PLANT PHYSIOLOGY IN THE TROPICS: TWO STUDIES ASSESSING THE EFFECTS OF ENVIRONMENTAL FACTORS ON PLANT FUNCTION AND DEVELOPMENT

An Undergraduate Research Scholars Thesis

by

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TABLE OF CONTENTS

ABSTRACT

Plant Physiology in the Tropics: Two Studies Assessing the Effects of Environmental Factors on Plant Function, Adaptation, and Development

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With a high species diversity, novel ecosystem functioning, and distinct topographic features, tropical forests are home to vegetation that is highly specialized and adapted to its environment. While this has resulted in many tropical species being confined to limited microclimatic conditions and elevations, certain phenotypically plastic species are able to survive across differing environmental gradients. To investigate this adaptation and plasticity, as well as, its implications for tropical species response to climate change, we assessed differences in leaf physiology and anatomy of *Carapa guianensis* Aubl and *Otoba novogranatensis* Moldenke, two emergent species found across a wide range of elevations within the Alajuela province of Costa Rica. Utilizing a portable leaf gas exchange system, A/C_i curves were generated for three replicate trees of both species at 600 m (Texas A&M University Soltis Center) and 820 m elevation (Pocosol Biological Preserve). Because trees were growing under varying light conditions, canopy cover of each individual was determined using the Leaf Area Index (LAI) measurements from hemispherical photos. Stomata density was determined for *C. guianensis* at both sites using stomata impressions. A/C_i curves were fitted using a revised Sharkey model to

determine maximum carboxylation rate of Rubisco (V_{cmax}), rate of electron transport (J), the rate of use of triose phosphates (TPU), daytime respiration (R_d), and mesophyll conductance (g_m). Results from this study depict stark differences in the photosynthetic capacity between our study plants with *C.* guianensis having significantly different V_{cmax} and Rd across sites while *O. novogranatensis*'s response did not differ between sites. C. *guianensis* also had significantly lower stomatal density at higher elevations, associated with shaded conditions, despite canopy cover being similar at both sites. This suggests that lower light intensity dictated primarily by clouds and fog, led to the observed differences between elevations.

Another common theme within tropical forests is the presence of tree fall gaps that occur and afford suppressed trees the opportunity for more light. While important drivers of species diversity within these systems, the effects of such small-scale disturbances on water use distribution among understory, mid-story, and dominant trees has not been explored in detail. To address this, we conducted a study exploring stand-level response to the death of a large dominant tree, *Mortoniodendron anisophyllum* Standl. & Steyerm (DBH > 220 cm; Height ~ 40 m). This study was conducted across four suppressed, four mid-story, and two dominant trees within a 50 × 50 m pre-montane tropical forest plot at the Texas A&M Soltis Center for Research and Education located in the Alajuela Provence, Costa Rica. We compared the proportion of water use by suppressed, mid-story, and dominant trees before (2014) and after the tree gap was created (2019) using thermal dissipation sap flow sensors. From our results, we found that, water usage of remaining trees in the gap had increased across all canopy levels; with suppressed trees, water usage now averaged proportionally closer to rates observed in dominant and mid-story trees. With increasing global temperatures and shifts in rainfall patterns increasing the likelihood of tree mortality coupled with the high environmental variability within tropical

forests, there is a greater need to enhance our fundamental understanding of tropical forest response to these phenomenon in order to better understand and predict possible changes in forest composition that may arise from climate change.

DEDICATION

This paper is dedicated to the Texas A&M Costa Rica REU cohorts of 2018 and 2019 as well as the students and faculty of Moore Lab.

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NOMENCLATURE

A/C_i: Net assimilation of CO_2/Intercellular CO_2 concentration

V_{cmax}: Maximum Carboxylation Rate of Rubisco

J: Rate of Electron Transport

TPU: Rate of use Triose Phosphates

R_d: Daytime respiration

g_m: Mesophyll Conductance

Js: Sap-flux

LAI: Leaf Area Index

Gap Fraction: Amount of sky visible from the understory of a forest

CHAPTER I

INTRODUCTION

The effects of climate change on forest ecosystems across the globe has been a topic well studied but poorly understood (Dale et al. 2001, Williamson et al. 2005). Particularly in systems as dynamic as tropical forests, predictions in forest structure, ecosystem function, and total productivity under a changing climate are continuously being refined through forest level models, large scale experimentations, and remote sensing technology (Norby et al. 2005, Koca et al. 2006, Bonan 2008). Through these methodologies and disciplines, many different approaches have been attempted in order to further our insight on the mechanisms that directly and indirectly drive tropical forest composition.

Of these mechanisms, understanding how changing climate will alter tropical forests is the central focus in many studies due to the important role that these environments play as both a global carbon sink and diversity hotspot (Mittermeier et al. 1998, Silver 1998, Ribeiro et al. 2011). However, the underlying effects that CO_2 has on a system can allow for a wide variety of conclusions to be reached among scientists. For example, a study conducted by Lloyd and Farquhar (2008) assessed the effects of elevated CO_2 on photosynthesis/respiration and reached the conclusion that tropical forest provide enough productivity to combat any reduced productivity that would occur from increased temperatures and water deficits while contrasting studies have reported that elevated CO_2 will reduce productivity (Clark 2004). Although this study only assessed physiological effects, others have predicted that such atmospheric change coupled with anthropogenic disturbance has the potential to alter tropical forests to the point of conversion into grassland savannahs (Cochrane et al. 1999, Brodie et al. 2012, Lyra et al. 2017).

To provide insight on future climate as well as the indirect effects it may have through increased tree mortality within tropical forests, we conducted two studies within the Alajuela Province of Costa Rica focused on plot level water usage and leaf level physiology.

Our first study seeks to understand how two pioneer species, *Carapa guianensis* and *Otoba novogranatensis*, respond to changing environmental conditions along an elevation gradient. While similar studies have been conducted within controlled environments (Huc et al. 1994), our observations were conducted in primary forest at two separate sites along an elevation gradient to not only observe differences between species, but observe within species response. The inclusion of an elevation gradient in this study was crucial to provide a more concrete comparison between both sample species due to the high amount of variation that occurs within tropical forest at the microclimatic, topographic, and vegetative scale (Fetcher et al. 1985, Clark and Clark 2000).

Both *C. guianensis* and *O. novogranatensis* are pioneer species with ranges extending from low-land coastal areas to pre-montane tropical forests and are found in both secondary and primary forest (Henriques and de Sousa 1989, Vozzo 2002). While characterized as emergent species both plants are also found in mature forests as mid-story and dominant trees. Due to the functional similarities between both species, this study is focused on exploring the differences in the immediate metabolic response to variable CO_2 that these functionally identical species may have. By conducting CO_2 response (A/C_i) curves on three seedling trees of each species at two sites separated by a 200 m elevation gradient, we found that, although similar in many aspects, *C. guianensis* and *O. novogranatensis* varied widely in their metabolic response to variable CO_2. Additionally, through microscopic analysis of our *C. guianensis* trees, we observed differences in stomatal densities across both sites despite similar growth conditions being observed through

leaf area analysis above our seedlings at either site. These results highlight how functionally similar species respond to changing environment, and stresses the importance of furthering our understanding of the physiological processes that dictate species response to altered CO_2, a crucial consideration when constructing predictive models for tropical systems (Huntingford et al. 2013, Zuidema et al. 2013).

Our second study explores how the death of a large dominant tree impacts the relative water usage of suppressed, mid-story, and dominant trees within the same tree plot; a phenomenon not fully understood in tropical rainforest. Current literature on tree fall gaps has shown the importance of this disturbance type to maintaining plant species diversity within tropical forests (Schnitzer and Carson 2001). However, there are few publications if any that explore how water usage has been altered at the stand level in response to dominant tree mortality, with the understanding of such a response potentially becoming crucial should we observe increased tree mortality within the tropics as a consequence of climate change. By comparing measurements of sap-flux in 4 suppressed, 4 mid-story, and 2 dominant trees with 2014 data collected by Aparecido et al. (2016) prior to the death of a large dominant tree *M. anisophyllum* (DBH > 220 cm; Height ~ 40 m), we investigated any changes in water usage across canopy levels that occurred in response to the death of a large dominant tree within the same tree plot.

CHAPTER II

METHODS

Study Sites

Both the leaf gas exchange and sap-flux studies were primarily conducted at the Soltis Center for Research and Education (Soltis Center) within the Alajuela Province, Costa Rica. This site is located at 10022’59.84’’N, 84037’03.21” W at an elevation of ~600 m within a 50m x 50m plot and receives ~4200 mm of precipitation annually (Teale et al. 2014). Leaf gas exchange measurements were also collected at a second site within the Alajuela Province, at the Pocosol Biological Station (Pocosol). This site is located at (10021’05.64’’N, 84040’03.04” W) ~820 m and is located within the Children’s Eternal Rainforest, a 23,000 ha preserve that serves as Costa Rica’s largest collection of protected land and receives ~4674 mm of rainfall a year (Montenegro 2010, Norris 2016). Both study sites are located within primary forest and are considered tropical evergreen broadleaf pre-montane forest. (Figure 1).

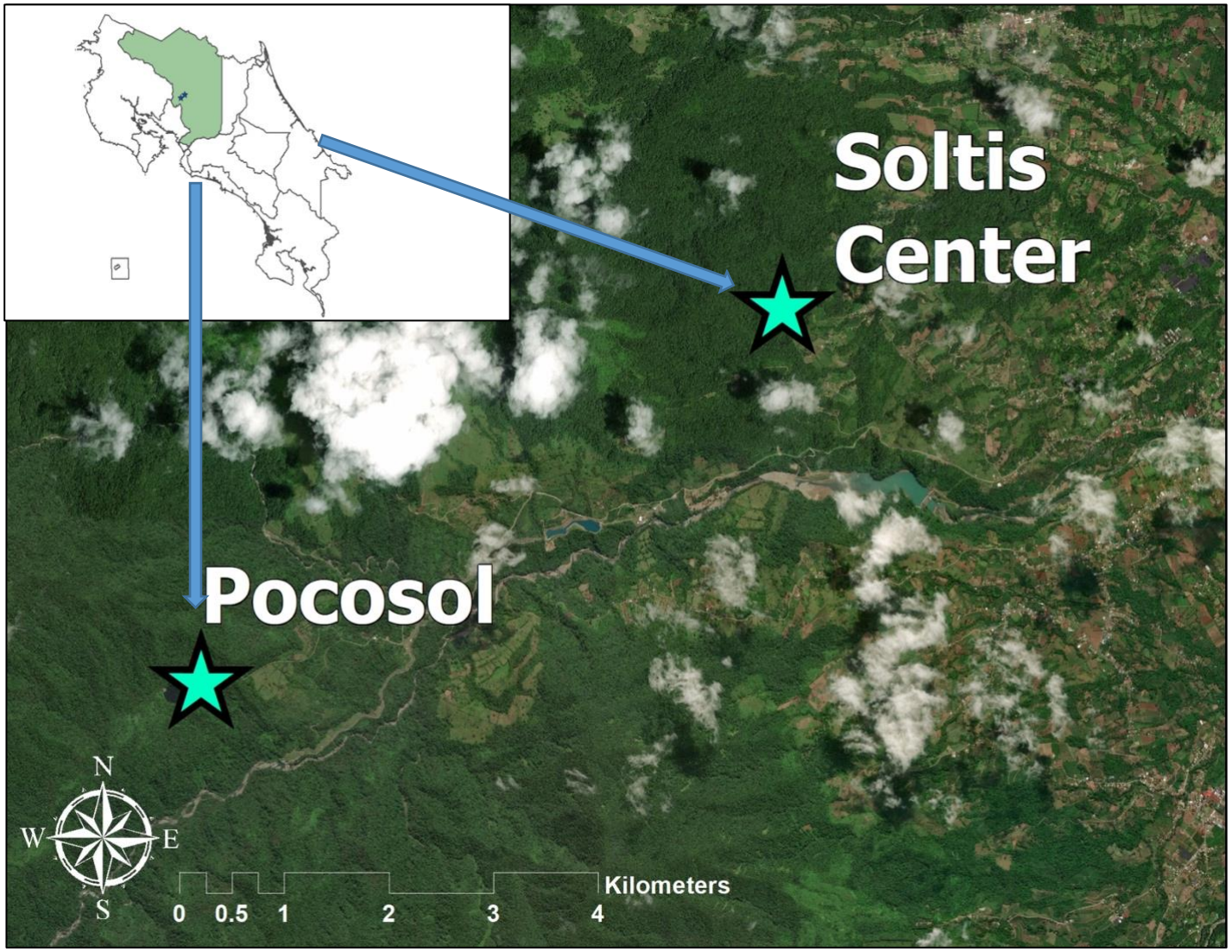


Figure 1. Map displaying the locations of the Soltis Center and Pocosol research stations. The stations are ~20km away from each other with elevation differing by ~200 m.

Leaf Gas Exchange Study

Tree Selection

A total of three wild saplings of *C. guianensis* and *O. novogranatensis* were identified within primary forest at both the Soltis Center and Pocosol under varying light conditions. Each sapling was a suppressed tree under the forest canopy and every measurement conducted was during daylight hours (0900 – 1700) on the most fully expanded, dry, and uppermost leaves of each tree.

A-Ci Measurements

Leaf gas exchange measurements were conducted in late June and early July of 2019. For each tree, three *A-Ci* curves were obtained using a Li-6400XT photosynthesis machine with a 6400- 02B LED light source (LI-6400XT, LICOR Inc., Lincoln, NE, USA). Each measurement conducted exposed each tree to CO_2 levels of 50, 100, 200, 300, 400, 600, 800, 1000, 1200, 1400, 1600, 1800, 2000, and 2200 µmol CO_2 m^{-2} s^{-1} (Figure 2) with 2 minutes allotted to each measurement in order to allow the leaf/leaflet being measured to acclimate to each level (Biosciences 2012).

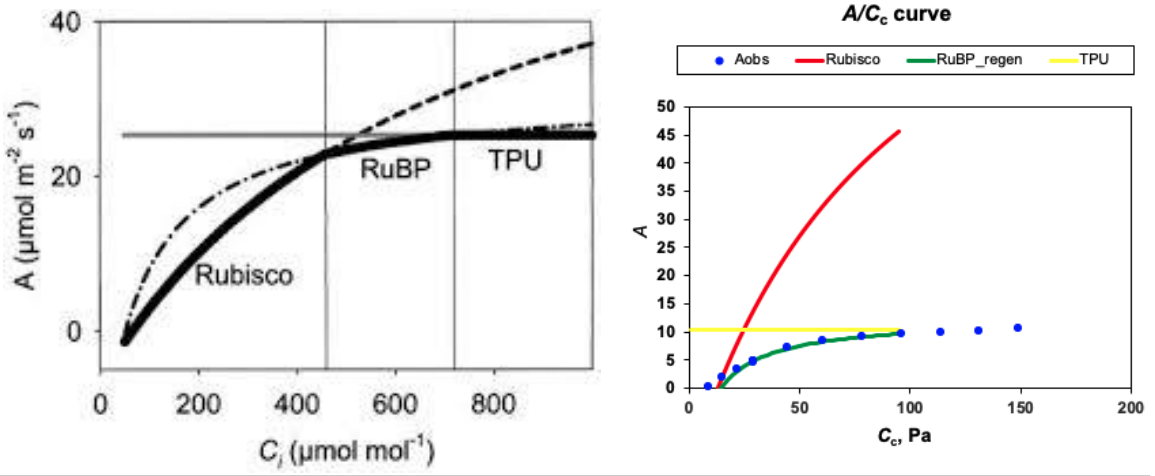


Figure 2. A concept of the parameters assessed in an *A/Ci* curve (left) along with a sample set of data (right).

For each measurement, several parameters were controlled to observe the effects of increasing CO_2 with flow rate = 500 mol s^{-1}, light intensity (PAR)= 2000 µmol m^{-2} s^{-1}, and leaf

area = 6cm$_2$. Relative humidity within the Li-6400XT chamber was kept between 50% and 80% across all *A*-C_i curves and chamber temperature was manually matched to ambient temperature before each measurement. Light saturation levels maintained during this study were consistent with other leaf gas exchange studies including *C. guianensis* or *O. novogranatensis* (Camargo and Marenco 2012, Loik et al. 2013). Data omission was structured so that only data that accurately represented plant behavior (i.e. nonnegative readings) was being compared between sites. Because of this, the first 6 data points for each curve were omitted so that only plant behavior under increasing CO_2 was included. Additionally, any data points with anomalous measurements, such as negative photosynthesis/conductance or spikes in data were omitted. Once all measurements were taken, each *A*-C_i curve was processed through a non-linear regression physiological model developed by (Sharkey et al. 2007). This model generates five parameters that allows us to assess metabolic differences in our sample plants, V_{cmax}: maximum velocity of Rubisco for carboxylation, *J*: rate of electron transport, *TPU*: the rate of use of triose phosphates, R_d: daytime respiration, and g_m: mesophyll conductance. This model accounts for the three metabolic limitations of CO_2 with Rubisco limitations, RuBP regeneration, and Triosephosphate Utilization processed through separate equations to estimate the aforementioned parameters (Equations 1-3). These limitations were manually assigned based on the estimated amounts of CO_2 within the intercellular spaces of the leaf, C_i, for all data points within each *A*-C_i curves (Sharkey et al. 2007).

Equation 1: $$A = V_{cmax}\left[\frac{C_c - \Gamma^*}{C_c + K_c\,(1 + O/K_o}\right] - R_d$$

Equation 2: $$A = J\,\frac{C_c - \Gamma^*}{4C_c + 8\Gamma^*} - R_d$$

Equation 3: $$A = 3TPU - R_d$$

Equations 1-3. Show all formulas used to estimate physiological parameters in (Sharkey et al. 2007).

In order to account for forest heterogeneity, Leaf Area Index (LAI) and gap fraction measurements were conducted under each sample tree at both sites. One image per tree was taken (n = 3) utilizing hemispherical photography (Nikon SLR with hemispherical lens) with each image taken at the base of the sapling with all foliage from each tree being shifted out of view in order to gain an accurate assessment of leaf coverage over each sapling. Each image was processed using HemiView software (Rich et al. 1999) and images across both species and sites were analyzed.

Stomatal Density

For *C. guianensis* and *O.novogranatensis*, stomatal imprints were collected from all leaves that had *A*-C_i curves conducted on them. Using methods defined by (Hilu and Randall 1984), these impressions were collected by applying acrylic paint to the abaxial surface of three leaves/leaflets from each sample tree at each site. For each leaf/leaflet, a total of three films were collected; however, viable imprints could only be obtained for *C.guianensis*. A Zeiss Axiophot (Zeiss Axiophot, Carl Zeiss Microscopy, LLC, Thornwood, NY, USA) light microscope at 20x magnification paired with MetaView image capturing software was utilized to take 0.06 x 0.06 mm^2 high resolution images from our stomatal imprints. Stomata density was then derived from this imagery by using ImageJ cell counting software (Ferreira and Rasband 2012) to collect accurate measurements of stomata present in each of the collected images. A total of three images were taken for each *C. guianensis* leaflet and averages were calculated across trees as well as sites.

Statistical Analysis

For measurements taken to facilitate our leaf gas exchange data (i.e. LAI/gap fraction and stomatal densities), a two-sample t-test assuming unequal variances was used to measure differences across sites at ($\alpha = 0.05$). All measurements across sites were compared as averages.

Parameters derived from our *A*-C_i curve data were analyzed through a one-way ANOVA analysis using the linear model function in R (RCTR Core Team 2013, RStudio Team 2015) to compare results across sites, within sites, between species, and within species at each site ($\alpha = 0.05$).

Sap-Flux Study

Sap-flux Measurements

Continuous measurements of sap-flux (*J*s) were collected over a ~6 month time period using 15 heat dissipation sensors (Granier 1985, Granier 1987) across 4 suppressed, 4 mid-story, and 2 dominant trees within a 50 × 50 m research plot at the Soltis Center. Each sensor consists of a reference and heater probe that allows for temperature differences between the two to be measured and stored as mV. Sensors were constructed from instructions detailed by Phillips et al. (1996) and installed in the outermost xylem over a 5 week period during the months of June and July of 2019. All sensors were installed above present tree buttresses and all probes contained probes 2 cm long, the same length of sensors used by Aparecido et al. (2016). Data from these sensors were collected every 30 seconds and averaged as 10-minute intervals using a CR1000 datalogger (Campbell Scientific Inc., Logan, UT). Sap-flux measurements used in this study were recorded over a 194-day period spanning over 6 months between July 22nd, 2019 and January 11th, 2020 and compared to final values in Table 1 of Aparecido et al. (2016) which were calculated from ~5 months of data collection between the months of July and December of 2014 (Appendix, Table 1). Additionally, LAI and gap fraction measurements were conducted at set

points and compared to 2014 LAI and gap fraction data obtained through similar methodology. This was done to capture any change in forest structure that may have occurred between 2014 (prior to mortality of the largest dominant tree) and 2019 (after mortality of the largest tree and associated reduction in shading by its canopy).

Data Processing/Analysis

By using an empirical calibration equation developed by Granier (1987) and automated through methods developed by (Aparecido et al. 2016), total tree J_s was calculated for each tree and, for trees housing multiple sensors, total tree J_s was calculated by averaging the number of sensors installed together to represent the tree (Equation 4). Sap-flux was then consolidated into hourly totals among individual trees before comparing data from the same trees in 2014.

Data omission for 2019/20 measurements occurred at two levels. The first was at the raw data level, where mV data points were omitted based off individual assessments of each sensor. Any negative or extreme outliers were omitted due to possible sensor failure, power loss, insect damage, or any other environmental variable not captured through this study. Additionally, interpolation and extrapolation were conducted within the 2019/20 data set to model any gaps in the data that occurred during our study period. Interpolation was conducted between sensor gaps with two points on either end and utilized within sensor data to model data through linear regression. Similar to this, extrapolation was also conducted through linear regression; however, the regression was derived from other sensors that correlated with the sensor being modelled (R^2 >= 0.6). Accounting for gap periods when all sensors malfunctioned, the resulting dataset included 15 sensor and 10 trees for the duration of our analysis. .

Comparisons of ratios for water usage among canopy levels were conducted between canopy levels within time-periods and between time-periods , while a two-sample t-test

assuming unequal variance ($\alpha = 0.05$) was conducted to observe any significant differences in total water usage across all canopy levels. Additionally, a two-sample t-test assuming unequal variance was conducted for LAI and gap fraction analysis to assess if any canopy structure change had occurred between 2014 and 2019 ($\alpha = 0.05$).

Equation 4: $$J_s = 0.199 \left(\frac{\Delta T_M - \Delta T}{\Delta T}\right)^{1.231} = 0.119K^{1.231}$$

CHAPTER III

RESULTS

Leaf Gas Exchange Study

Leaf Gas Exchange Results

For measurements comparing *C. guianensis* between elevations: V_{cmax} was 2.65 times greater at our higher elevation site, Pocosol (30 ± 7 mmol^{-2} s^{-1}) than at our lower elevation site, the Soltis Center (11.3 ± 1.1 mmol^{-2} s^{-1}, P = 0.002). Values for J did not differ between sites with Soltis Center J being 50.3 ± 7.1 mmol^{-2} s^{-1} and Pocosol J being 42.5 ± 3.3 mmol^{-2} s^{-1} (P = NS) Values for *TPU* did not differ between sites with Soltis Center *TPU* being 3.7 ± 0.7 mmol^{-2} s^{-1} and Pocosol *TPU* being 4.7 ± 0.6 mmol^{-2} s^{-1} (P = NS). Values for R_d was 9.72 times greater at the Soltis Center (5.1 ± 1.5 mmol^{-2} s^{-1}) than Pocosol (0.5 ± 0.4 mmol^{-2} s^{-1}, P = 0.001). Values for g_m did not differ between sites with Soltis Center g_m being 23 ± 0.4 mmol^{-2} s^{-1} Pa^{-1} and Pocosol g_m being 22 ± 1.9 mmol^{-2} s^{-1} Pa^{-1} (P = NS).

For measurements comparing *O. novogranatensis* between elevations: V_{cmax} did not differ between sites with Soltis Center V_{cmax} being 9.7 ± 0.1 mmol^{-2} s^{-1} and Pocosol V_{cmax} being 25.8 ± 16.2 mmol^{-2} s^{-1} (P = NS). Values for J did not differ between sites with Soltis Center J being 60.3 ± 3.7 mmol^{-2} s^{-1} and Pocosol J being 62 ± 8.8 mmol^{-2} s^{-1} (P = 0.798). Values for *TPU* did not differ between sites with Soltis Center TPU being 4.8 ± 0.3 mmol^{-2} s^{-1} and Pocosol TPU being 4.7 ± 0.6 mmol^{-2} s^{-1} (P = NS). Values for R_d did not differ between sites with Soltis Center R_d being 6.1 ± 0.5 mmol^{-2} s^{-1} and Pocosol R_d being 6.1 ± 0.6 (P = NS). Values for g_m did not differ between sites with Soltis Center g_m being 22.5 ± 0.2 mmol^{-2} s^{-1} Pa^{-1} and Pocosol g_m being 23.3 ± 0.9 mmol^{-2} s^{-1} Pa^{-1} (P = NS.).

For comparisons between species at our lower elevation site (Soltis Center): V_{cmax} was 1.17 times greater for *C. guianensis* (11.3 ± 1.1 mmol^{-2} s^{-1}) than for *O. novogranatensis* (9.7 ± 0.1 mmol^{-2} s^{-1}, P = 0.005). Values of *J* were marginally insignificant with *O. novogranatensis J* being 60.3 ± 3.7 mmol^{-2} s^{-1}and *C. guianensis J* being 50.3 ± 7.1 mmol^{-2} s^{-1} (P = 0.063). Values of *TPU* were 1.27 times greater for *O. novogranatensis* (4.8 ± 0.3 mmol^{-2} s^{-1}) than for *C. guianensis* (3.7 ± 0.7 mmol^{-2} s^{-1}, P = 0.045). Values of R_d did not differ between species with *O. novogranatensis* R_d being 6.1 ± 0.5 mmol^{-2} s^{-1} and *C. guianensis* R_d being 5.1 ± 1.5 mmol^{-2} s^{-1}, P = NS). Values for g_m were similar between sites with *O. novogranatensis* g_m being 22.5 ± 0.2 mmol^{-2} s^{-1} Pa^{-1} and *C. guianensis* g_m being 23 ± 0.4 mmol^{-2} s^{-1} Pa^{-1} and (P = NS).

For comparisons between species at our higher elevation site (Pocosol): V_{cmax} was 1.16 times greater for *C. guianensis* (30 ± 7 mmol^{-2} s^{-1}) than for *O. novogranatensis* (25.8 ± 16.2 mmol^{-2} s^{-1}, P = 0.005). Values for *J* were 1.46 time greater for *O. novogranatensis* (62 ± 8.8 mmol^{-2} s^{-1}) than for *C. guianensis* (42.5 ± 3.3 mmol^{-2} s^{-1}, P = 0.008). *TPU* was 1.5 times greater *O. novogranatensis* (4.7 ± 0.6 mmol^{-2} s^{-1}) than for *C. guianensis* (3.2 ± 0.3 mmol^{-2} s^{-1}, P = 0.004). Values for R_d were 11.57 times greater for *O. novogranatensis* (6.1 ± 0.6 mmol^{-2} s^{-1}) than for *C. guianensis* (0.5 ± 0.4 mmol^{-2} s^{-1}, P = 0.0001). Values for g_m did not differ between both species with *C. guianensis* g_m being 22 ± 1.9 mmol^{-2} s^{-1} Pa^{-1} and *O. novogranatensis* g_m being 23.3 ± 0.9 mmol^{-2} s^{-1} Pa^{-1} (P = NS)

For comparisons of all *C. guianensis* and all *O. novogranatensis* across both sites: V_{cmax} did not differ between plants with *C. guianensis* V_{cmax} being 20.7 ± 5.2 mmol^{-2} s^{-1} and *O. novogranatensis* V_{cmax} being 17.8 ± 8.1 mmol^{-2} s^{-1} (P = NS). Values for *J* were 1.32 times greater for *O. novogranatensis* (61.1 ± 4.3 mmol^{-2} s^{-1}) than for *C. guianensis* (46.4 ± 3.9 mmol^{-2} s^{-1}, P = 0.001). Values for *TPU* were 1.38 times greater for *O. novogranatensis* (4.8 ± 0.3

mmol^{-2} s^{-1}) than for *C. guianensis* (3.4 ± 0.4 mmol^{-2} s^{-1}, P = 0.0004). Values for R_d were 2.16 times higher for *O. novogranatensis* (6.1 ± 0.4 mmol^{-2} s^{-1}) than for *C. guianensis* (2.8 ± 1.3 mmol^{-2} s^{-1}, P = 0.001). Values for g_m did not differ between species with *C. guianensis* g_m being 22.5 ± 0.9 mmol^{-2} s^{-1} Pa^{-1} and *O. novogranatensis* g_m being 22.9 ± 0.4 mmol^{-2} s^{-1} Pa^{-1} (P = NS).

For comparisons of all plants at our lower elevation site (Soltis Center) between all plants at our higher elevation site (Pocosol): V_{cmax} was 2.66 times greater at Pocosol (27.9 ± 7.9 mmol^{-2} s^{-1}) than at the Soltis Center (10.5 ± 0.6 mmol^{-2} s^{-1}, P = 0.005). Values for J did not differ across sites with overall Soltis Center J being 55.3 ± 4.2 mmol^{-2} s^{-1} and overall Pocosol J being 52.3 ± 6.1 mmol^{-2} s^{-1} (P = NS). Values for *TPU* did not differ across sites with overall Soltis Center *TPU* being (4.2 ± 0.4 mmol^{-2} s^{-1}) and overall Pocosol *TPU* being 4 ± 0.5 mmol^{-2} s^{-1} (P = NS). Values for R_d were 1.69 times greater at the Soltis Center (5.6 ± 0.8 mmol^{-2} s^{-1}) than for Pocosol (3.3 ± 1.3 mmol^{-2} s^{-1}, P = 0.031). Values for g_m did not differ between both sites with Soltis Center g_m being 22.8 ± 0.2 mmol^{-2} s^{-1} Pa^{-1} and Pocosol g_m being 22.6 ± 1 mmol^{-2} s^{-1} Pa^{-1} (P = NS). (Table 1 and Figures 3-7)

Table 1. Results of Sharkey et al. (2007) output parameters compared across sites, within sites, between species, and within species at each site, ($\alpha = 0.05$).

Carapa Site Comparison					
Variables	Average Carapa Soltis	Standard Error	Average Carapa Pocosol	Standard Error	p-value
Vcmax	11.32	1.13	30.01	7.02	2.3E-03
J	50.31	7.09	42.54	3.34	1.2E-01
TPU	3.74	0.68	4.75	0.62	2.2E-01
Rd	5.14	1.52	0.53	0.44	6.2E-04
gm	23.04	0.35	21.98	1.93	6.6E-01

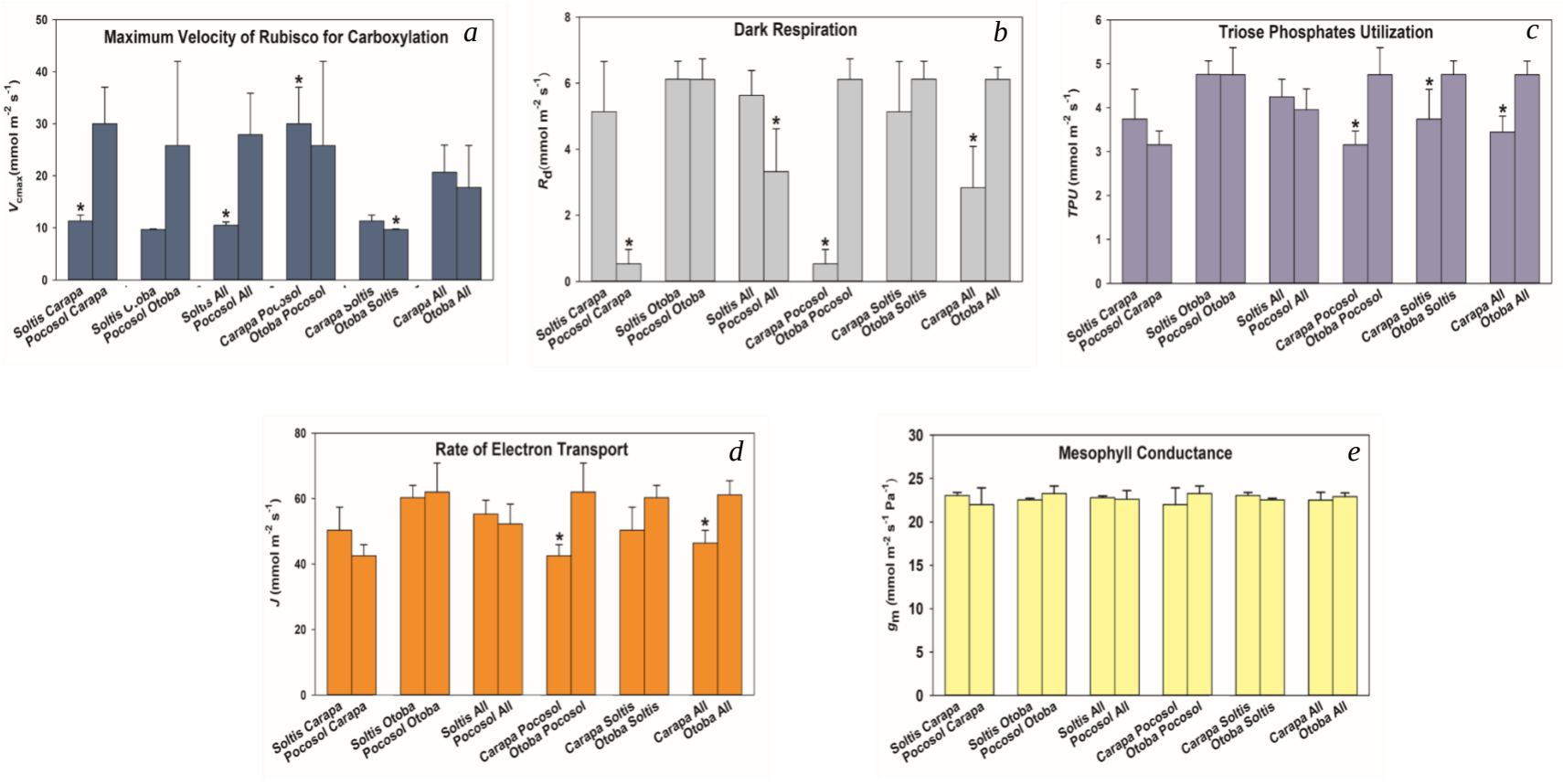
Otoba Site Comparison					
Variables	Average Otoba Soltis	Standard Error	Average Otoba Pocosol	Standard Error	p-value
Vcmax	9.70	0.10	25.81	16.19	0.147
J	60.27	3.74	62.01	8.81	0.798
TPU	4.75	0.31	4.75	0.62	0.995
Rd	6.12	0.55	6.11	0.62	0.998
gm	22.55	0.16	23.26	0.87	0.219

Total Soltis vs Total Pocosol Comparison					
Variables	Total Soltis	Standard Error	Total Pocosol	Standard Error	p-value
Vcmax	10.51	0.62	27.91	7.95	0.005
J	55.29	4.22	52.28	6.06	0.532
TPU	4.25	0.40	3.95	0.47	0.464
Rd	5.63	0.76	3.32	1.29	0.031
gm	22.80	0.21	22.62	0.99	0.883

Carapa vs. Otoba Pocosol Comparison					
Variables	Carapa Pocosol	Standard Error	Otoba Pocosol	Standard Error	p-value
Vcmax	30.01	7.02	25.81	16.19	0.005
J	42.54	3.34	62.01	8.81	0.008
TPU	3.16	0.31	4.75	0.62	0.004
Rd	0.53	0.44	6.11	0.62	0.000
gm	21.98	1.93	23.26	0.87	0.594

Carapa vs. Otoba Soltis Comparison					
Variables	Carapa Soltis	Standard Error	Otoba Soltis	Standard Error	p-value
Vcmax	11.32	1.13	9.70	0.10	0.005
J	50.31	7.09	60.27	3.74	0.063
TPU	3.74	0.68	4.75	0.31	0.045
Rd	5.14	1.52	6.12	0.55	0.403
gm	23.04	0.35	22.55	0.16	0.398

ALL Carapa vs. Otoba Comparison					
Variables	Total Carapa	Standard Error	Total Soltis	Standard Error	p-value
Vcmax	20.67	5.25	17.75	8.09	0.654
J	46.43	3.91	61.14	4.30	0.001
TPU	3.45	0.36	4.75	0.31	0.000
Rd	2.83	1.25	6.12	0.37	0.001
gm	22.51	0.91	22.90	0.43	0.742



Figures 3*a*-*e*. Graphs of Sharkey et al. (2007) output parameters compared across sites, within sites, between species, and within species at each site, * = p-value < 0.05.

Stomata Density and LAI/Gap Fraction Results

Results show that *C. guianensis* trees at our lower elevation site (Soltis Center) had 1.85 times more stomata, 529 ± 146.9 mm^{-2} than our higher elevation site (Pocosol), 212.4 ± 378.1 mm^{-2}, $P = 0.000054$ (Figure 4*a-c*). LAI and gap fraction analysis showed no significant differences when comparing stomatal density between *C. guianensis* at the Soltis Center (2.79 ± 0.01, 0.06 ± 0.002) and Pocosol (2.84 ± 0.04, 0.06 ± 0.002, P = NS, P = NS). Total plant comparisons between sites for both LAI and gap fraction were marginally insignificant between the Soltis Center (2.91 ± 0.09, 0.05 ± 0.005) and Pocosol (2.57 ± 0.1, 0.08 ± 0.01, $P = 0.07$, $P = 0.07$). However, *O. novogranatensis* LAI and gap fraction were significantly different across with Pocosol (3.3 ± 0.1, 0.1 ± 0.01) having higher LAI and lower gap fractions than the Soltis Center (3.03 ± 0.2, 0.05 ± 0.01, $P = 0.02$, $P = 0.03$). (Figure 5*a-f*)

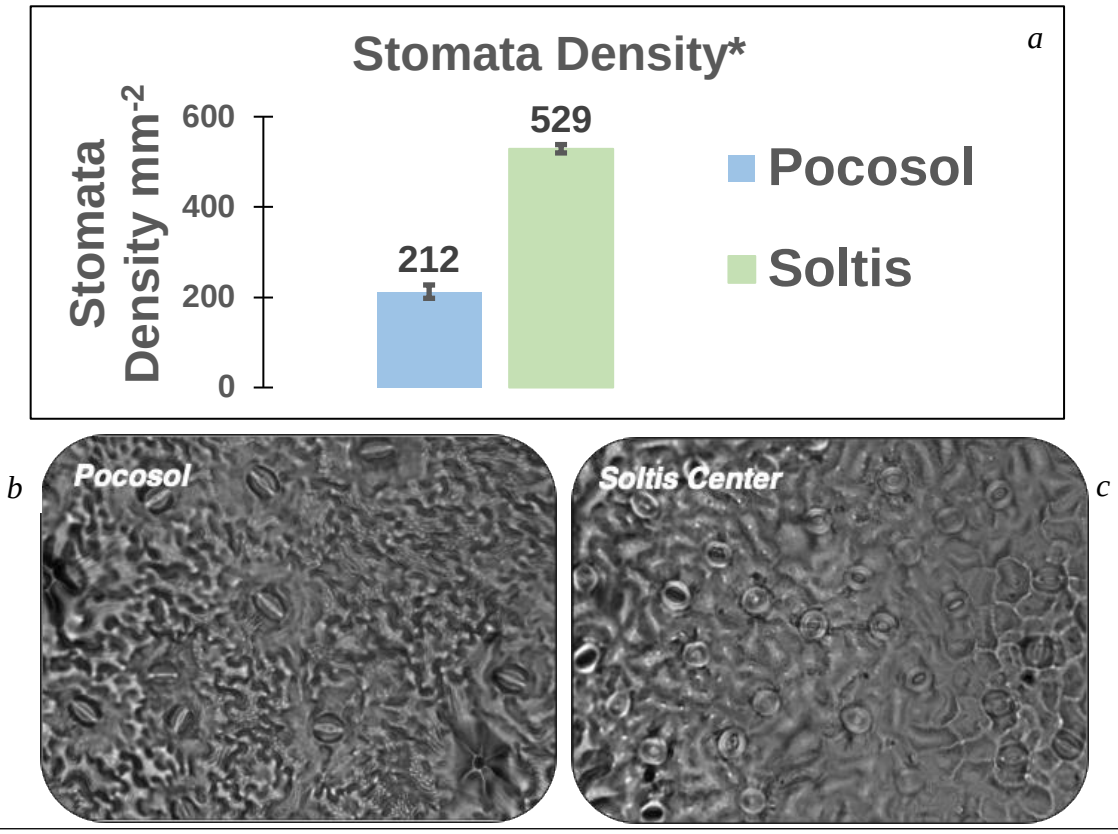


Figure 4*a-c*. Results of stomata density analysis (*a*) with images of *C. guianensis* stomata collected from Pocosol (*b* left) and the Soltis Center (*c* Right), ***** = p-value < 0.05.

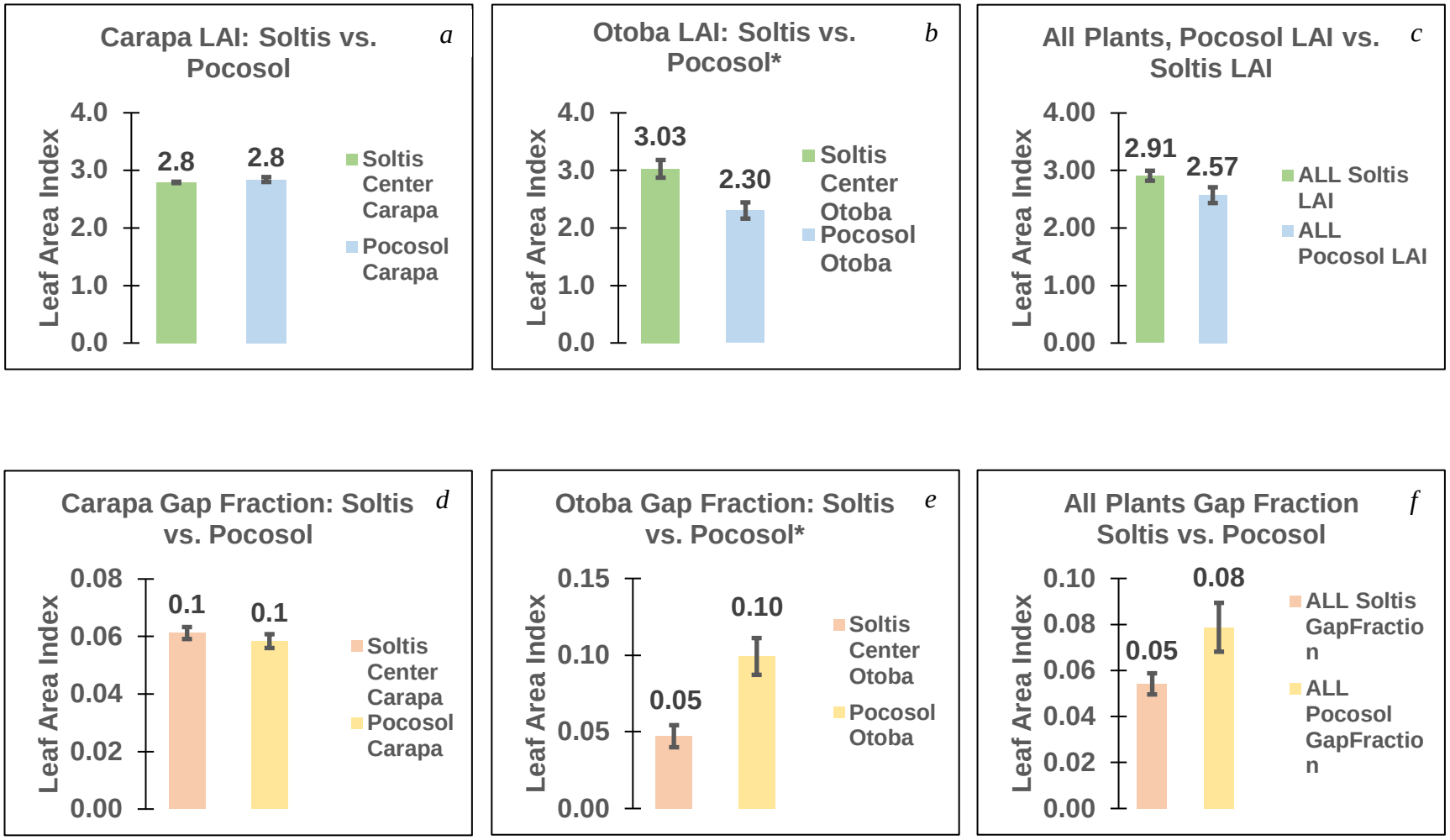


Figure 5. Results for LAI and Gap Fraction analysis comparisons of growth environments between sites for *C. guianensis* (*a* and *d*), *O. novogranatensis* (*b* and *e*), and all plants of each site (*c* and *f*) ***** = p-value < 0.05.

Sap Flow Study

LAI and Gap Fraction Results

Leaf Area Index was not statistically different between 2014 (3.32 ± 0.1) and 2019 (3.19 ± 0.4, *P* = NF) while gap fraction (i.e. the amount of visible sky) was significantly higher in 2019 (0.07 ± 0.01) than in 2014 (0.04 ± 0.002, *P* = 0.0004, Figure 6*a-b*).

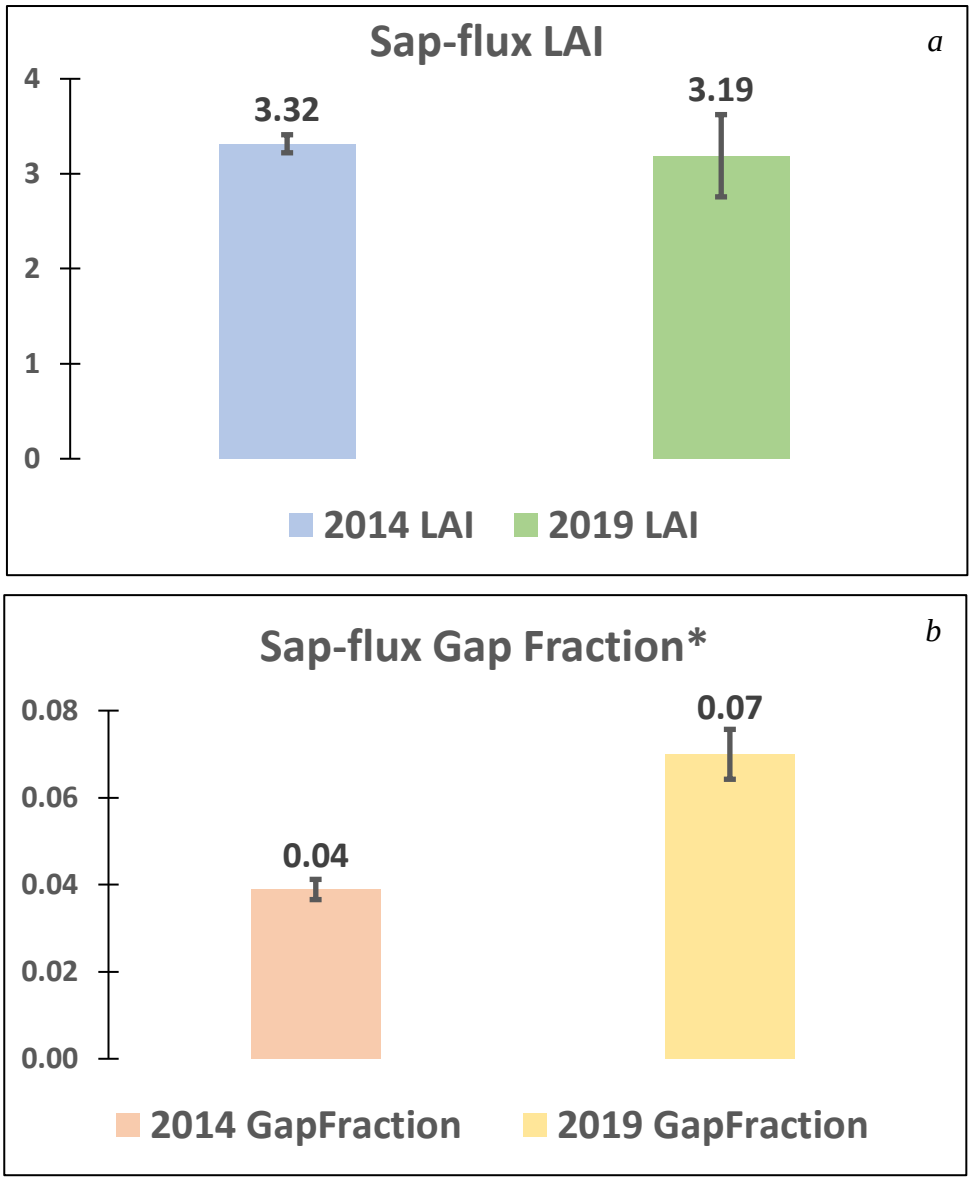


Figure 6*a-b*. Depiction of LAI (*a*) and gap fraction (*b*) results used to detect change in forest structure between 2014 and 2019/20.

Water Usage Comparisons

Overall, the rates of sap flux were higher after the tree gap was created than before and the ratios of water use between the dominant, mid-story, and suppressed trees shifted markedly. After the death of the large dominant tree, mid-story trees used only ~14% more water than suppressed trees in post tree death compared with ~22% more water than suppressed trees prior to tree death. Similarly, dominant trees used only ~3% more water than suppressed trees post tree death compared with ~29% more water than suppressed trees prior to tree death. Interestingly, mid-story trees used ~12% more water than dominant trees post tree death and ~10% less water than dominant trees prior to tree death. Sap-flux for suppressed trees was, on average, higher for trees post tree death (48.65 ± 10.34 kg m^{-2} h^{-1}) than for trees prior to tree death (27.65 ± 5.47 kg m^{-2} h^{-1}). For mid-story trees sap-flux was, on average, higher for trees post tree death (56.84 ± 9.76 kg m^{-2} h^{-1}) than for trees prior to tree death (35.33 ± 5.77 kg m^{-2} h^{-1}). Dominant tree sap-flux was, on average, higher in for trees post tree death (49.91 ± 6.93 kg m^{-2} h^{-1}) than for trees prior to tree death (38.85 ± 5.65 kg m^{-2} h^{-1}). From total tree comparisons across sites, post tree death sap-flux was significantly higher (48.8 ± 4.9 kg m^{-2} h^{-1}) than sap-flux prior to tree death (32.96 ± 3.4 kg m^{-2} h^{-1}, P = 0.02). (Figures 7-9, Table 2)

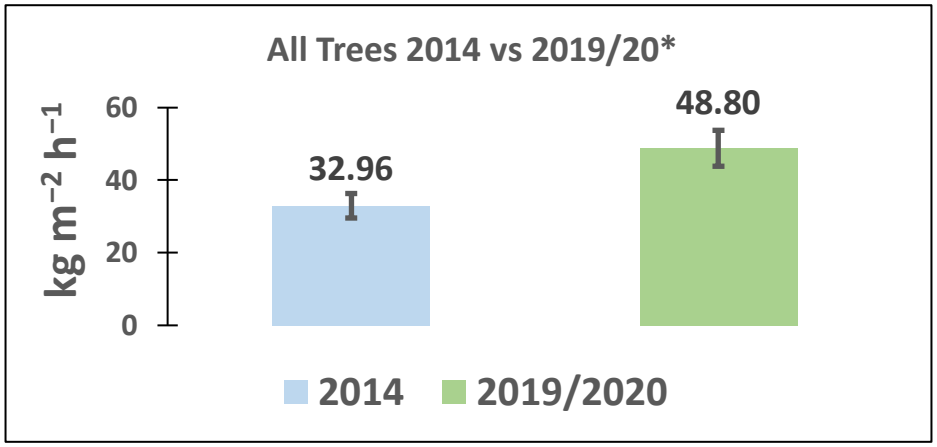


Figure 7. Graphed total average tree comparisons between 2014 and 2016 (*b*), ***** = p-value < 0.05.

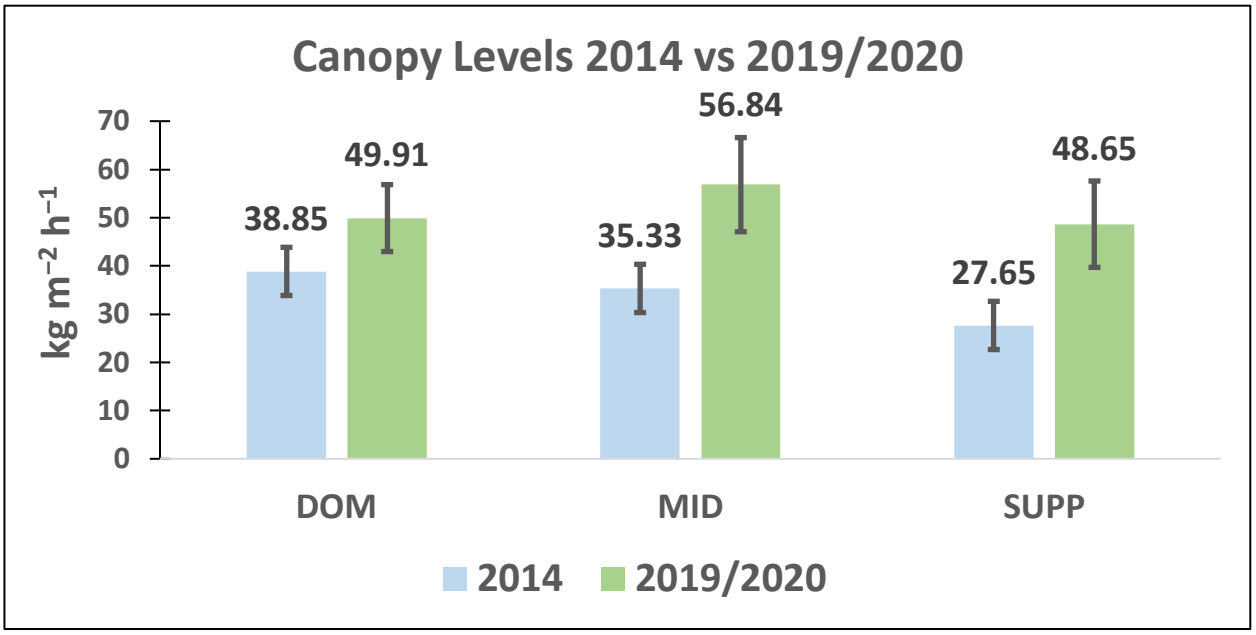


Figure 8. Graphed total average hourly sap-flux of dominant (DOM), mid-story (MID), and suppressed (SUPP) trees for both 2014 (pre tree death) and 2019/20 (post tree death).

Table 2. Total hourly J_s averages from each tree with additional 2014 measurements from Aparecido et al. (2016).

Canopy Level	Tree Species	2014 Diameter at Breast Height (cm)	2014 Tree Height (m)	2014 J_s (kg m^{-2} h^{-1})	2019/20 J_s (kg m^{-2} h^{-1})
Dominant	*Otoba novogranatensis*	62.8	29	44.5 ± 16.7	56.8 ± 28
Dominant	*Genipa americana*	46.2	28	33.2 ± 18.0	43 ± 20.3
Mid-story	*Ampelocera macrocarpa*	15.6	16	35.3 ± 18.5	45 ± 29.3
Mid-story	*Carapa guianensis*	17.3	16	26.1 ± 12.4	23.1 ±11.7
Mid-story	*Ampelocera macrocarpa*	32	26	28.3 ± 14.3	56.4 ± 20.4
Mid-story	*Eschweilera* sp.	30.5	27	51.6 ± 24.7	69.1 ± 36.5
Suppressed	*Trophis mexicana*	10	11	42.1 ± 19.4	36.7 ± 19.9
Suppressed	*Carapa guianensis*	8.3	9	21.9 ± 11.5	35.6 ± 16.5
Suppressed	*Cupania macrophylla*	6.9	10	29.6 ± 11.3	74.1 ± 34.2
Suppressed	*Pouteria cf. viridis*	11.1	11	17 ± 8.6	48.1 ± 56.2

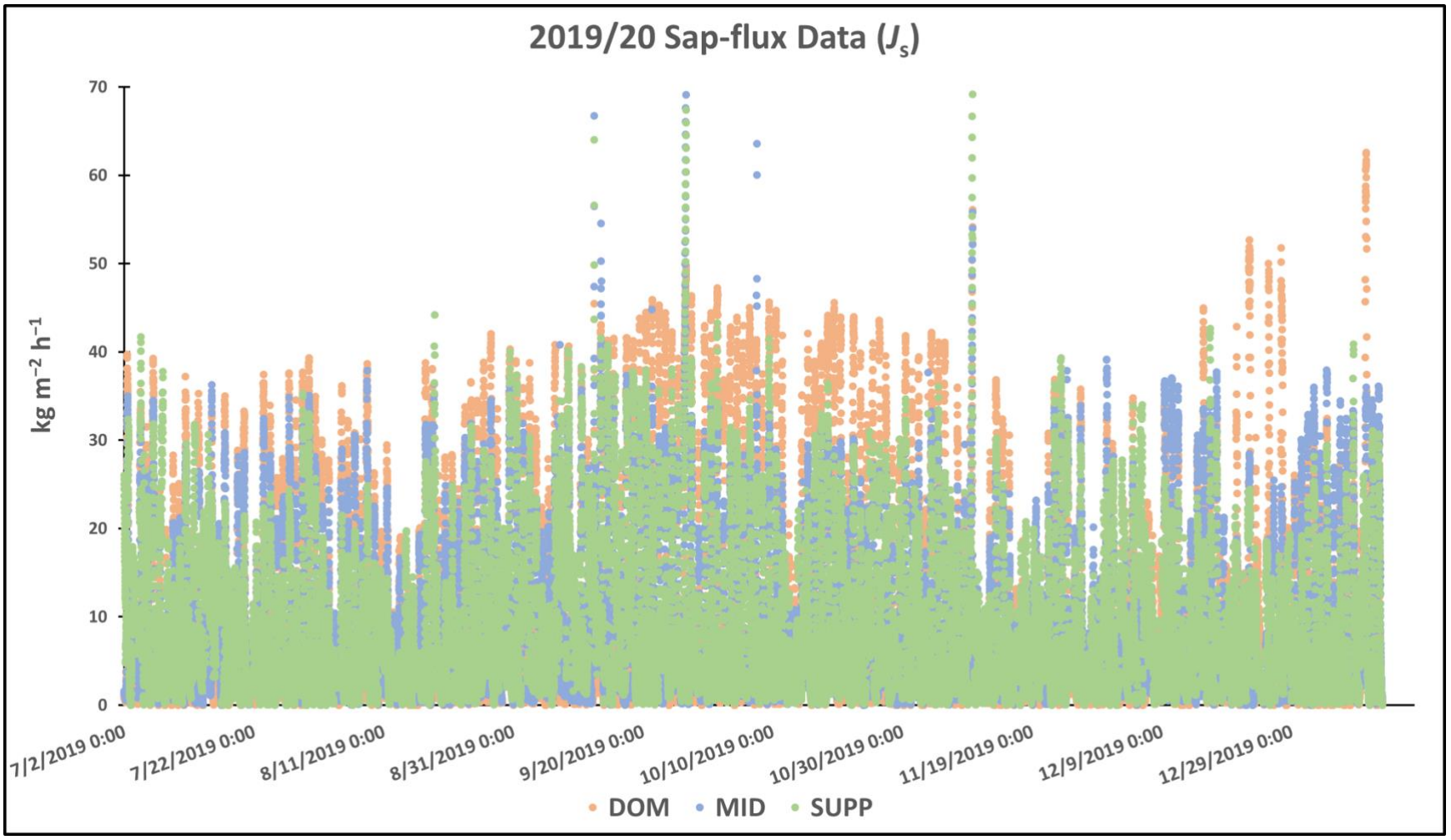


Figure 9. Graphical illustration of dominant (DOM), mid-story (MID), and suppressed (SUPP) 2019/20 sap-flux data across the entire measurement period.

Discussion

Leaf Gas Exchange Study

From leaf gas exchange results, there was a clear difference in the photosynthetic apparatus of both *C. guianensis* and *O. novogranatensis* under environmental variability both within sites and between them. Significant differences were present between these species for three of the five parameters tested (day respiration, electron transport, and Triose Phosphate Utilization) when comparing total values across sites, highlighting the overall species differences in photosynthetic capacity under environmental variability. Of the two species, *C. guianensis* appears to be the more phenotypically plastic due to greater maximum velocity of Rubisco for carboxylation at the Soltis Center and higher daytime respiration at Pocosol. Additionally, *O. novogranatensis* comparisons between sights yielded no significant differences across sites despite the variability in growing conditions found through LAI and gap fraction analysis, further highlighting its inability to alter its photochemical response to environmental variability along elevation gradients. Within site comparisons also depicted a somewhat inversion of physiological response with *C. guianensis* containing higher maximum velocity of Rubisco for carboxylation values at both sites and *O. novogranatensis* containing significantly higher electron transport electron transport values at Pocosol, and consistently (yet not significantly) higher values of electron transport at the Soltis Center. These results emphasize the physiological variability that can occur in species that are functionally similar with the inverse trend between *C. guianensis* and *O. novogranatensis* perhaps being the most apparent evidence of this. The preference of either increased maximum velocity of Rubisco for carboxylation or electron transport could potentially be indicators of differences in survival strategy that occur within these species,

allowing them to occupy similar niches. However, the ability to conduct such an analysis is outside the scope of this study.

Additionally, while total LAI and gap fraction comparisons were not deemed significantly different, the greater average total LAI recorded at the Soltis Center conflicts with our findings in stomatal densities for *C. guianensis*. For *C. guianensis* trees in Pocosol, where total average LAI was lower and gap fraction higher, we calculated a significantly smaller stomatal density when compared to the Soltis Center. This finding coupled with the fact that stomatal density is proven to be higher in sun exposed plants (Voleníková and Tichá 2001, Camargo and Marenco 2012), leads us to hypothesize that stomatal density within *C. guianensis* is primarily driven by sun exposure limited by cloud cover, and not forest heterogeneity. It is also important to note that while LAI/gap fraction measurements for *O. novogranatensis* could be the primary reason for our difference in averages, insignificant differences in LAI/gap fraction measurements recorded for *C. guianensis* site comparisons still support the aforementioned hypothesis.

Sap-flux Study

Following the death of a large canopy tree and subsequent increases in light available to the remaining trees in our plot, sap-flux in trees of all canopy layers starkly increased their total water usage when compared to sap flow measured in 2014 when that tree was still alive. This finding highlights the immediate redistribution in plant water usage that occurred among dominant, suppressed, and mid-story trees ~7 months after the death of the *M. anisophyllum* tree. This observation demonstrates how drastically suppressed species competing for light can increase their transpiration in order to take advantage of such a tree fall gap, and to what extent, this water uptake and associated rapid growth can compete with that of larger more developed

over-story species. Should this type of tree fall gap become more frequent as rain patterns and temperature change with increasing atmospheric CO_2, we hypothesize that the tree behavior demonstrated in this study could potentially affect species survival and ultimately, forest structure. It is also important to note that, although this comparison was made using the same trees as Aparecido et al. (2016), the number of sensors per tree and total time frame for measurements was not equal between study periods. Particularly for our 2019 data, mid-story and dominant tree measurements often included one sensor whereas measurements conducted by Aparecido et al. (2016) installed two or more sensors within these same class of trees to reduce error imposed by the variance of sapwood depth within trees.

CHAPTER IV

CONCLUSION

The first study reported sought to investigate how two early successional tropical species alter their photochemical response to climate variation along an altitudinal gradient. From this study, we found that *C. guianensis* has a higher photosynthetic capacity along elevation gradients than *O. novogranatensis*. Additionally, we provide evidence that variation in *C. guianensis* leaf anatomy along this gradient is primarily driven by climatic variation as opposed to forest heterogeneity. In its entirety, this study highlights the fact that species within the same functional groups are not guaranteed to respond similarly to environmental variation and stresses the importance of understanding key physiological processes within individual species.

The second study addresses effects of tree fall gap on water usage across varying canopy levels prior to dominant tree mortality. We found that suppressed trees increased their average water usage to levels near that of mid-story and dominant trees in the same stand; most likely in response to the increases in tree gaps present post-death of the dominant tree. We also found significant evidence that all trees in the plot may have increased their water use substantially relative to what it was before the tree death occurred. These findings stress the importance of better understanding how tree fall gaps alter site hydrology and species water use in order to understand what potential effects may occur should tree mortality increase within the tropics as a result of climate change.

By exploring the physiological mechanisms that drive plant species response to environmental variation, as well as plot level response to dominant tree mortality, this research provides new insights into the dynamic nature of tropical rainforests by investigating key

characteristics within them that dictate their function/composition and that may be crucial to predicting how such systems will develop under a changing climate.

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APPENDIX

Table 1. Aparecido et al. (2016).

Table I. Individual description of trees measured using sap flux probes.

Category	Diameter at breast height (cm)	Height (m)	Basal area (m^2)	Sapwood area (m^2)	%	Average max J_s ($kg\,m^{-2}\,h^{-1}$)
Dominant	45.2	27	0.160	0.100	62%	61.6 ± 16.9
Dominant	200	32	3.142	1.230	39%	41.7 ± 13.2
Dominant	19.7	27	0.030	0.029	94%	30.2 ± 12.9
Dominant	80	30	0.503	0.253	50%	36.6 ± 15.7
Dominant	62.8	29	0.310	0.192	62%	44.5 ± 16.7
Dominant	46.2	28	0.168	0.102	61%	33.2 ± 18.0
Dominant	220	38	3.801	1.478	39%	56 ± 15.1
Dominant	150	30	1.767	—[a]	—	47 ± 18.2
Midstory	11.6	13	0.011	0.010	93%	41.7 ± 13.2
Midstory	21.2	13	0.035	0.030	86%	48.4 ± 15.1
Midstory	42.6	22	0.143	0.069	48%	57.2 ± 23.7
Midstory	40.1	25	0.126	0.113	90%	70.2 ± 25.7
Midstory	15.6	16	0.019	0.012	65%	35.3 ± 18.5
Midstory	17.3	16	0.024	0.016	69%	26.1 ± 12.4
Midstory	18.5	15	0.027	0.024	90%	32.5 ± 14.4
Midstory	32	26	0.080	0.066	82%	28.3 ± 14.3
Midstory	40	30[b]	0.126	0.068	54%	57.8 ± 31.7
Midstory	30.5	27[b]	0.073	0.053	73%	51.6 ± 24.7
Suppressed	7.7	6	0.005	0.005	100%	25.7 ± 9.9
Suppressed	12.7	6	0.013	0.011	86%	33.7 ± 16.4
Suppressed	10	11	0.008	0.006	82%	42.1 ± 19.4
Suppressed	17	10	0.023	0.019	83%	32.7 ± 11.6
Suppressed	8.3	9	0.005	0.004	78%	21.9 ± 11.5
Suppressed	6.9	10	0.004	0.003	82%	29.6 ± 11.3
Suppressed	12	10	0.011	0.010	90%	28.3 ± 9.8
Suppressed	11.1	11	0.010	0.009	90%	17.0 ± 8.6

[a] Unable to retrieve xylem core samples.
[b] Labelled midstory because they are located under a larger, 40-m tall tree.