was no significant relationship between the environment in which the *M. adansonii* plants grew and the amount of herbivory in my study, previous research has indicated that plants found in the sun experienced significantly less damage by herbivores than leaves in the shade (Coley et al. 1996). This study also measured rates of herbivory in the canopy layer and the understory and stated that a possible explanation for different levels of herbivory may be due to the rate of increased predation on insect herbivores along the canopy where birds reside most (Coley et al. 1996).

Previous research that examined herbivory in mammalian herbivores has found that they significantly preferred to consume young, new leaves as opposed to mature leaves in tropical rainforest ecosystems (Coley 1983). Another study found that due to the higher nutritional quality of younger leaves, the daily rates of herbivore damage can be 5-25 times higher than for mature leaves (Coley et al. 1996). Another study found that in 70% of sampled species, young leaves were significantly more damaged by herbivory, even though phenols and other chemical defenses are much higher in younger leaves (Coley 1983).

Previous research has indicated that raphides play a role in protecting a plant from an herbivore attack (Hanley et al. 2007). Other previous research states the opposite and found that raphides have low efficiency in plant protection against herbivores (Sousa 2021). A possible explanation for this theory may have to do with the type of herbivores present. For example, herbivorous insects contain more structured chewing mouthparts that protect them from being damaged by raphides (Sousa 2021).

Future Directions

Future directions in this research might include further examination of the impact of light on the structural and chemical defenses of plants within the same species in an experimental setting, such as a greenhouse, where light levels could be controlled. In addition, it would be interesting to develop a long-term study about phenotypic differences in structural defenses among individuals or populations of the same species. It would also be interesting to utilize technology that gives the exact level of sunlight in both sun and shaded regions so that the light factor could be in the form of a gradient to examine relationships further. Furthermore, examining the types of herbivores who consume plants in the shade versus the sun could lead to more information on the extent to which raphides play in anti-herbivore defense.

Deforestation and other anthropogenic changes have consequences on the environment such as its effect on plant morphology and toxicity. In this research, the open areas that were determined as ‘sun’ areas were categorized as such because there was no tree canopy above and the plants were in direct sunlight. However, these open areas are not a natural phenomenon but are roads that have been logged and cleared to make room for hiking paths and roads (Jacobi, personal observation). This change can have great effects such as reducing trait diversity (Pessoa et al. 2017). A combination of observational data and experiments could be used to examine the consequences of environmental modification more specifically on plant traits such as those examined in this study.

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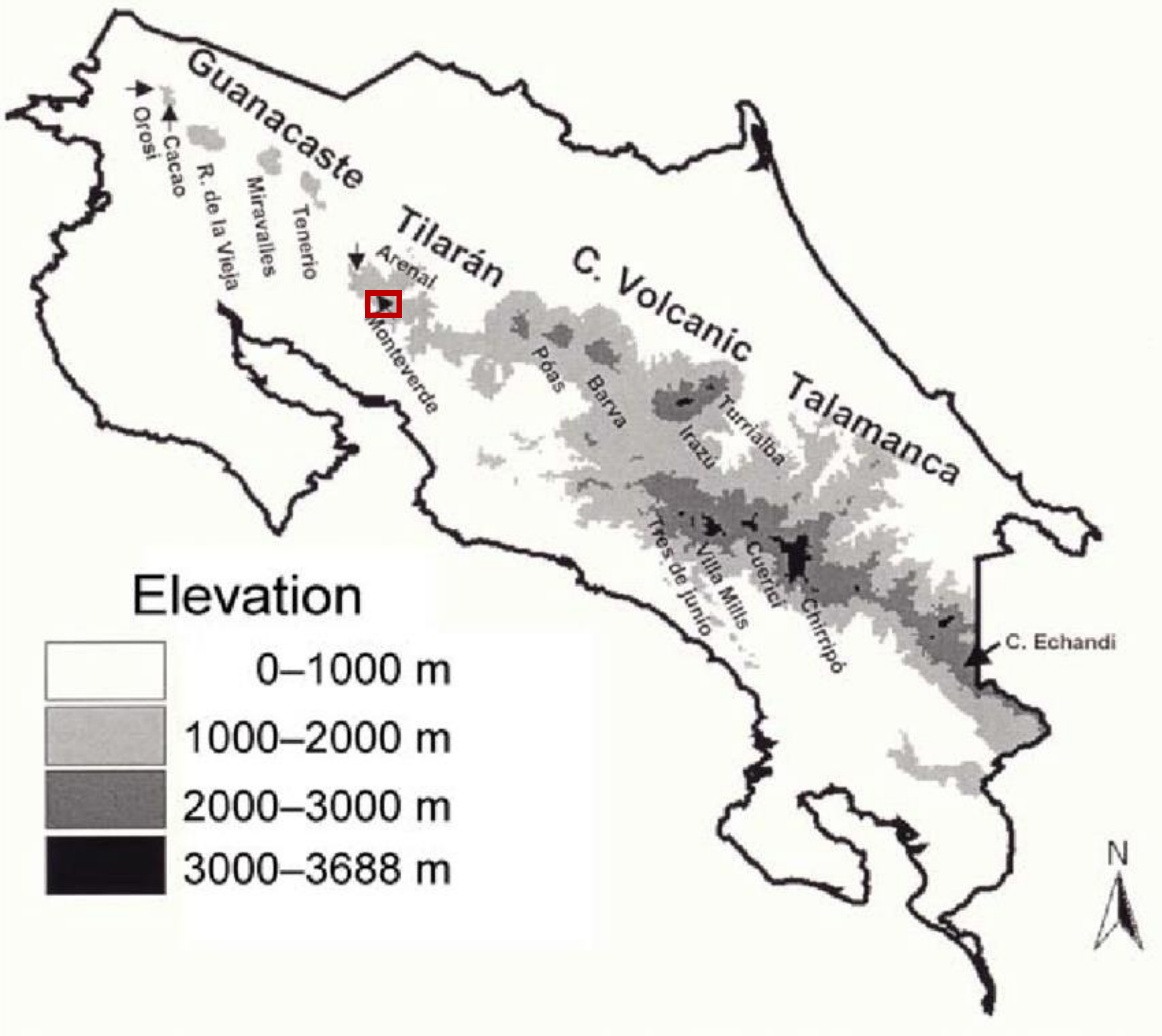

FIGURE 1. Map of Costa Rica and Mountain Range. From Barrantes et al. 2002. Field site outlined in red.

FIGURE 2. *Monstera adansonii.* Individual plants located in the shade (left) and the sun (right).

Found in the premontane wet forest in Monteverde, Costa Rica

FIGURE 3. Forest cover example of “sun” vs “shade” areas for sampling *Monstera adansonii.*

FIGURE 4. Sampling methods and measurement technique using iPhone and LeafByte application (Getman-Pickering et al 2019).

FIGURE 5. Visual of data collection process of *Monstera adansonii* individual “number 1” and its leaves (1, 3 & 5). Photo on the right is samples after they were sliced, and solution was added after 60 seconds on vortex.

FIGURE 6. Raphides as shown when examined in Low Power Objective Lens (10x).

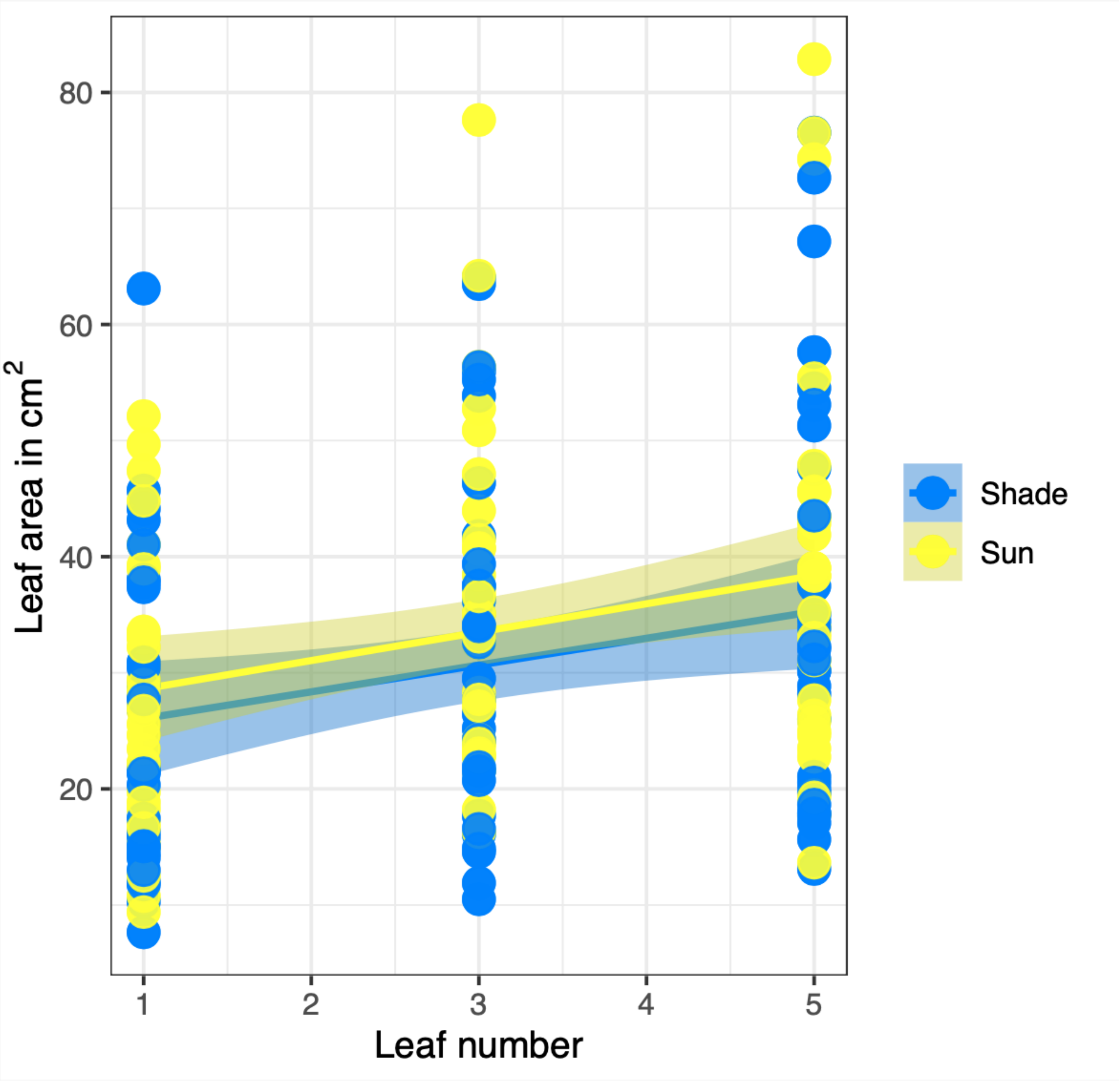

FIGURE 7. Relationship of leaf area to leaf age.

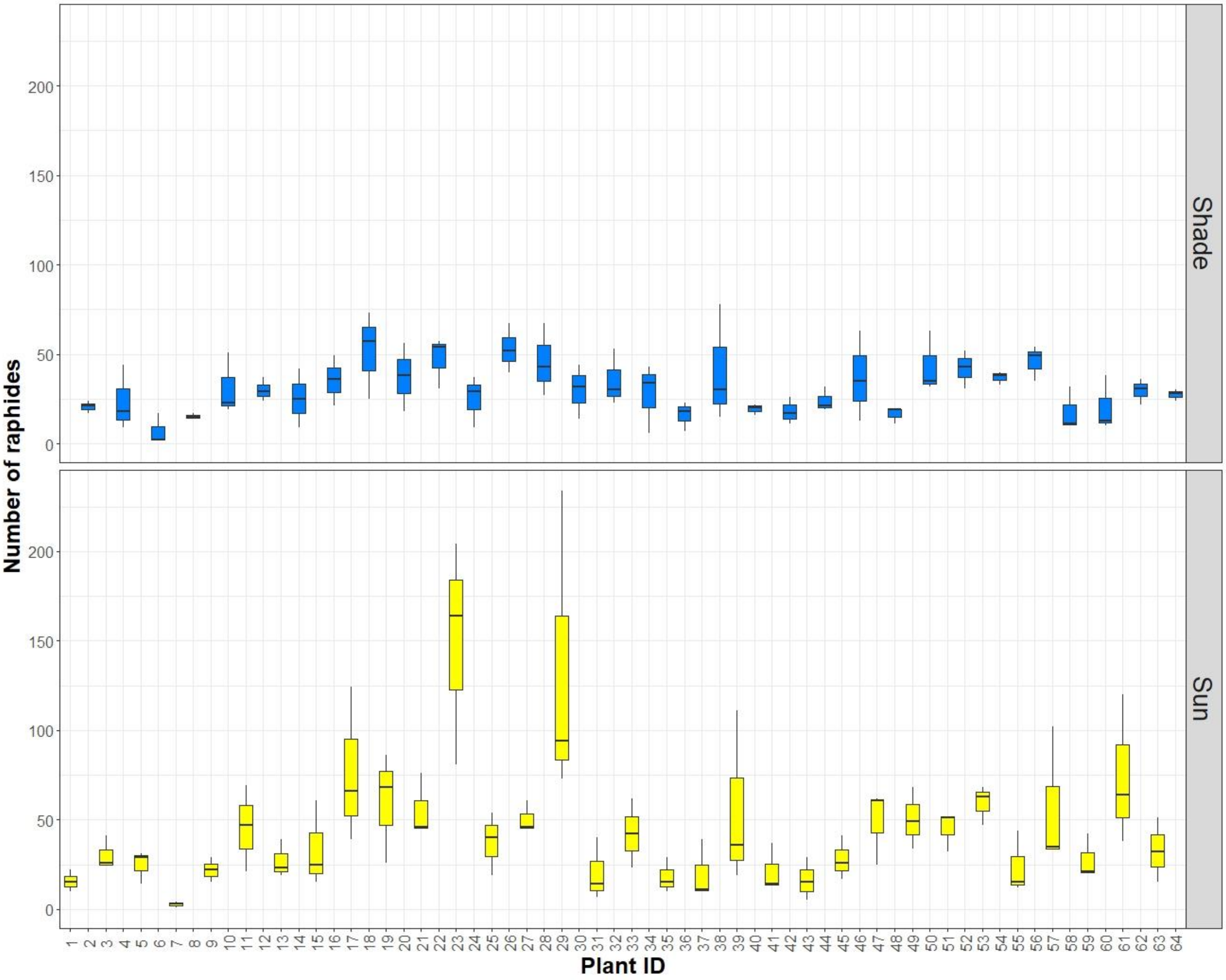

FIGURE 8. Visualization of variation across plants to illustrate the random effect. These data represent the mean and standard error across 3 leaves in the sun and shade.

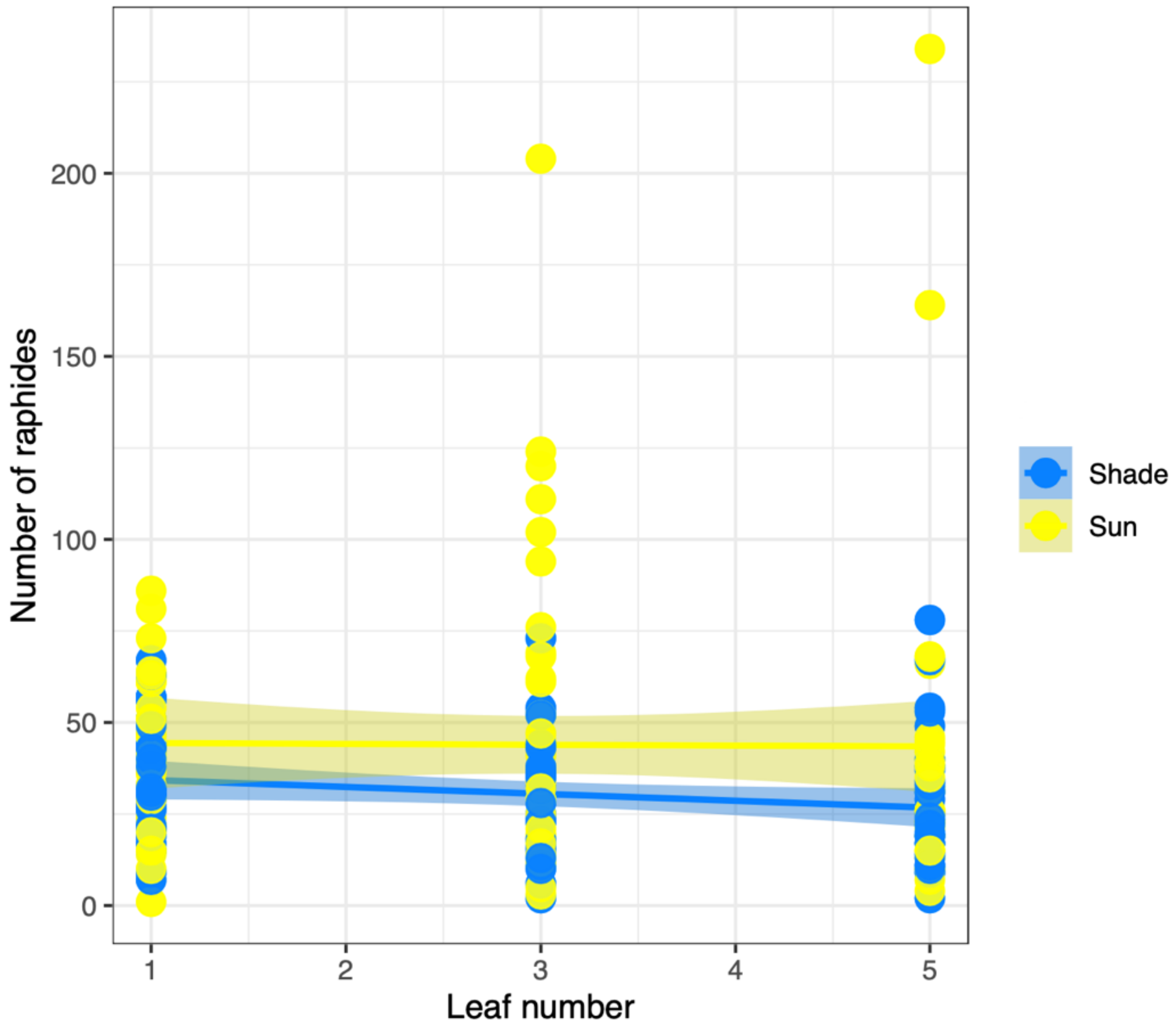

FIGURE 9. Number of raphides in the sun and shade by leaf number.

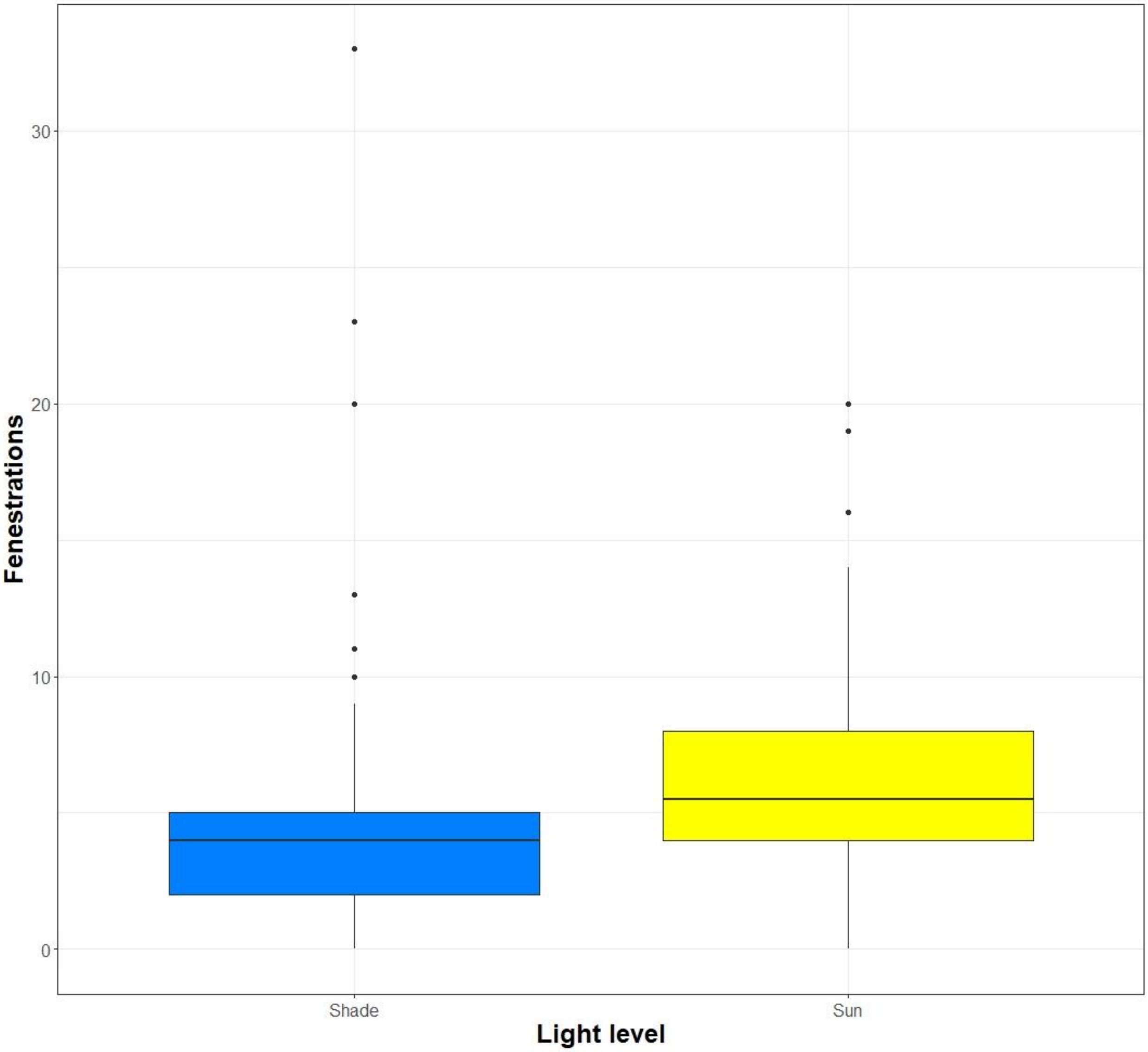

FIGURE 10. Relationship of fenestrations to light level.

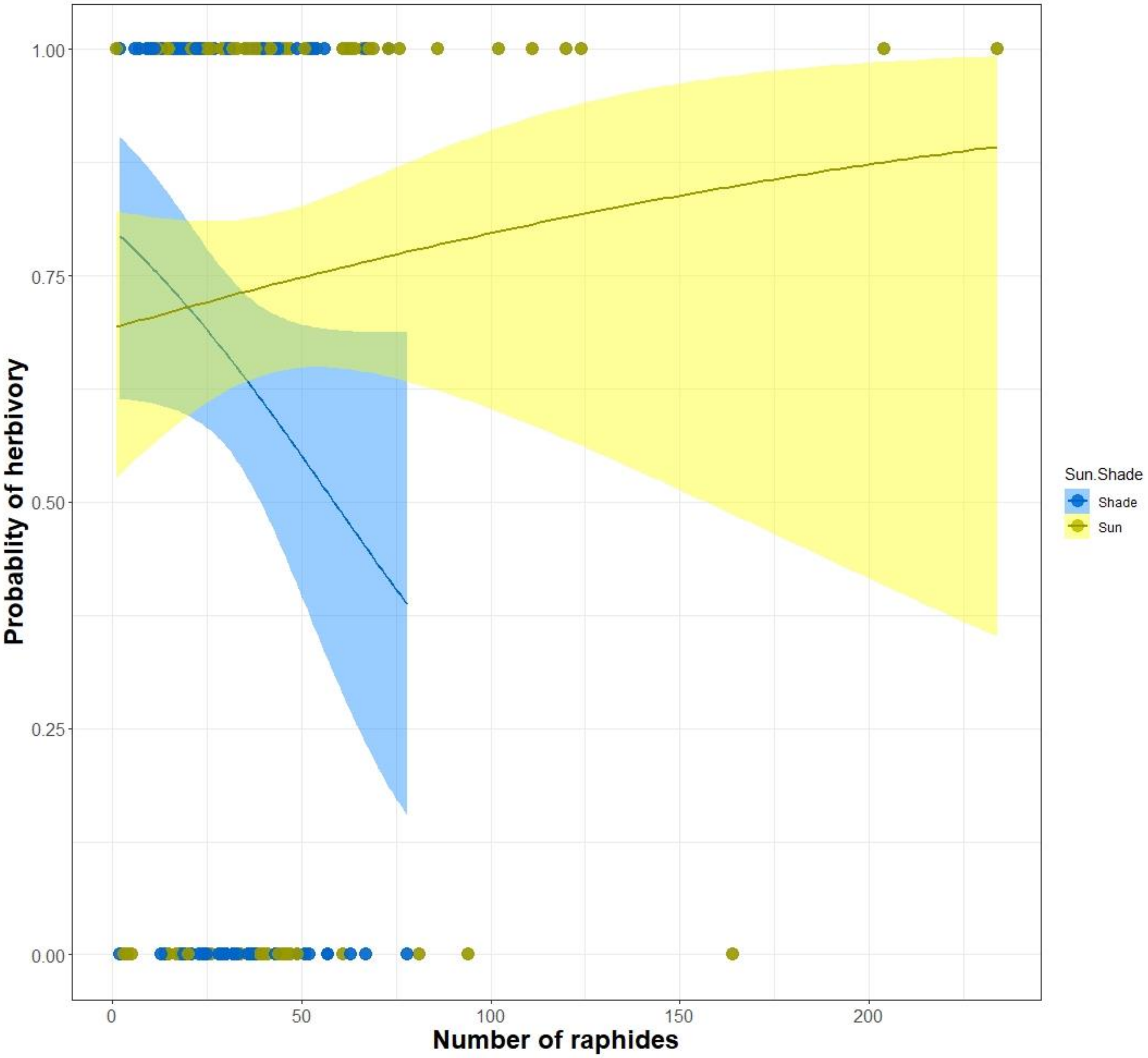

FIGURE 11. Probability of herbivory in relation to number of raphides in the sun and shade. Results show that in the sun, number of raphides has a positive effect on herbivory, but in the shade number of raphides has a negative effect on herbivory.