Phenotypic plasticity and stability of the size and number of adventitious roots of the climbing vine *Monstera dubia* Kunth (Engler & Krauze), Araceae

Edgardo I. Garrido-Pérez[1, 2]

[1]Coiba Scientific Station -COIBA-AIP, Gustavo Lara Street, Bldg.145B, City of Knowledge, Panama

[2]Asociació Americanistes de Catalunya, Calle Aragó 565, bajos, Barcelona, Spain

Corresponding Author: egarrido@coiba.org.pa

Abstract: Some 30% of Tropical Rainforests' plant species use roots for anchoring on trees, yet such root-bark interactions remain poorly studied. Hypothetically, bark-surface micro-sites differently offer resources to *Monstera dubia* roots altering roots' dry weight, length and number. I studied N=12 juvenile *Monstera dubia* individuals growing upon *Anacardium excelsum* while classifying *Anacardium excelsum*'s bark micro-sites into plates, fissures, juxtapositions, sub-plates, and sub-juxtapositions. Since *Monstera dubia* grows as a series of segments from the ground to the canopy, I determined the relative age of *Monstera dubia* segments from the youngest to the oldest to explore age-related changes of roots' size and number. No *Monstera dubia* individual had enough segments for single-genotype tests of plasticity in response to micro-sites. Therefore, I ran Dunn's tests for classifying all *Monstera dubia* individuals having similar root weights (groups a-b), and lengths (groups a', b', and c'). Segment-age had no-effect on the length and number of roots per segment (Linear regressions, p>0.35), and poorly explains root's weight (p<0.0001, r^2=0.05). Heavier segments and inter-nodes had more roots than lighter segments (p<0.0001) but such a trend is weak (r^2=0.24 for segment's weight; r^2=0.08 for inter-node's weight). The same was valid for root length *vs* inter-node's weight (r^2=0.06, p<0.0001), and for number of roots per segment *vs* inter-node's weight (r^2=0.18, p<0.0001). For all *Monstera dubia* individuals, roots into host's fissures were lighter than in juxtapositions, sub-plates and sub-juxtapositions (KW, p<0.0001), and shorter than in all other micro-sites (KW; p<0.001). The later also occurred for groups a (p<0.001) and a' (p<0.0005), while roots into sub-juxtapositions were larger than in other micro-sites for group b' (p<0.005). Root numbers were similar on both left and right sides along *M.dubia*'s body. All these suggest that root's size phenotypic plasticity, besides the stability of roots' number, evolved as part of one single anchoring strategy contributing to *Monstera dubia*'s fitness.

Keywords: *Anacardium excelsum*, Anchoring strategy, Neotropical rainforest, Panama canal, Secondary hemiepiphyte, Vine-host interactions.

INTRODUCTION

Vines, epiphytes, and hemi-epiphytes are vascular, canopy plants living on trees and typifying Tropical Rainforests (Leigh, 1975; Gentry & Dodson, 1987; Benzing, 1990; Gentry, 1991; Schnitzer *et al*., 2015). Secondary hemi-epiphytes like climbing Araceae germinate on the ground and then climb and stay attached to trees by means of adventitious roots (Strong & Ray, 1975; Madison, 1977; Ray 1981; Ray, 1983; Putz & Holbrook, 1986; Mantovani *et al*., 2018). Once on top, secondary hemi-epiphytes receive light, expand their area for spreading pollen and seeds, and escape from predators and pathogens of the understory; all these without spending large amounts of energy by producing a trunk as trees must do (Putz & Holbrook, 1986). Yet the adventitious roots of both epiphytes and secondary hemi-epiphytes are challenged by the variety of tree-bark textures resulting from the high tree diversity of Tropical Rainforest (Putz & Holbrook, 1986; Slik *et al*., 2015). For instance, the populations of Neotropical *Monstera dubia* (Kunth) Engl. &. K. Krause (Araceae, Fig. 1A) are exposed to communities of trees whose surfaces range as follows. (1) Very smooth barks (e.g. *Cecropia* spp., *Ficus* spp., and some Arecaceae), (2) exfoliating barks (*Terminalia* spp., *Albizzia guechepele* (Kunth) Dugand), (3) sinuous barks (*Dypteryx oleifera* Benth.), (4) deeply fissured barks (*Tabebuia rosea* (Bertol.), *Callophyllum* spp.), and (5) protuberant barks (*Zanthoxyllum setulosum* P. Wilson, *Ceiba pentandra* (L.) Gaertn.). Reportedly, adventitious-rooted canopy plants represent some 30% of the species of Tropical Rainforests (Gentry & Dodson, 1987; Benzing, 1990). On a worldwide scale, about 10% of the world's Magnoliophyta species are (hemi)epiphytes using roots to attach to their host trees and hosting vast numbers of insects and other life forms (Benzing, 1990). In spite of such an importance of vascular (hemi) epiphytes, little is known about how their adventitious roots interact with the changing surface of their host trees.

As a working hypothesis, trees with different barks should differentially accumulate water and nutrients to be further

offered to the adventitious roots of plants like *Monstera dubia* (Nadkarni, 1984; Talley *et al*., 1996; Catinon *et al*., 2011). In response to the changing substrate, single *Monstera dubia* individuals expectably activate genetic switches for producing different sizes and numbers of adventitious roots. This kind of variation of the phenotype, generated by single genotypes in response to environmental change, is called phenotypic plasticity and is well-known to occur to the roots of terrestrial plants (Trewavas, 1986; Fitter, 1996; Gutierrez, *et al*., 2009). Another, non-direct reason to expect the phenotype of *Monstera dubia*'s roots to be plastic is the outstanding plasticity displayed by other organs of the same species. Thus, ground-living seedlings of *Monstera dubia* have small bracts separated by long internodes (Fig. 1A). At the same time, seedling's stem performs a kind of negative phototropismn called 'skototropism' consisting on the growth towards a dark point on the horizon, thereby locating a host tree (Strong & Ray, 1975). After contacting a host, *Monstera dubia* stem switches from skototropism into positive phototropism, while the leaves switch from bracts into larger, tounge-like leaves with short inter-nodes and the vine gets attached to its host tree using adventitious roots (Fig. 1A) (Madison, 1977; Ray, 1981; Ray, 1983; Brito *et al*., 2022). The mentioned studies also report that, if *Monstera dubia* looses contact with its host, the climber performs the following. (1) A switch from positive phototropism into gravitropism. (2) A reduction of the size of its leaves while enlarging the inter-nodes. (3) A growth towards the ground for further creeping until contacting another host tree (Fig. 1A). Thus, the well-confirmed phenotypic plasticity displayed by *Monstera dubia* makes reasonable to predict that its adventitious roots should display phenotypic plasticity in response to the surface changes of its host trees. The general, and the specific questions guiding this research were the following: How do the climbing organs of *Monstera dubia* respond to the changing micro-sites of a host tree? Do the dry weight, length, and number of adventitious roots of *Monstera dubia* change depending on the micro-sites offered by a given host tree?
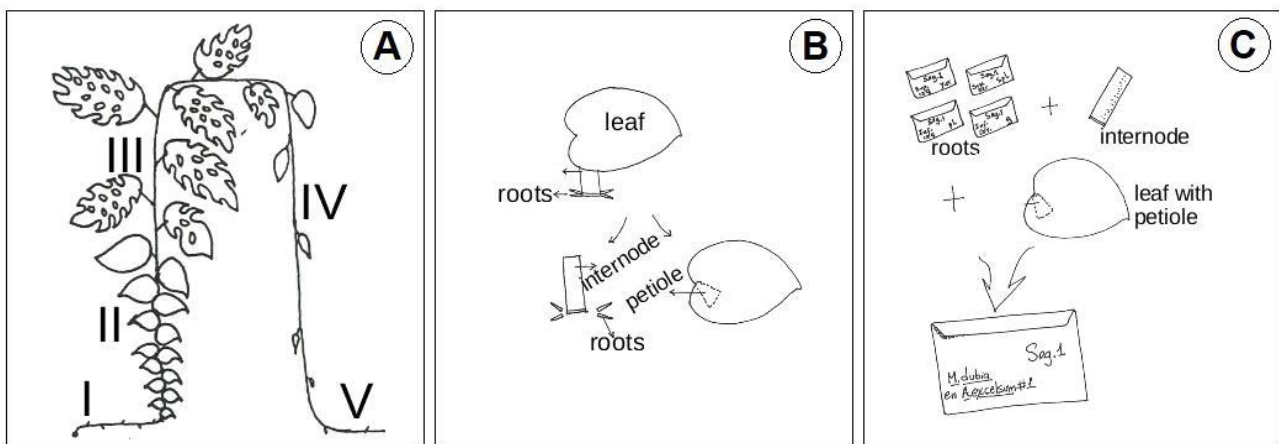

Figure 1. Drawings of the climbing, secondary hemi-epiphytic vine *Monstera dubia* (Kunth) Engl. &. K. Krause (Araceae), its segments, and dissection: **A**, Whole plant showing: (I) skototropic, terrestrial seedling, (II) climbing juvenile -which was the only stage covered by this study, (III) climbing adult (the stage producing flowers), (IV) gravitropic hanging phase produced after loosing contact with host tree, and (V) terrestrial phase creeping for another host (after Madison, 1977; see also Strong & Ray, 1975 as well as Ray, 1981); **B**, Dissected parts of a segment of *Monstera dubia* climbing-juvenile just before being prepared for dehydration; **C**, Each root was tagged and put into a small envelope, then deposited into larger envelopes with the rest of the parts of the segment, and then put into a 68°C oven per ≥3 weeks for further dry weight and root-length measurements.

MATERIALS AND METHODS

Field-and-laboratory work

In order to reduce uncertainties due to changing host-tree species, I studied only *Monstera dubia* individuals growing upon one single tree species *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels (Anacardiaceae); also referred here as the *host-tree*. *Anacardium excelsum*'s bark-relief comprehends many of the changing surfaces I visually observed on other trees during five years exploring Neotropical Rainforest. After exhaustive walks, the fairly acceptable number of N=12 *Anacardium excelsum* trees hosting *Monstera dubia* were found on two combined areas of the Panama Canal (Panama): the Barro Colorado Island Biological Station (9°10'N, 79°51'W), and the *Sendero El Charco* of the Soberanía National Park (9°5'N, 79°40'W) (Fig. 2).

Recurrently finding *Monstera dubia* individuals hosted on *Anacardium excelsum* was very rare. That was because the high alpha-diversities of the studied sites (for instance, BCI holds > 300 tree species (Condit *et al*., 2019) strongly reduces the chances of the same vine species to climb upon the same host tree species (Garrido-Pérez & Burnham, 2010). Therefore, each of the 12 *Anacardium excelsum* trees hosting *Monstera dubia* on was separated from its co-specifics hosting the same vine species by distances larger than the conservative estimation of 350 m. *Anacardium excelsum*'s bark micro-sites were classified as follows (Fig. 3). (1) Fissures which are produced when tree's secondary
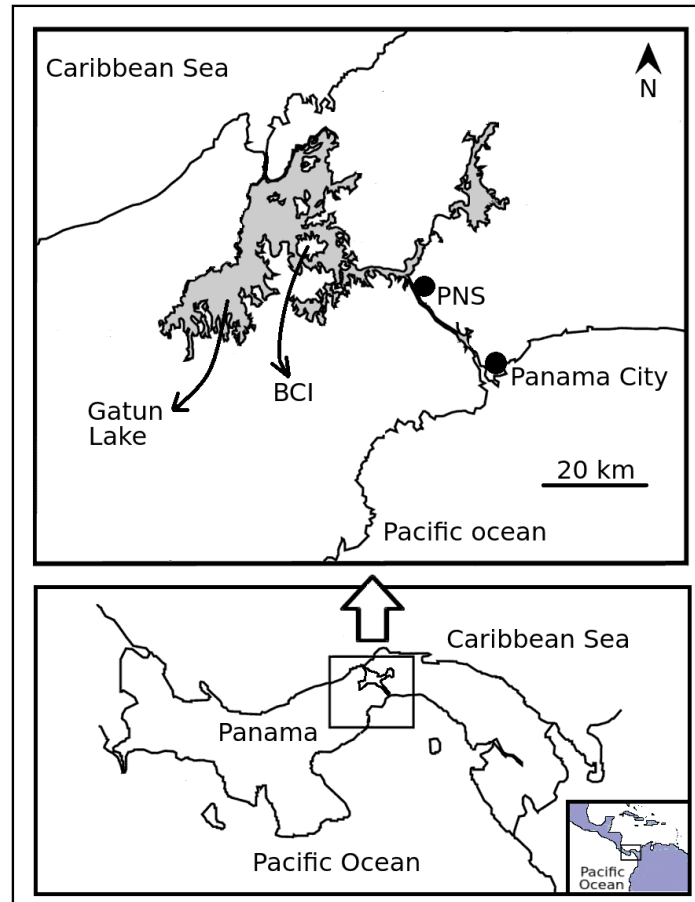
Figure 2. Location of the Barro Colorado Island (BCI 9°10'N, 79°51'W) and the Soberanía National Park (PNS, 9°5'N, 79°40'W; El charco trail) in the Panama Canal (Central America). Twelve *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels trees hosting juvenile *Monstera dubia* (Kunth) Engl. &. K. Krause vines were located in both sites after exhaustive walks in order to study the here reported anchoring mechanism of *Monstera dubia* on such trees.
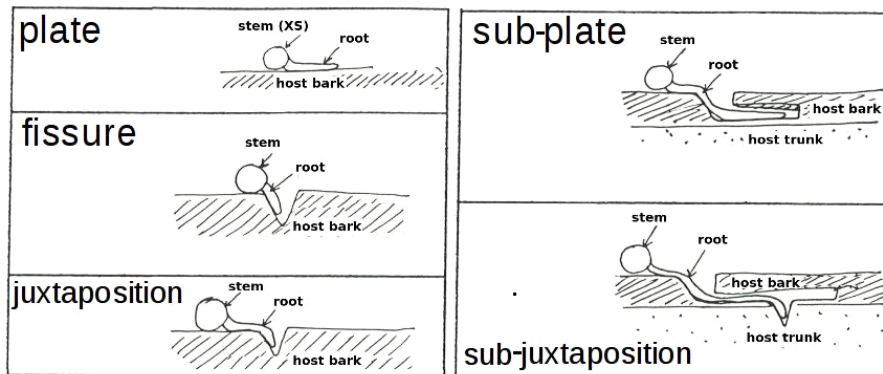
Figure 3. Drawings of the five bark micro-sites of *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels trees occupied by roots of the vine *Monstera dubia* (Kunth) Engl. &. K. Krause on Barro Colorado Island and the Sendero El Charco of the Soberanía National Park, Panama Canal. All drawings were made from the point of view of the cross section of the *Monstera dubia* stem.

growth makes the bark to collapse, (2) plates: non-collapsed parts of the bark, (3) juxtapositions (any fissure after a plate), (4) sub-plates: any plate under another plate due to slow exfoliation of the collapsing bark, and finally (5) sub-juxtapositions (any juxtaposition under a plate). For each *Monstera dubia* individual, only juvenile segments found from the ground up to 2.25 m above ground level were studied because they were reachable with my extended arms and hands. For each *Monstera dubia* individual, all segments were numbered from the ground to the top. Each segment included (Fig. 1B): adventitious roots, one leaf with petiole, and one inter-node; all these with clearly defined abscission zones. Using a sharpened HB pencil, each adventitious root was gently separated from its surrounding host bark. While making the later, I registered: (1) the number of the segment each root belonged to, (2) the micro-site occupied by each root, (c) its occupied side (left or right respect to *Monstera dubia*'s stem), and (d) whether the root was in an upper or lower position respect to other roots on the same side of the same segment. Once separated away of its host, each *Monstera dubia* was moved to the laboratory, softly cleaned, and dissected (Fig. 1B). All dissected parts of the body

were put into envelopes like in figure 1C. These envelopes were put into a 68°C oven per ≥3 weeks until reaching a stable dry weight. Then, the dry weight of each separated organ for each segment was measured using an analytical balance. For reducing uncertainties due to balance fluctuations, roots <0.0003g were excluded of further analysis regarding roots' dry weights. Roots were too small for accurately measuring their lengths so I used a non-direct measurement method. In concrete, already weighed roots were glued on bond paper using fast-drying transparent, thin glue while writing all its envelope's information. Each paper with roots was photocopied to 142% enlargement. Then, I measured the lengths of root silhouettes following their contours, and re-settled the resulting values to 100% thereby obtaining a reliable value of the length of each root.

Data analysis
Reducing risks of spurious results

Ontogenic (segment-age-related) switches, instead of host micro-sites, could affect the size and number of *Monstera dubia* roots generating false answers to my research questions. In order to cope with this, I studied the seven found individuals having the youngest, poorly lignified segment. For these individuals, I re-numbered the segments in an ordinal scale 1, 2, 3, and so on from the youngest segment (on top) to the oldest segment (near the ground) to use such digits as proxies of the segment age. Then, I used linear regressions for exploring whether segment age was related to the weights, lengths, and number of roots per segment. Also, gradual increase of segment weight due to ontogeny and/or accumulated photosyntate may result in a concomitant increase of root size and number. The later was a potential source of spurious answers to my research questions. Therefore, I ran linear regressions for all 12 individuals in order to explore the effect of the dry weight of the segments on the dry weight, lengths, and number of roots per segment. Moreover, many leaves suffered size and weight reductions due to herbivory that occurred prior my fieldwork, potentially affecting my further data analysis. Therefore, I repeated the aforementioned regressions using the dry weight of inter-nodes as a descriptor instead of the dry weights of segments.

Roots size and number vs host-bark micro-sites

For detecting a general trend on the plastic response of root sizes, I explored the change of root-dry weights and lengths depending on host-bark micro-sites for all *Monstera dubia* individuals together (Kruskal-Wallis tests -KW). Such a procedure offers an idea on the plastic response of *Monstera dubia*'s population, particularly considering that studied *Monstera dubia* individuals were spatially spread (Gianoli & Valladares, 2012). I recognize that such a method does not neutralize the effects of genetic differences among individuals. However, no *Monstera dubia* individual had enough roots for single *Monstera dubia* genotype comparisons of roots among micro-sites. That imposed the necessity of collating *Monstera dubia* into groups of individuals fairly similar from a genetic point of view; at least for the alleles encoding root size. Fortunately, I was able to reduce the variation of the environment by means of comparing root sizes among individuals for just one single micro-site: the plates, which were the micro-site where most of the roots were growing onto. Indeed, I ran Dunn's-tests for detecting among-individual root-size differences for roots growing on plates. After applying such a procedure, two groups (a and b) were found for root dry-weights, and three groups (a', b', and c') emerged for root lengths. Within such groups, I ran KW and Dunn's post-hoc tests for detecting root-size differences among micro-sites of the barks of the host *Anacardium excelsum*.

RESULTS AND DISCUSSION

After linear regressions, segment age had no effect on the dry weight (p=0.99) and number of roots per segment (p=0.35), but younger segments had roots with higher dry weight (p<0.0001) being such a trend very weak (r^2=0.05). As a more visible, still weak trend (r^2=0.24; p<0.0001) heavier segments had higher numbers of roots than lighter segments. A similar, but at the same time weaker pattern was detected when using the dry weight of inter-nodes as a descriptor of the number of roots per segment (r^2=0.08). Root lengths exhibited similarly weak patterns (linear regression for inter-node dry weight *vs* root lengths r^2=0.06, p<0.0001). At the same time, inter-node's dry weight was fairly better as a descriptor of the number of roots per segment (r^2=0.18, p<0.0001). All these suggest that, for the young *Monstera dubia* individuals studied, the age and weight of single segments are barely useful for explaining the variation of the size and number of adventitious roots.

In contrast, the changing host-bark relief seemingly altered both the weight and the lengths of *Monstera dubia* roots (Table 1). That was visible before, and after splitting the N=12 individuals into groups according to their root-sizes on plates (Table 1). In general, *Monstera dubia* roots growing into fissures were lighter and shorter than the roots growing into juxtapositions, sub-plates, sub-juxtapositions, and even plates (Table 1). That suggests a plastic response of the biomass and length of *Monstera dubia* roots presumably triggered by the moisture, nutrients, and degree of darkness offered by the micro-sites of the host bark. Interestingly, *Monstera dubia*'s root dry weights (group b) as well as root lengths (group c') did not change in response to host-bark micro-sites (Table 1). For group b, root weights were one

order of magnitude (10^{-4} g) lower than the root weights of group a (10^{-3} g) (Table 1). Group b was generally composed by small, light individuals after summing the dry weights of all segments for each individual. That suggests that small individuals should have a genetically determined root-size minimum enough for ensuring the attachment to host trees. If this is true, then the plastic response of roots for acquiring the "prize" of the resources offered by some host-bark micro-sites gets triggered when *Monstera dubia* reaches a certain, still unknown body size. On another hand, the number of adventitious roots (two to three) on the left and right sides of the segments and the whole *Monstera dubia* body was consistently similar for all individuals. A major implication is that the torsion moment generated by each root was neutralized by its opposite root of the same segment thereby keeping *Monstera dubia* individuals consistently appressed to their host trees.

Table 1. Comparisons of the adventitious root-dry weights (DW) and lengths for 12 *Monstera dubia* individuals according to the bark-micro-sites of the host tree species *Anacardium excelsum* on Barro Colorado Island and Sendero El Charcho, Panama Canal, Central America.

	Fissures (f)	Plates (p)	Juxta-positions (y)	Sub-plates (sp)	Sub-juxta-positions (sy)	p-value after KW	Interpretation after Dunn's test
DW without grouping individuals (g)	$\bar{X}=4.7\times10^{-3}$ SD=2.2×10^{-2} n=31	$\bar{X}=1.1\times10^{-3}$ SD=8.9×10^{-4} n=388	$\bar{X}=1.7\times10^{-3}$ SD=1.2×10^{-3} n=88	$\bar{X}=1.8\times10^{-3}$ SD=2.2×10^{-3} n=130	$\bar{X}=1.7\times10^{-3}$ SD=1.5×10^{-3} n=22	**<0.0001**	f < (y, sp, sy)
Length without grouping individuals (mm)	$\bar{X}=6.7$ SD=2.4 n=36	$\bar{X}=10.9$ SD=8.7 n=472	$\bar{X}=13.7$ SD=9.8.9 n=87	$\bar{X}=23.6\times10^{-3}$ SD=24.2×10^{-3} n=95	$\bar{X}=16.6$ SD=9.9 n=23	**0.001**	f < (p, y, sp, sy)
DW group a (g)	$\bar{X}=7.6\times10^{-3}$ SD=2.9×10^{-2} n=18	$\bar{X}=1.6\times10^{-3}$ SD=1.1×10^{-3} n=170	$\bar{X}=2.0\times10^{-3}$ SD=1.2×10^{-3} n=68	$\bar{X}=2.7\times10^{-3}$ SD=1.9×10^{-3} n=69	$\bar{X}=2.4\times10^{-3}$ SD=1.9×10^{-3} n=11	**<0.0001**	f < (p, y, sp, sy)
DW group b (g)	$\bar{X}=7.0\times10^{-4}$ SD=3.5×10^{-4} n=11	$\bar{X}=7.5\times10^{-4}$ SD=3.4×10^{-4} n=160	$\bar{X}=7.4\times10^{-4}$ SD=3.2×10^{-4} n=19	$\bar{X}=8.5\times10^{-4}$ SD=4.5×10^{-4} n=41	$\bar{X}=1.0\times10^{-3}$ SD=4.7×10^{-4} n=12	0.24	root weights were similar among micro-sites
Length group a' (mm)	$\bar{X}=6.5$ SD=2.2 n=14	$\bar{X}=12.7$ SD=8.8 n=158	$\bar{X}=14.8$ SD=10.3 n=54	$\bar{X}=20.8$ SD=19.5 n=54	$\bar{X}=23.0$ SD=17.2 n=11	**<0.0005**	f < (p, y, sp, sy)
Length group b' (mm)	$\bar{X}=7.0$ SD=3.2 n=11	$\bar{X}=8.3$ SD=2.8 n=195	$\bar{X}=7.0$ SD=2.1 n=15	$\bar{X}=10.3$ SD=4.5 n=19	$\bar{X}=12.4$ SD=3.9 n=12	**<0.005**	sy > (f, p, sp)
Length group c' (mm)	$\bar{X}=6.8$ SD=2.1 n=10	$\bar{X}=6.4$ SD=2.8 n=78	$\bar{X}=7.7$ SD=3.2 n=67	$\bar{X}=15.1$ SD=2.5 n=60	NO ROOTS	0.71	root lengths were similar among micro-sites

Note: Groups a and b emerged after Dunn-test cross-individual comparisons of roots' dry weights on plates; groups a', b', and c' emerged after similar comparisons for roots' lengths. Boold-typed p-values are statistically significant ($\alpha=0.05$) after KW=Kruskall Wallis test.

Altogether, the mentioned results suggest that the anchoring of juvenile *Monstera dubia* on the barks of trees comprises one single adaptive strategy for climbing upon trees (Gentry, 1991). Such a strategy integrates the following three features. First: a similar number of adventitious roots on the left *vs* the right side of each segment and, consequently, for the whole individual. When the individual is still light, small roots are strong enough for keeping *Monstera dubia* attached to its host tree independently of the relief changes of the later. Second: a low variation of the dry weight, lengths, and number of roots per segment with respect to the dry weight of such segments. That suggests the evolution of *Monstera dubia* has determined that fairly small, well-distributed roots are enough for the juveniles of such species to climb and stay attached on host trees. Finally (third): Roots changing their size in response to host-bark micro-sites, mainly from the moment when *Monstera dubia* individuals reach a still non-determined body size (Ray, 1983).

CONCLUSION

Tropical Rainforests hold many tree species with different bark textures. That excerpts complex selective pressures favoring the phenotypic plasticity of the size of *Monstera dubia*'s adventitious roots (Bradshaw & Hardwick, 1989; Gianoli & Valladares, 2012). Yet the mentioned plasticity is complemented by the phenotypic stability of the number and spatial distribution of the adventitious roots *Monstera dubia* uses for anchoring on its host trees, which is consistent

with the reported complementarity between physiological change and morphological stability for leaves of the climbing aroid *Philodendron hederaceum* (Jacq.) Schott (Mantovani *et al.*, 2018).

The phenotypic plasticity of a given organ is not only as an adaptation, but also a response to the environment functionally complemented by the phenotypic stability of other characteristics of the organ and the system it belongs to. Thus, systems' phenotypic plasticity and stability work in a "tandem" fashion: they belong to a functional unit evolving by natural selection. The plasticity-stability tandem requires further studies for a better understanding of the relationships between two major components of tropical forests flora: canopy plants and their host trees.

ACKNOWLEDGMENTS

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