PLANT-ATMOSPHERE RESPONSES TO WET CANOPY CONDITIONS IN A MATURE TROPICAL FOREST

A Dissertation

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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May 2017

Major Subject: Ecosystem Science and Management

ABSTRACT

Spatial and temporal variation in wet canopy conditions following precipitation events can influence processes such as transpiration and photosynthesis, which can be further enhanced as upper canopy leaves dry more rapidly. As part of a larger study aimed at improving land-surface modeling in a wet tropical forest of Costa Rica, this dissertation: I) compared transpiration among trees with exposed and shaded crowns under various leaf wetness conditions; II) evaluated responses of seven tropical and three semiarid savanna plant species to simulated leaf wetness; and III) tested stomatal and canopy conductance model performance while canopies were wet. To address these goals, I mainly relied on 43 sap flux sensors (J_s), gas exchange measurements under dry and wet conditions, and one year and a half of micrometeorological measurements from a 40-m tower inside a mature rainforest plot.

Overstory trees (13% of the plot) contributed ~76% to total stand transpiration. Transpiration and J_s was driven by vapor pressure deficit and solar radiation, but leaf wetness had a significant role by reducing as much as 28%. Dry days had equal quantities of J_s between overstory and midstory trees; while on wet days, all trees had low J_s rates. Meanwhile, photosynthetic responses (A_{net}) while leaves were wet varied greatly among species, but all plants maintained a baseline of activity. A_{net} responses, among all ten species, varied between -48% and +21%, when compared to their dry condition performance. Due to the canopy and atmospheric complexity of the study site, most canopy models tested did not depict leaf wetness periods appropriately. Even during dry days, low vapor pressure deficits interfered with model accuracy. Also, intermittent rain, during semi-dry and wet days, caused large fluctuations in canopy and stomatal conductance estimates, especially between shaded and sunlit leaves.

Thus, this dissertation found compelling evidence that leaf wetness may partially or substantially suppress physiological responses in function of leaf anatomy and inter-canopy microclimate. Therefore, further studies on tropical plant traits across a wide range of species, and on leaf-level gas exchange and sap flow measurements are needed to improve the accuracy of climatic modelling of wet tropical ecosystems.

DEDICATION

I dedicate this dissertation to my family and to the endless mysteries of tropical forests around the world.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Georgianne W. Moore, and my committee members, Dr. Gretchen R. Miller, Dr. Anthony T. Cahill, and Dr. James L. Heilman, for their guidance and support throughout the course of this research. Specifically, thank you, Georgianne (and family), for being such an amazing mentor and friend. You will always be an inspiration to me! Additionally, I would like to thank the staff of the Texas A&M University Soltis Center for Research and Education for the field and logistics support for the entire data collection of this dissertation, and for helping me with my Spanish.

Thanks also go to my friends and colleagues, faculty and staff of the department of Ecosystem Science and Management for making my time at Texas A&M University a great experience. Also, special thanks to the “Aggieland/BCS community” for embracing me as their own. I am proud to be an Aggie and call this place “home”.

Special thanks to the Moore Ecohydrology Lab (Caitlyn Cooper, Rosaleen March, Amelia Min-Venditti, Paul Klockow, Ajinkya Deshpande and Aline Jaimes) and the Geoecohydrology Research Group (Ryan Andrews and Jaeyoung Song) for not only supporting my research (data collection and writing reviewers), but for being my good friends inside and out of the laboratory. This friendship will for sure extend after this doctoral period.

I would also like to recognize the outside support provided by friends of the Brazilian Student Association of Texas A&M University and Brazilian friends (Ilha

Solteira-SP, Curitiba-PR (especially to the Dendrometry Laboratory – LADEN), Manaus-AM and Campinas-SP) and abroad (specifically, Norbert Kunert from Max Planck) that made themselves present throughout this difficult period away from home.

Finally, thanks to my mother (Maria Inês da Silva) and father (João Batista Aparecido) for their encouragement in letting me pursue a challenging career and dealing with their daughter residing ~5,000 miles away. Hope my hard work will always make you proud! Thanks also to my brother (André Luiz T. Aparecido) and niece (Gabriela B. T. Aparecido) for seeing me as their role model and incentivizing me to succeed. Special thanks to my partner (Pedro M. Risso) for being my emotional fortress and for enduring along with me the challenges in sustaining a relationship from afar. I would not have been able to complete this journey without your support.

I will be eternally grateful for all of you involved in my life before and after this PhD. THANK YOU!

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a dissertation committee consisting of Associate Professor Dr. Georgianne W. Moore of the Department of Ecosystem Science and Management, and Associate Professors Dr. Gretchen R. Miller and Dr. Anthony T. Cahill of the Department of Civil Engineering, and Dr. James L. Heilman of the Department of Soil and Crop Sciences.

All work for the dissertation was completed by the student, in collaboration with Dr. Eugenio Gonzalez and staff of the Texas A&M University Soltis Center for Research and Education.

Funding

This work was made possible in part by the Department of Energy – Office of Science (BER) under Grant Number DE-FOA-0000749 and entitled “Improving land-surface modeling of evapotranspiration processes in tropical forests”. Its contents are solely the responsibility of the authors and do not necessarily represent the official views of the Department of Energy – Office of Science (BER).

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Introduction

Tropical forests have a major role in the global atmosphere dynamics. These forests are responsible for 50% of water recycling (Shuttleworth 1988) and at least 35% of the aboveground carbon storage (biomass) (Baccini et al. 2012), making their conservation crucial for a steady output and input of water and carbon fluxes to the atmosphere. However, tropical forests would not be as productive without an efficient precipitation recycling regime that could maintain a steady source of water, which directly affects growth and precipitation rates regionally and even globally (Baker et al. 2003). High biodiversity is also an important characteristic of these ecosystems. Non-degraded tropical forests can house over 200 species of trees per hectare (Gentry 1988), along with a variety of other plant functional types, like palms (ter Steege et al. 2013), lianas (DeWalt et al. 2006) and a wide range of epiphytes (Ding et al. 2016). Large precipitation amounts (year-round or seasonally), high relative humidity, and constant warm temperatures throughout the year (Malhi and Wright 2004) are the main factors to which they have adapted to. Additionally, a species heterogeneous forest stand leads to unique microclimatic conditions within canopy layers that can favor a wide range of plant individuals (Pausas and Austin 2001).

Tropical rainforests are composed of complex canopy structures with emergent tree crowns with an even more complex inter-canopy level. This multi-layered vertical structure creates distinguishable differences in environmental factors that will further influence the biological functioning of the existent tree species (e.g, photosynthesis and transpiration) (Kumagai et al. 2001). Vertical variability of inter-canopy microclimate is also increased when topography plays a role in enhancing wind exposure, elevation and day-length shift (Dobrowski 2010). The most important factors to consider when assessing vertical profiles of forest stands are: overstory canopy absorption of solar radiation and reducing the amount that reaches the understory; less fragmented canopies will partially block air mixing in lower canopy levels; and less air mixing leads to warmer and more humid understory (Kumagai et al. 2001, Loescher et al. 2002, Hardwick et al. 2015). When considering an energy-limited, wet, montane and biodiverse forest stand, the vertical profile dynamics may lead to wide range of physiological responses throughout the profile due to their dependence on favorable conditions (e.g., wind and solar radiation) to dry out leaves significantly to continue functioning (Dietz et al. 2007).

The wide variety of plant species spans through multiple distinct plant morpho-physiological traits. Tropical plant physiology (water use, biomass production, nutrient allocation, etc.) directly influences morphological traits (leaf shape, canopy size, rhizosphere, etc.) (Valladares et al. 2002, Kenzo et al. 2004, Sanches et al. 2010). A classic example is the difference between dominant, pioneer trees and suppressed, late-successional trees, in which high photosynthetic capability of dominant individuals (due to light availability) will allow a large production of branches and small, dispensable leaves; while suppressed individuals will maintain few branches and long-living, large leaves to be more photosynthetically efficient (King 1994, Kitajima et al. 2005, Binkley et al. 2010). Although distinct, both tree dominance groups are influenced by highly variable micrometeorological conditions. Dominant tree leaves have to cope with high solar radiation incidence and higher vapor pressure deficits during dry, sunny days (Turner 2004), while suppressed trees have limited light access and elevated humidity levels that may promote the growth of physiologically detrimental leaf epiphytes (Holder 2007).

In montane tropical forests, low radiation due to cloud coverage and leaf wetness (rain and fog) requires more specialized plant species or species with high plasticity. With increase in altitude, plants have developed some traits such as foliar water uptake, reduced photosynthetic rates (and growth) with lower photosynthetically active radiation (PAR) and decrease in root-to-shoot ratio with altitude (Letts and Mulligan 2005, Soethe et al. 2006, Oliveira et al. 2014). While under a different or changing environment, little or lack of plasticity to drought of tropical forest species (e.g., acclimation through change in plant anatomy traits) (Binks et al. 2016) will consequently limit a certain number of species to its habitat, due to small probabilities of migration and survival (Aitken et al. 2008). Hence, adapted plant morphological traits, such as large and coriaceous leaves (Grubb 1977), leaves with drip-tips (Malhado et al. 2012), leaf water uptake (Goldsmith et al. 2012), shoot size correlated to incident light (Valladares et al. 2000), leaf pubescence or repellency (Brewer et al. 1991, Holder

2007), and reduced rates of stomatal conductance and water uptake (Granier et al. 1996, Bourne et al. 2015), are crucial to survive in these environments (Gratani 2014). Other environmental variables, like leaf wetness, strong winds (structural damage) and forest gap conditions (natural or anthropogenic) can also suppress plant physiological processes (Zhu et al. 2004, Letts and Mulligan 2005, Sanches et al. 2010).

Among the climatic variables cited, leaf wetness is the least studied and considered as one of the most detrimental factors for tropical tree growth (Monteith 1963). Leaf wetness has been described as a gas exchange diffusional resistance factor (Fogg 1947), but very few studies have acknowledged its possible benefits to leaf-canopy processes. Additionally, their adaptations to cope with recurrent large amount of precipitation, in comparison to lowland, premontane forests, or high density of fog occurrence in montane, cloud forests have also been little addressed. Leaf wetness could have a measurable impact on photosynthesis and transpiration, since water being intercepted by the forest canopy can range from 20 to 80% of precipitation in the tropics (Sollins and Drewry 1970, Loescher et al. 2005, Teale et al. 2014). In some tropical montane environments, other hydrological phenomena, like dewfall and fog are also significant (Bruijnzeel and Veneklaas 1998, Gotsch et al. 2014). In transitional montane ecosystems, this phenomenon is even more important since these environments are subjected to the combination of large rainfall amounts, occasional fog and indirectly affected by dense cloud coverage. The fact that this variable is understudied is extremely inscrutable, considering the climatic and biological significance of these environments in the global scenario, especially with global climate predicted to change dramatically in future years.

Recently, development and usage of global climate models (e.g., GCM - General Circulation Model, such as CLM - Community Land Model; Oleson and Lawrence 2013) has become increasingly popular and powerful to predict these future climate scenarios. Unfortunately, the micrometeorological, remote sensing and plant functional trait data collected and used to represent tropical forests are very few (only 6% of FLUXNET data; Williams et al. 2009) when compared to drier and more accessible ecosystems (Akkermans et al. 2002, Buytaert et al. 2010) and most likely underrepresents the actual hydrological processes and growth limitations when these forests are wet, which is, in most tropical forests, more than half of the year. Although CLM has been improving global climate models by introducing plant functional traits (e.g. photosynthetic parameters, like V_{cmax} and J_{max}), models still need to improve the range of their datasets to include plant species from wet, energy-limited environments. Otherwise, these model estimates may be underestimating their productivity and hydraulic efficiency under highly variable climatic conditions, especially canopy wetness.

Literature Review

Plant water relations

The foundation of plant water conductance depends on the water capillary rise, which is described as a certain volume of water inside a tube confinement, with smooth and rigid walls, and that through adhesion of strong, cohesive water molecules to the wall creates an upward force that result in an upward meniscus (Kramer and Boyer 1995). Capillary rise occurs when adhesion forces to the walls is larger than the cohesive forces of water molecules in a certain tube volume (height and diameter). The pressure gradient driving force, also known as diffusion pressure deficit, is assumed to be the necessary tension for the “Cohesion-Adhesion Tension” theory (Kramer and Boyer 1995). Angiosperm woody plants vessel dimensions, in which vessel diameters rarely exceed half a millimeter (Jones 1992), can determine the amount of flux density (sap flow) and released into the atmosphere (transpiration) at a certain pressure gradient. Leaf or canopy to atmosphere pressure gradient is also known as “atmospheric vapor pressure deficit” (δe - kPa). δe is the difference between the amount of moisture the air contains and the amount of moisture it can actually hold when 100% saturated.

With leaves transpiring, there is a reduction of water potential (flows from less negative to most negative) that causes the movement of water upwardly in direction of the leaves and, consequently, the atmosphere (Kramer and Boyer 1995). This loss of water consequently produces tension that is transmitted through the water column, which reduces the water potential and results in water uptake by the roots from the soil.

Tropical lowland tropical forests have been documented to transpire between 500-1,000 mm year^{-1}, while montane tropical forests transpire less (250-500 mm year^{-1}) (Bruijnzeel and Veneklaas 1998). This significant reduction in transpiration with increase in altitude has been attributed to lower leaf areas (LAI), dense cloud coverage and fog occurrence (Oliveira et al. 2014). In seasonally dry tropical forests, soil water deficits (Kumagai et al. 2004, Kumagai et al. 2005) and elevated vapor pressure deficits (above 2 kPa) also impose constraints to transpiration rates (Motzer et al. 2005).

During very dry days, it is expected that solar radiation, vapor pressure deficit and temperature will be increased and, consequently, causing soil evaporation. It has been reported that atmospheric pressure can decrease from -100 MPa to -300 MPa in extremely dry days (Kramer and Boyer 1995). On these days, it is common that plants transpire more than they can actually absorb from the roots (large soil resistance due to large pores/air pockets). Excessive transpiration can cause leaf wilting and/or stomata closure (negatively affecting gas exchange), which may lead to carbon starvation or hydraulic failure through cavitation (Tyree and Sperry 1989). Broadleaves are the most affected because they possess large conduits and have a lack of a margo membrane in their pits, that helps diminish the passage way for this “air bubbles” (Sperry et al. 2006).

Tropical trees are not only vulnerable due to wood type, but are mainly affected due to their sensitivity to high vapor pressure deficits and soil water deficits that normally do not occur in wet tropical forests (Bourne et al. 2015). Species with little adaptations to drought will likely die of hydraulic failure (Rowland et al. 2015, Binks et al. 2016, Torres-Ruiz et al. 2016). Bucci et al (2016) discusses that tree species from wet tropical ecosystems, that do not experience seasonal droughts, have stems and leaves with similar vulnerability to cavitation, while trees from dry tropical ecosystems have leaves that are more vulnerable to drought induced cavitation compared to stems. Hence, are able to shed their leaves while preserving their hydraulic system. For long term strategies, wet tropical forests may cope with drought by restricting shoot growth and increasing root expansion (Brunner et al. 2015). It has also been shown in wet tropical forests that root-to-shoot ratio doubles when annual precipitation regimes are reduced by ~80% (Mokany et al. 2006). Additionally, due to large growth rates, tropical species can cope with some embolized conduits by producing new xylem tissues, especially considering that they are not dormant during the winter like temperate broadleaved species (Tyree and Zimmermann 2002). But, it is important to highlight that daily variations are as important as seasonal variations (Ford et al. 2004a).

Soil-plant-atmosphere interactions

The main compromising factor of water uptake and stomata aperture through the soil-plant-atmosphere continuum is water availability. In plant water relations, it is essential to maintain sufficiently high water content, from the soil to stomata guard cell turgidity, so that physiological processes function properly (Kramer and Kozlowski 1960). Therefore, any biotic or abiotic factor that affects water supply (source availability or resistance/conductance) is a threat to the mechanisms that involves ascent of sap, transpiration and photosynthesis. Since soil water content in tropical forests is almost always saturated, it can be assumed that the most influential abiotic factor for transpiration and photosynthesis is vapor pressure deficit of the air (δe) (Renninger et al. 2010). Leaf gas exchange occurs when vapor pressure in their leaves exceeds that in the surrounding air. Therefore, any other variable that increases this pressure difference may be considered as another important abiotic factor. Temperature and relative humidity are some of those variables, especially considering that these variables are used to estimate this parameter. Increase in leaf temperature has been associated to increase in photosynthetic rates until a thermal optimum is exceeded (Way et al. 2015), which may lead to stomatal closure or photosynthetic enzyme degradation. In tropical montane ecosystems, leaf temperature also has an important role in promoting leaf drying after rain events (Goldsmith et al. 2016).

Other abiotic factors that affect leaf gas exchange are solar radiation and wind. Solar radiation is an important factor in stomata aperture/conductance since it is a source of energy for photosynthesis. Also, solar radiation is the source of latent heat (vaporizes the water released by stomata or from the soil into the atmosphere) and sensible heat (increases surface temperature) (Bonan 2008b). Although surface vaporization has a large contribution to the water balance, there has been some evidence that little and large vaporization rates may have negative effects (Rocha et al. 2009). Leaf surface vaporization can majorly affect plants with thin cuticles, which release water even if their stomata are closed on a dry, hot day (Kramer and Boyer 1995). Oppositely, the lack of surface aeration can also hinder gas exchange. Wet surfaces from rain, dew or fog are believed to suppress plant physiological processes due to lower gas diffusion rate in water (increased resistance) (Smith and McClean 1989). Some species that occur in regions with high precipitation amounts (e.g. tropical forests) have shown adaptations to cope with this phenomena, such as leaf repellency and pubescence, leaf angle, foliar water uptake and take advantage of the wetness for cooling effects (Aryal and Neuner 2010, Bruijnzeel et al. 2011, Goldsmith et al. 2013, Rosado and Holder 2013, Oliveira et al. 2014).

The role of wind or turbulent fluxes is important in many ways, but mainly alters the leaf boundary layer so it can perform water and gas exchange with the atmosphere properly (Martin et al. 1999). This can lead to positive and negative effects. If wind speed is moderate, the main effects will be leaf cooling and air mixing (Hardwick et al. 2015). If the wind speed is too low or non-existent, the leaf boundary layer can become thick enough with saturated air that the pressure gradient will not be large enough for CO_2 and water exchange (O'Brien et al. 2004, Kim et al. 2014).

Examples of secondary biotic factors caused by frequent and prolonged leaf wetness such as diseases, surface epiphytes, and fungal growth can affect the integrity of leaves, stems and roots. Although some of these factors do not affect the pressure gradient, they can promote interruption of water transport and gas exchange. Wet leaves and roots are prone to pathogen invasions, and can lead to mortality of these tissues, which consequently will affect the plant physiologically.

Leaf wetness and morphological traits

Leaf wetness consists of water droplets or film that settles on the leaf surface and temporarily occludes stomata until it evaporates or drains (Ishibashi and Terashima

1995, Pandey and Nagar 2003). Most studies consider the susceptibility of wet surfaces to pathogen invasion (Hirano and Upper 2000, Jackson et al. 2006) and the proliferation of algae, moss and other biofilms (Coley et al. 1993) or determine how irrigation intensity affects crop yield (Cavero et al. 2009, Urrego-Pereira et al. 2013). Other studies focus on how foliar application of pesticides can affect photosynthesis (Kramer and Kozlowski 1960). Several of the above-mentioned studies are based on the assumption that when water covers open stomata, gas exchange (water and carbon dioxide) is reduced, since diffusion in water is extremely low when compared to diffusion in air (1:10,000) (Fogg 1947, Smith and McClean 1989). Although this diffusion limitation is known, some researchers argue that most plants species are hypostomatous, thus less affected (Dietz et al. 2007, Letts et al. 2010) or that leaf wetness resultant from fog or dewfall are considered physiologically insignificant (Monteith 1963).

However in wet environments, leaf wetness could have a measurable impact on photosynthesis and transpiration, since water being intercepted by the forest canopy can range from 20 to 80% of precipitation in the tropics (Sollins and Drewry 1970, Loescher et al. 2005, Teale et al. 2014). In some tropical montane environments, other hydrological phenomena, like dewfall and fog are also significant (Bruijnzeel and Veneklaas 1998, Gotsch et al. 2014). Given that tropical forest ecosystems can have mean annual precipitation from 2,000-5,000 mm, with peaks of up to 10,000 mm year^{-1} (Juo and Franzluebbers 2003, Holzman 2008), and that rainfall can occur daily and last throughout continuous days, the potential physiological impact of leaf wetness cannot be ignored.

Although decrease in photosynthesis and transpiration has been reported in other studies (Brewer and Smith 1995, Ishibashi and Terashima 1995, Letts and Mulligan 2005, Reinhardt and Smith 2008, Alvarado-Barrientos et al. 2014, Lin et al. 2015), the increase in photosynthetic activity has also been reported. Smith and McClean (1989) which 60% of the studied species formed water beads that enhanced stomatal opening and 34% of photosynthetic rates. Urrego-Pereira et al. (2013) also observed that alfalfa photosynthetic rates increased between 14 and 57% in irrigated crops, when compared to non-irrigated, due to leaf hydrophobicity. Similarly, Hanba et al. (2004) observed that hydrophobic pea leaves had a 22% increase in photosynthetic rates after 72 h of artificial misting due to a 12.5% increase in stomatal conductance (improved stomatal regulation). The optimum conditions created by wetness (cooler temperatures, high humidity) combined with favorable leaf anatomy traits are probably key elements for the species that show photosynthetic increase.

Structurally and biologically diverse tropical rainforests, with a mixture of distinct and unique traits within plant functional groups, are likely to possess specialized adaptations for wet leaves. Photosynthesis and transpiration may be inhibited when the leaf surface is partially or completely covered with water droplets due to these features (Fogg 1947, Smith and McClean 1989, Brewer and Smith 1997, Hanba et al. 2004, Letts et al. 2010, Alvarado-Barrientos et al. 2014). Adaptations to promote water shedding may include trichome coverage (Levin 1973, Brewer and Smith 1994), surface roughness, leaf angle (Fogg 1947) and repellency features like cuticular wax (Kaul 1976, Rosado and Holder 2013). These adaptations help to mitigate or prevent the effects of water on stomata and enable photosynthesis during and after rain, fog, or dewfall events (Holder 2007). Along with degree of leaf surface wettability, leaf arrangements within canopy will dictate leaf wetness duration and its possible suppression of gas exchange.

When precipitation falls on such a canopy, it creates a number of unique microclimates with wetness varying by height and tree characteristics. Vertical canopy leaf distribution directly affects sub-canopy humidity and subsequently affects transpiration and photosynthetic rates within these different layers. However, in wet tropical rainforests, it is unlikely that the entire canopy will be completely dry, with some portions remaining wet for a significant fraction of daylight hours (Dietrich et al. 1982). Such complex relationships between plant traits and atmospheric or biotic drivers present difficulties in the study of gas exchange (water and carbon dioxide) (Katul et al. 2012).

Forest canopy processes

The importance of water and its respective drivers are well-known, the modeling and delineation of its processes is as important as knowing its benefits, but extremely complex to be executed. The first step to understand water exchange between atmosphere and biosphere is having a clear knowledge of atmospheric boundary layer (ABL). ABL consists of the lowest portion of the atmosphere and is mainly influenced by its contact to the planet’s surface, which directly affect turbulent fluxes (Brutsaert 2005), since friction or shear stress decreases with height (Foken 2008). Therefore, this layer is not a simple system, since it includes a diurnal component (daytime convections and nighttime stratification), complex terrain issues (surface roughness and emissivity variations) and large weather events (tropical storms to extensive droughts). The main subdivisions are outer and inner region with intermittent transition layers (between each other, to the free atmosphere layer or to the surface layer) (Brutsaert 2005).

The inner region of ABL, at midday, can reach up to 1-2 km in thickness during midday and as low as 500 m at dawn, and is mainly defined as the region in which the wind direction remains constant with height due to its independent effect from the Earth's rotation and large pressure gradients from weather events (Brutsaert 2005). This inner region is mainly affected by the ground surface, whether it is vegetation or urban areas, and normally has vertical turbulent fluxes not too divergent from the ground surface (~10%). But it is important to highlight that this layer does not reach the ground surface and its main drivers are sensible heat flux and water vapor concentrations in the air, which directly affects air flow and momentum. Oppositely, these variables at the lowest portion of this layer are considered negligible, since heat flux and water vapor are passive admixtures (Brutsaert 2005). Therefore, it can be assumed that most atmospheric fluxes occur slightly above the ground or canopy height until the transition into the outer region. This assumption can be exemplified by observing a height profile of potential temperature, in which the ground to canopy temperatures are normally cooler than above the upper layer when submitted to the same wind intensity. This is mainly due to water vapor advection, and is even more distinct during cloudless nights. Although negligible, alternative measurements for near-surface fluxes and drivers need to be conducted for better understanding of the amount and pattern of fluxes observed above the canopy.

Therefore, acknowledging these distinct drivers leads to the distinction of "atmospheric surface layer", that is considered as the lowest layer adjacent to surface (or the lowest 10% of the atmospheric boundary layer) (Foken 2008). This layer takes in consideration turbulent exchange coefficients, height displacement and effects of roughness that will later be used in prediction models of surface fluxes and near-surface profiles. These models assume that in a plan-parallel flow wind velocity increase in the vertical direction will create a downward momentum flux and sink at the surface according to its respective shear stress and height (Brutsaert 2005). But, in general, these models are very generalist (Foken 2006) (e.g. considering the atmosphere in a neutral or stable condition, when in reality it is a mixture of unstable and stable conditions) and the need of more in depth investigations lead to Monin and Obukhov (1954) proposition of a new and more robust model based on wind velocity and temperature gradient. Due to its consideration of buoyancy forces along a wind and temperature gradient in the ABL, the Monin-Obukhov Similarity Theory (MOST) has been the basis of various climate models, including CLM (Community Land Model) (Bonan et al. 2002).

The Community Land Model, currently on its 5th version, has been considered as a promising climate model since it considers biogeophysical and biogeochemical parameters that simulate multiple land cover processes and atmosphere-land interactions; mainly to improve estimates of global and regional carbon cycle, vegetation dynamics and river routing (Oleson and Lawrence 2013). Since the beginning of CLM development, further improvements have been implemented to incorporate recent scientific advances in land surface processes, newer datasets and higher resolution data inputs. The latest version has been updated to incorporate revised canopy radiation incidence and warming, and improvements for leaf processes scaling (i.e. canopy conductance), mostly aiming to revise co-limitations on photosynthesis and, consequently, stomatal conductance.

Most land surface models have been mainly calibrated with fluxes measured within the extra-tropical Northern hemispheres (Akkermans et al. 2002). Similar to these models, CLM has an obvious deficit and biased observation data for artic and tropical (dry and humid) scientific insights. The data deficit is mostly due to few field sites in these ecosystems and also due to inconsistent field measurements within the sites (Akkermans et al. 2002, Buytaert et al. 2010). Additionally, some CLM parameters have been known to overestimate fluxes in the tropics, e.g., enlarged transpiration and productivity estimates based on large leaf area index (LAI) values, and non-realistic increase in albedo estimations due to soil albedo-soil wetness relationships if the model has parameters based on dry conditions/seasons (Lawrence et al. 2011). Hence, the implantation of long-term stand monitoring data (micrometeorological, hydrological, ecological and leaf-level measurements) in mature tropical forests (with highly heterogeneous canopy roughness, layers and species diversity and size) under various climatic conditions is essential for more accurate predictions from climate models (Barron 1995), especially CLM (Oleson and Lawrence 2013).

Objectives

Thus, to serve as a basis for future improvement of global climate models, this dissertation's major objective was to better understand how leaf wetness can affect tropical plants' physiological processes. My goal was to assess how transpiration, photosynthesis and canopy conductance of a Costa Rican premontane tropical forest perform under this condition.

Specifically, I aimed to address the following objectives, which represent each chapter of this dissertation:

I. Analyze the variation of plant water uptake during different wetness conditions for three tree canopy exposure categories (dominant, midstory, and suppressed) in a tropical premontane forest environment under frequent rain events. I hypothesized that leaf wetness would substantially reduce water assimilation on larger, more exposed trees in comparison to shaded understory trees.

II. Evaluate tropical and semiarid savanna species responses to simulated leaf wetness and test the hypothesis that leaf wetness reduces rates of photosynthesis (A_{net}); identify leaf traits that affect leaf wetness duration such as surface features, repellency, and stomatal arrangement and density; and address species traits generalization across habitats (tropical and semiarid) and highlight the main physiological process drivers.

III. Explore how leaf wetness affects canopy (g_c) and stomatal (g_s) conductance to water vapor across a range of environmental conditions. This objective relied on sap flux derived transpiration to test multiple models of g_c and g_s to determine their strengths and weaknesses for use in tropical forest canopies under frequent wet conditions. I hypothesized that some conductance models will perform better than others if they adequately represent the radiation and driving gradient of leaf-to-atmosphere vapor fluxes.

CHAPTER II

COMPARISON OF TREE TRANSPIRATION UNDER WET AND DRY CANOPY CONDITIONS IN A COSTA RICAN PREMONTANE TROPICAL FOREST[*]

Overview

Spatial and temporal variation in wet canopy conditions following precipitation events can influence processes such as transpiration and photosynthesis, which can be further enhanced as upper canopy leaves dry more rapidly than the understory following each event. As part of a larger study aimed at improving land-surface modeling of evapotranspiration processes in wet tropical forests, this chapter compared transpiration among trees with exposed and shaded crowns under both wet and dry canopy conditions in central Costa Rica, which has an average 4200 mm annual rainfall. Transpiration was estimated for 5 months using 43 sap flux sensors in 8 dominant, 10 midstory, and 8 suppressed trees in a mature forest stand surrounding a 40-m tower equipped with micrometeorological sensors. Dominant trees were 13% of the plot's trees and contributed around 76% to total transpiration at this site, whereas midstory and suppressed trees contributed 18% and 5%, respectively. After accounting for vapor pressure deficit and solar radiation, leaf wetness was a significant driver of sap flux, reducing it by as much as 28%. Under dry conditions, sap flux rates (J_s) of dominant trees were similar to midstory trees and were almost double that of suppressed trees. On wet days, all trees had similarly low J_s. As expected, semi-dry conditions (dry upper canopy) led to higher J_s in dominant trees than midstory, which had wetter leaves, but semi-dry conditions only reduced total stand transpiration slightly and did

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not change the relative proportion of transpiration from dominant and midstory. Therefore, models that better capture forest stand wet-dry canopy dynamics and individual tree water use strategies, are needed to improve accuracy of predictions of water recycling over tropical forests.

Introduction

Evapotranspiration (ET) is the combination of physical abiotic water evaporation (transport of water into the atmosphere from surfaces) and biotic leaf transpiration (exchange of water vapor that occurs between plants and the atmosphere) driven by an external source of energy (Katul et al. 2012). This process is one of the most important components of the global water budget since it is directly related to precipitation and land cover. Evapotranspiration from terrestrial surfaces is responsible for around 60% of the atmosphere's water moisture (Shiklomanov 1998). Within that percentage, 10% comes from vegetation (Hanson 1991), of which 30% of incoming precipitation is from temperate forests (Ohte and Tokuchi 2011) and 50% is from tropical forests (Shuttleworth 1988). Tropical forest systems are also well known carbon sinks, having among the largest gross primary productivity in the world (Clark et al. 2003, Malhi and Phillips 2005). However, tropical forests would not be as productive without an efficient precipitation recycling regime that could maintain a steady source of water, which directly affects growth and precipitation rates regionally and even globally (Baker et al. 2003). Therefore tropical forest ET comprises a large and important component of the global water cycle, much of which (around 70% in rainforests) is lost through transpiration (Schlesinger and Jasechko 2014).

Independent of total rainfall, the frequency of rain events influences vegetation growth and plant species composition in tropical forests (Baker et al. 2003). Tropical forest species range from those that require a large amount of water to supply their fast growth and high transpiration losses to those that require a smaller amount of water to sustain their slower growth (Horna et al. 2011). These differences in growth rates and water use result in the wide variation in tree diameter and height within the closed canopy structure, as is predominant in mature tropical forests. When precipitation falls on such a canopy, it creates a number of unique microclimates with wetness varying by height and tree characteristics. Vertical canopy leaf distribution directly affects sub-canopy humidity and subsequently affects evapotranspiration rates and photosynthesis within these different layers. However, in wet tropical rainforests, it is unlikely that the entire canopy will be completely dry, with some portions remaining wet for a significant fraction of daylight hours (Dietrich et al. 1982).

Wet canopy conditions may also affect plant growth and functional characteristics. Photosynthesis may be inhibited when the leaf surface is partially or completely covered with water droplets (Fogg 1947, Smith and McClean 1989, Brewer and Smith 1997, Hanba et al. 2004, Letts et al. 2010, Alvarado-Barrientos et al. 2014). Another factor to consider is the possible adaptive strategies some species might possess, such as leaf traits, i.e. trichomes and repellency (Levin 1973, Brewer and Smith 1994), and leaf angle (Fogg 1947) that may influence evapotranspiration. Such complex relationships between plant traits and atmospheric or biotic drivers present difficulties in the study of evapotranspiration, such as evaporative cooling (Katul et al. 2012).

Beyond the leaf scale, spatial arrangements of leaves within complex forest stands require the characterization of tree size and canopy position for precise transpiration rates estimation (Andrade et al. 1998, Motzer et al. 2005). Several studies have documented how large, dominant trees are responsible for a disproportionate amount of water being released back to the atmosphere (Nadezhdina et al. 2002, Horna et al. 2011). Additionally, transpiration rates can vary drastically when considering stand position, species composition, canopy architecture (branch number and angling, and leaf area) and ecological succession (Granier et al. 1996, Andrade et al. 1998, Nadezhdina et al. 2002, Horna et al. 2011, Kunert et al. 2015b). Differences between canopy strata levels and closeness to forest gaps can alter the microclimate surrounding these trees that can affect not only transpiration, but also canopy photosynthesis (Campbell and Norman 1998). The effects of tree size and canopy exposure (in terms of energy availability) on tropical stand transpiration have been accounted for in the literature. Some studies showed that tall dominant trees transpired 4 to 10 times more than understory/suppressed trees due to vapor pressure deficit and/or exposure to radiation (Granier et al. 1996, Horna et al. 2011), but the effects of leaf wetness on these tropical trees' water use has been little studied (O'Brien et al. 2004). In these frequently wet forests, dominant trees are likely to dry out more rapidly than suppressed understory trees, which could further enhance differences in gas exchange between canopy layers.

The objectives of this study were to analyze the variation of plant water uptake during different wetness conditions for three tree canopy exposure categories (dominant, midstory and suppressed) in a tropical montane forest environment under frequent rain events. This chapter relied on sap flux and micrometeorological measurements to determine if sap flux rates in three tree size groups (dominant, midstory and suppressed) were impacted by different wetness conditions (dry, “semi-dry” and wet). Then, the relative contribution of each group to stand transpiration was compared to each wetness conditions. These results are important for quantifying the contribution of a constantly moist canopy to the plant-atmosphere water balance, and consequently improving global scale land surface models for more accurate climate predictions.

Materials and Methods

Site description

The study site is located at the Texas A&M University Soltis Center for Research and Education near San Isidro de Peñas Blancas in the Alajuela Province, Costa Rica (10^{o}23’13”N - 84^{o}37’33”W). The site is approximately 600 meters above sea level and shares a border with the Children’s Eternal Rainforest, near the Monteverde-Arenal Mountain Cloud Forest Reserve (Figure 1).

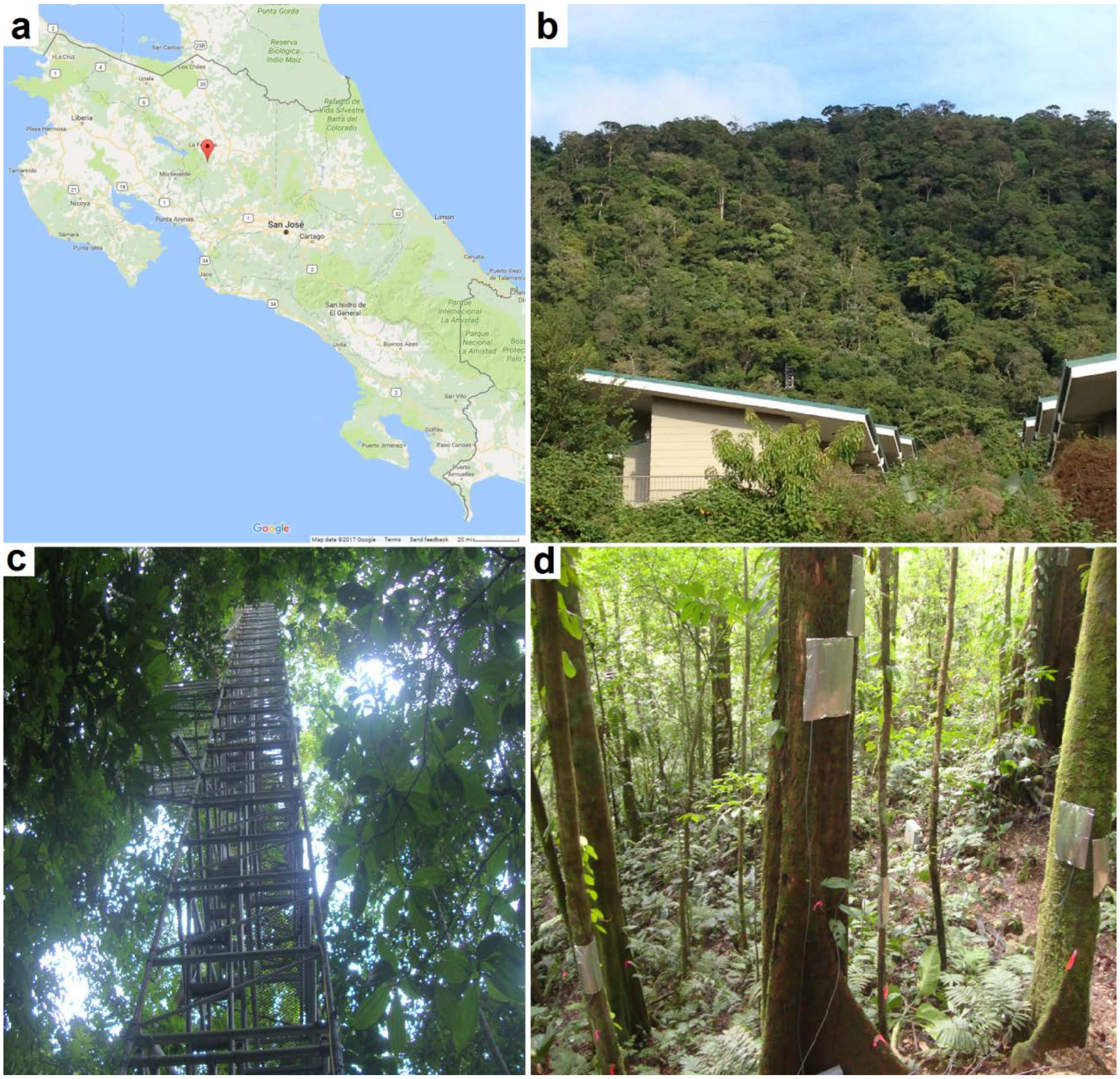

Figure 1. Study site location, characterization and instrumentation. A) Red pin represents the location of the Texas A&M Soltis Center for Research and Education in the country of Costa Rica (Map data: Google INEGI Terms (2017)); B) Landscape view of the mountain with the study site; C) 40-m micrometeorological tower located in the middle of the study plot (also seen on image B); D) Various tree individuals with different sizes equipped with sap flux sensors in the steep slope terrain of the study plot.

The study area has an average annual temperature of approximately 24°C, average relative humidity of 85%, and average annual rainfall of approximately 4200 mm. The rainy season extends from May to December (470 mm month^{-1}), with a relatively “dry” season from January to April (195 mm month^{-1}) (Teale et al. 2014). Based on the Holdridge Classification system, the vegetation is a transitional tropical premontane moist forest (Holdridge 1967). Trees at the study site range from 25-45 m in height, reaching upper canopy at around 25 m with dense foliage, multiple interlacing crowns, but with frequent canopy gaps. The most common species was *Carapa guianensis* Aubl. and the largest trees (DBH>100 cm) were mostly *Mortoniodendron anisophyllum* (Standl.) Standl. & Steyerm (Table 1).

The site hosts a 42 m tower equipped with micrometeorological instrumentation. Around the tower, a 2200 m² plot was designated, containing 151 heterogeneous tree individuals ranging from 6 to >200 cm in diameter and 6 to 40 m in height. The steep terrain is volcanic in origin and has an average slope of 45 degrees.

All trees in the plot were categorized by field observations (canopy structure and height) as dominant, midstory, or suppressed based on tree height and canopy exposure. Dominant trees were the tallest and received 80 to 100% canopy exposure to solar radiation. Subsequently, midstory trees had closer to 50% canopy exposure and suppressed had 30% or less exposure. I selected 8 dominant trees, 10 midstory trees, and 8 suppressed trees for this study.

Table 1. Individual descriptions of trees measured using sap flux probes. Notes: *Unable to retrieve xylem core samples. ** Labeled midstory since they are located under a larger, 40-m tall tree.

Species	Category	DBH (cm)	Height (m)	Basal Area (m^2)	Sapwood Area (m^2)	%	Average Max J_s (kg m^{-2} h^{-1})
Pouteria viridis (Pittier) Cronquist.	Dominant	45.2	27	0.160	0.100	62%	61.6±16.9
Mortoniodendron anisophyllum (Standl.) Standl. & Steyerm.	Dominant	200	32	3.142	1.230	39%	41.7±13.2
Aspidosperma desmanthum Benth.	Dominant	19.7	27	0.030	0.029	94%	30.2±12.9
Otoba novogranatensis Moldenke.	Dominant	80	30	0.503	0.253	50%	36.6±15.7
Otoba novogranatensis Moldenke.	Dominant	62.8	29	0.310	0.192	62%	44.5±16.7
Genipa americana L.	Dominant	46.2	28	0.168	0.102	61%	33.2±18.0
Mortoniodendron anisophyllum (Standl.) Standl. & Steyerm.	Dominant	220	38	3.801	1.478	39%	56±15.1
Pouteria sp.	Dominant	150	30	1.767	-*	-	47±18.2
Gymnanthes riparia (Schltdl.) Klotzsch	Midstory	11.6	13	0.011	0.010	93%	41.7±13.2
Meliosma idiopoda S. F. Blake	Midstory	21.2	13	0.035	0.030	86%	48.4±15.1
Carapa guianensis Aublet.	Midstory	42.6	22	0.143	0.069	48%	57.2±23.7
Inga sp.	Midstory	40.1	25	0.126	0.113	90%	70.2±25.7
Ampelocera macrocarpa Forero & A. H. Gentry	Midstory	15.6	16	0.019	0.012	65%	35.3±18.5
Carapa guianensis Aublet.	Midstory	17.3	16	0.024	0.016	69%	26.1±12.4
Brosimum alicastrum Sw.	Midstory	18.5	15	0.027	0.024	90%	32.5±14.4

Table 1. Continued.

Ampelocera macrocarpa Forero & A. H. Gentry	Midstory	32	26	0.080	0.066	82%	28.3±14.3
Macrolobium costaricense W. C. Burger	Midstory	40	30**	0.126	0.068	54%	57.8±31.7
Eschweillera sp.	Midstory	30.5	27**	0.073	0.053	73%	51.6±24.7
Meliosma idiopoda S. F. Blake	Suppressed	7.7	6	0.005	0.005	100%	25.7±9.9
Gymnanthes riparia (Schltdl.) Klotzsch	Suppressed	12.7	6	0.013	0.011	86%	33.7±16.4
Trophis mexicana (Liebm.) Bureau.	Suppressed	10	11	0.008	0.006	82%	42.1±19.4
Pleuranthodendron lindenii (Turcz.) Sleumer	Suppressed	17	10	0.023	0.019	83%	32.7±11.6
Carapa guianensis Aublet.	Suppressed	8.3	9	0.005	0.004	78%	21.9±11.5
Cupania macrophylla Mart.	Suppressed	6.9	10	0.004	0.003	82%	29.6±11.3
Gymnanthes riparia (Schltdl.) Klotzsch	Suppressed	12	10	0.011	0.010	90%	28.3±9.8
Pouteria viridis (Pittier) Cronquist.	Suppressed	11.1	11	0.010	0.009	90%	17.0±8.6

Micrometeorological measurements

Leaf wetness was estimated using dielectric leaf wetness sensors (LWS, Decagon Devices, Pullman, WA) installed at 5 heights above the ground surface (5, 11, 22, 33, and 38 m). The sensor located at 38 m was more embedded inside the forest canopy, and the sensor installed at 33 m was more exposed due to a gap in the canopy. Data were collected every 30 seconds and averaged at 5-minute intervals. Leaf wetness is output in mV; values around 100 mV indicate dry conditions, from 145 and 190 mV indicate partially wet leaves, and >200 mV indicate fully wet leaves. Therefore, a leaf wetness index for daylight hours (6 AM to 6 PM) was developed through the sum of all 5-minute values expressed on a scale from 0-100%. Days when mean index values fell below 15% wet were considered to be “dry”; between 10% and 50% was considered “semi-dry”; and above 50% as “wet”. “Semi-dry” days were further filtered to include only the days that had a dry upper canopy (sensors at 33 and 38 m average less than 10%) and wet understory (sensors at 5 m above 50%); these days had atmospheric conditions (higher δe and radiation) which dried the overstory canopy but not the understory. In total, 37 days of each category were considered in the data analysis.

Photosynthetic active radiation (PAR) (LI-190SA, LI-COR, Lincoln, NE) was measured at the same heights as the leaf wetness sensors (except at 5 m) and an additional height (27 m). Daily average and maximum PAR measured during daylight hours was averaged through the days selected for each wetness conditions to show the amount of radiation the canopy was receiving, specifically the average maximum low and high for each day of the study period within each category. PAR sensors located at

11 m were designated to represent suppressed trees; sensors between 11 and 27 m as midstory; and between 27 and 38 m as dominant. Occurrence and duration of rain events was measured in a nearby clearing using a tipping bucket rain gage (TE525WS, Texas Electronics, Dallas, Texas). Air temperature was measured using temperature probes (model 107, Campbell Scientific, Logan, UT) placed at the same levels as leaf wetness sensors and was also used to estimate vapor pressure deficit (δe) along with atmospheric and ambient pressure and water vapor concentration (Campbell and Norman 1998) from a gas profile system (AP200, Campbell Scientific, Logan, UT) (eq. 1, 2 and 3).

$$\delta e = e(T_a) - e_s \qquad \text{(eq. 1)}$$

In which, $e(T_a)$ is the saturation vapor content of air at temperature (T_a) (kPa), and e_s is actual vapor pressure (kPa). Where:

$$e(T_a) = 0.614 \cdot e^{\left(\frac{17.5 \cdot T_a}{240.9 + T_a}\right)} \qquad \text{(eq. 2)}$$

$$e_s = \frac{W \cdot P}{1000} \qquad \text{(eq. 3)}$$

in which, W is water vapor concentration (mmol mol^{-1}) measured by the AP200 and P is atmospheric pressure (kPa).

Sap flux and sapwood area measurements

Sap flux density (J_s) was measured continuously using 43 thermal dissipation sensors (Granier 1987) constructed using the method described in (Phillips et al. 1996) and installed in 26 trees during a 5 month period ranging from July 5, 2014 to November

30, 2014. This method consists of a reference and heated probe inserted in the outer 20 mm of the active xylem.

The number of sensors installed per tree differed by size. Trees less than 20 cm in diameter received one sensor (14 individuals); between 21-80 cm, two sensors (8 individuals); above 80 cm, three sensors (3 individuals) or four sensors (1 individual). The first sensor was placed perpendicular to the slope, roughly facing the north, with the others (if any) spaced evenly around the tree. The sensors were installed at a height of 1.5 m height, or as low as possible above tall buttresses, up to 7 m. Data were collected every 30 seconds and later averaged over 10-minute intervals and stored on a datalogger (CR1000, Campbell Scientific Inc., Logan, UT). Temperature differences between the reference and heated probe were converted into J_s (kg m^{-2} s^{-1}) based on Granier (1987) empirical calibration equation (eq. 4):

$$J_s = 0.119 \cdot \left(\frac{\Delta T_M - \Delta T}{\Delta T}\right)^{1.231} = 0.119 \cdot K^{1.231} \qquad \text{(eq. 4)}$$

Where ΔT_M is the maximum temperature difference when sap flux is assumed to be zero, and ΔT is the actual temperature difference. Herein, J_s is expressed as hourly (kg m^{-2} h^{-1}) and daily (kg m^{-2} day^{-1}) totals, where daily total sap flux density was the sum of all J_s in a 24-h period. Nighttime data fluctuations were small, but more erratic on wet, rainy days likely because of weak lower limit of temperature detection (Burgess et al. 2001) or temporarily elevated nighttime vapor pressure deficit (Rosado et al. 2012). However, vapor pressure deficit was confirmed to reach zero every day.

Active sapwood area was determined for all trees with sap flux sensors using safranin-fucsin dye injections on fresh tree cores (Vertessy et al. 1995, McDowell et al.

2002, Gebauer et al. 2008). Sapwood area ranged from 0.003 to 1.47 m^2, equivalent to ~80% of active xylem for an average cross-section. An exponential model was developed to predict sapwood area for the rest of the plot trees from basal area ($A_s=0.4713\cdot A^{0.8493}$; $r^2=0.992$, where A_s is sapwood area and A is basal area, both in m^2) (Figure 2). All trees had a sapwood radius greater than the sensor depth (>20mm) (Clearwater et al. 1999). Sapwood area was used to estimate stand transpiration following the methodology used by (Moore et al., 2004) with separate size categories for dominant trees (n=20 sensors on 8 trees), midstory trees (n=15 sensors on 10 trees), and suppressed trees (n=8 sensors on 8 trees), but also including 125 additional trees in the plot without sap flux sensors assigned to each size category. The average daily total of sap flux density (J_s) for dominant, midstory, and suppressed trees was multiplied by the ratio of total sapwood area to total plot area for each size category and summed to estimate stand transpiration (eq. 5) (Moore et al. 2004, Horna et al. 2011).

$$E_t = \sum \bar{J}_s \cdot \left(\frac{A_s}{A_g}\right) \qquad \text{(eq. 5)}$$

Where, E_t is strand transpiration (mm day^{-1}), A_s is sapwood area (m^2) and A_g is ground-plot area (m^2).

While others have shown that J_s can vary with depth in the sapwood (James et al. 2002, Poyatos et al. 2007, Zhang et al. 2015), J_s was not measured at depths beyond 20 mm in the sampled trees because an independent analysis of radial profiles in a subset of nearby trees did not show consistent declines in J_s trends with depth. In this case, there was consideration that any potential errors in scaling J_s to stand transpiration were minor

(~15%, e.g., Miller et al. 2013), as the estimates were within the range observed by others in similar forests (Bruijnzeel and Veneklaas 1998). To corroborate this assumption, a transpiration correction equation for angiosperms developed by Pataki et al. (2011) was applied and compared to the current database to the resulting corrected database. However, this correction was found to cause gross biases in the tree size comparison and was not applied.

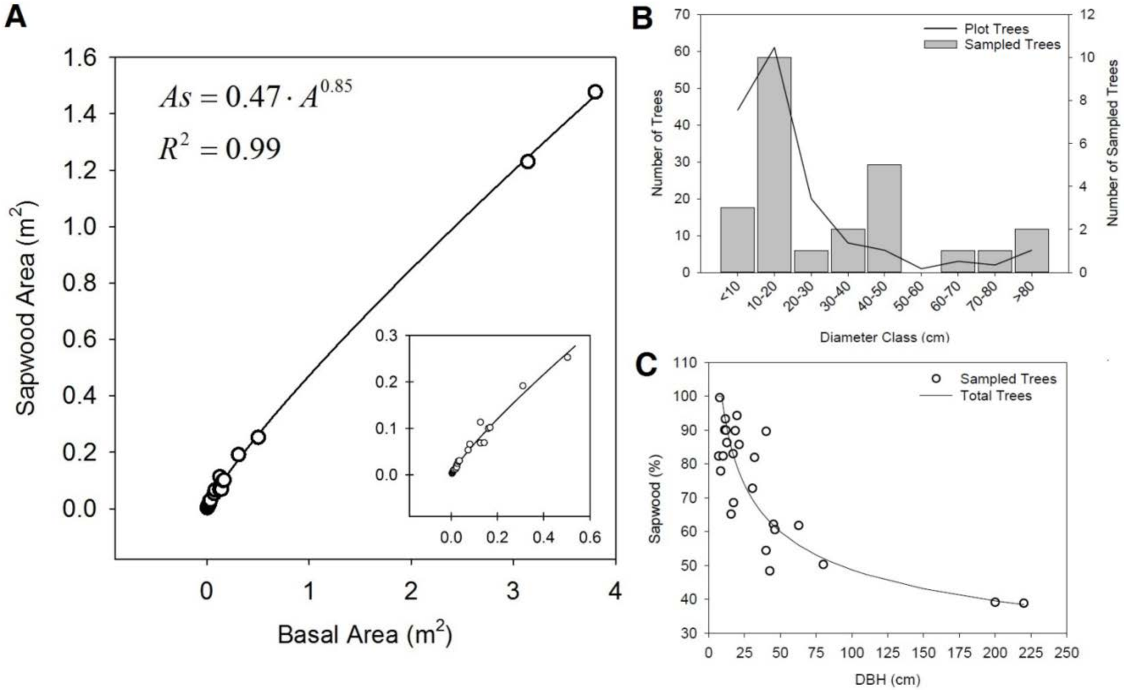

Figure 2. (A) Allometric relationship between sapwood area (*As*) and basal area (*A*). Inset graph highlights clustered data points, which correspond to tree individuals with basal area < 1 m^2. (B) Diametric distribution classes for total plot (n=151) and total sampled trees (n=26); (C) Sapwood area percentage as a function of diameter at breast height (DBH) for all sampled trees.

Statistical analyses

Analysis of Variance (ANOVA) was used to test for differences (p-values, α=0.05 and 0.001) between tree size categories and wetness conditions; followed by the Tukey HSD multi-comparison post-hoc test. Generalized least squares (simple and multiple regressions) models were also fitted. Additional analyses included stepwise multiple linear regression and Pearson correlation to evaluate relationship between sap flux rates and micrometeorological variables (leaf wetness index, δe, PAR and air temperature) under different wetness conditions. The response variable was daily total sap flux (J_s) and the independent variables were leaf wetness index, δe and PAR. Regression models were evaluated based on goodness of fit determined from the highest significant R^2-values and entailed sequential (forwards) addition of independent variables in the order PAR, δe, leaf wetness index plus interaction terms using a manual procedure. Relationships within canopy strata were also assessed. Final multiple regression models were selected using a sequential F-test procedure (Ott and Longnecker 2010). In this test, for each variable not already included in the model, an F-statistic (α=0.05) was calculated and the final model was selected from all possible models. Statistical analyses were performed with R version 2.6.2 software (R Core Team 2013).

Results

Micrometeorological drivers

A total of 2573 mm rainf fell over the five month study period. The month of July was the wettest, with a total of 900 mm of rain, and August was the driest with 341 mm. August had 42% more water uptake than July, which resulted in higher daily J_s rates overall and for all tree size categories. PAR was likewise highest during August. Diurnal average PAR was 108 ± 36 μmol m^{-2} s^{-1} over all days in the month of August, and the peak hour of the day that month averaged 445 ± 226 μmol m^{-2} s^{-1} at a height of 33 m. Air temperature measured at 33 m averaged 22 ^{o}C and varied by less than 1 ^{o}C between months and vertically within the canopy (Figure 3). Tower heights of 38 and 33 m correspond with the dominant zone, 27 and 22 m corresponds with the midstory zone, and 11 m corresponds with the suppressed zone. PAR differed by an order of magnitude between canopy heights and peaked at 33 m because the sensor at 38 m was partially obscured by a tree branch (Figure 3), but it also greatly differed throughout the day due to intermittent cloud coverage. Cloud free days were rarely observed throughout the study period (around 3 days), but during those conditions PAR would reach as much as 1500 μmol m^{-2} s^{-1} for short periods of time.

Mean daily temperatures were highest at 6 m, at the level of suppressed tree canopies, but only differed by 1^{o}C throughout the canopy. Leaf wetness followed the same profile pattern as air temperature (Figure 3), but contrasted greatly between levels. Between the most exposed (at 33 m) and the least exposed (at 5 m) sensors, leaf wetness ranged from 25% to 80%, respectively. This implies that since there is not much air temperature variation throughout levels and decreasing gradients of PAR and leaf wetness, less energy is available to dry the leaves of lower level trees.

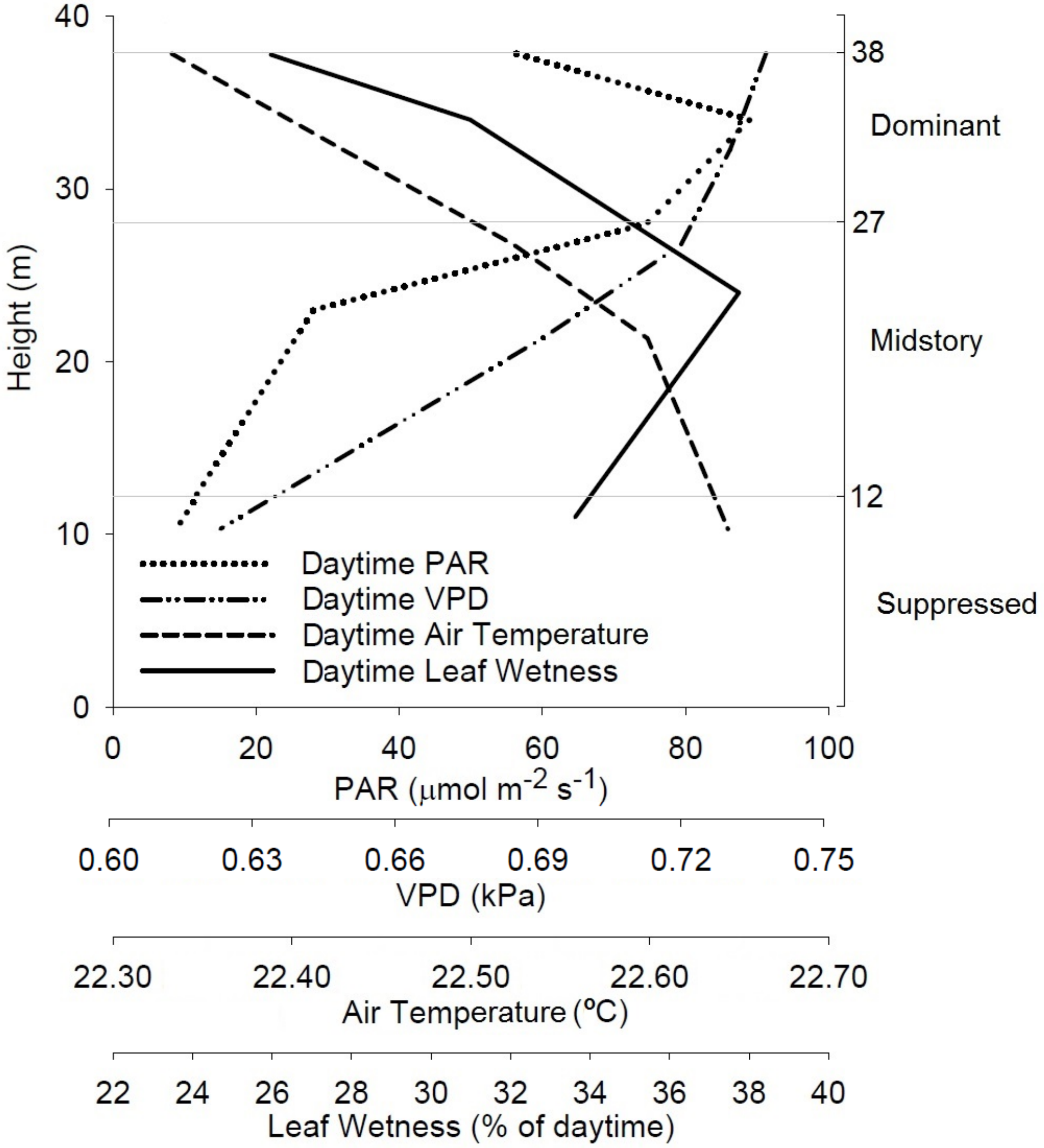

Figure 3. Height profiles of average daytime air temperature (^{o}C), leaf wetness (% of daytime), VPD (kPa) and PAR (µmol m^{-2} s^{-1}) for the study period. Canopy height classifications are noted.

On dry and semi-dry days, J_s was negatively correlated with leaf wetness ($r=-0.42$), which was also associated with low PAR and δe (Figure 4). PAR was 38% and 73% lower on semi-dry and wet days, respectively, when compared to dry days. Across the three wetness conditions, J_s increased at a similar rate as PAR increased ($r^2=0.31$); however, J_s was consistently lower for the same level of PAR if leaves were wet (43% less; $r=0.13$) or semi-dry (30% less; $r=0.40$). Lower δe and higher leaf wetness both contributed to this. δe was an important covariate with wetness condition ($r^2=0.45$). Regression analyses show that the effects of δe and PAR on J_s were dependent on leaf wetness condition. An additional 6% of variation in J_s was explained by leaf wetness after accounting for the effects of δe and PAR ($P<0.05$). When leaf wetness was 50%, J_s decreased by 10% under average δe and PAR conditions; and when leaves were completely wet (100%), J_s decreased by as much as 28%. Due to large range in PAR conditions observed throughout the day, PAR had little to no influence on sap flux rates when leaves were wet ($r=0.13^{ns}$) or dry ($r=0.29^{ns}$), and some influence during semi-dry days ($r=0.40$, $P<0.05$). The above correlations were further broken down by canopy level (Figure 4b-d), which similarly indicated differences with wetness condition, especially in dominant and midstory trees.

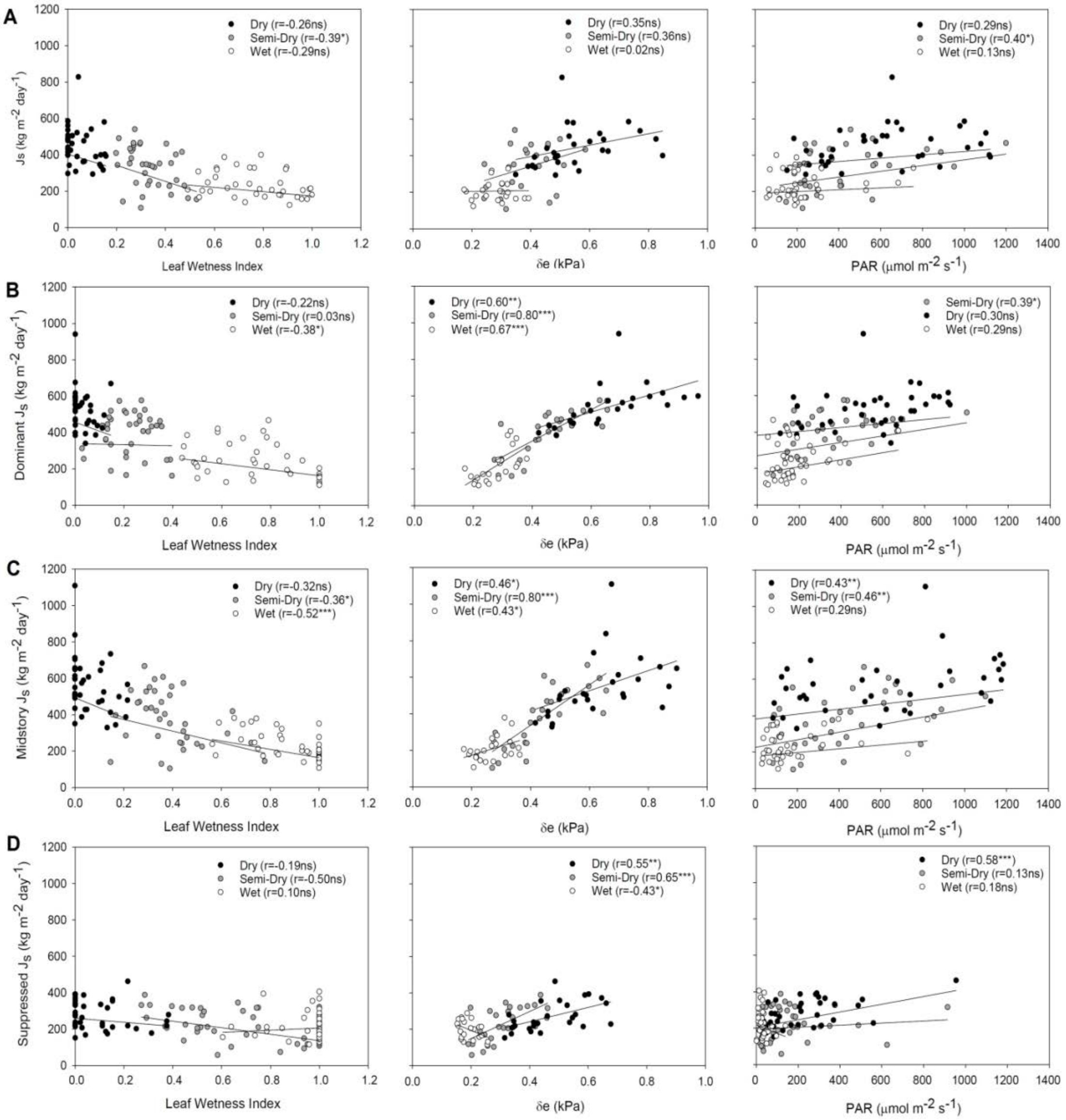

Figure 4. Total daily sap flux related to micrometeorological variables (daily leaf wetness index at 33 m of height, daily average vapour pressure deficit (δe - kPa) and daily maximum photosynthetically active radiation (PAR - μmol m^{-2} s^{-1}), respectively from left to right) under different wetness conditions and canopy levels, as indicated by Pearson correlation coefficient (α=0.05) and regression lines. (A) Average canopy conditions. (B) Dominant canopy conditions. (C) Midstory canopy conditions. (D) Suppressed canopy conditions. Notes: significance levels labeled with *** $P<0.001$; ** $P<0.01$; *$P<0.05$; and ns = non-significant ($P>0.05$).

Sap flux rates by category and wetness conditions

In general, J_s was highest in canopy trees and lowest in suppressed trees, but the relative differences between groups were not consistent as wetness condition changed (Figure 5). Peak J_s of canopy and midstory trees were similar on dry days (47.6 ± 11.4 and 48.6 ± 1.5 kg m^{-2} h^{-1}, respectively), but on semi-dry days, midstory trees had slightly lower J_s rates than overstory trees. Between dry and semi-dry conditions, J_s daily total was reduced enough to be considered as different for both size categories ($P<0.001$). As expected, whether wet or not, suppressed trees had lower J_s than overstory or midstory trees and were much more variable.

On dry days, suppressed tree J_s was practically half that of dominant and midstory trees ($P<0.001$) and peaked later in the day, 12:30 PM as opposed to 12:00 PM for the other groups, with maximum daily values of 56.8 ± 13.6 kg m^{-2} h^{-1}, 58.7 ± 1.8 kg m^{-2} h^{-1} and 28.9 ± 13.9 kg m^{-2} h^{-1} for dominant, midstory and suppressed, respectively (Figure 5). Average total daily values for J_s on dry days was 498 ± 98, 493 ± 127, and 290 ± 75 kg m^{-2} day^{-1} in the three groups, respectively (Figure 6). PAR at dominant and midstory level peaked around 10 AM, while suppressed trees peaked at 11 AM; δe peaked at 1:30 PM for dominant and midstory levels, later than maximum J_s, and at noon for suppressed, with similar intensities between midstory and dominant.

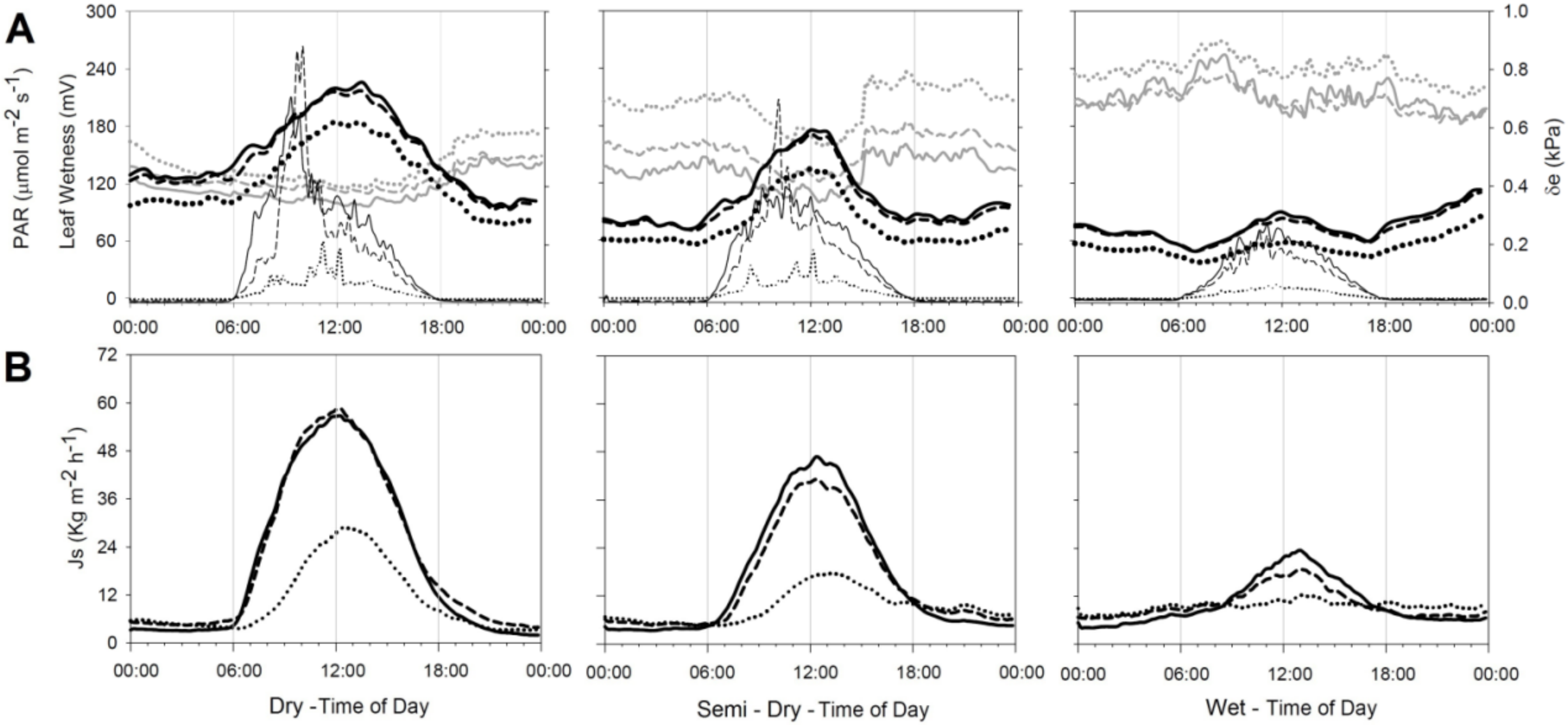

Figure 5. Diurnal average sap flux curves (*Js*) for each tree category (dominant, midstory and suppressed) at each wetness condition (from left to right: dry, semi-dry and wet, respectively) and respective diurnal micrometeorological condition. (A) Micrometeorological variables: vapor pressure deficit (δe) – thick black lines; leaf wetness (mV) – thick gray lines; photosynthetically active radiation (PAR) – thin black lines. (B) Dominant – solid line; midstory: dashed line; suppressed: dotted line (same patterns for figures A).

When compared to dry days, J_s on “semi-dry” days proportionally decreased by only 24%, 27% and 18% in canopy, midstory, and suppressed trees, with the later reducing less because suppressed trees had low rates even on dry days (Figure 6). On “semi-dry” days, dominant trees had a slight advantage over midstory trees of 6% (or 18 kg m^{-2} day^{-1}), with 14% greater peak of J_s; however, tree-to-tree variability was too high for the difference to be significant (*ns*). Suppressed trees again peaked later in the day (1:00 PM), while dominant and midstory peaked both at 12:20 PM. Suppressed trees’ daily maximum J_s were 59% lower than dominant trees and 53% lower than midstory trees ($P<0.001$). Because suppressed trees remain wet more frequently across all wetness conditions, their J_s differed the least. On semi-dry days, with less intensity, PAR peaked at the same time for dominant and midstory as dry days, but was at noon for suppressed; while δe peaked at noon for all three levels, slightly before maximum J_s. On these days, leaf wetness was lower at the top of the canopy and increased at the understory level, but with a distinct drop around midday. PAR and δe were not the only factors influencing these trends. Maximum daily PAR for dominant trees averaged 20% and 44% less than for midstory trees on dry and “semi-dry” days, respectively, due to gap in the middle section of the canopy. Likewise, δe for dominant trees averaged 3% and 2% higher than for midstory trees on dry and “semi-dry” days, respectively.

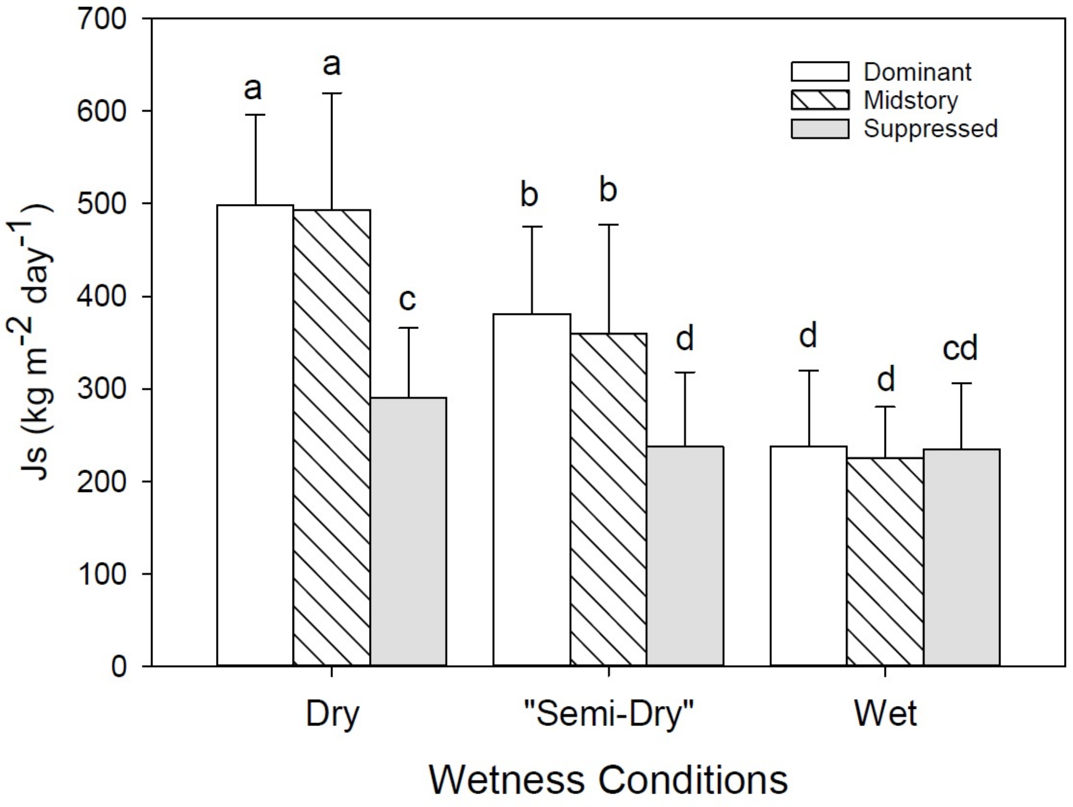

Figure 6. Comparison of total sap flux per day (kg m^{-2} day $^{-1}$) for each wetness conditions (dry, semi-dry and wet) and for each tree category (dominant, midstory and suppressed). Tukey HSD denoted with letters and standard error bars indicate categories with significance differences, as indicated by ANOVA (P<0.05).

On wet days, all the size categories had reduced J_s (Figure 6), signified by uniform wetness through the entire canopy and uniformly low δ*e* throughout the day, with lower values at the understory level. Daily total J_s had a 45% reduction on wet days, when compared to dry days. PAR was reduced to values below 70 µmol m^{-2} s^{-1}. Peak J_s occurred at 1:00 PM for all the categories, while peak δ*e* was before maximum J_s at noon for dominant and midstory, and 12:30 PM for suppressed (Figure 5). These values did not differ from each other (P<0.001), even though dominant trees presented the highest J_s values. Although all of the size categories had significant decrease in sap flux rates and had a delayed peak, suppressed trees differed the least between wetness conditions, with only 2% difference (*ns*) in daily total J_s between wet and semi-dry conditions. Dominant trees uptake was greater by 38% and 52% on wet days when compared to “semi-dry” and dry days, respectively. Midstory trees reduced J_s by 38% and 55%, respectively.

Transpiration rates by category and wetness conditions

Daily stand transpiration rates for the entire period of study averaged 1.38 ± 0.53 mm day^{-1} and average transpiration of 41.4 mm month^{-1} (497 mm year^{-1}). Dominant trees, independent of wetness conditions, accounted for around 76% of total stand transpiration from only 13% of the plot’s trees, which represent 76% of the stand’s active sapwood area. Midstory trees contributed approximately 19% of stand transpiration from 38% of the plot’s trees and 18% of active sapwood; and suppressed accounted for only 5%, from 48% of trees with 6% of sapwood area (Figure 7a & 7b).

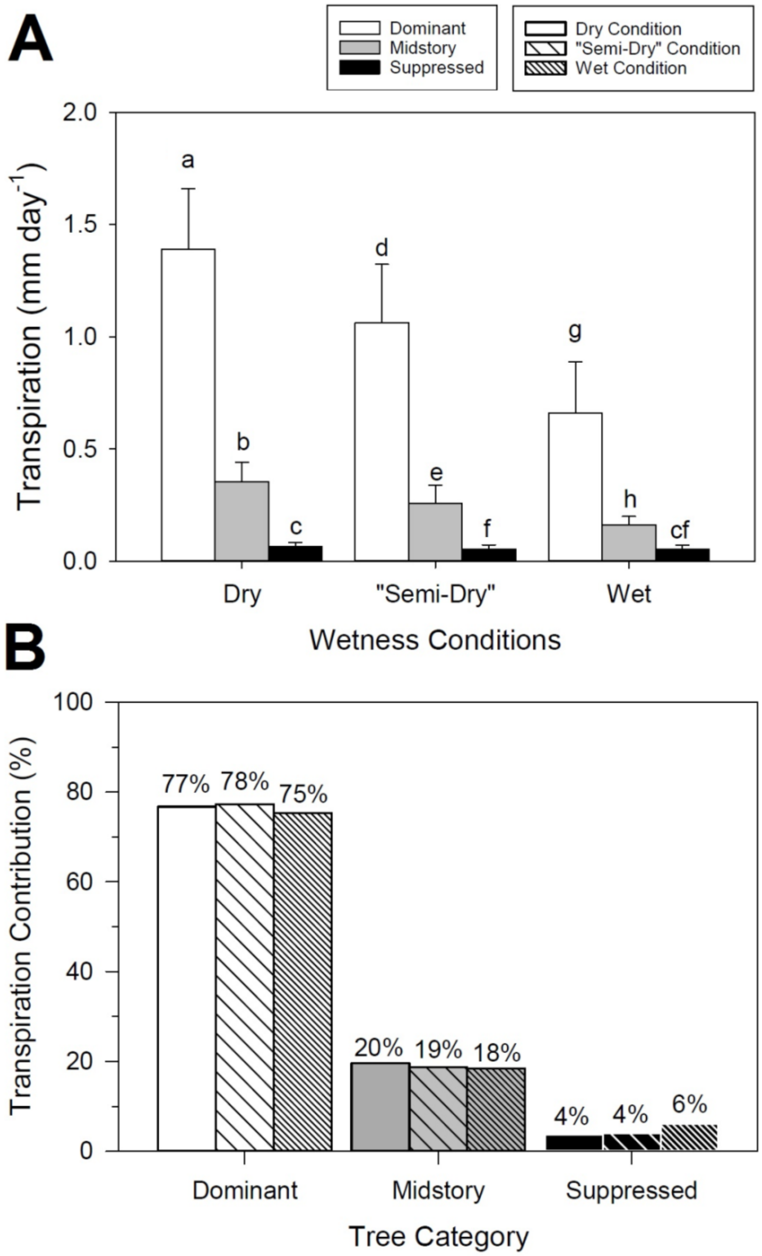

Figure 7. Stand transpiration partitioned per period and percentage transpired from each tree category. (A) Comparison of total transpiration per day (mm day^{-1}) for each wetness conditions (dry, semi-dry and wet) and for each tree category (dominant, midstory and suppressed). Tukey HSD letters with standard error bars indicate categories with significance differences, as indicated by ANOVA (P<0.05). (B) Stand transpiration contribution (%) from each tree category under different wetness conditions.

Wet conditions were associated with a 52% decrease of daily total transpiration, when compared to dry days. Semi-dry conditions reduced stand transpiration of dominant trees by 24% ($P<0.001$) compared with a 52% reduction with wet conditions ($P<0.001$). Midstory trees responded similarly by reducing stand transpiration by 27% ($P<0.001$) when semi-dry and 54% when wet ($P<0.001$). However, suppressed tree transpiration only differed between dry and semi-dry conditions ($P<0.05$), but overall differed very little ($P<0.05$) between all wetness conditions, resulting in an average rate of 0.05 mm day $^{-1}$ for all conditions.

Discussion

At this frequently wet tropical rainforest site, while PAR and δe were major drivers of transpiration variation between wet and dry days, the added effect of leaf wetness appeared to further reduce transpiration. Further, the effect of leaf wetness on J_s differed between exposed trees in the upper canopy and less-exposed trees in the understory. This implies that δe and/or PAR were coupled with other environmental variables, like leaf wetness, to significantly influence water uptake. O’Brien et al. (2004) , when studying environmental variables that influence tree transpiration in another Costa Rican site, found strong negative correlations with sap flux rate and leaf wetness (-0.62) or relative humidity (-0.96); while, δe (0.96), irradiance (0.84), air temperature (0.90) and wind speed (0.72) were all strongly positive correlated. However, they did not control for the interacting effects between these drivers. Moreover, I assessed whether leaf wetness condition affects the relative contribution of dominant, midstory, and suppressed trees under varying conditions typical of tropical forests. Surprisingly, while the proportion of J_s was affected by wetness condition, the relative proportion of each group to total stand T remained constant (Figures 6 and 7).

Although wet leaf conditions significantly reduced dominant and midstory water uptake, semi-dry conditions did not reduce J_s as much as we expected. This illustrates that transpiration does not respond proportionally to canopy wetness. Models with simple linear reductions in transpiration with leaf wetness on days with less intense rainfall events, in which upper canopies dry faster, would drastically underestimate evapotranspiration and tree growth. Maintaining dry conditions in the upper canopy is significant for precipitation recycling in the tropics. Because these forests remain wet for prolonged periods after precipitation events, effects were long-lasting. At their Indonesian rainforest site, Horna et al. (2011) found that sap flux rates were lower for as long as 16-22 hours after a rainfall event when air humidity was higher than usual and when leaf wetness affected 44-55% of the canopy. They concluded that transpiration estimations were lower than expected for all the tree height categories due to these wetness conditions.

Suppressed trees assimilated less water, as expected, since they receive much lower levels of PAR, which results in slower rates of leaf drying (Kume et al. 2006) and less energy to photosynthesize. Brewer and Smith (1997) highlight how forest growth is driven by microclimate variation that can result in very patchy wetness conditions, especially within canopy strata, since the most shaded level is less affected by radiation and wind turbulence than upper levels. Therefore, trees classified as suppressed would probably grow faster if they were less wet or dried more rapidly, e.g. near natural forest clearings (Kunert et al. 2015b).

From the results, it can be inferred that water droplets on leaf surfaces are an important physical factor limiting water uptake after accounting for the primary drivers δe and PAR. Another is the establishment of epiphytic organisms on foliage that act like trichomes, which are hair-like leaf appendages that extend across the epidermis' surface (Levin 1973), by creating a barrier between the leaf surface and water droplets (Dietz et al. 2007). Considering the microclimate in which suppressed trees are growing (constant high humidity and low solar radiation), they are highly susceptible to harboring these organisms, as observed in the leaves of the study site. A layer of water over the leaves can potentially inhibit photosynthesis, as has been reported previously (Fogg 1947, Smith and McClean 1989, Brewer and Smith 1997, Hanba et al. 2004, Letts et al. 2010, Alvarado-Barrientos et al. 2014). On the other hand, tropical species may actually be adapted to optimize function under low PAR intensities (<1000 µmol m^{-2} s^{-1}) and saturated δe (<0.7 kPa) given frequent wet and foggy conditions (Gotsch et al. 2014), or by optimizing physiological processes during short dry periods. Additional adaptations to wet environments have been reported, such as rapid leaf drying (O'Brien et al. 2004) or the ability to maintain photosynthesis when wet (Smith and McClean 1989). This effect may be driven by sensitivities to leaf temperatures. According to Katul et al. (2012), there is a cooling effect minutes after rainfall whereby the humidity and leaf temperatures become ideal for optimum tree physiological functioning. Therefore, on semi-dry days, trees in transitional tropical premontane moist forests may actually become more efficient water users right after rain, dew, or/and fog events during the dry-down phase. Since there was no evidence of midday stomatal suppression with semi-dry conditions, the trees showed a more pronounced decreasing hierarchical pattern (dominant, midstory, and then suppressed) than during dry days (Figure 6).

The response to leaf wetness may also vary due to species leaf anatomy. Tree species that occur in locations in which dewfall, rainfall, and fog are extremely frequent have strategies to repel water on their leaves. Smith and McClean (1989) show that habitat and microclimate is also a factor to be considered as environments under dense fogs and dewfall frequently host specialized species with leaf features that reduce the effect of long duration of leaf wetness. These adaptations are evidence that these trees have developed strategies to be as productive as possible under such normally suppressing conditions. Studies show that trees from wet montane forested environments can develop features like foliar water uptake, and leaf repellency and/or presence of trichomes that can reduce the area exposed to water beads to prevent photosynthesis and water uptake suppression (Smith and McClean 1989, Brewer and Smith 1994, Ishibashi and Terashima 1995, Brewer and Smith 1997, Holder 2007, Gotsch et al. 2014). Although leaf anatomy was not analyzed for this study, the trees in the site show evidence that they are specialized to endure prolonged wetness characteristic to this region, like possessing ovate and lanceolate shapes that can facilitate water drainage during a rain event.

The amount of transpiration estimated in this study, although low, is consistent to other findings in literature for other vegetation types, especially in tropical montane cloud forests that are known to have transpiration around 250-300 mm year^{-1} (Bruijnzeel and Veneklaas 1998). The daily rates also were similar to previously reported values in tropical forests (Bruijnzeel et al. 2011, Horna et al. 2011, Alvarado-Barrientos et al. 2014, Kunert et al. 2015b). The Pataki et al. (2011) correction, which was developed for a range of temperate angiosperms, was investigated and deemed inappropriate for this study. Applying the correction across all trees and dates severely dampened the extreme rates that occurred on drier and wetter days (Figure 8). This decision was further corroborated by an independent analyses (Miller et al. 2013). However, future work is needed to develop robust estimates of radial profiles in tropical forests, given the unique microclimate conditions and high diversity in these ecosystems. As others have indicated, tropical species show major sapwood area inconsistencies due to different sizes, species, individual traits (e.g. age and susceptibility to cavitation and/or tyloses) and microclimate (e.g. seasonal and diurnal vapor pressure deficit variations) as observed in the site (Jimenez et al. 2000, Meinzer et al. 2001, James et al. 2003, Ford et al. 2004a, Ford et al. 2004b).

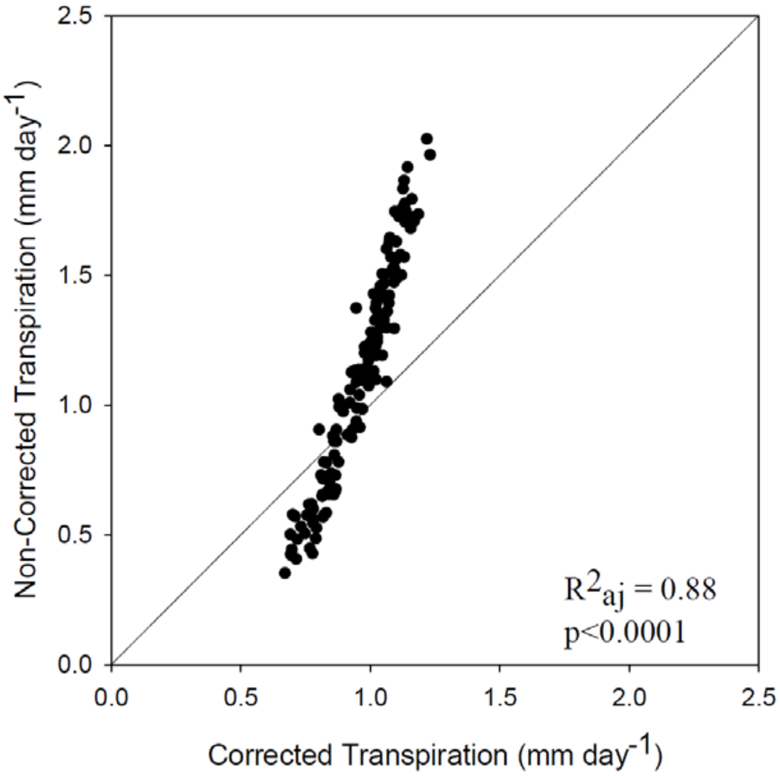

Figure 8. Cross-validation between corrected (proposed by Pataki et al. 2011) and non-corrected (following Granier et al. (1987) calibration) transpiration values.

Not only were rates of transpiration impacted by wetness, but the relative proportion of exposed trees in the stand disproportionately influenced stand transpiration. Dominant trees comprised the greatest total sapwood in the stand and largest water use per unit sapwood than the midstory on semi-dry days. The strong relationship between sapwood and basal area or diameter at breast height has been widely studied (Wullscheleger et al. 1998, West et al. 1999, Meinzer et al. 2001, Lundblad and Lindroth 2002, Nadezhdina et al. 2002, Meinzer et al. 2005). In the study, total sapwood area had a strong influence on the relative contribution of each size category to total stand transpiration.

Total sapwood area varied among groups, which strongly impacted stand transpiration estimates. Even though dominant trees amounted to only 13% of the plot's trees, they contributed an estimated 76% to stand transpiration. Sapwood area of dominant trees averaged approximately 56% of the cross-sectional area, while the average for the stand was 87%. However, it is important to note that this percentage is over cross-sections that can reach ~3 m^2 per tree compared with only ~0.004 m^2 for a typical suppressed tree. This underscores the importance of using a representative sampling method based on the size distribution appropriate for the forest type (Andrade et al. 2005, Kunert et al. 2015a).

Conclusions

The findings confirm the distinctive influence of leaf surface wetness on plant water uptake, even for trees adapted for very wet environments. It is reasonable to assume that these trees are adapted to take advantage of the short-term leaf dryness that occurs between frequent rain events, in order to perform adequately photosynthesis. Tree size also has a crucial role in plant and atmosphere interactions in rainforests, as a minority of large trees are responsible for most of the transpiration. Not only does canopy exposure (not necessarily tree height) directly affect transpiration rates, but the ratio of sapwood area to basal area is also a key factor to consider when quantifying how much water is used by an individual tropical tree versus a stand of tropical trees. This suggests that harvesting of large dominant trees could cause a large hydrological disequilibrium to an ecosystem.

Future studies should address how neglecting leaf wetness and its apportionment within the canopy can affect the accuracy of climate modeling, particularly in regions in which precipitation recycling is high. Global circulation models need to more accurately predict latent and sensible heat (Akkermans et al. 2002), interception, evapotranspiration (Amthor et al. 2001, Hobbins et al. 2001, Akkermans et al. 2002, Davies-Barnard et al. 2014), precipitation amount (Lloyd et al. 1988, Martins et al. 2015) and duration (Lorenz et al. 2014), and even forest greenness and coverage estimations (Bonan and Levis 2006), all of which are affected by canopy wetness. This study suggests that improvements in evapotranspiration parametrizations may be needed for more accurate atmosphere-land models, particularly for predictions under varying climate scenarios where rainfall frequency is altered.

CHAPTER III

PHOTOSYNTHETIC RESPONSES TO LEAF SURFACE WETNESS IN TROPICAL AND SEMIARID SAVANNA PLANTS WITH VARYING LEAF TRAITS

Overview

While it is reasonable to predict that photosynthetic rates are inhibited while leaves are wet, leaf gas exchange measurements during wet conditions are challenging to obtain due to equipment limitations and complexity of canopy-atmosphere interactions in forested environments. Thus, the objective of this study was to evaluate responses of seven tropical and three semiarid savanna plant species to simulated leaf wetness and test the hypotheses that (1) leaf wetness reduces photosynthetic rates (A_{net}), (2) leaf traits explain different responses among species, and (3) leaves from wet environments are better adapted for wet leaf conditions than those from drier environments. The two sites were a tropical rainforest in northern Costa Rica with ~4200 mm annual rainfall and a savanna in central Texas with ~1100 mm. Gas exchange measurements were collected under dry and wet conditions on five sun-exposed leaf replicates from each species. Additional measurements included leaf wetness duration and stomata density. Measurements showed that A_{net} responses varied greatly among species, but all plants maintained a baseline of activity under wet leaf conditions, suggesting that abaxial leaf A_{net} was a significant percentage of total leaf A_{net} for amphistomatous species. Among tropical species, A_{net} responses immediately after wetting ranged from -31% (*Senna alata*) to +21% (*Zamia skinneri*), while all savanna species declined (up to -48%). After

10 minutes, savanna species, *Quercus macrocarpa* and *Quercus stellata*, showed a 14% increase and 13% decrease, respectively. Leaf wetness duration and stomata density also contrasted greatly between species and partially explained differences in A_{net}. This variability between species suggests that leaf traits may be critical for optimizing photosynthesis under wet conditions. A better understanding of leaf wetness inhibiting photosynthesis is vital for accurate modeling of growth in forested environments; however, species adapted for wet environments may possess compensatory traits that mitigate for these effects.

Introduction

Leaf wetness consists of water droplets or film that settles on the leaf surface and temporarily occludes stomata until it evaporates or drains (Ishibashi and Terashima 1995, Pandey and Nagar 2003). Most studies consider the susceptibility of wet surfaces to pathogen invasion (Hirano and Upper 2000, Jackson et al. 2006) and the proliferation of algae, moss and other biofilms (Coley et al. 1993) or determine how irrigation affects crop yield (Cavero et al. 2009, Urrego-Pereira et al. 2013). Other studies focus on how foliar application of pesticides can affect photosynthesis (Kramer and Kozlowski 1960). Several of the above-mentioned studies are based on the assumption that when water covers open stomata, photosynthesis is reduced, since carbon dioxide diffusion in water is extremely low when compared to diffusion in air (1:10,000) (Fogg 1947, Smith and McClean 1989). Although this diffusion limitation is known, some researchers argue that most plants species are hypostomatous, thus gas exchange would be less affected (Dietz et al. 2007, Letts et al. 2010) or that leaf wetness resultant from fog or dewfall are considered physiologically insignificant (Monteith 1963).

However in wet environments, leaf wetness could have a measurable impact on photosynthesis, since water being intercepted by the forest canopy can range from 20 to 80% of precipitation in the tropics (Sollins and Drewry 1970, Loescher et al. 2005, Teale et al. 2014). In some tropical montane environments, other hydrological phenomena, like dewfall and fog are also significant (Bruijnzeel and Veneklaas 1998, Gotsch et al. 2014). Given that tropical forest ecosystems can have mean annual precipitation from 2,000-5,000 mm, with peaks of up to 10,000 mm year^{-1} (Juo and Franzluebbers 2003, Holzman 2008), and that rainfall can occur daily and last throughout continuous days, the potential physiological impact of leaf wetness cannot be ignored.

Although a decrease in A_{net} due to leaf wetness has been reported in some studies (Brewer and Smith 1995, Ishibashi and Terashima 1995, Letts and Mulligan 2005, Reinhardt and Smith 2008), an increase in photosynthetic activity has been reported in others. Smith and McClean (1989) found that 60% of the studied species formed water beads that enhanced stomatal opening and photosynthetic rates by 34%. Urrego-Pereira et al. (2013) associated higher leaf hydrophobicity with higher A_{net} in irrigated alfalfa crops. Similarly, Hanba et al. (2004) observed that hydrophobic pea leaves had a 22% increase in photosynthetic rates after 72 h of artificial misting, which they attributed to a 12.5% increase in stomatal conductance (improved stomatal regulation). The optimum conditions created by wetness (cooler temperatures, high humidity) combined with favorable leaf anatomy traits are assumed to be the key elements for the species that increased photosynthesis.

Structurally and biologically diverse tropical rainforests, with a mixture of distinct and unique traits within plant functional groups, are likely to possess specialized adaptations for wet leaves. Adaptations to promote water shedding may include trichome coverage, surface roughness, and repellency features like cuticular wax (Kaul 1976, Rosado and Holder 2013). These adaptations help to mitigate or prevent the effects of water on stomata and enable photosynthesis during and after rain, fog, or dewfall events (Holder 2007). Along with degree of leaf surface wettability, leaf arrangements within the canopy will dictate leaf wetness duration and its resulting photosynthetic suppression.

While tropical forests have the most frequent leaf wetness due to pronounced rainfall regimes, semiarid or water deficient environments may require fewer adaptations to cope with sporadic rain events interspersed by prolonged dry periods. On the other hand, semiarid plants experience frequent dew formations on plant surfaces (Monteith 1963), which can actually become an alternative water source through foliar uptake in some adapted species (Breshears et al. 2008, Limm et al. 2009), or can improve leaf and soil water content, consequently enhancing photosynthetic conditions (Zhuang and Ratcliffe 2012). Species from the *Quercus* genus that occur in semiarid regions are characterized as possessing trichomes (diverse in types, patterns, and amount) on the bottom surface (Hardin 1979, Stein et al. 2003) to avoid damage caused by high radiation intensity and to help regulate leaf temperature and prevent dehydration on hot, dry days (Fernandez et al. 2014). However, they also feature a highly water-repellent abaxial surface, and some species even display foliar water uptake from the upper surface (Oliveira et al. 2005, Breshears et al. 2008, Fernandez et al. 2014, Yan et al. 2015).

Although these leaf traits are scientifically well-known and characterized extensively in the literature (e.g., Fernandez et al. (2014)), their implications on physiological processes have not been well described, especially for *Quercus* species. Despite being relevant in various research fields (botany, atmospheric sciences, etc.) and across a global range of locations (Ishibashi and Terashima 1995), leaf wetness experiments are logistically challenging, especially since conducting measurements on rainy days or using high moisture levels can lead to equipment damage.

To study the effects of leaf wetness on rates of photosynthesis across a wide range of plant species, leaf level gas exchange measurements were performed under a controlled wetness gradient. Ten species were selected based on differences in leaf characteristics and growth habits. Species were further described in terms of their leaf water retention, stomatal features, temperature response, and light response. The study aimed to: (1) evaluate tropical and semiarid savanna species responses to simulated leaf wetness and test the hypothesis that leaf wetness reduces rates of photosynthesis (A_{net}); (2) identify leaf traits that affect leaf wetness duration such as surface features, repellency, and stomatal arrangement and density; and (3) address species traits generalization across habitats (tropical and semiarid) and highlight the main physiological process drivers. Ultimately, these data can be used to improve models of photosynthesis under wet leaf conditions based on a mechanistic understanding of leaf-level processes and feedbacks in ecosystems spanning from wet to semiarid.

Materials and Methods

Study sites and plant selection

Tropical site

The study was conducted at Texas A&M University Soltis Center for Research and Education near San Isidro de Peñas Blancas in the Alajuela Province, Costa Rica (10^{o}23’13”N, - 84^{o}37’33”W). The center is bordered by the Children’s Eternal Rainforest, near the Monteverde-Arenal Mountain Cloud Forest Reserve. Measurements were performed between ~450 m a. s. l. and ~600 m a. s. l. within a transitional tropical premontane moist forest and in a clearing at its edge (Holdridge 1967). This study site, denoted as “wet site”, has an average annual temperature of approximately 24^{o}C, average relative humidity of 85%, and mean annual rainfall of approximately 4200 mm, in which the “dry season” can reach up to 200 mm month^{-1} and the “wet season” ~500 mm month^{-1} (Teale et al. 2014).

In order to represent a variety of leaf traits (Table 2), seven distinct tropical species were selected (*Stachytarpheta jamaicensis* (L.) Vahl; *Tibouchina heteromalla* Cogn.; *Zamia skinneri* Warsz. Ex. A. Dietr.; *Calathea crotalifera* S. Watson; *Costus laevis* Ruiz & Pav.; *Carapa guianensis* Aublet.; *Senna alata* (L.) Roxb.), among which six were located in the open areas and one, was located inside the forest (Figure 9, Table

2). All plants are native to Costa Rica or the Caribbean region. Leaf traits were distinct for each species, but were mainly related to mesophyll surface coverage (bare or covered with trichomes), roughness, shape (including drip-tip, which was determined following Malhado et al. (2012)) and size. An additional trait was the observation of leaf surface water retention patterns or, referred in this study as, “leaf ponding”. Leaf ponding was observed and noted immediately after rainfall events. This trait consists on how the water settles and drains from the leaf surface.

Table 2. Leaf or leaflet traits of the ten selected plant species. Note: *Classification according to Malhado et al. (2012).

N°.	Species	Habitat	Height (m)	Average Leaf Size (cm^2)	Leaflet Count	Other Morphology Features	Texture	Trichomes	Drip-tip category*
1 SJA	*Stachytarpheta jamaicensis* (L.) Vahl	Partially shaded	1-2	40.6 ± 10.5	N/A	Thin and serrated margins	Rough with multiple veins	Large and sparse on both sides	Acute
2 THE	*Tibouchina heteromalla* Cogn.	Full sun	~3	248.2 ± 59.7	N/A	Intermediate thickness	5 midribs, multiple veins	Large and dense on both sides, mostly bottom	Acute
3 ZSK	*Zamia skinneri* Warsz. Ex A. Dietr.	Shaded	1-1.5	127.8 ± 43.0	20.8 ± 1.4	Thick and rigid	Parallel, dentated veins	None	Drip-tip
4 CCR	*Calathea crotalifera* S. Watson	Partially shaded	1-2	238.0 ± 11.8	N/A	Thin and flexible	Smooth, waxy	None	Small tip
5 CLA	*Costus laevis* Ruiz & Pav.	Shaded	2-3	149.3 ± 0.9	N/A	Thick and firm	Smooth, waxy	Short (abaxial); none adaxial	Drip-tip
6 CGU	*Carapa guianensis* Aublet.	Late successional/ Shade tolerant	15-35	79.6 ± 33.2	10.3 ± 0.6	Intermediate thickness and undulated margins	Smooth	None	Rounded
7 SAL	*Senna alata* (L.) Roxb.	Full sun	5-10	21.2 ± 4.9	26.0 ± 0.6	Thin	Smooth, water repellent	Short and numerous (abaxial); large and few (adaxial)	Rounded
TX1 PO	*Quercus stellata* Wangenh.	Full sun	~6	72.6 ± 10.3	N/A	Thin and lobed margins	Moderately coarse	Intermediate density on both sides	Absent
TX2 CO	*Quercus muehlenbergii* Engelm.	Full sun	~6	77.4 ± 14.0	N/A	Thin and sinuated margins	Smooth	Dense (abaxial); none (adaxial)	Absent
TX3 BO	*Quercus macrocarpa* Michx.	Full sun	~4	73.3 ± 11.1	N/A	Thin and lobed margins	Coarse	Intermediate density (abaxial); none adaxial	Absent

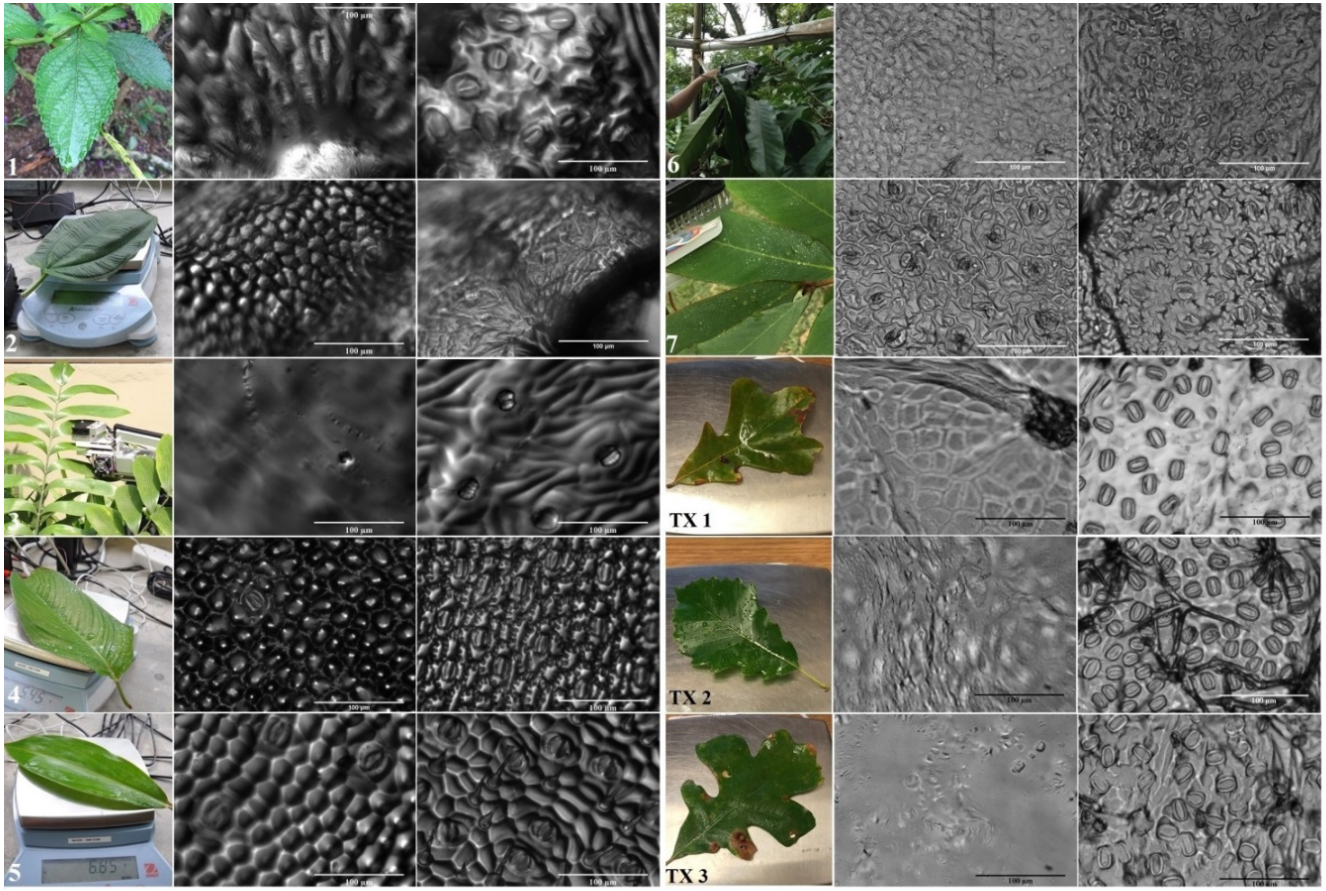

Figure 9. Selected tropical and semiarid species submitted to wetness gas exchange experiment and followed by each adaxial and abaxial leaf surface photomicrograph at 20× resolution, respectively.1) *Stachytarpheta jamaicensis* (L.) Vahl (SJA); 2) *Tibouchina heteromalla* Cogn. (THE); 3) *Zamia skinneri* Warsz. Ex. A. Dietr. (ZSK); 4) *Calathea crotalifera* S. Watson (CCR); 5) *Costus laevis* Ruiz & Pav. (CLA)*;* 6) *Carapa guianensis* Aublet. (CGU)*;* 7) *Senna alata* (L.) Roxb. (SAL)*;* TX1) *Quercus stellata* Wangenh. (PO);TX2) *Quercus muehlenbergii* Engelm. (CO); TX3) *Quercus macrocarpa* Michx. (BO).

The species ranged from 1 m to ~35 m in height (accessed through an adjacent 42-m micrometeorological tower) with leaf areas of individual leaves from 16.3 cm^2 to 307.9 cm^2. All measurements were made on sun-exposed leaves. To facilitate access, six species were sampled from open areas; however, all of them were commonly observed inside the forest understory, usually associated with dense epiphyll coverage and/or low light intensity.

Semiarid site

The second study site was at the Texas A&M University Ecology and Natural Resources Training Area (30^{o}59’01” N, -96^{o}35’65” W). The annual conditions for this study site (henceforth “dry site”) include 1032 mm total annual precipitation, average annual temperature of 21 ^{o}C, and average annual relative humidity of 70% (NOAA 2015) (Figure 10). Tthree *Quercus* species were chosen to examine potential contrasting plant adaptions between wet and dry biomes. Three distinct and geographically widespread oak species were selected (*Quercus stellata* Wangenh. (Post oak - PO); *Quercus muehlenbergii* Engelm. (Chinkapin oak – CO); *Quercus macrocarpa* Michx. (Bur oak – BO)) due to their known resistance to harsh conditions (e.g. droughts and poor soil) and occurrence in the semiarid savanna forests of the state of Texas (Stein et al. 2003, Mickelbart and Jenks 2010). Each oak species had unique leaf surface texture, trichome presence, and leaf area (58 – 105 cm^2) (Table 1).

Figure 10. Site location (Bottom right – Map data: Google, INEGI Terms (2017)) and gas exchange measurements in post oak (Quercus stellata Wangenh.) (Left) and chinkapin oak (*Quercus muehlenbergii* Engelm.) (Upper right).

Leaf wetness duration categories

To determine leaf wetness duration, two fresh leaf replicates from each species were weighed over a precision scale and later artificially misted in the same manner as the leaves selected for wet gas exchange measurements. After thorough wetting, leaves were weighed continuously until dry to obtain dry-down curves for each species. Leaves were considered to be dry when they reached their original fresh weight. Leaf surface water retention (g/cm^2) was determined as maximum water retained on the surface (g) divided by the leaf area (cm^2). Plant species were grouped according to similarities in leaf surface water retention or dry-down rates to determine the significance of leaf traits in photosynthetic responses to leaf wetness. Simple linear regression models were applied to the dry-down curves for each replicate and, later, the resulting slopes and intercepts were averaged between the replicates.

Gas exchange measurements

Wet site measurements were collected at midday over seven days between June 9th and 15th, 2015 and dry site measurements were collected on August 26, 2015 under full-sun and occasional clouds. Midday gas exchange measurements were executed using a portable photosynthesis system (LI-6400XT, LICOR Inc., Lincoln, NE) on five leaf replicates from each species. The physiological variable of interest was photosynthetic rate (A_{net}, µmol CO_2 m^{-2} s^{-1}); and the environmental variables were leaf temperature (T_{leaf}, °C), vapor pressure deficit (δe, kPa), and temperature difference between leaf and air (T_{diff}, °C). Unfortunately, this method precluded the measurement of stomatal conductance and transpiration, since the equations used by the LI-6400XT to calculate these parameters were based on water concentrations inside the chamber. Due to the nature of the experiment design presented, these equations would not produce realistic values.

Measurements were conducted with fixed flow rate = 500 mol s^{-1}, PAR = 1500 µmol s^{-1}, leaf area = 6 cm^2, and constant CO_2 concentrations ≅400 mol CO_2 m^{-2} s^{-1}, stabilized by a buffer volume. Measurements were all conducted with ambient dry conditions. First, baseline dry leaf measurements were collected over a three-minute period. Later, leaves were thoroughly wetted, and then again placed inside the chamber for an additional 10 minutes of continuous measurements. At the time of wetting, leaves were wet completely through artificial misting using a spray bottle with fixed nozzle flow for a uniform application to simulate a recent rain event. Leaves were misted enough to cover the entire upper surface, but not forming large oversized droplets. We were careful to only mist the upper surface, since water droplets remain on the top leaf surface of broadleaved plants under typical field conditions, unless leaf orientation is vertically upward or downward, which is rare (Bohman 2004, Dietz et al. 2007). Wet leaf measurements were logged at 1 minute intervals up to 10 minutes during which time leaves became increasingly drier inside the chamber.

Optimum PAR and leaf temperature was determined under sunny conditions through light and temperature curve measurements over a 10-day period between January 26th and February 4th, 2016 for tropical species, while savanna species were measured on May 25th and September 27th. Temperature curves were generated under optimum PAR for each species, as determined by light curves. The LI-6400XT chamber conditions established for light curves were the same adopted for the wet gas exchange measurements. Light curves followed a commonly applied PAR sequence (LI-COR 2012) of 800, 600, 400, 200, 500, 800, 1000, 1200, 1400, 1600, 1800, 2000, 2200, 2400, 2600, 2100, 1500, 800 µmol s^{-1}. Most of the species showed optimum PAR of 1500 µmol s^{-1}, except for *Senna alata* and *Tibouchina heteromalla*, which peaked around 1800 and 2000 µmol s^{-1}, respectively. Adding these light intensity preferences into the chamber settings, we performed the temperature curves that followed the sequence: 27, 25, 23, 24, 27, 29, 31, 33, 35, 37, 32, 29, 27 °C (LI-COR 2012). It is important to highlight that the instrument uses water vapor to reduce the temperature from the ambient air until it reaches the desired leaf temperature; and to increase, the opposite occurs. Therefore, leaf temperature was kept above 23 °C to prevent malfunctions due to excessive relative humidity and condensation in its interior. Also, maximum leaf temperatures did not exceed 34^{o}C due to cooler ambient temperatures. Curves were fitted using Verhulst's (1838) proposed logistic model for growth or decay of population dynamics model (Zwanzig 1973, Archontoulis and Miguez 2015), except the temperature curve for species *Stachytarpheta jamaicensis,* which was better fitted with a quadratic equation. Light and temperature response curves were not recorded for *Zamia skinneri* due to seasonal dormancy at the time these measurements were conducted. Since *Zamia skinneri* is a well-known understory plant species in Costa Rica and Panama (Taylor et al. 2008, Acuña-Castillo and Marín-Méndez 2013), it was assumed optimum temperatures were below 25 °C and light intensities not higher than 1500 µmol m^{-2} s^{-1}.

Stomatal density

Leaf surface impressions were used to determine stomatal density and to categorize each species as amphistomatous (stomata present on both abaxial (bottom) and adaxial (upper) surfaces) or hypostomatous (only on the bottom) (Preininger 2013). Following a method similar to Long and Clements (1934) and Taft (1950), clear acrylic paint was applied on the adaxial and abaxial sides of three leaf replicates per species. After dry, the paint was carefully removed and stored in vials and microscope slides.

The samples were analyzed at Texas A&M Microscopy and Imaging Center using an upright, lighted microscope at 20× objectives with phase contrast (Zeiss Axiophot, Carl Zeiss Microscopy, LLC, Thornwood, NY) and coupled with a high resolution digital camera (DXM1200, Nikon Corporation). Image acquisition was controlled via MetaView software and resulting captured images processed using FIJI image processing software (Schindelin et al. 2012). Four 0.06 × 0.06 mm monochrome photomicrographs at 100 µm scale were obtained from each side (See Appendix A). These images were then used to collect stomata counts, which were later averaged to obtain stomatal density. Stomata ratio (n^o of stomata on adaxial/n^o of stomata on the abaxial) was also assessed; stomata ratios close to one represent leaves with adaxial and abaxial surfaces with similar or equal number of stomata, whereas those equal to zero represent hypostomatous leaves.

Unfortunately, the dense layer of trichomes on both surfaces of the species *Tibouchina heteromalla* and the top surface of *Stachytarpheta jamaicensis* prevented the collection of reliable stomata impressions. Therefore, I relied on other studies, like Reis et al. (2005) and Iroka et al. (2015), to assume that its subfamily and species, respectively, are characterized as predominantly hypostomatous and amphistomatous, respectively. Likewise, stomata characterization was confirmed with prior studies in the literature (Meyer and Meola 1978, Reis et al. 2005, Camargo and Marenco 2012, Acuña-

Castillo and Marín-Méndez 2013, Begum et al. 2014, Rozali et al. 2014, Singh et al. 2014, Iroka et al. 2015).

Statistical analyses

Multiple regressions (additive and interaction terms) were used to compare photosynthesis response to leaf wetness within and among species and site. To determine the main photosynthesis drivers under wet conditions, A_{net} was considered as the independent variable, environmental conditions (T_{diff}, T_{leaf}, δe), species and site (categorical variables) were the dependent variables. Best model fit was determined through stepwise analyses and based on R^2_{adj}, P-value and Mallow's Cp. Also, dry and wet conditions were compared through ANOVA and Tukey HSD multi-comparison post-hoc test per species and between conditions (no site distinction). All statistical analyses were performed with R version 2.6.2 software (R Core Team 2013).

Results

Leaf wetness duration and stomata density

Dry-down curves were separated into in three categories: 1) large leaf surface water retention, long drying period (LR/LD; slope = $-7.4 \cdot 10^{-5} \pm 3.9 \cdot 10^{-6}$; intercept = 0.005 ± 0.004), which included *Tibouchina heteromalla* and *Zamia skinneri*; 2) small leaf surface water retention, small drying period (SR/SD; slope = $-1.3 \cdot 10^{-4} \pm 8.0 \cdot 10^{-6}$; intercept = 0.004 ± 0.0004), which included *Starchytarpheta jamaicensis*, *Senna alata* and all three savanna oak species (*Quercus stellata*, *Quercus muehlenbergii*, *Quercus macrocarpa*); and 3) small leaf surface water retention, long drying period (SR/LD; slope = -4.7·10^{-5} ± 5.4·10^{-6}; intercept = 0.003 ± 0.0009), which included *Calathea crotalifera*, *Costus laevis* and *Carapa guianensis* (Figure 11).

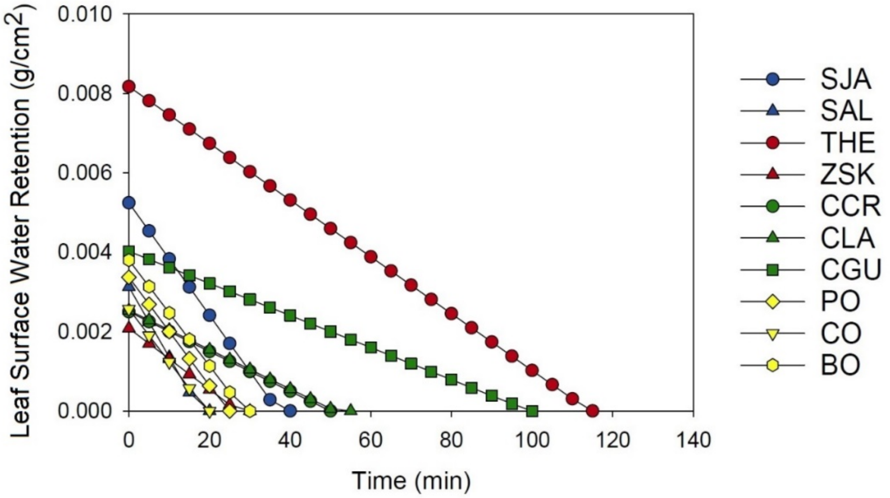

Figure 11. Dry-down curves and leaf categories. Blue: small leaf surface water retention, short drying period (SR/SD); Red: large leaf surface water retention, long drying period (LR/LD); Green: small leaf surface water retention, long drying period (SR/LD); Yellow: semiarid oak species - small water leaf surface water retention, short drying period (SR/SD).

Stomata density varied greatly between all species. All savanna oak species were hypostomatous and had a stomata density that ranged from 676 to 1298 mm^{-2}, higher than the density found on the abaxial surface of most of the tropical species (between 58 and 743 mm^{-2}) (Table 3). In contrast, among the tropical species, only two were hypostomatous (*Tibouchina heteromalla* and *Carapa guianensis*). The other five species were amphistomatous with stomatal ratios ranging from 0.03 to 0.75. Species with no trichomes on either surface were *Tibouchina heteromalla*, *Costus laevis* and *Carapa guianensis*. Only *Zamia skinneri* possessed stomatal crypts (Figure 9), which are pits in the mesophyll, covered by epidermis, that contain the stomata; they are known to protect the cells from excessive water loss during drought (Mauseth 2008) and to facilitate carbon dioxide diffusion through the tissue between the abaxial and adaxial surfaces of thick leaves (Hassiotou et al. 2009).

Gas exchange measurements

Measurement conditions (ambient and leaf)

At the wet site, after applying artificial misting, leaves inside the chamber experienced 9% higher RH and 26% lower δe relative to dry conditions that were observed prior to artificial wetting. Leaf temperature was only 2% lower after wetting, but that amounted to nearly 6-fold decrease in T_{diff}. (Table 4). Similarly, at the “dry site”, wetted leaves inside the chamber experienced 7% higher RH and 3% lower leaf temperatures associated, again, with a 6-fold decrease in T_{diff}. However, those leaves at the dry site experienced only a 4% decrease in δe, since the ambient conditions at this site was much warmer (+5 ^{o}C) and drier (nearly double) than the “wet site”.

Table 3. Summary per species of respective stomata density (abaxial and adaxial, mm^{-2}), stomata ratio, dry-down category, initial (at 1 minute) photosynthetic percentage in relation to average dry state (A_{net} Dry – Wet 1 min), long-term (10th minute) percentage in relation to average dry state (A_{net} Dry – Wet 10 min), and given status according to dry-down pattern (Dry-down A_{net} status). Note: * highlights measurement uncertainties due to dense trichomes.

Species	Adaxial Stomata Density (mm^{-2})	Abaxial Stomata Density (mm^{-2})	Stomata Ratio	Dry-Down Category	Initial response	Long term response	Dry-Down A_{net} Status
SJA	200 ± 49*	267 ± 14	0.75	SR/SD	-20%	-3%	Fast Recovery
SAL	271 ± 57	551 ± 24	0.57	SR/SD	-31%	-1%	Fast Recovery
CCR	8 ± 10	255 ± 46	0.03	SR/LD	-15%	-3%	Recovery
CLA	29 ± 25	167 ± 24	0.18	SR/LD	-12%	-31%	Decrease/ Late recovery
ZSK	13 ± 16	58 ± 22	0.22	LR/LD	21%	7%	Increase
THE	0	Unknown*	0	LR/LD	-4%	10%	Increase
CGU	0	689 ± 86	0	SR/LD	-9%	-6%	Recovery
PO	0	676 ± 49	0	SR/SD	-11%	-13%	Decrease
CO	0	1298 ± 13	0	SR/SD	-48%	-31%	Late Recovery
BO	0	731 ± 51	0	SR/SD	-11%	14%	Increase

Table 4. Upper-half of the table: Ambient and leaf/chamber conditions during measurements (dry, wet and average with respective standard deviation). Bottom-half: leaf/chamber conditions while dry and wet for each species and overall average per variable with respective standard errors. Note: Environmental variables: air temperature (T_{air}), relative humidity (RH%), photosynthetically active radiation (PAR) and water concentration (H_2O concentration); Chamber variables: vapor pressure deficit (δe), leaf temperature (T_{leaf}) and leaf-to-air temperature difference (T_{diff})).

Costa Rica – Tropical Environment					
Ambient	Average	Leaf / Chamber	Average	Dry	Wet
T_{air} (^{o}C)	32.8 ± 2.4	T_{leaf} (^{o}C)	32.5 ± 1.9	32. 9 ± 1.2	32.3 ± 1.0
RH (%)	54.7 ± 4.5	T_{diff} (^{o}C)	-0.35 ± 0.4	0.07 ± 0.3	-0.48 ± 0.4
PAR (µmol m^{-2} s^{-1})	427.0 ± 250	δe (kPa)	1.5 ± 0.3	1.9 ± 0.3	1.4 ± 0.3
H_2O Concentration (mol H_2O mol air^{-1})	28.9 ± 3.3	H_2O Concentration (mol H_2O mol air^{-1})	35.5 ± 4.6	32.9 ± 4.5	36.0 ± 4.6
		RH (%)	67.1 ± 4.1	62.2 ± 4.3	68.6 ± 4.2
Texas – Semiarid Environment					
Ambient	Average	Leaf / Chamber	Average	Dry	Wet
T_{air} (^{o}C)	38.4 ± 0.8	T_{leaf} (^{o}C)	38.3 ± 0.9	38.4 ± 0.5	38.3 ± 0.6
RH (%)	28.2 ± 1.8	T_{diff} (^{o}C)	-0.1 ± 0.13	-0.02 ± 0.3	-0.12 ± 0.1
PAR (µmol m^{-2} s^{-1})	564.4 ± 240	δe (kPa)	4.4 ± 0.2	4.5 ± 0.2	4.3 ± 0.3
H_2O concentration (mol H_2O mol air^{-1})	19.1 ± 2.1	H_2O concentration (mol H_2O mol air^{-1})	24.1 ± 2.0	22.7 ± 1.7	24.5 ± 2.1
		RH (%)	35.5 ± 2.0	33.4 ± 1.1	36.1 ± 2.3

Table 4. Continued.

Species	Average δe - Dry	Average δe – Wet	Average T_{leaf} - Dry	Average T_{leaf}- Wet	Average T_{diff} - Dry	Average T_{diff} - Wet
SJA	1.97 ± 0.4	1.23 ± 0.3	35.93 ± 1.4	34.21 ± 1.4	-0.57 ± 0.5	-1.91 ± 1.3
SAL	1.79 ± 0.4	1.66 ± 0.4	32.41 ± 1.4	32.05 ± 1.4	1.11 ± 0.3	1.13 ± 0.3
THE	1.44 ± 0.2	0.98 ± 0.1	30.64 ± 0.3	30.23 ± 0.3	-0.23 ± 0.3	-0.80 ± 0.3
ZSK	2.22 ± 0.4	1.39 ± 0.4	34.02 ± 1.4	33.38 ± 1.1	0.25 ± 0.2	-0.58 ± 0.4
CCR	2.06 ± 0.2	1.31 ± 0.2	34.08 ± 0.6	33.24 ± 0.6	-0.24 ± 0.2	-0.86 ± 0.3
CLA	2.37 ± 0.4	2.04 ± 0.3	33.80 ± 1.2	33.75 ± 1.3	-0.14 ± 0.2	-0.41 ± 0.1
CGU	1.56 ± 0.3	1.33 ± 0.2	29.37 ± 1.2	29.57 ± 0.7	0.34 ± 0.2	0.09 ± 0.2
PO	4.17 ± 0.3	4.07 ± 0.4	37.35 ± 0.8	37.37 ± 1.1	-0.08 ± 0.1	-0.22 ± 0.1
CO	4.61 ± 0.2	4.52 ± 0.2	38.44 ± 0.3	38.40 ± 0.3	0.05 ± 0.1	0.03 ± 0.2
BO	4.66 ± 0.1	4.35 ± 0.1	39.28 ± 0.5	39.04 ± 0.4	-0.03 ± 0.1	-0.18 ± 0.2
Average	2.68 ± 0.3	2.29 ± 0.3	34.35 ± 0.9	34.12 ± 0.9	0.05 ± 0.2	-0.37 ± 0.3

Photosynthesis measurements

Light response curves confirmed the assumptions regarding the species' habitat preference (Figure 12a). Species classified as shaded (Table 2), in this case only *Costus laevis*, showed a sharp decline at 1600 µmol m^{-2} s^{-1} after a constant optimum photosynthetic rate starting at low light intensities (200 µmol m^{-2} s^{-1}). This trend was not observed for any of the other sampled species. Another interesting trend was observed for *Carapa guianensis*, in which the light response curve depicts the plasticity of a late successional species that are able develop under shade and later adjust itself to higher light intensities (Fetcher et al. 1987). Although not showing an apparent stabilization of photosynthetic rates, this species maintained the lowest photosynthetic rates among the tropical species. All other species (tropical and semiarid) showed strong increase in photosynthetic rates with increase of light intensities, but stabilization occurred at different intensity levels for each species. Stabilization over 1000 µmol m^{-2} s^{-1} was observed for most of the species; while *Tibouchina heteromalla* stabilized at 2200 µmol m^{-2} s^{-1}, followed by *Stachytarpheta jamaicensis* and *Quercus stellata*, showing an inflection point at 3000 µmol m^{-2} s^{-1}. The average optimum light intensity among all species was 1671 ± 734 µmol m^{-2} s^{-1}.

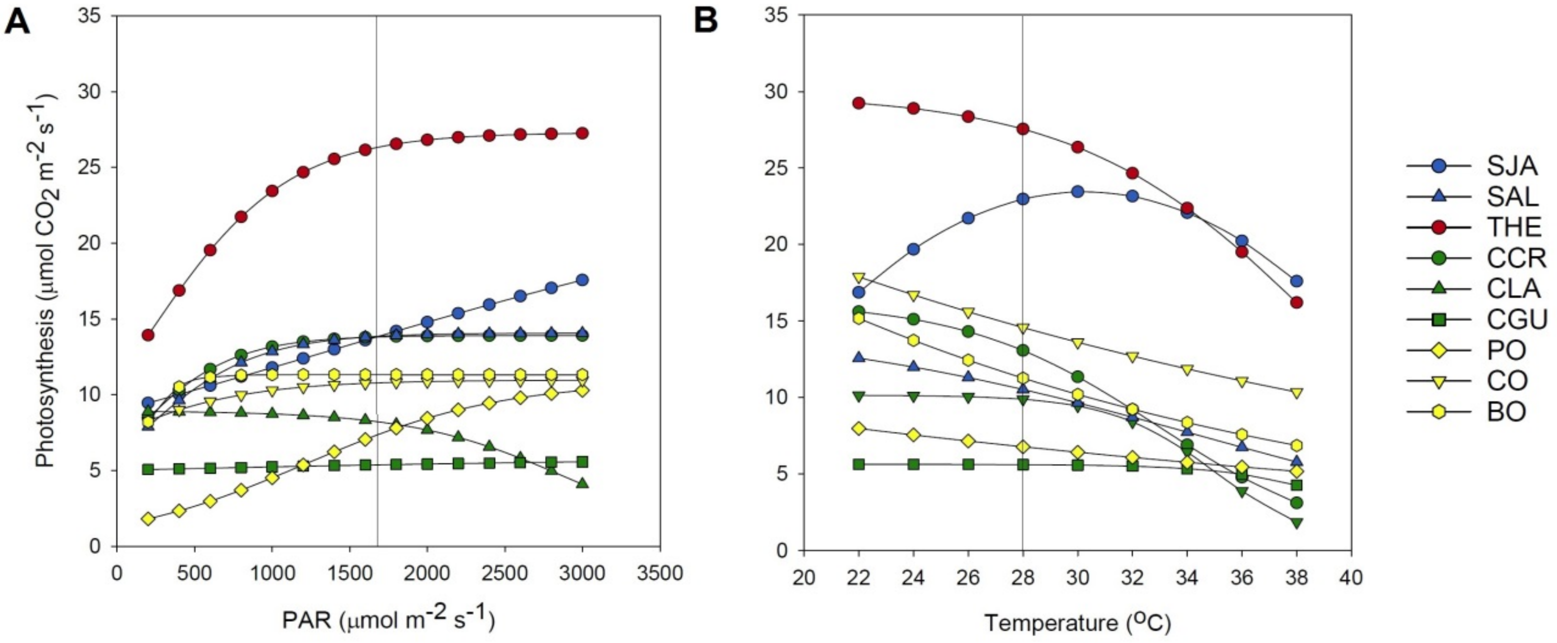

Figure 12. Fitted (A) light response curve (200-3000 µmol m^{-2} s^{-1}) and (B) leaf temperature response curve (22-38 °C) for each species. Grey vertical line represents average optimum condition among species (PAR$_{opt}$=1700 µmol m^{-2} s^{-1}; $T_{leaf\text{-}opt}$=28 °C (tropical)). Species represented by their leaf wetness duration color [blue: small leaf surface water retention, short drying period (SR/SD); red: large water leaf surface water retention, long drying period (LR/LD); green: small water leaf surface water retention, long drying period (SR/LD); yellow: semiarid oak species - small water leaf surface water retention, short drying period (SR/SD)].

Overall, species which were intolerant of intense light had a higher tolerance for leaf wetness. Plants with small leaf surface water retention and long drying periods were also the ones that needed less light to photosynthesize (<1500 µmol m^{-2} s^{-1}); three of the species, however, had notably different behavior. *Quercus muehlenbergii* (PAR_{opt} = 1300 µmol m^{-2} s^{-1}) and *Quercus macrocarpa* (PAR_{opt} = 700 µmol m^{-2} s^{-1}), which had short drying times, had the lowest light intensity optimum among all species. *Tibouchina heteromalla* had a long drying period, but did not experience the photoinhibition; since the presence of trichomes provides protection under high light intensity (Ripley et al. 1999).

In contrast to the relationship observed between wetness duration and light tolerance, a species' photosynthetic response to temperature did not show a relationship with leaf wetness duration. However, there was a clear distinction between sites, in which savanna species showed more tolerance to warmer temperatures (above 40 ^{o}C). Among both sites, temperature response curves showed that photosynthesis in all but one species declined with increasing temperatures. Photosynthesis in *Stachytarpheta jamaicensis* appeared parabolic, with an optimum temperature of 30 ^{o}C (Figure 12b). The main difference among the other species was at which temperature level photosynthetic rates declined and the relative sensitivity of A_{net} to temperature. Tropical species had the largest declines with increasing temperature when compared to the optimum conditions. Experimentally, when extrapolating temperature responses over the highest temperature measured (38 ^{o}C) using the fitted models, five of the tropical species (Figure 12b) reached zero or near-zero rates of A_{net} (<3 µmol CO_2 m^{-2} s^{-1}) when leaf temperature was over 40 ^{o}C. *Tibouchina heteromalla* did not reach zero but had a photosynthetic reduction of 81% between 20 ^{o}C and 45 ^{o}C. In contrast, semiarid species had a less steep decline of photosynthetic rates compared to tropical species, with none of species' A_{net} below 4 µmol CO_2 m^{-2} s^{-1}. Among the species, between 20 ^{o}C and 45 ^{o}C, *Quercus stellata* had the smallest reduction of photosynthetic rates (49%) and *Quercus macrocarpa* the largest (71%). Even though species optimum temperature level varied, we believe that temperatures between 24^{o}C and 32^{o}C would still maintain an optimum photosynthetic rate for all species ($T_{leaf\text{-}opt} = 31.9 \pm 8.1$ ^{o}C, while: $T_{tropical} = 28.2 \pm 5.0$ ^{o}C and $T_{semiarid} = 43.0 \pm 1.4$ ^{o}C).

Distinct leaf traits and ecological succession stage, also observed through the light and temperature response curves, influenced photosynthetic rates during dry and wet conditions. As a result, species and sites varied greatly ($P<0.05$) (Figure 13). Hence, we cannot accept the hypothesis that leaf wetness reduced A_{net}, since results varied greatly among species. Some species showed higher A_{net} when dry or wet, while others were reduced. As a result, mean A_{net}-dry and A_{net}-wet did not differ ($P=0.32$). When assessing the trends in A_{net}-wet over the course of drying inside the chamber, most leaves experienced an initial reduction in A_{net} followed by a full or partial recovery to values similar to A_{net} dry. Species photosynthetic response variability was also reflected on light and temperature responses for each species. The large species variability (morphologically and physiologically) led us to further evaluate photosynthetic behavior based on whether a species was hypostomatous or amphistomatous.

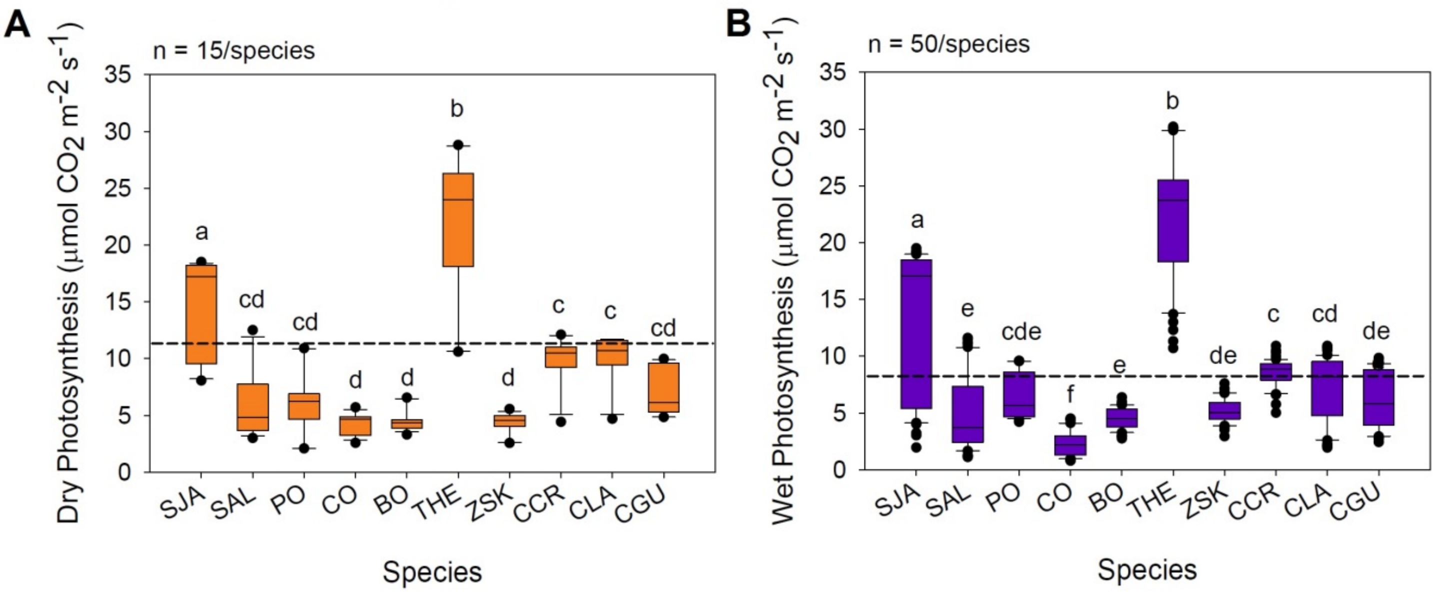

Figure 13. Range of photosynthesis measurements for dry (A) and wet (B) conditions for each species. Grey dashed line across each graph indicates the overall mean photosynthetic value for each condition (dry = 8.8 ± 6.0 µmol CO_2 m^{-2} s^{-1}; wet = 8.2 ± 6.5 µmol CO_2 m^{-2} s^{-1} and number of measurements per species is indicated above each graph. Order of species in the X-axis follow leaf wetness duration categories (from left to right: SR/SD (SJA, SAL, PO, CO and BO), LR/LD (THE and ZSK), SR/LD (CCR, CLA and CGU). Box plots characterize this distribution, with the bottom and top part of the box indicating the 25th and 75th percentile, respectively; the two dashes the 10th and the 90th percentile, respectively; and the horizontal line within the box the median value. Tukey HSD denoted with letters indicate categories with significance differences, as indicated by ANOVA (*P*<0.05).

Hypostomatous species

Even though all “dry site” species were hypostomatous with relatively small leaf surface water capacity and short drying period, all three displayed distinct photosynthetic patterns while drying (Figure 14a). All three species showed an immediate decline, but after 10 minutes of wetting, *Q. stellata* continued responding negatively (to -13% of A_{net} dry), *Q. muehlenbergii* recovered partially (-48% to -31% of A_{net} dry), and *Q. macrocarpa* recovered fully, ending with 14% higher A_{net} than recorded under dry conditions (Table 3).

At the “wet site”, *Tibouchina heteromalla* and *Carapa guianensis* were also hypostomatous, yet differed markedly in wetness duration and photosynthetic patterns while drying (Figure 14a). Even though *Tibouchina heteromalla* showed a slight decrease during the first 2 minutes (-4%), afterwards there was a constant increase that reached 10% above the dry condition rates. Oppositely, *Carapa guianensis* had a late reaction to leaf wetness by showing its largest decrease in photosynthetic rates after 4 minutes (-28%), but almost fully recovered by 10 minutes (-6%) (Table 3).

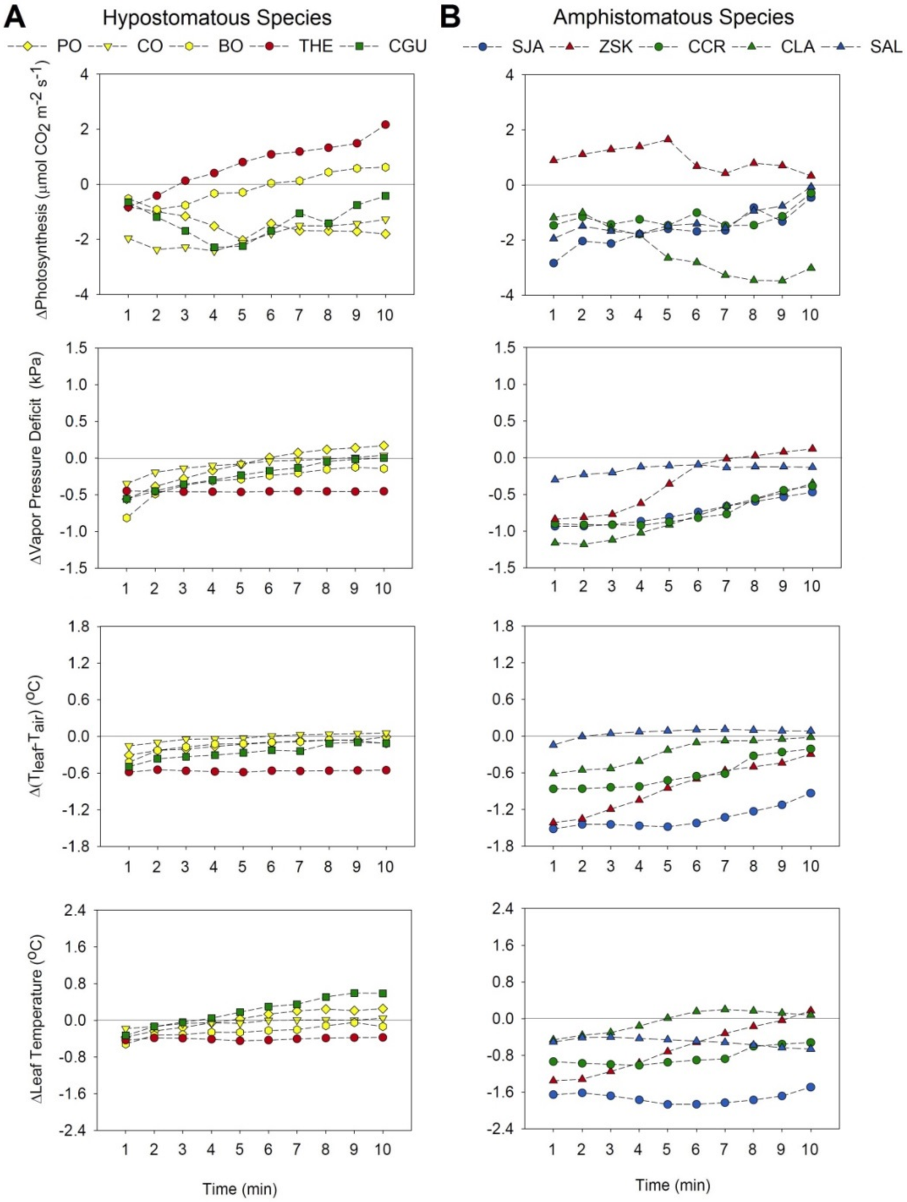

Figure 14. Normalized average photosynthetic response of the sampled species to simulated wetness and subsequent dry-out [$x(t_0)=0 \rightarrow$ dry] and their respective micrometeorological drivers. (A) Hypostomatous species; (B) Amphistomatous species. Notes: From left to right, respectively: photosynthesis (μmol CO_2 m^{-2} s^{-1}), vapor pressure deficit (kPa), difference between leaf temperature and air temperature (^oC) and leaf temperature (^oC). Leaf wetness categories are represented in "blue" for small leaf surface water retention, short drying period (SR/SD), "red" for large water leaf surface water retention, long drying period (LR/LD), "green" for small water leaf surface water retention, long drying period (SR/LD), and "yellow" for savanna oak species - small water leaf surface water retention, short drying period (SR/SD).

Amphistomatous species

At the “wet site”, *Stachytarpheta jamaicensis* and *Senna alata* were categorized as amphistomatous with small leaf surface water capacity and short drying period. Consequently, both species showed the largest immediate decrease in A_{net}. These species were also the ones to possess the largest stomata ratios within the tropical species (Table 3). But interestingly, both species were almost fully recovered after 10 minutes when the leaves were almost or fully dry (Figure 14b).

Amphistomatous species with small leaf surface water capacity and a *long* drying period (*Calathea crotalifera* and *Costus laevis*) displayed different responses to wetness. *Calathea crotalifera* had an initial decrease of 15%, but like those that dried more quickly was almost fully recovered after 10 minutes (-3%). Although *Costus laevis* had a similar initial photosynthetic rate decrease (-12%) as *Calathea crotalifera, Costus laevis* A_{net} continued decreasing up to 9 minutes and started a late recovery afterwards (Table 3 and Figure 14b).

Zamia skinneri was the only amphistomatous species with large leaf surface water capacity and long drying period. Similarly to *Tibouchina heteromalla*, this species had an immediate improvement (21%) of A_{net} dry, but subsequently started decreasing after 5 minutes and was almost equivalent (7%) to its dry condition rates at 10 minutes despite the fact that it was most likely still relatively wet at that time.

Environmental variable relationships

The environmental variables (δe, T_{leaf} and T_{diff}) varied greatly between species, due to variable leaf traits (e.g. trichomes and surface roughness held water longer; hence, affecting leaf temperature and δe), but hypostomatous species showed a smaller range of variation throughout the dry-down than amphistomatous species (Figure 14). While leaves were wet, the variables that showed the largest variations were temperature difference and δe for most of the studied species and sites, consequently influencing the observed A_{net} trends. Also, the effects on T_{diff} on A_{net} were found to be slightly weaker or stronger, depending on species' leaf morphology. Vapor pressure deficit was highly correlated with photosynthetic response for most species or habitat group, although its influence is mainly dependent in the interaction with temperature difference (Table 5).

Table 5. Best model fit obtained through linear or multiple regressions between chamber variables (leaf temperature (T_{leaf}), leaf-to-air temperature difference (T_{diff}) and vapor pressure deficit (δe)) and each species, each plant functional group (numerical and categorical) and all species combined (numerical and categorical) chosen through the largest adjusted coefficient of determination (R^2_{adj}). Notes: significance value labels represented by "*** P<0.001", "** P<0.01", "* P<0.05" and "*ns* as non-significant". Superscript "*n*" and "*c*" represents how "*Species*" was treated in the model (as numerical or categorical variables, respectively).

Species	Best Model	R^2_{adj}
SJA	δe	0.77***
SAL	$T_{\mathrm{leaf}}\cdot \delta e$	0.91**
THE	$T_{\mathrm{leaf}}\cdot \delta e$	0.39^{ns}
ZSK	δe	0.49**
CCR	δe	0.35^{ns}
CLA	$T_{\mathrm{diff}}\cdot \delta e$	0.98***
CGU	$T_{\mathrm{leaf}}\cdot \delta e$	0.79**
PO	δe	0.72**
CO	$T_{\mathrm{diff}}\cdot \delta e$	0.96***
BO	$T_{\mathrm{diff}}\cdot \delta e$	0.98***
All Tropical Species^n	$T_{\mathrm{leaf}}\cdot \delta e$	0.57***
All Tropical Species^c	Species$\cdot T_{\mathrm{diff}}$	0.99***
All Semiarid Species^n	T_{diff}	0.53***
All Semiarid Species^c	Species$\cdot \delta$e	0.97***
All Species (Tropical and Semiarid)^n	$T_{\mathrm{leaf}}\cdot \delta e$	0.44***
All Species (Tropical and Semiarid)^c	Species$\cdot T_{\mathrm{diff}}$	0.99***

Discussion

Rather than finding consistent reductions in A_{net} under wet leaf conditions, plant species were distinctly different from each other, as reflected in divergent photosynthetic responses that seemed to be related to leaf traits: leaf wetness duration, leaf architecture, stomata placement and successional stage. Species with higher wet A_{net} relative to dry conditions held more water on the surface, suggesting a preference for cooler and more humid conditions along with leaf architecture mechanisms to cope with this water retention (trichomes and grooved leaves, *Tibouchina heteromalla* and *Zamia skinneri*, respectively) (Figure 15a,d). Others with longer drying periods and low water retention, immediately reduced their photosynthetic rates, but later recovered due to stomata placement and subsequent drier condition resulted from leaf surface evaporation. Contrary to my expectations, having stomata on the adaxial surface of leaves did not consistently reduce A_{net} when wet. Apparently, other traits, such as faster drying times or lower water retention on the upper leaf surface, mitigated the impacts of wet upper stomata. This finding suggests that tropical species may be better adapted to wet leaf conditions than semiarid species. It is notable that the species sampled were not consistent with the literature regarding stomata placement, in which xeric species are usually amphistomatous (Mott et al. 1982, Smith et al. 1998, Williams et al. 2004), and tropical species hypostomatous (Smith et al. 1998, Camargo and Marenco 2011).

Tibouchina heteromalla possesses a dense layer of trichomes that could potentially help alleviate the excessive transpiration, due to increase in leaf boundary layer thickness. Literature suggests that some tropical montane species can perform foliar water uptake, as an alternative water source or to temporarily enhance cell turgidity (Eller et al. 2013, Goldsmith et al. 2013, Eller et al. 2016, Fu et al. 2016, Goldsmith et al. 2016); *T. heteromalla* appears to be a good candidate for such behavior. Holder (2007) described *Tibouchina urvilleana* as having very similar leaf characteristics as *T. heteromalla* from this study, particularly its “wettability” (i.e. water droplets spread and adhere to the leaf surface, rather than form a bead on the surface) (Figure 15b), while possessing an almost repellent abaxial surface (i.e., a 98^o droplet contact angle just under the 110^o threshold). Hence, the geographical occurrence of *T. heteromalla* (coastal or inland high altitude mountainous regions) and its preference for cooler temperatures (Luttge et al. 2015), also shown its temperature curve (Figure 12b), leads to the assumption that leaf wetness actually creates a favorable boundary layer condition surrounding the leaves by retaining water droplets suspended from the leaf surface by the trichome tips. This type of retention can actually stimulate greater stomatal opening and higher water use efficiency (Smith and McClean 1989, Brewer et al. 1991).

Figure 15. Examples of leaf water retention (“leaf ponding”) in species with varying leaf traits. Only image A depicts artificial misting, while the others show intercepted rain. A) *Zamia skinneri* Warsz. Ex. A. Dietr.: water channeled through leaflet indented venation; B) *Senna alata* (L.) Roxb.: water beading on repellent leaf surface; C) *Calathea crotalifera* S. Watson: thin, adhered water film on wettable surface; D) *Tibouchina heteromalla* Cogn.: acute leaf tip water ponding on wettable, trichome covered surface.

Favorable conditions can also be linked to the increase of A_{net} for *Zamia skinneri*, as this species is mainly restricted to the tropical understory, which has low light intensity and high humidity. Although this species is amphistomatous, Acuna-Castillo et al. (2013) report several features that could allow for continued photosynthetic activity during wetness events: crypt stomata and adaxial stomata located in the elevated, ridged portions of the leaflet. In other words, stomata located in the elevated portions of the leaves are still dry and capable to continue photosynthetic activity, while stomata located inside the depressed portion are wet ("leaf ponding" - Figure 15a). Considering that tropical understory plants remain wet longer than more exposed overstory plants, these adaptations would enhance photosynthetic activity even under suboptimal conditions. As seen on figure 14, *Zamia skinneri* photosynthetic rates started declining when vapor pressure deficit ($R^2=0.49$, $P<0.01$) exceeded the initial dry state after 5 minutes.

Not only was leaf ponding important for highly complex anatomical species (Figure 15), but was also predominant in species with small water volume and long drying period. The species considered in this category had different volumes of water puddled on the surface depending upon leaf anatomy. One of the strategies shown by tropical plant species to minimize water ponding is the presence of drip tips (Malhado et al. 2012, Goldsmith et al. 2016). *Calathea crotalifera* and *Costus laevis* showed a prominent and a small one, respectively; and *Zamia skinneri* (from the other wetness category) also had leaflets with drip-tips (Table 1). Interestingly, all three sampled species with drip-tips are species commonly found in tropical understories. Malhado et al. (2012) found that Amazonian species that showed this leaf feature were short plants with smaller trunk girths found in the understory. Additionally, Farji-Brener et al. (2002) and Meng et al.(2014) found that drip-tips were less common on canopy-exposed trees in Costa Rica and China, respectively, since leaf drying from solar radiation, wind and higher vapor pressure deficit is more dominant than at understory tree canopy level. Meng et al. (2014) also found that shaded species with drip-tips showed smaller leaf inclination angles than sun-exposed species (~10^o (flatter) and ~40^o (sloped), respectively) for optimized sun exposure to enhance carbon gain. Hence, drip-tip, leaf shape (mainly thick midrib with folded leaf margins) to facilitate water drainage, and flatter leaf angles can result in water ponding in portions of the leaves.

The surface area covered by the puddle along with leaf surface wettability can lead to longer drying period and, consequently, photosynthetic suppression in amphistomatous species or hypostomatous species with warmer leaf temperature preferences. Therefore, I theorized that the difference in A_{net} recovery from wetting events between *Costus laevis* and *Calathea crotalifera* can be attributed to the latter showed less surface wettability (thinner and smoother waxy surface than the thicker, rougher waxy *Costus laevis* leaves) and solar tracking (variable leaf angles) (Herbert and Larsen 1985). These features would lead to a better leaf drainage and result in a smaller area being affected by the drip-tip puddle, while the major dry reminiscent area can continue gas exchange (Holder 2011) (Figure 15d). Additionally to *Costus laevis* less favorable leaf features that lead to larger water puddles on the surface, this species also had higher stomata ratios than *Calathea crotalifera* (0.18 and 0.03, respectively).

Carapa guianensis leaflets, although hypostomatous, also showed to have a design that favored leaf ponding (flat midrib and wavy mesophyll margins), but large pulvinus in the base of the leaflets and leaves can facilitate water drainage and leaf surface exposure to radiation to evaporate thin, retained water film (Figure 15c). Even though this species' photosynthetic rates varied little with leaf temperature variation (Figure 12b), the A_{net} reduction and later recovery was assumed to be due to the combination of the vapor pressure deficit drop immediately after wetting along with the increase in leaf temperature ($R^2=0.79$, $P<0.01$). Since conditions inside the chamber contrasted strongly with the large surface area of leaves outside the chamber (i.e. temperature and light intensities), this could have caused disequilibrium conditions inside the chamber (Long et al. 1996, Kaipiainen and Pelkonen 2007). Hence, showing that leaf wetness lower δe and cooling effect, even in species with stomata on the top, can cause a suppression effect without directly affecting stomata CO_2 diffusion rate. Urrego-Pereira et al. (2013) also found irrigated maize reduced A_{net} by 10−41% due to decrease in temperature below the optimum range. The same result was found by Hanba et al. (2004) on wettable soybean leaves.

Time of drying was a major indicator of rapid recovery from wetness. Water repellency has been documented as a major feature to cope with wetness (Rosado and Holder 2013), along with trichomes (Brewer et al. 1991), which were present on both species of this category (*Senna alata* and *Stachytarpheta jamaicensis*, respectively). Unlike *Tibouchina heteromalla*, *S. jamaicensis* had a less dense layer of trichomes, which could have contributed to the drying process, but also with the initial photosynthetic decrease. Brewer and Smith (1994), while studying soybean leaves with low trichome densities compared to native, non-agricultural species (Brewer et al. 1991), found that trichome layers retained water longer in patches and, consequently, reduced CO_2 assimilation by 15% compared to non-misted plants; however, leaf surface area beneath these patches of water film was small (when compared to bare leaf surfaces), promoting rapid evaporation. While water retention in the form of water film can reduce gas exchange, Brewer et al. (1991) states that more spherical water droplets on repellent leaf surfaces, as observed for *Senna alata* (Figure 15b), will insure gas exchange on the dry reminiscent surfaces. Droplet roll-off also increases drying rate.

Leaf hypostomaty provides extra protection against excessive transpiration and consequent dehydration of plant tissues (Brown and Wilson 1905). In drier environments, some savanna tree species (including the three sampled in this study) have thick leaves covered with trichomes. Additionally, a large volume and long period of water retention on the top surface can lead to pathogen invasions and fungi or lichen growth that can permanently disable stomata on an amphistomatous plant. Having stomata on the abaxial surface can primarily avoid surface wetness decreasing gas exchange during rain events, since it is rare to wet the abaxial surface (Dietz et al. 2007). Similarly to *Carapa guianensis* hypostomaty and its response to wetness, leaf anatomy traits and stomata distribution required further environmental conditions assessment when analyzing the mixed responses among the semiarid species. Although all three species showed different A_{net} responses to wetness (Figure 14a), all were strongly influenced by the resulting combination of temperature difference and vapor pressure deficit variation (Table 4). Not only were all three species hypostomatous, but they also have a dense trichome layer on the abaxial surface; whereas, the adaxial surface had variable surface roughness and trichome density (Table 2). Hence, I hypothesized that A_{net}-wet responses were influenced by adaxial surface potential for retaining water and the subsequent cooling effect and/or leaf boundary layer thickening of each species.

Among the oak species, only *Quercus stellata* is considered drought tolerant while the other two are considered intermediate (Dickson and Tomlinson 1996). Compared to *Quercus macrocarpa*, *Quercus muehlenbergii* may be more tolerant to high temperatures (Hamerlynck and Knapp 1994, Balok and Hilaire 2002) and its dominance in xeric environments (Abrams 1986). The evidence gathered through this study support this since *Q. macrocarpa* responded favorably to wetness and its associated cooler leaf temperatures. Oppositely, even though *Quercus muehlenbergii* showed the same reduction on those three variables, photosynthetic rates reduced immediately after wetting and only started improving after dry conditions were reached again after 7 minutes. I also believe that the rough-textured (wax granules (Balok and Hilaire 2002)) adaxial epidermis surface of *Q. macrocarpa*, even though trichome-free (Hardin 1979), lead to a more prolonged optimum microclimatic condition on the leaf by retaining water for a longer period. Also, Balok and Hilaire (2002) found that *Q. macrocarpa* had less epicuticular wax content than *Q. muehlenbergii*, which not only shows a vulnerability to drought due to high heat transmissivity through the mesophyll, but can possibly enhance the cooling effect on these species' leaves after rain events on hot, dry days.

Quercus stellata, as a drought-tolerant plant, has shown high tolerance to dry, hot conditions (Will et al. 2013). Contrary to the finding in this study, leaf wetness was expected to have a beneficial effect of cooling the leaves of trees at the dry site and even possibly allow for foliar water uptake, both of which may lead to greater stomatal conductance and stimulate A_{net}. Although there are some studies on dry environment or semiarid tree's capacity in performing foliar water uptake (Breshears et al. 2008, Limm et al. 2009, Fernandez et al. 2014), there is little to no studies on the effect of leaf wetness on physiological processes for these types of trees. Compared to wet site species, it was surprising to find such similar responses to leaf wetness between biomes, given the large contrasts in plant adaptations to local environmental conditions. It is possible that these species converge on a relatively muted response to wetness, each for divergent purposes (cooling, avoiding stomatal occlusion, or by several unique means of rapid drying).

Conclusions

The findings show strong evidence that leaf wetness duration was the main factor driving photosynthesis reduction or increase. However, this variable was only insightful if linked to one or more leaf traits, like stomata distribution and trichome presence or leaf surface repellency/wettability. I surmise that tropical species have developed distinct adaptations to cope with wetness without drastically affecting photosynthetic rates, or have evolved strategies to enhance photosynthesis by using leaf wetness to their advantage. Unfortunately, there have been predictions that tropical regions will be affected by more frequent and extreme droughts in the near future, which could dramatically affect these species that depend on leaf wetness for their optimum physiological conditions. Additional studies to examine interactions between leaf traits and leaf wetness, and potential functional adaptions in highly biodiverse ecosystems are crucial for a better understanding of canopy-atmosphere interactions and how that will affect forest yield and global climate modelling.

CHAPTER IV

RESPONSE OF LEAF AND WHOLE-TREE CANOPY CONDUCTANCE TO WET LEAF CONDITIONS WITHIN A MATURE PREMONTANE TROPICAL FOREST IN COSTA RICA

Overview

Tropical water recycling and carbon storage are dependent on highly variable canopy-atmosphere dynamics. Canopy fluxes are substantially enhanced or reduced when, for example, rainfall occurs. Hence, models based on climate to estimate the conductance of water and carbon fluxes from canopies may have been used without major consideration of temporal variability of wetness. The goal of this chapter was to estimate stomatal and canopy conductance to water vapor of a mature tropical forest of Costa Rica under a gradient of leaf wetness conditions at 30-min intervals for the year 2015. To address this goal, I relied on sap flux measurements from 26 trees and micrometeorological measurements made from 40-m tower for the entire year of 2015. Actual transpiration was derived from sap flux measurements (E_c). The models tested were stomatal conductance (g_s) models proposed by Jones (1992) ($g_{s\text{-J}}$) using shaded and sunlit leaf temperatures, and Monteith and Unsworth (1990) ($g_{s\text{-MU}}$) using air temperature, and canopy conductance (g_c) models proposed by McNaughton and Jarvis (1983) and Penman-Monteith. Cumulative g_c and g_s estimates in this study matched those reported for similar sites in the literature, and were enhanced by extensive observations of sap flux. Between stomatal and canopy conductance, g_c had the largest differences within models. However, during wet periods, the estimates were the most similar among models. Stomatal conductance estimates differed substantially when considering shaded or sunlit leaves. Shaded leaves averaged 26% higher g_s than sunlit leaves. Yet, most g_c and all g_s models estimated that conductance on wet days was at least as high on dry days, indicative of their insensitivity to leaf wetness. Also, large shifts of diurnal peaks (up to 2 hours earlier than E_c) were observed for most g_c and g_s estimates, indicative of the influence exerted by net radiation and air temperature. Additionally, the decoupled interface (Ω>0.90) reflected the multiple environmental drivers that may influence conductance (e.g. vapor pressure deficit and leaf temperature). This model comparison led to three major insights: 1) g_c and g_s cannot accurately be predicted under wet conditions without accounting for leaf wetness, 2) even during dry days, low vapor pressure deficits interfere with model accuracy, and 3) intermittent rain during semi-dry and wet days cause large fluctuations in g_c and g_s estimates. Thus, it is advised that sub-daily scale (5- or 10-min intervals) and direct physiological measurements of conductance under wet conditions should be adopted. While methodologically challenging, improved estimates of conductance of water vapor at leaf to canopy scales is critical for improving our mechanistic understanding of plant water fluxes in wet environments.

Introduction

Tropical ecosystems are known for their biodiversity and warm, humid climate. These ecosystems are also extremely threatened by human development and climate change (Buytaert et al. 2005, Buytaert et al. 2011). The prediction is that more prolonged or more intense dry seasons will occur in the tropics and may lead to higher tree mortality (IPCC 2014), especially through cavitation in drought sensitive species (Bourne et al. 2015). Other extreme events, like frequent rainfall, can also lead stomata to decrease or enhance their sensitivity to a range of vapor pressure deficit in conjunction to leaf anatomical features (Hanba et al. 2004). Stomata are responsible for triggering water uptake and carbon assimilation and, subsequently, release water to the atmosphere or allocate carbon to biomass. These processes are known as transpiration and photosynthesis, respectively. For these processes to occur, stomata respond negatively or positively to certain degrees of sensitivity. This sensitivity refers to the magnitude in which stomatal conductance is reduced as vapor pressure deficit increases (Oren et al. 1999). Stomata are influenced by the physical barrier of leaf boundary layer thickness, which is proportional to the ratio of leaf size and wind speed, to determine the magnitude in which gas exchange will occur (Schuepp 1993). The thickness of the leaf boundary layer will determine the stomatal resistance (r_s) or conductance ($g_s=1/r_s$) (Bonan 2008a).

Therefore, stomatal conductance is not only dependent on external factors, but is also significantly affected by phylogenetic characteristics. Leaf position inside the canopy, size, age, number and position of stomata and leaf anatomical features (e.g., pubescence) are a few examples of variables which enhance or reduce stomatal conductance, especially by creating small-scale leaf microclimates (Pincebourde and Woods 2012). Leaf-level measurements have shown that some species can continue transpiring or quickly recover from wetting events through specialized leaf traits that enable fast drying, protects the stomata from wetting or even enhances stomatal aperture following rain events (Smith and McClean 1989, Hanba et al. 2004, Urrego-Pereira et al. 2013). Hence, when acknowledging the biodiversity of plant species in the tropics, the task of measuring or modelling stomatal conductance becomes even more challenging.

For many decades, to simplify plant resistance studies, empirical models based on climate have been developed to facilitate the estimation of stomatal conductance. To better represent stomatal responses to climate and canopy heterogeneity, researchers have proposed models to estimate canopy conductance (g_c), which is driven by both g_s and leaf boundary layer conductance. While stomatal conductance to water vapor can be easily estimated using leaf transpiration (as a biological parameter), temperature and vapor pressure deficit (Monteith and Unsworth 1990), g_c additionally considers wind, solar radiation, and air and water physical proprieties throughout the canopy. Essentially, g_c is the parallel sum of the individual leaf conductances per unit projected leaf area (or leaf area index). However, models are not able to dissociate the “physiological” component from the “phylogenetic leaf” component, and most certainly will not depict the horizontal and vertical variation with a forest stand (Jones 1992). Jarvis and McNaughton (1986) state that even leaves with equal conductances do not necessarily contribute equally to the canopy transpiration and vice-versa due to highly variable microclimatic conditions within the canopy (O'Brien et al. 2004, Dietz et al. 2007). As the physiological component of g_c, g_s fluctuations will proportionately cause fluctuations in transpiration (Landsberg and Gower 1997). Hence, when modelling g_c, actual measurements for transpiration and/or g_s are necessary for a more accurate estimation.

Transpiration can be modelled through robust models like Penman-Monteith (Monteith and Unsworth 1990) and Priestley-Taylor (Priestley and Taylor 1972), direct leaf measurements from infrared gas analyzers, volumetric methods (i.e. potometers) (Kramer and Boyer 1995) and direct plant organ (e.g. stem, roots, branches) measurements through heat-based sensors, also known as sap flux sensors (Granier 1987, Cermak and Nadezhdina 1993, Čermák et al. 2004). All available methodologies have advantages and disadvantages, but to monitor continuous and long-term variation, sap flux sensors, combined with weather stations, have been widely used across biomes. Sap flux derived transpiration has been used in multiple studies (Granier et al. 2000, Wullscheleger et al. 2001, Motzer et al. 2005, McDowell et al. 2008, Han et al. 2011) and has been shown to be a reliable parameter to estimate g_s and g_c (Zhao et al. 2005, Liu et al. 2008, Mereu et al. 2009).

The Penman-Monteith model (Penman 1948, Monteith 1965) was developed to estimate the rate in which wet surfaces exchanged sensible and latent heat with the air, considering that this exchange is dependent on temperature and vapor pressure deficit. Aerodynamic and stomatal resistances are also used in this equation to incorporate leaf and canopy dynamics, even though those parameters are more difficult to acquire or estimate (Flint and Childs 1991). The difficulty in obtaining these latter parameters led to simplifications of this equation, such as the Priestley-Taylor model (Appendix B). Although their applicability has been proven through the years in various ecosystems (Sumner and Jacobs 2005), some assumptions from this model makes it difficult to apply them in certain environments. The main assumption of the Penman-Monteith model that the canopy is “a big leaf” while the vertical structure of forest stands is complex (Shi et al. 2008), may lead to large estimation errors in tropical forests with highly diverse canopy structures and wetness gradients. This also applies to g_s models. While the Monteith and Unsworth (1990) model has been adapted (Jones 1992) and been widely used, the calibration of this model to temperate ecosystems can lead to large estimation errors in other ecosystems, like the tropics. One of the conditions implied in this model, which may not be always applicable to tropical forests, is that leaf and air temperature are considered as equal when leaves are small and air mixing is high within the canopy. Thus, atmospheric vapor pressure deficit can also be considered as equal to air-to-leaf vapor pressure deficit (Ewers and Oren 2000).

An energy-limited environment with highly variable climate, as is common in wet montane tropical forests, can lead to reduced stomatal responses under these conditions (Bruijnzeel and Veneklaas 1998) that further hinders our ability to predict this parameter to be predicted using models. When assessing wet canopy conditions, the theory behind g_c is that stomata exert no influence on transpiration ($g_c \rightarrow \infty$ and decoupling coefficient (Ω) = 1) (Landsberg and Gower 1997). Additionally, constantly wet environments will maintain thicker atmospheric and leaf boundary layers if turbulence and latent heat are not enough to dissipate this resistance. Ewers and Oren (2000) advise that to avoid g_s and g_c estimate errors, the calculation should be limited to conditions of vapor pressure deficit above 0.6 kPa, due to uncertainties in sap flux, relative humidity and temperature measurements. However, most tropical environments with substantial rainfall amounts and warm temperatures have an average annual or seasonal vapor pressure deficit below 0.6 kPa (Grip et al. 2005, Vourlitis et al. 2006, Clark et al. 2013, Berry et al. 2016).

Hence, the goal of this chapter was to explore how leaf wetness affects canopy (g_c) and stomatal (g_s) conductance across a range of environmental conditions in a frequently wet and energy-limited tropical forest. This objective relied on sap flux derived transpiration to test multiple models of g_c and g_s to determine their strengths and weaknesses for use in tropical forest canopies under frequent wet conditions. I hypothesized that some conductance models will perform better than others if they adequately represent the driving gradient of leaf-to-atmosphere vapor fluxes. Results of this study will clarify the complexity of tropical canopy processes while wet and will provide useful insights for further studies to improve climatic modelling in these biomes.

Materials and Methods

Study site and tree selection

This study was conducted at a forest plot located in the Texas A&M University Soltis Center for Research and Education near San Isidro de Peñas Blancas in the

Alajuela Province, Costa Rica (10^{o}23’13”N - 84^{o}37’33”W). The forest plot is approximately 600 m.a.s.l. It is bordered by the Children’s Eternal Rainforest and in the proximity of the Monteverde-Arenal Mountain Cloud Forest Reserve. The forest plot was delineated through a rectangular-shaped 2200 m^{2} in area with a 42-m tall micrometeorological tower at its center.

The study area has an average annual temperature of approximately 24^{o}C, relative humidity on average >70% and mean annual rainfall can reach over 5000 mm year^{-1} (Dr. Eugenio Gonzalez, *Pers. Comm.*) , with the “dry season” (~200 mm month^{-1}) between January and April (Teale et al. 2014). Vegetation is characterized as transitional tropical premontane moist forest (Holdridge 1967). *Carapa guinanesis* Aubl. is the most frequent tree species among the 53 species surveyed at this plot. Average canopy height of the plot is 19.6 ± 10.1 m and the overstory averages 30.6 ± 11.3 m.

Micrometeorological measurements

The micrometeorological measurements of this study were mostly taken at 33-m and 44-m above the ground. The plot is located in a 45-degree slope terrain. Net radiation (R_{net}, W m^{-2}) was measured using a net radiometer (CNR1, Kipp & Zonen, Bohemia, NY) hoisted to 44 m above the ground on a mast. The eddy covariance system, composed of a three dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, UT) and infrared gas analyzer (AP200, Campbell Scientific, Logan, UT), was installed at 33 m, and measured wind speed (u, m s^{-1}), air temperature (T_{air}, K) and atmospheric pressure (P, kPa). Other micrometeorological sensors installed at this level included: dieletric leaf wetness sensors (*LW*, mV converted into %) (LWS, Decagon Devices, Pullman, WA) and two infrared temperature sensors (T_{leaf}, ^{o}C) measuring shaded and sunlit leaves (IRTS-P, Apogee Instruments Inc., Logan, UT).

The eddy covariance system measurements were stored in the gas analyzer data logging interface (LI-7550, LI-COR, Lincoln, NE) at 10 Hz intervals and later processed and averaged through the EddyPro software (LI-COR, Lincoln, NE) at 30-min intervals. Vapor pressure deficit (δe, kPa) and leaf-to-air vapor pressure (δl, kPa) were estimated using air and leaf temperature, respectively, and water vapor concentration (AP200, Campbell Scientific, Logan, UT) by following equation 2 highlighted in Chapter II. All other micrometeorological sensors were stored in a data logger (CR1000, Campbell Scientific, Logan, UT) and, when necessary, collected by a multiplexer (AM25T, Campbell Scientific, Logan, UT) and averaged in 5-min intervals, which were later converted into 30-min intervals to match the eddy covariance system measurements.

The two measurements outside of the forest plot were precipitation amount and relative humidity (%). Daily precipitation amounts were collected using a manual rain gauge along with relative humidity (HC2S3-L60, Campbell Scientific, Logan, UT) at an open location less than 400 m away from the study area tower.

Sap flux measurements, stand transpiration and leaf area index

This study used the same 26 sampled tree species from Chapter II, independently of their respective size category (Table 1). Heat dissipation sap flux measurements (J_s) (Granier 1987) described in Chapter II, were also used for this study. The sap flux monitoring was extended throughout the year of 2015 (Jan. 01 – Dec. 31, 2015). Canopy transpiration (E_c, mm day^{-1}) was estimated in the same manner as Chapter II (eq. 2), but was converted into a smaller time-scale (mm s^{-1} or kg m^{-2} s^{-1}) and the estimates were not partitioned by canopy level.

Leaf area index (LAI) was determined through hemispherical images (Englund et al. 2000). The images were taken using a high-resolution camera (D90, Nikon, Melville, NY) coupled with an 8-mm fisheye lens with hood (F3.5-HD, Rokinon, New York, NY). The measurements were taken at 9 points within the plot. The LAI points were located 15-m horizontally and vertically from the nearest points. Measurements were taken during overcast conditions in January and June, 2015, and February and August, 2016. The instrument was leveled at 1-m from the ground using a tripod. The hemispherical images were analyzed through a canopy analysis software (HemiView 2.1, Delta-T Devices, Cambridge, UK) (Rich et al. 1999) that calculated LAI using a threshold value of 217. Leaf area index was, on average, 3.3 ± 0.5 m^2 m^{-2}.

Calculations of canopy, stomatal, aerodynamic conductances and decoupling coefficient

Daytime canopy conductance to water vapor (g_c, m s^{-1}) was estimated using daytime stand transpiration converted into canopy transpiration (E_l, kg m^{-2} s^{-1}). Daytime (5:00 AM to 6:30 PM) was based on net radiation and sap flux diurnal trends and did not differ throughout the study period. The conversion from stand transpiration to canopy transpiration followed the methodology used by Tang et al. (2006) (E_l=E_c/LAI, assuming that time lags between sap flux rates and environmental variables are negligible).

Furthermore, the models used to estimate canopy conductance were: the inverted Penman-Monteith equation (Monteith and Unsworth 1990, Lundblad and Lindroth 2002, Lu et al. 2003) (eq. 6) and a simplified equation of the Penman-Monteith proposed by McNaughton and Jarvis (1983) (eq.7).

$$g_{c-PM} = \frac{\gamma \lambda E_c g_a}{\Delta \cdot R_{net} + \rho C_p \delta_e g_a - \lambda(\Delta + \gamma) \cdot E_c} \qquad \text{(eq. 6)}$$

$$g_{c-MJ} = \frac{(E_c \cdot \gamma \cdot \lambda)}{(\rho \cdot C_p \cdot \delta_e)} \qquad \text{(eq. 7)}$$

where, E_c is the canopy transpiration derived from sap flux measurements (Kumagai et al. 2008), R_{net} is net radiation (W m^{-2}), Δ is the rate of change of saturation of water vapor pressure with temperature (kPa K^{-1}) and γ is the psychometric constant (kPa K^{-1}), ρ is density of dry air (=1.183 at 25 ^{o}C), C_p is the specific heat of air at constant pressure (=1005 J kg^{-1} K^{-1} at 25 ^{o}C), δe is vapor pressure deficit (kPa). Δ and γ were calculated according to Zotarelli et al. (2010). g_a (m s^{-1}) is aerodynamic conductance, which was estimated through the following equation (Choudhury and Monteith 1988, Granier et al. 2000) (eq. 8):

$$g_a = \left[\frac{(k^2 \cdot u)}{(\ln(z-d)/z_0)^2}\right] \qquad \text{(eq. 8)}$$

in which, k is von Karman's constant (=0.41), u is wind speed (m s^{-1}), z is height of measurement (= 33 m in this study), d is displacement height (= 2/3·canopy height, which hc = 30.6 m; Brutsaert 2005) and z_0 is roughness length (= $0.08 \cdot h_c$ = 2.45) (Hansen 1993).

Stomatal conductance to water vapor (g_s, m s^{-1}) was determined through the adapted versions of Fick's Law ($g_s = E_l/\delta_l$) proposed by Jones (1992), which considers leaf temperature instead of air temperature (eq. 9). The other equation was proposed by Monteith and Unsworth (1990) and used by Ewers and Oren (2000), Ewers et al. (2001) and McDowell et al. (2008) to model g_s using air temperature (eq. 10). Other g_s models that estimate conductance of carbon dioxide were taken in to consideration for this study (e.g. Ball-Berry and Jarvis-Loustau models) (Wijk et al. 2000), but, unfortunately, there were not enough measurements conducted to be implemented properly to these models (e.g. diurnal photosynthetic and actual stomatal conductance rates).

$$g_{s-J} = \frac{E_l}{\left(\frac{2.17}{T_l}\right) \cdot \delta_l} \qquad \text{(eq. 9)}$$

$$g_{s-MU} = \frac{(E_l \cdot K_T)}{\delta_e} \qquad \text{(eq. 10)}$$

where, E_l is the leaf transpiration ($E_l = E_c/LAI$), K_T is a temperature conductance coefficient (=$115.8 + 0.423 \cdot T_{air}$ (kPa m^2 kg^{-1}), T_{leaf} (^oC) is leaf temperature for shaded and sunlit leaves, δ_l (kPa) is air-to-leaf vapor pressure deficit, also for shaded and sunlit leaves, and 2.17 is the ratio between the molecular weight of water (M_w=18.02 g mol^{-1})

and the universal gas constant (R=8.31 J mol^{-1} K^{-1}). The temperature conductance coefficient (K_T) assumes that leaf temperature is equal to air temperature and, consequently, enables the use of δe (Ewers and Oren 2000, McDowell et al. 2008).

The decoupling coefficient (Ω) was calculated according to Jarvis and McNaughton (1986) (eq. 11):

$$\Omega = \frac{(\varepsilon+1)}{\left(\varepsilon + \left(1+\frac{g_a}{g_c}\right)\right)} \qquad \text{(eq. 11)}$$

Where, ε is the molecular weight of water vapor/dry air ratio, which can be determined by (Δ/γ). In other words, the decoupling coefficient is the ratio between the leaf, canopy surface conductance and the boundary layer. Hence, this parameter determines the relative effect of aerodynamic conductance (e.g., wind effects) and canopy conductance (e.g., resistance in the exchange of water fluxes) in the stomatal control of transpiration. This dimensionless parameter varies between 0 (perfect coupling) and 1 (complete isolation) (Jones 1992).

Conversion of canopy, stomatal and aerodynamic conductance (m s^{-1}) into molar based units (mol m^{-2} s^{-1}) was conducted according to Pearcy et al. (1989) (eq. 12). P is atmospheric pressure (kPa) and air temperature in Celsius.

$$g(mol\ m^{-2}s^{-1}) = g\ (m\ s^{-1}) \cdot 446\left(\frac{273}{T_{air}+273}\right) \cdot \left(\frac{P}{101.3}\right) \qquad \text{(eq. 12)}$$

Data analyses

Similarly to Chapter II, leaf wetness categories were stipulated according to wetness percentage thresholds. Dry periods were classified when daily average *LW*% ranged within 0-9.9%, semi-dry periods within 10%-49.9%, and wet periods within 50-100%. Dry period threshold was reduced to 10%, in comparison to Chapter II's 15%, to reassure the dry canopy conditions. To evaluate the relationship between conductance estimates and environmental variables at each wetness condition, model fits (linear and non-linear) were evaluated according to the adjusted coefficient of determination (R^2_{adj}) and *P*-value. Due to data gaps, data filtering was required to proceed with the analyses. Statistical analyses were performed with R version 2.6.2. software (R Core Team 2013).

Results

Micrometeorological measurements, aerodynamic conductance, and Ω

In 2015, precipitation totaled 5213 mm year^{-1} with an average of 434 ± 189 (sd) mm month^{-1}. March was the driest month (115 mm) and July was the wettest (669 mm). Air temperature showed little variation throughout the year, with an annual average of 23.3 ± 2.6 ^{o}C. The highest temperatures mainly occurred during the dry days with an average of 24.6 ± 1.6 ^{o}C) and slightly lower temperatures were recorded during wet days (21.8 ± 1.6 ^{o}C). It is important to highlight that wet days did not always occur during the cooler, rainy season, leading to certain days with higher air temperatures and slightly higher vapor pressure deficit. The opposite also applies to dry days. In contrast, leaf temperatures were cooler as leaf wetness increased. Shaded T_{leaf} during wet days was, on average, 17.2 ± 2.1 ^oC, followed by semi-dry days (19.2 ± 2.5 ^oC) and dry days (21.4 ± 2.9 ^oC).Sunlit T_{leaf} was higher than shaded leaves, but also decreased with increase in wetness (wet: 22.2 ± 1.2 ^oC; semi-dry: 23.0 ± 1.2 ^oC; dry: 25.2 ± 1.7 ^oC). However, shaded leaf to air temperature difference was on average -3.9 ± 1.9 ^oC with the highest difference during wet days (-4.7 ± 1.4 ^oC). Meanwhile, sunlit leaves had the smallest difference within wetness conditions (-0.2 ± 0.5 ^oC) with dry days usually having leaf temperatures warmer than air (0.1 ± 0.6 ^oC); but, overall, sunlit leaves were almost identical to air temperature ($R^2_{adj} = 0.93$, $P<0.001$). Consequently, leaf-to-air pressure deficit was on average 44% lower for shaded leaves than sunlit leaves. Wind speed averaged 1.1 ± 0.4 m s^{-1} across the entire study period and varied little among wetness conditions (dry = 1.1 ± 0.4 m s^{-1}, semi-dry = 1.1 ± 0.4 m $s^{-1}$and wet = 1.3 ± 0.3 m s^{-1}) (Figure 16a).

Net radiation averaged 205 ± 88 W m^{-2}. In contrast to air temperature and wind speed, net radiation varied greatly across the wetness conditions. During dry days, daily average net radiation during daylight hours was 242 ± 74 W m^{-2}. While on semi-dry and wet days, daily average net radiation was 155 ± 77 W m^{-2} and 119 ± 73 W m^{-2}, respectively, since wet conditions often coincide with intermittent or long periods of cloud coverage. Likewise, vapor pressure deficit declined, but little among wetness conditions (Figure 16 and 17). Wet days had the lowest δe (0.2 ± 0.1 kPa), followed by semi-dry (0.4 ± 0.2 kPa) and dry days (0.6 ± 0.2 kPa) (Figure 16c). Additionally, relative humidity was generally above 80% throughout the year. Relative humidity averaged 79.2 ± 8.2 % across all days, while dry days averaged 81.7 ± 9.6 %, semi-dry 77.6 ±16.5 % and wet days 74.4 ± 17.2 %.

Although constant throughout the year, wind speed's diurnal variation was greater during semi-dry (5.8 ± 2.9 m s^{-1}) and wet days (5.1 ± 2.7 m s^{-1}), which consequently affected aerodynamic conductance and decoupling coefficient within wetness conditions. Decoupling coefficients (Ω) were on average 0.98 decreasing to as low as 0.62, but mainly stayed above 0.90 during the day. Although similar, dry days' small variation in wind speed throughout the day led to slightly higher Ω ($P<0.001$), differentiating itself from semi-dry and wet days ($P=0.06$). Lowest Ω values were observed during the first 2 morning hours (5-7AM) and during elevated vapor pressure deficit periods (Figure 16c).

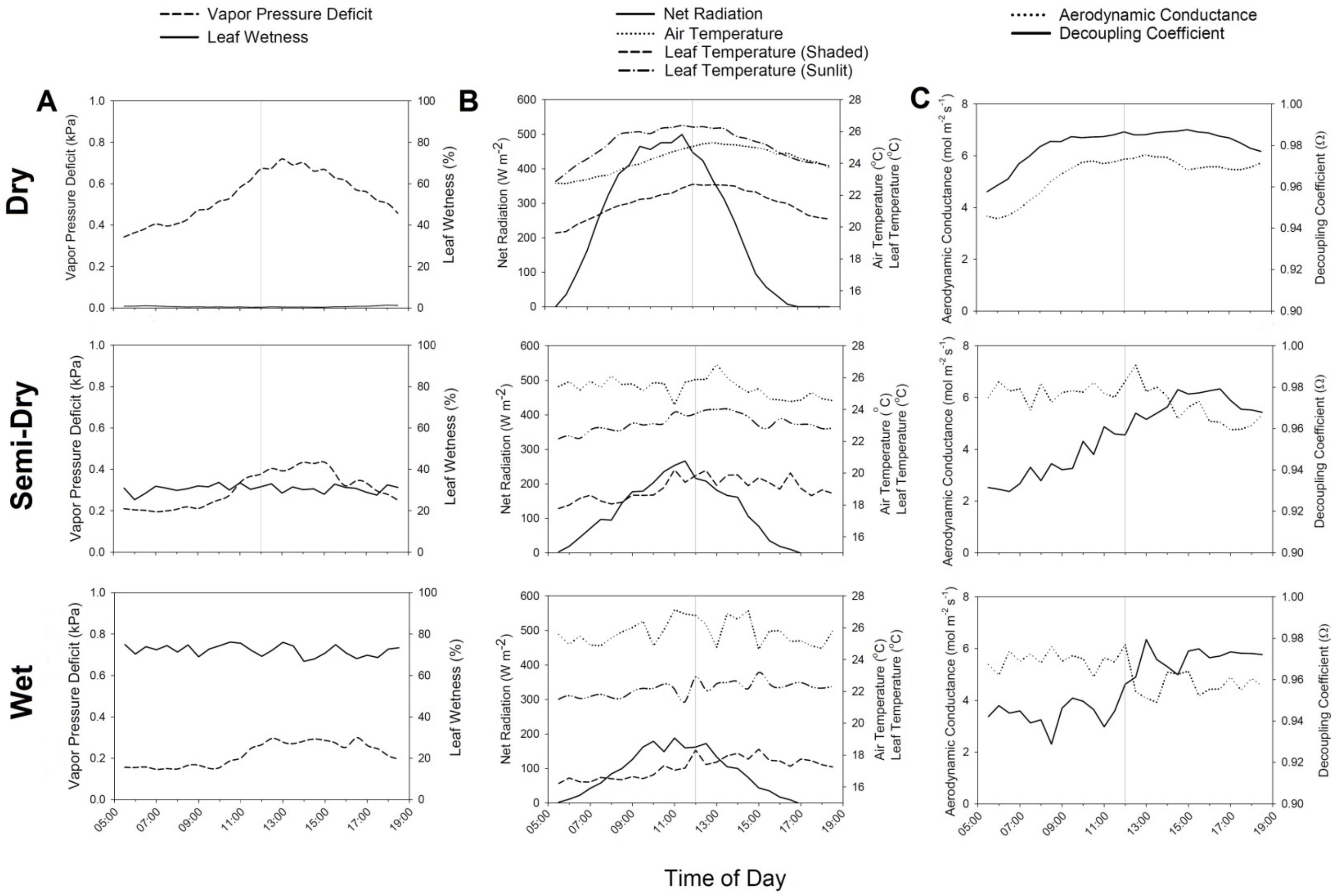

Figure 16. Diurnal micrometeorological trends across wetness conditions. Groupings: A) Vapor pressure deficit (kPa), wind speed (m s^{-1}) and leaf wetness (%); B) net radiation (W m^{-2}), air and leaf temperature (^{o}C, shaded and sunlit); C) aerodynamic conductance (mol m^{-2} s^{-1}) and decoupling coefficient (dimensionless). Note: Grey vertical line indicates midday (12PM).

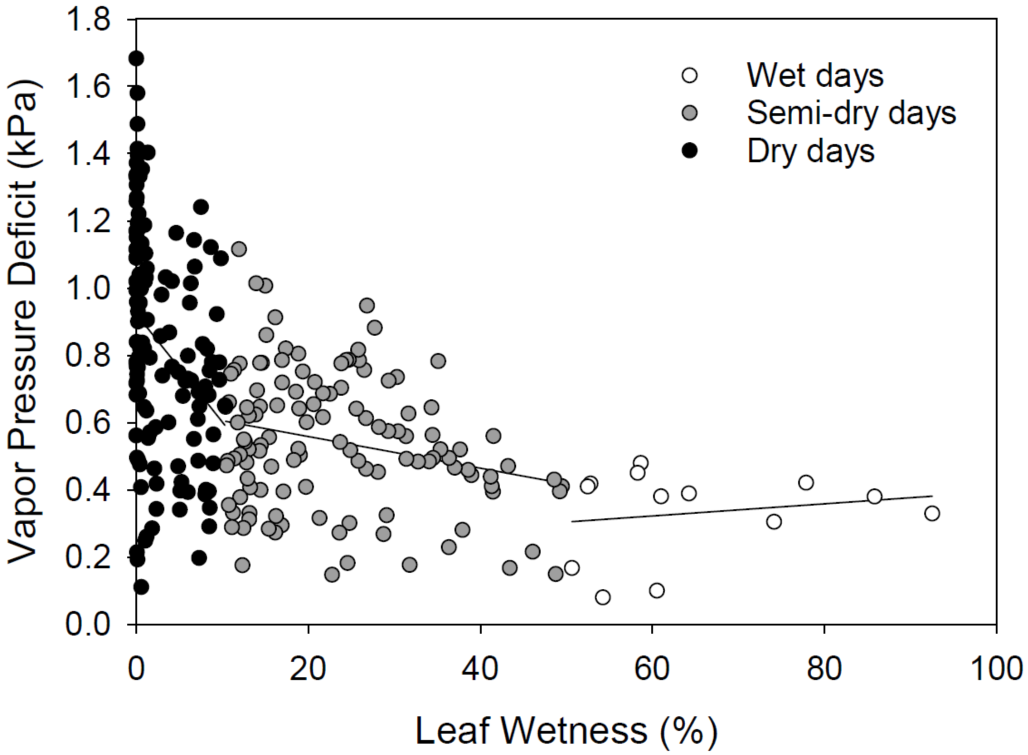

Figure 17. Vapor pressure deficit (kPa) relationship with leaf wetness (%) ($R^2_{adj} = 0.27$, $P<0.001$; dry: $R^2_{adj} = 0.10$, $P<0.001$; semi-dry: $R^2_{adj} = 0.06$, $P<0.05$; and wet days: $R^2_{adj} = 0.03^{ns}$).

Canopy transpiration: observed and estimated

Canopy transpiration (E_c) derived from sap flux measurements totaled 540 mm year^{-1}, with a daily average of 1.4 ± 0.6 mm day^{-1}. Daily total transpiration rates declined with wetness conditions, similarly to Chapter II. E_c on wet days was 73% and 57% less than dry and semi-dry days, respectively. E_c mainly peaked between 12PM and 1PM, with wet days being the latest to peak (Figure 18 and Table 6). This peak was similar to vapor pressure deficit and leaf temperature, but not net radiation, which peaked around

10AM due to the slope of the mountain (Figures 16 and 18). Nonetheless, these climatic trends observed during dry days suggest that light might trigger the initiation of E_c in the morning, but fading sunlight in the afternoon did not exert as strong an influence as δe, since it remains high for longer into the afternoon. Meanwhile, semi-dry and wet days were driven mostly by δe throughout the day, since sunlight inputs were significantly lower than dry days. Due to the possibility of nighttime transpiration and trunk capacitance, conductance estimates were solely focused on daytime to avoid non-realistic values during the night.

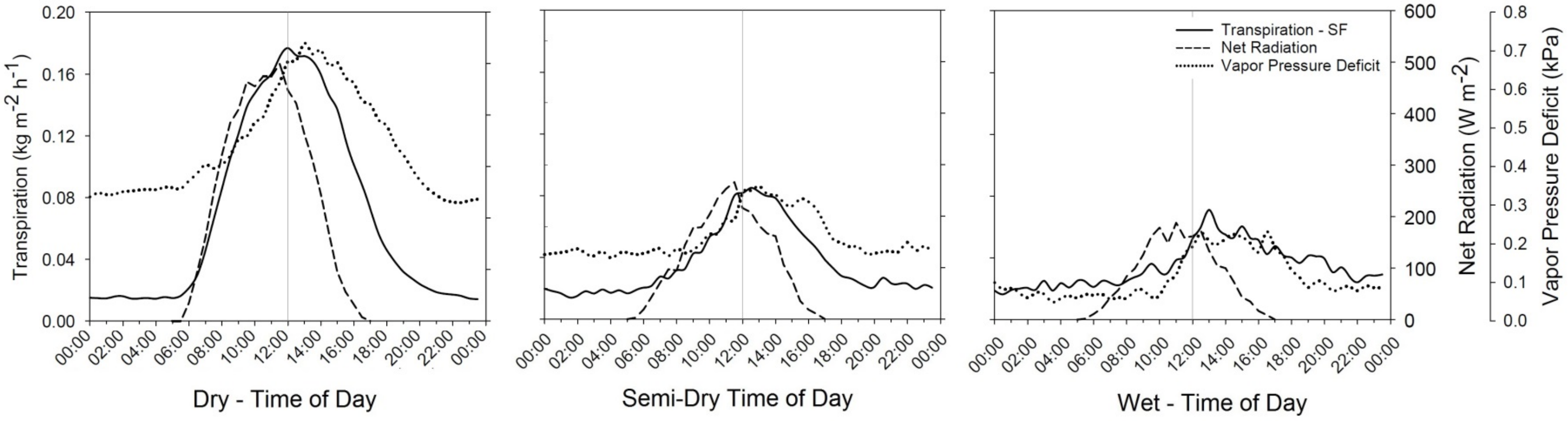

Figure 18. Diurnal trends of transpiration rates (kg m^{-2} h^{-1}) derived from sap flux measurements (E_c– solid line), vapor pressure deficit (dotted line) and net radiation (W m^{-2} – dashed line) across wetness conditions (From left to right: dry, semi-dry and wet).

Canopy and stomatal conductance

When comparing $g_{s\text{-J}}$ (Jones 1992) and $g_{s\text{-MU}}$ (Monteith and Unsworth 1990), there was only a -11% difference between sunlit $g_{s\text{-J}}$ and $g_{s\text{-MU}}$, while shaded $g_{s\text{-J}}$ was 30% and 22% higher, respectively (Figures 19 and 20). Considering that g_s of sunlit leaves and air temperature were more strongly correlated, in comparison to g_s of shaded leaves ($R^2_{\text{adj}} = 0.49$, $P<0.001$).

Sunlit $g_{s\text{-}J}$ was 27% higher than $g_{s\text{-}J}$ of shaded leaves during wet days and 34% lower during semi-dry days. Sunlit $g_{s\text{-}J}$ were also higher than $g_{s\text{-MU}}$ (+17%) during wet days. This difference was mainly attributed to the higher δ_l from sunlit leaves during wet days in comparison to the shaded leaves with ~50% less δ_l. During dry days, shaded leaf $g_{s\text{-}J}$ was 8% higher than $g_{s\text{-MU}}$, while sunlit $g_{s\text{-}J}$ was 20% lower.

Overall, g_c estimates were the least similar within all models tested. On average, $g_{c\text{-MJ}}$ was on average 11% higher than $g_{c\text{-PM}}$ across wetness conditions. Opposite to g_s, g_c estimates had the largest reduction during semi-dry conditions for both MJ and PM models (Figure 21b). Semi-dry day $g_{c\text{-MJ}}$ was on average 11% less than wet days and 9% less on dry days; while $g_{c\text{-PM}}$ was on average 16% less and 2% less, respectively. The models were most similar during wet days with $g_{c\text{-MJ}}$ only 1% higher; while, $g_{c\text{-MJ}}$ estimates on dry days and semi-dry days were 7% and 14% higher, respectively. Although dry and semi-dry day model differences were similar, semi-dry days had the lowest g_c values within wetness conditions.

At the diurnal scale, although g_s and g_c show similar daily trends, there is a clear shift of the diurnal peak (before and after midday) between all g_s and g_c estimates

(Figure 21a and Table 6). Although E_c usually peaked at midday, $g_{\text{s-J}}$ shaded, $g_{s\text{-MU}}$ and $g_{c\text{-MJ}}$ peaked before 11AM, with exception on mostly wet days (Table 6). In contrast, $g_{c\text{-PM}}$ peaked after midday during all wetness conditions. Hence, these g_s and g_c estimates suggest that transpiration when associated with multiple climatic parameters may lead to different periods of conductance optima. Additionally, relying only on air or leaf temperature, which varies greatly throughout wet and semi-dry days, may lead to unrealistic spikes (day and night) that were possibly minimized by other climatic variables, such as wind speed or net radiation. Hence, g_c models with humidity, net radiation and aerodynamic parameters (eq. 4) seemed more reliable than models with only humidity (eq. 5) or heat parameters (g_s equations).

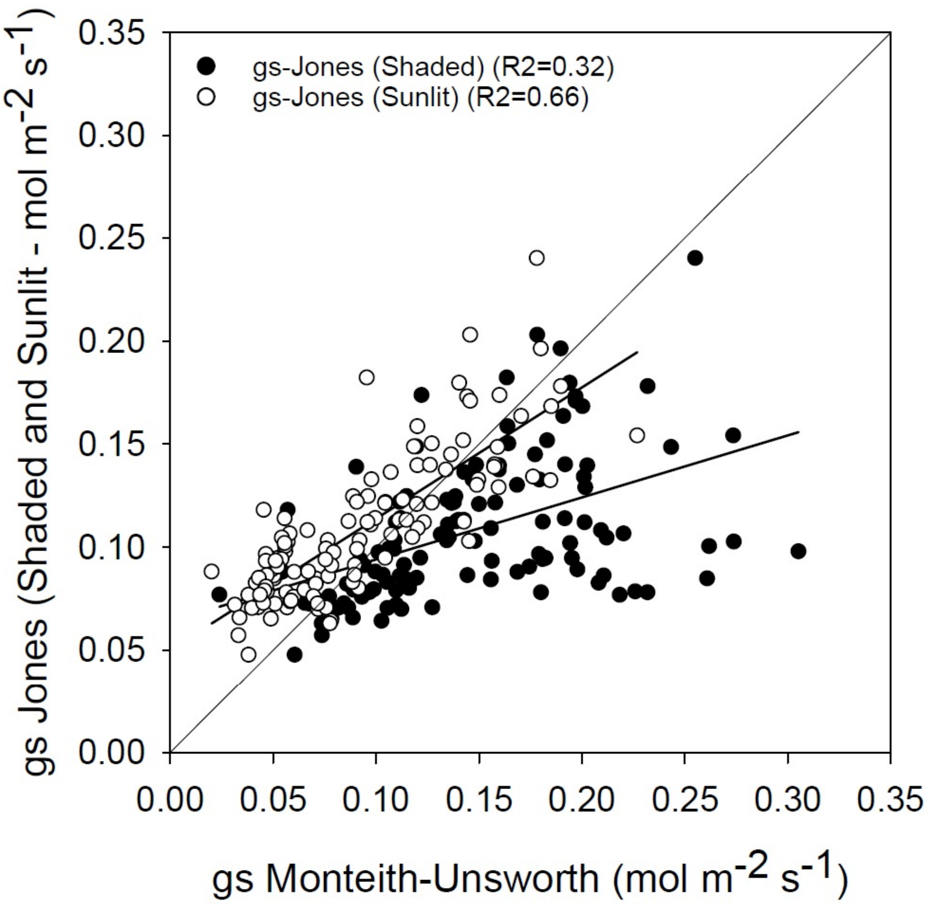

Figure 19. Relationship between stomatal conductance derived from Monteith-Unsworth model with stomatal conductance derived from Jones model with shaded and sunlit leaf temperature.

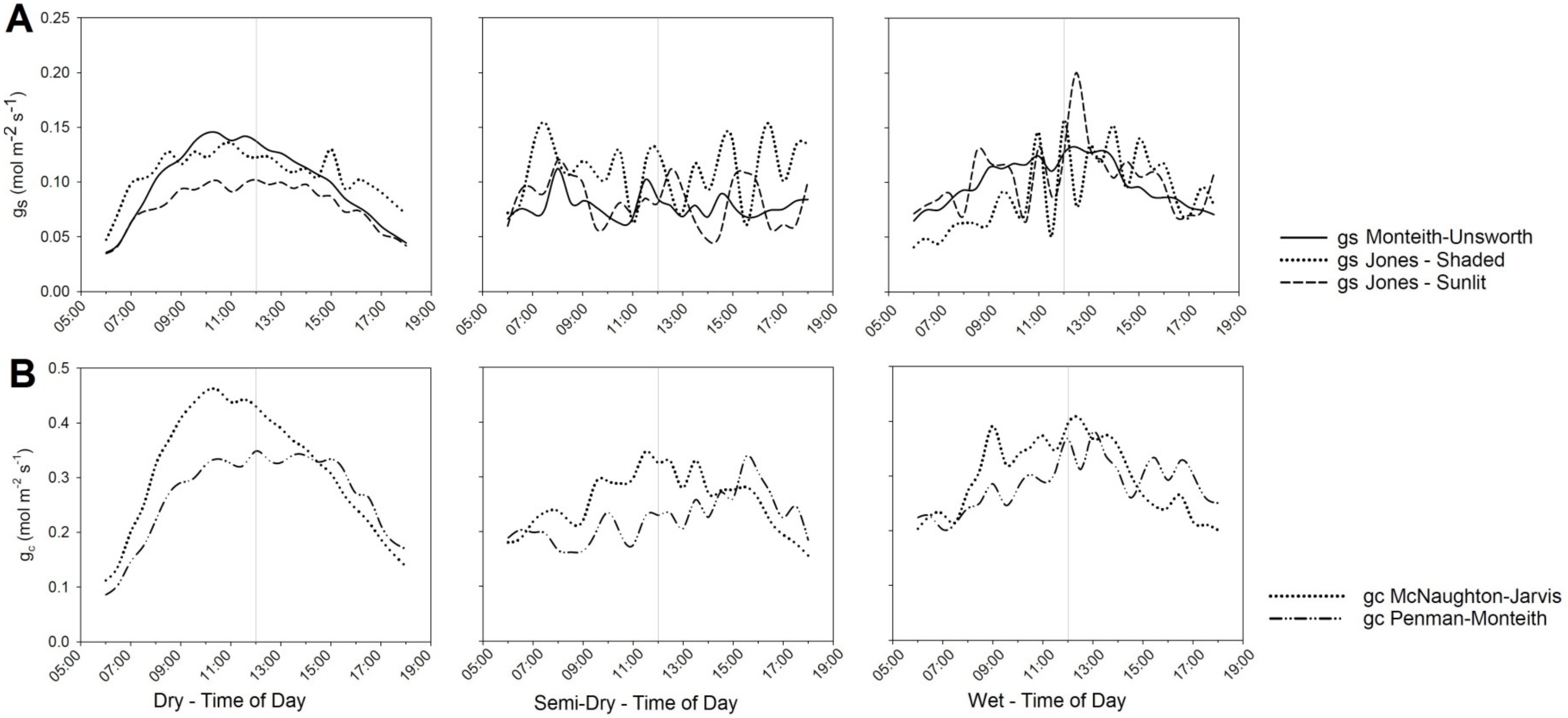

Figure 20. Daytime diurnal trends of stomatal conductance - g_s (A) (Jones (1992) using shaded and sunlit leaf temperatures (T_{leaf}) and Monteith & Unsworth (1990) using T_{air} models) and canopy conductance - g_c (B) (McNaughton & Jarvis (1986) and Penman-Monteith models) estimated for different wetness conditions.

Table 6. Daytime average peak of canopy transpiration (E_c – kg m^{-2} h^{-1}) canopy (g_c), stomatal (g_s), aerodynamic (g_a) conductances (mol m^{-2} s^{-1}) and decoupling coefficients for the entire year and each wetness condition. Note: MJ = McNaughton and Jarvis equation using sap flux derived transpiration; PM = Penman-Monteith equation using sap flux derived transpiration; J is equivalent to Jones (1992) equation and MU to Monteith and Unsworth (1990). Tukey HSD denoted with letters as indicated by ANOVA (*P*<0.05). Capital letters represent difference within model averages (MJ vs. PM and J shaded, sunlit vs. MU) and lower case represents difference within wetness for each parameter

Period	E_c	g_c MJ	g_c PM	g_s J_Shaded	g_s J_Sunlit	g_s MU	g_a	Ω PM_SF	Ω MJ_SF
Overall	0.16±0.04	0.43±0.17^{A}	0.34±0.15^{B}	0.18±0.11^{A}	0.11±0.08^{B}	0.14±0.07^{C}	5.96±2.57	0.98±0.01^{A}	0.98±0.01^{B}
Time	12PM	1030AM	12PM	2PM	1230PM	11AM	12PM	3PM	3PM
Dry	0.18±0.03^{a}	0.46±0.15^{a}	0.35±0.14^{a}	0.12±0.07^{a}	0.09±0.06^{a}	0.11±0.13^{a}	6.04±2.64^{b}	0.99±0.01^{a}	0.99±0.01^{a}
Time	12PM	1030AM	12PM	11AM	130PM	2PM	1PM	3PM	3PM
Semi-dry	0.09±0.03^{b}	0.35±0.18^{b}	0.34±0.18^{b}	0.15±0.13^{a}	0.12±0.11^{a}	0.11±0.06^{b}	7.24±2.22^{a}	0.98±0.02^{b}	0.98±0.02^{b}
Time	1230PM	1130AM	330PM	730AM	8AM	8AM	1230PM	430PM	230PM
Wet	0.07±0.03^{c}	0.40±0.19^{c}	0.37±0.20^{c}	0.16±0.13^{b}	0.20±0.15^{b}	0.14±0.10^{a}	5.12±2.76^{b}	0.98±0.02^{b}	0.97±0.02^{b}
Time	1PM	1230PM	12PM	12PM	1230PM	1PM	3PM	1PM	1PM

Environmental control on canopy conductance

Although there were differences between the canopy conductance models, McNaughton & Jarvis did not follow the same diurnal trend in E_c. Therefore, in this section, I decided to only analyze $g_{c\text{-PM}}$ to identify their environmental drivers. Likewise, since $g_{s\text{-J}}$ was similar to g_s-$_{\text{MU}}$ under sunlit conditions, $g_{s\text{-J}}$ shaded and sunlit were analyzed separately (Figure 21).

The extremely heterogeneous conditions of the study site affected the relationship of canopy conductance and the various environmental parameters analyzed (Figure 21). Surprisingly, leaf wetness had no effect on canopy conductance ($R^2_{ad\ j}$= 0.002ns) and sunlit stomatal conductance ($R^2_{ad\ j}$= 0.01ns), and was only marginally a factor under shaded conditions ($R^2_{ad\ j}$= 0.03, $P<0.05$) (Figure 21a). Similarly, air and leaf temperature also had little to no relationship (data not shown) with g_c (T_{air}-R^2_{adj} = 0.007ns; $T_{leaf(shaded)}$-R^2_{adj} = 0.07ns; $T_{leaf(sunlit)}$-R^2_{adj} = 0.003ns) and, within g_s, only had a positive correlation between shaded $g_{s\text{-J}}$ and air temperature (R^2_{adj}=0.13, $P<0.001$). The model for $g_{s\text{-J}}$ accounts for T_{leaf} and δ_l, but actual plant responses are also sensitive to the leaf to air temperature difference (T_{diff}). In sunlit leaves, T_{diff} was coupled to $g_{s\text{-J}}$ (increased with cooler temperatures), even though there was only small variation (± 1^{o}C) between air and leaf temperature (R^2_{adj} = 0.11, $P<0.001$) (Figure 21b). Oppositely, shaded leaves were never warmer than the air, and were as much as 7 ^{o}C cooler; $g_{s\text{-J}}$ models for shaded leaves were decoupled with T_{diff}(R^2_{adj} = 0.01ns). During wet days, shaded leaves were always cooler –by 3 ^{o}C than sunlit leaves; during dry and semi-dry days T_{diff} contrasted even more between shaded and sunlit leaves (Figure 21b).

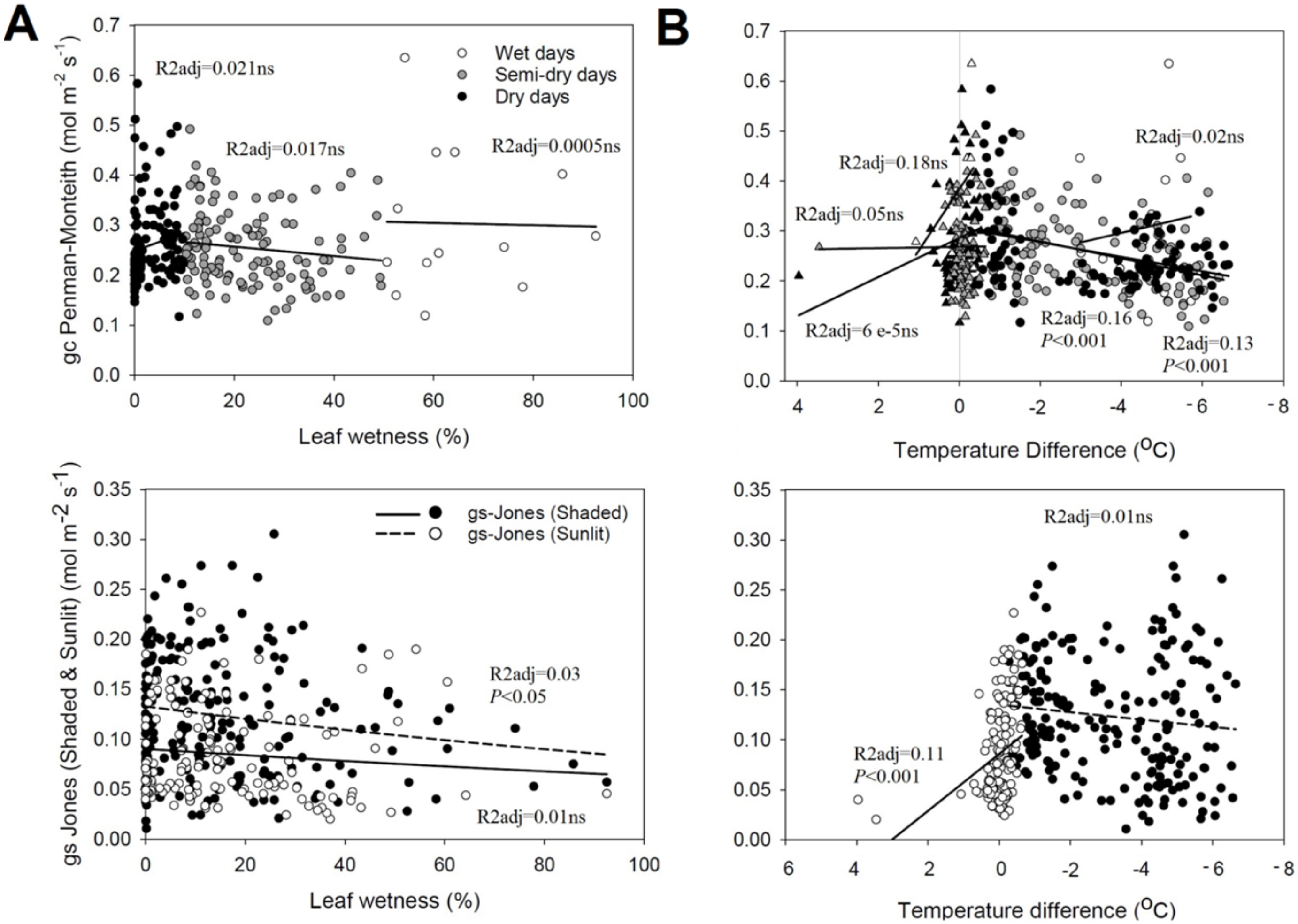

Figure 21. Relationship between daily average canopy and stomatal conductance rates and: A) leaf wetness (%); B) temperature difference (°C).

Discussion

This model comparison led to three major insights: 1) g_c and g_s cannot accurately be predicted under wet conditions without accounting for leaf wetness, 2) even during dry days, low vapor pressure deficits interfere with model accuracy, and 3) intermittent rain during semi-dry and wet days cause large fluctuations in g_c and g_s estimates. As expected, the estimates obtained from the stomatal and canopy conductance models differed due to varying inputs (R_{net} and δe), which revealed the relative importance of driving variables in this system associated with wet canopies and thick leaf boundary layer conditions ($\Omega > 0.90$).

All estimates obtained through this study were consistent with results from other tropical forest studies. Maximum g_s in tropical montane cloud forests have been documented to vary on average 0.2–0.3 mol m^{-2} s^{-1} (Bruijnzeel and Veneklaas 1998); Ecuadorian Andean forests between 0.09–0.17 mol m^{-2} s^{-1} (Motzer et al. 2005); and Brazilian and Colombian Amazon between 0.13–0.5 mol m^{-2} s^{-1} (Meinzer et al. 1993, Roberts et al. 1993, Letts and Mulligan 2005). The g_s estimates found at this study also are consistent with the average g_s measurements conducted during midday dry conditions of Chapter III (0.16 ± 0.11 mol m^{-2} s^{-1}). The observation of increase of conductance variability under wetter conditions indicates that the integration of air or leaf temperature with vapor pressure deficit in the equations was significant enough to enhance g_s by 1/5 when canopies were wet compared to dry conditions.

Canopy conductance estimates were also consistent with other findings from tropical forests. Studies from Borneo and South American Amazon found that maximum canopy conductance range between 0.3 and 1.0 mol m^{-2} s^{-1} (Granier et al. 1996, Meinzer et al. 1997, Malhi et al. 2002, Kumagai et al. 2004, Vourlitis et al. 2006). Also, the heterogeneity in daily microclimate variability are unaccounted in climate models, which may lead to an underestimation of the climatic tolerance of the species if, for example, certain climatic peaks only occur for a short period of the day (Logan et al. 2013). This is even clearer when analyzing the distinct temporal shift in peak midday g_c during semi-dry and wet days, and a smaller shift when dry. Hence, I re-emphasize the importance of smaller, sub-daily temporal scales (e.g. 5 or 15 minute intervals) (Meinzer et al. 1993) when estimating physiological parameter through climatic variables.

Current conductance models do not depict the physical suppression of gas exchange caused by leaf surface wetness. Leaf wetness also affected the accuracy of the models through highly variable climatic conditions and frequent wet-dry cycles, especially due to intermittent rain events. Another challenge for estimating conductance in wet environments is that the range of vapor pressure might be too small to accurately depict the biophysical constraints of leaf wetness simply by reducing the $\delta e/\delta_l$ parameter in the equation.

Although our findings are consistent with other studies, there is still the possibility that the model formulations overestimate conductance to water vapor, since δe was the denominator for all the equations used. Oren et al. (1999) logarithmic exponential decay relationship between δe and conductance considers that g_s or g_c will only decline with increase of δe and enhance only with lower δe, but only as low as 0.6 to avoid large estimation errors (Ewers and Oren 2000). Therefore, highly decoupled forested sites with low δe and wet canopies, even during dry days, may be subjected to overestimation of g_s and g_c, especially since there was strong evidence that transpiration and photosynthesis were mostly suppressed by leaf wetness. Energy-limitation and low δe conditions prevailed ($\delta e < 1$ kPa, $R_{net} \sim 250$ W m^{-2}), even on dry days, which led the models to overestimate stomatal and canopy conductance, but especially on semi-dry and wet days. Although g_s and g_c had clearer diurnal trends under dry canopy conditions, most of the days at this site were atmospherically dry (e.g., $\delta e \sim 1.0$ kPa, $T_{air} \sim 24$ ^{o}C), while canopies may still be wet from nighttime rainfall.

The evidence that g_s and g_c can be enhanced when leaves were more than 10% wet (threshold of dry days) and that the ratio of δe and R_{net} is tightly related to dry conditions (data not shown), suggest tropical canopies can achieve an optimum rate of conductance in unfavorable atmospheric conditions. Leaf wetness has been known to affect (positively and negatively) gas exchange through other studies (Smith and McClean 1989, Brewer and Smith 1995, Ishibashi and Terashima 1995, Hanba et al. 2004, Reinhardt and Smith 2008). However, the results indicating that leaf wetness had little to no effect on conductance suggest that the models do not depict or fully account for leaf wetness biophysical effects to the leaves and whole canopy. Furthermore, this study exposes the deficiency of these models, in which low δe is expected to represent wet canopy and atmosphere conditions. This assumption is even more pronounced during days that morning or evening rainfall may result in higher δe than days with intermittent rainfall throughout the day.

Our findings are consistent to other studies that found that a saturated atmosphere may enhance conductance due to the increase in stomata acclimation to low δe and/or higher soil water content (Hanba et al. 2004, Bourne et al. 2015) or even enhancement through stronger diffuse light during cloudy days (Reinhardt et al. 2010). Kumagai et al. (2004) found that canopy conductance was higher during the rainy season in Borneo, which was attributed to soil moisture increase after dry seasons. While Meinzer et al. (1993) attributed higher g_s, during wet periods, to seasonal variation in leaf age; and Letts and Mulligan (2005) to leaf hypostomaty. Wang et al. (2009) found that Ball-Woodrow-Berry (using relative humidity) model underestimated g_s, while the Leuning model (using δe) overestimated g_s. Although the authors concluded that Ball-Woodrow-Berry model was erroneous, since the expectation was that g_s should enhance with low δe, like other studies, the authors failed to acknowledge the effects of leaf wetness at their study site. Meanwhile, Garcia-Santos et al. (2009) acknowledged the effects of morning dewfall, but decided to neglect it and only consider results from wet soil conditions. The present study site has not yet detected significant soil moisture deficits, thus indicating that the species that occur at this site do not reach sufficient vapor pressure or soil moisture deficits to induce xylem cavitation or changes in mesophyll physiology (Oren et al. 1999). In other words, these species will have a smaller absolute reduction in g_s and g_c with increasing vapor pressure deficit (Ewers et al. 2005). Other authors advise that sensitivity to vapor pressure deficit and decoupling coefficient vary greatly among tropical species and their canopy position, which should be taken in consideration (Meinzer et al. 1997, Wullscheleger et al. 1998, O'Brien et al. 2004).

The model outcome predicted that shaded $g_{s\text{-}J}$ increased, rather than decreased, with wetness, further indicating that the model likely failed to capture the effects of wetness. Although this could be explained through the benefits of leaf cooling, it may also be explained by the rapid response to light inputs that possibly occurs at random periods throughout the day (Schymanski et al. 2013). Additionally, variability in sunlight will also determine the leaf drying rate, which can be enhanced or decreased according to anatomical features (Kuiper and Lapre 2004, Urrego-Pereira et al. 2013). These differences in g_s suggest that each model depicted the distinct leaf boundary layer resistance created by T_{air} or T_{leaf}, and/or δ_l or δe due to the different degrees of air mixing and leaf drying rates within the canopy. Considering that the canopy at the study site is composed of ~25% of sunlit leaves (*unpublished data*), these results imply that g_s estimations in tropical ecosystems should not consider air temperature in their formulations since the leaf boundary layer impedes leaf temperature from increasing linearly with air temperature (Meinzer et al. 1993). This deceleration in leaf heating was even more pronounced during wet periods due to reduced net radiation and inconsistent aerodynamic conductance (Figure 16c). However, the increase in g_s for sunlit leaves during wet conditions may suggest that leaf cooling must be playing an ultimate role.

Following the findings of Chapter II, transpiration increased in the morning in tandem with sunrise, but remained high into the mid-afternoon as sunlight began to decline. Conductance most likely peaks when both R_{net} and δe are maximized, and continues as long as the driving gradient for evaporation persists. This effect was strongest on dry days, however, there was also evidence of higher understory transpiration contribution during the afternoon of wet days, since their canopies were less wet and microclimate had higher vapor pressure deficit than overstory and midstory trees. Loescher et al. (2005) also found higher g_c values during late afternoons. The authors attributed this fact to understory tree transpiration contribution. This explanation fits our study site. Due to intermittent rain events on semi-dry and wet days, g_s and g_c did not follow a clear diurnal trend as dry days and E_c. High climatic variability during those days lead to a sizeable interference on the resulting model estimates, which made it difficult to compare the models and their responses during wet days. These negative, but stronger relationships between shaded leaves, leaf wetness and air temperature suggest that these leaves have little tolerance for overheating or increase of the atmospheric pressure gradient (Gotsch et al. 2014, Binks et al. 2016). Additionally, the significant relationship between shaded g_s and leaf wetness may indicate a larger constraint in drying leaves while in the shade.

In contrast to g_s, g_c estimates had larger differences within the models tested. According to Granier et al. (1996), as the atmosphere and canopy were less decoupled (Ω closer to zero), the Jarvis and McNaughton equation was as accurate as Penman-Monteith (only 6% difference). However, the present study showed Ω was predominantly above 0.90 (complete isolation of the leaf/canopy surface to the atmosphere), indicating that the Jarvis & McNaughton equation is applicable to environments subject to contrasting climatic conditions. The mostly high Ω indicated, independently of wetness conditions, there was little stomatal control over transpiration due to a large leaf boundary layer and, thus, water exchange will rely on external factors (e.g., net radiation, and wind) to occur (Jarvis and McNaughton 1986). Our estimates of decoupling coefficients are consistent with those of Jarvis and McNaughton (1986) and Meinzer et al. (1993) for a few tropical species. Loescher et al. (2005) estimated Ω>0.85 on most days at a study site also in Costa Rica. The authors attributed this to net radiation and aerodynamic conductance. This was not the case at our site where our analyses suggested that wind speed had a very weak or non-existent relationship with canopy conductance. Considering the elevated Ω and conductance values consistent with the literature, it can be assumed that tropical canopies subjected to daily rainfall events are somewhat adapted to limiting climatic conditions (low R_{net}, low δe, leaf wetness and constant air temperature) if the combination of environmental variables becomes favorable.

Conclusions

This study surfaced the positive and negative aspects of physiological modelling. Transpiration had a large role in dominating stomatal and canopy conductance trends, which indicated that this parameter should be accurately estimated or properly measured. While sap flux measurements are laborious and may lead to over or underestimations due to calibration issues, nighttime transpiration and reverse flow, our study indicated that lack of physiological measurements may lead to model overestimations since wet tropical environments have very little variability between wetness conditions.

Even though g_c was grossly overestimated when using the McNaughton and Jarvis equation, both g_c equations tested depicted similar diurnal trends. However, relying solely on two or three climatic parameters was not enough to actually represent the extremely heterogeneous canopy of the study site, especially during semi-dry and wet days. Clearly, leaf wetness was not depicted by the models, since g_s and g_c were not influenced by it. Solely relying on low δe to represent rainy days leads to unreliable estimates, especially in a highly decoupled environment, in which δe below 1kPa occurs even during dry days.. The estimates corroborated our hypothesis that intermittent rain events and sharp diurnal variabilities are not accounted for in these models, since g_s and g_c were enhanced with increase in wetness. Specifically, the influence of sunlit leaves in the estimation of g_s resulted in the opposite effect expected in a saturated environment; while, shaded leaves, although more realistic to tropical canopy conditions were more difficult to model. Hence, use of alternative models (e.g., Ball-Berry model based on photosynthesis) or improvement of the models tested is needed for these resistance parameters to be further implemented in global climate models to accurately represent wet tropical forests.

CHAPTER V

SUMMARY & CONCLUSIONS

Tropical forests are essential components of the global carbon and water cycle. Tropical forest composition is extremely heterogeneous. Not only are these ecosystems composed by a multitude of species, but are also composed of various tree sizes and degrees of exposure to the atmosphere or inter-canopy microclimates. The heterogeneity of tree size and age will inherently determine the amount of water used to grow and maintain healthy plant organs. Tree water use is directly influenced by micrometeorological conditions, such as rainfall, solar radiation and vapor pressure deficit. Atmospheric conditions are already extremely variable in lowland tropical rainforests, but it embeds other factors when considering montane ecosystems.

The study site of this dissertation, located in Costa Rica (Texas A&M Soltis Center of Research and Education), is classified as a premontane or lower montane tropical rain forest, which is characterized by little seasonal variability in climate, large precipitation amounts (~5,000 mm year^{-1}), lower solar radiation due to cloud coverage, and air temperature averaging around 24 ^{o}C year round. Additionally, stand structure comprises of a 30 m tall multi-layer canopy and terrain with 45 degree slope. Hence, the combination of complex canopy structure, wet climate and biodiverse composition leads to unique responses to a changing environment (short or long-term), especially when considering a phenomenon like leaf wetness (i.e. rain and fog). The assumption that a film of water over stomata reduces gas diffusion (1:10,000 compared to air) (Smith and

McClean 1989) is reasonable, if not impractical considering how frequently this system gets wet. This is especially important, since tropical tree species from Brazil and Indonesia alone stock 35% of the world's carbon (Baccini et al. 2012). Hence, this dissertation aimed to answer the following questions: I) How was sap flux (and transpiration) affected by the variation of leaf wetness, and was the response equal throughout canopy levels?; II) Were photosynthetic responses actually altered by leaf wetness? To what extent were these responses dependent on leaf anatomical traits and habitat?; and III) Did stomatal and canopy conductance models accurately depict leaf wetness effect on canopy dynamics across environmental conditions?

Through the use of sap flux sensors in individual trees differing in species and size, I was able to find evidence of the influence of leaf surface wetness on plant water uptake (up to 45% less). Trees were adapted to take advantage of short-term dryness in between rain events to perform gas exchange, which was probably enhanced on trees capable to dry their leaves faster than others. The traits involved in leaf drying were only successful if coupled with favorable environmental conditions. There was a disproportional effect of canopy exposed trees under dry conditions that was partially offset during wet conditions, when midstory trees used a higher proportion of water relative to dry conditions. In other words, during rain events, overstory conditions led to wetter canopy levels (higher interception) and lower vapor pressure deficit than some midstory and understory trees. Hence, the forest stand continued transpiring when wet, even if in a lower rate (~30%), due to distinct vertical microclimates at each canopy level. Furthermore, this study clarified the importance of the ratio of sapwood area and basal area as a key factor when quantifying how much water was used by an individual tree versus a stand of tropical trees.

After acknowledging the effects of leaf wetness in transpiration and sap flux, the leading question helped elucidate more in depth what occurred at the stomata level. This study indicated strong evidence that leaf wetness duration was the main factor driving photosynthesis reduction or increase. Furthermore, the responses were not solely dependent on the physical obstacle of water covering the stomata. The photosynthetic responses gathered were also a function of stomata distribution and leaf anatomy traits that hastened or extended drying times. When considering species habitat, savanna trees indicated mixed responses to the change in leaf boundary layer conditions. Even though most savanna species were hypostomatous, certain leaf features changed the boundary layer conditions enough to trigger a positive or negative response without blocking the stomata. Among the hypostomatous tropical species measured, only one reduced its photosynthetic rate, but recovered quickly afterwards; while the other increased substantially. Hence, I provided evidence to support the hypothesis that tropical species have developed distinct adaptations to cope with frequent wetting events (almost daily) without drastically affecting photosynthetic rates, or evolved strategies to enhance photosynthesis by using leaf wetness to their advantage.

At the canopy scale, there was also evidence that leaf wetness is inadequately accounted for in stomatal and canopy conductance models. However, the physiological benefits of leaf cooling and preference for weaker atmospheric pressure gradient to guarantee hydraulic safety may be an adaptive behavior that is poorly understood. . I gained important insights into how model inputs affect our ability to predict conductance to water vapor under a range of conditions common in wet tropical forests. Leaf wetness conditions led to various model discrepancies; for example, g_s had the largest variation on dry days, due to difference between air and leaf temperature; while, wet days had the most similar results within all models. Although enhancing g_s, wetness also increased the scatter of g_s and g_c estimates. Leaf wetness has been known to affect (positively and negatively) gas exchange through other studies, but my observation that leaf wetness had little to no effect on conductance suggests that the models do not depict or fully account for leaf wetness' biophysical effects to the leaves and whole canopy. Additionally, high climatic variability during those days lead to a sizeable interference on the resulting model estimates, which made it difficult to compare the models and their responses during wet days. This suggests that this largely decoupled forest stand (average $\Omega > 0.90$) may lead to great estimations errors, in which the applicability of both models may not be ideal for these types of environments.

Overall, this dissertation undertook an underrated climate phenomenon (leaf wetness) and provided compelling evidences of its importance to the study of tropical forest ecophysiology and functional ecology. I recommend that further studies about tropical species specific traits (e.g. leaf, stem, root, and crown) in their natural environment should be conducted more in depth, so that more information is gathered to link plant physiological functioning and environmental variability to water and carbon flux contribution of tropical plants. Furthermore, the improvement of canopy conductance or resistance to water vapor estimates is essential to create a more robust database for these environments to be properly used in land surface models, regionally and globally. For that, there is a necessity for more leaf-level gas exchange and sap flow measurements (Hogg et al. 1997), technologically updated flux towers and weather stations with continuous maintenance in the tropics to validate these models.

The findings of this dissertation indicated that the biophysics of tropical wet forests behave differently from other tropical environments and even more from temperate. Furthermore, the assessment of tropical ecophysiology of wet leaves at different scales (stem, leaf and canopy-atmosphere) and across a complex vertical canopy profile demonstrated strong influence of leaf wetness at every scale and its effects were further enhanced with microclimate variability along the forest structure. Future studies should acknowledge the inter-canopy dynamics as much as the overstory, when quantifying and analyzing the dynamics of water and carbon fluxes. As climate change predictions indicate longer, drier periods, the microclimatic vertical profile of tropical ecosystems will be altered along with a functioning shift of ecologically distinct species.

Although leaf wetness partially or substantially suppressed plant physiological processes, the depletion of this phenomenon may lead to a higher sensitivity to vapor pressure deficit that could induce tree mortality through cavitation. Nevertheless, in a changing environment, stomatal conductance to water vapor modelling or measurements are essential to better assess the degrees of sensitivity of a group of ecologically distinct species or divergence inside some species. Yet, certain constraints embedded in the modelling and measurements should be considered, so that the imposed conditions from the formulation or from the equipment will be equal or similar to the ambient conditions. Finally, improvement of climatic modelling of environments with challenging conditions (thick atmosphere and leaf boundary layers) should not be standardized with other tropical systems with dry or drier seasons.

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APPENDIX A

SUPPLEMENTARY FIGURES FOR CHAPTER III

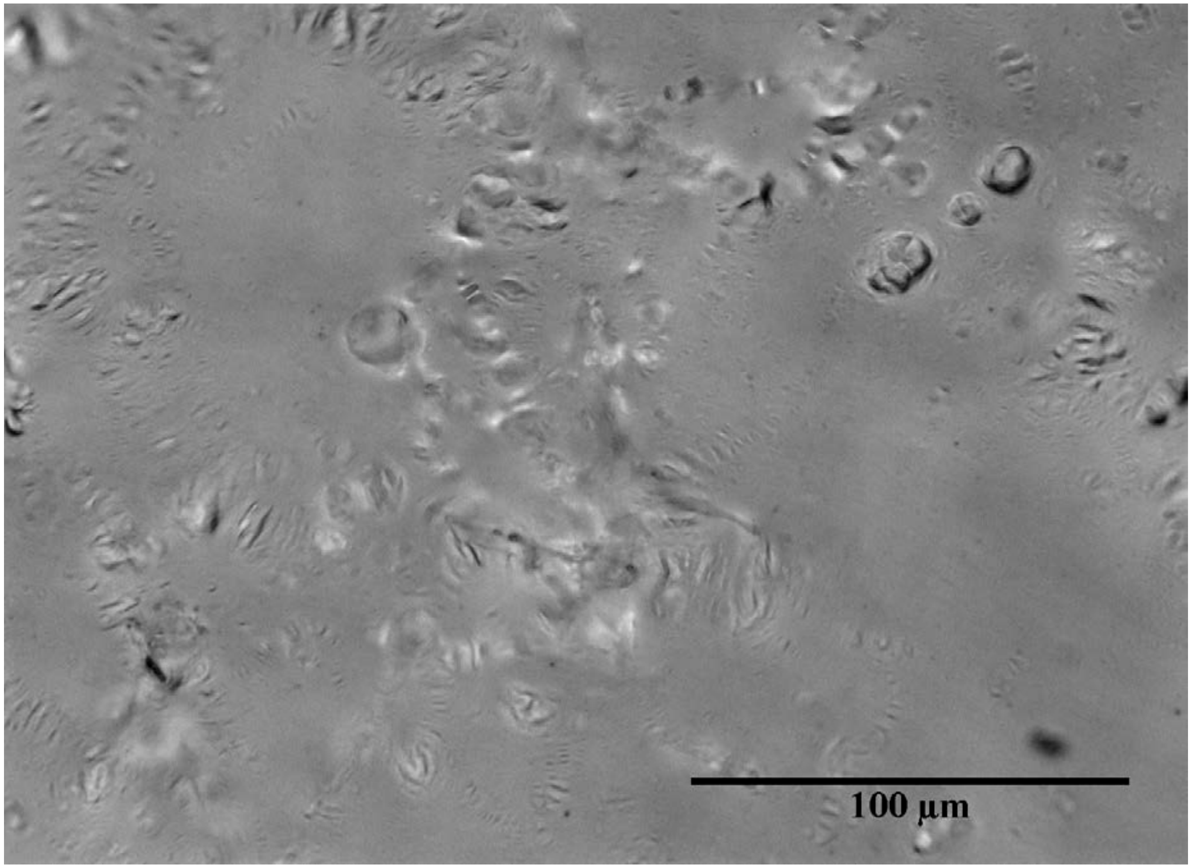

Figure 22-A. Adaxial leaf surface photomicrograph at 20× resolution of *Quercus macrocarpa* Michx. (BO).

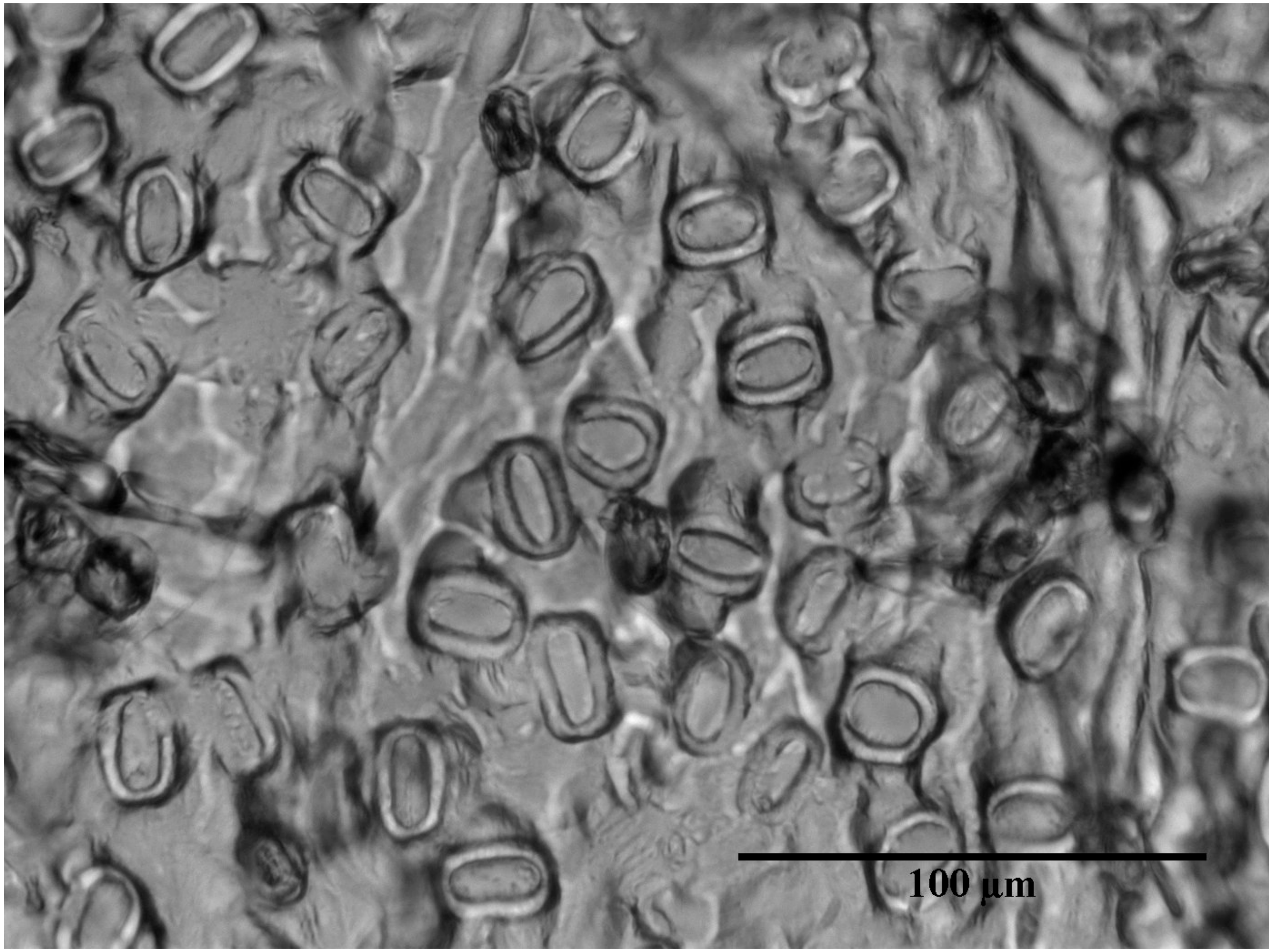

Figure 23-A. Abaxial leaf surface photomicrograph at 20× resolution of *Quercus macrocarpa* Michx. (BO).

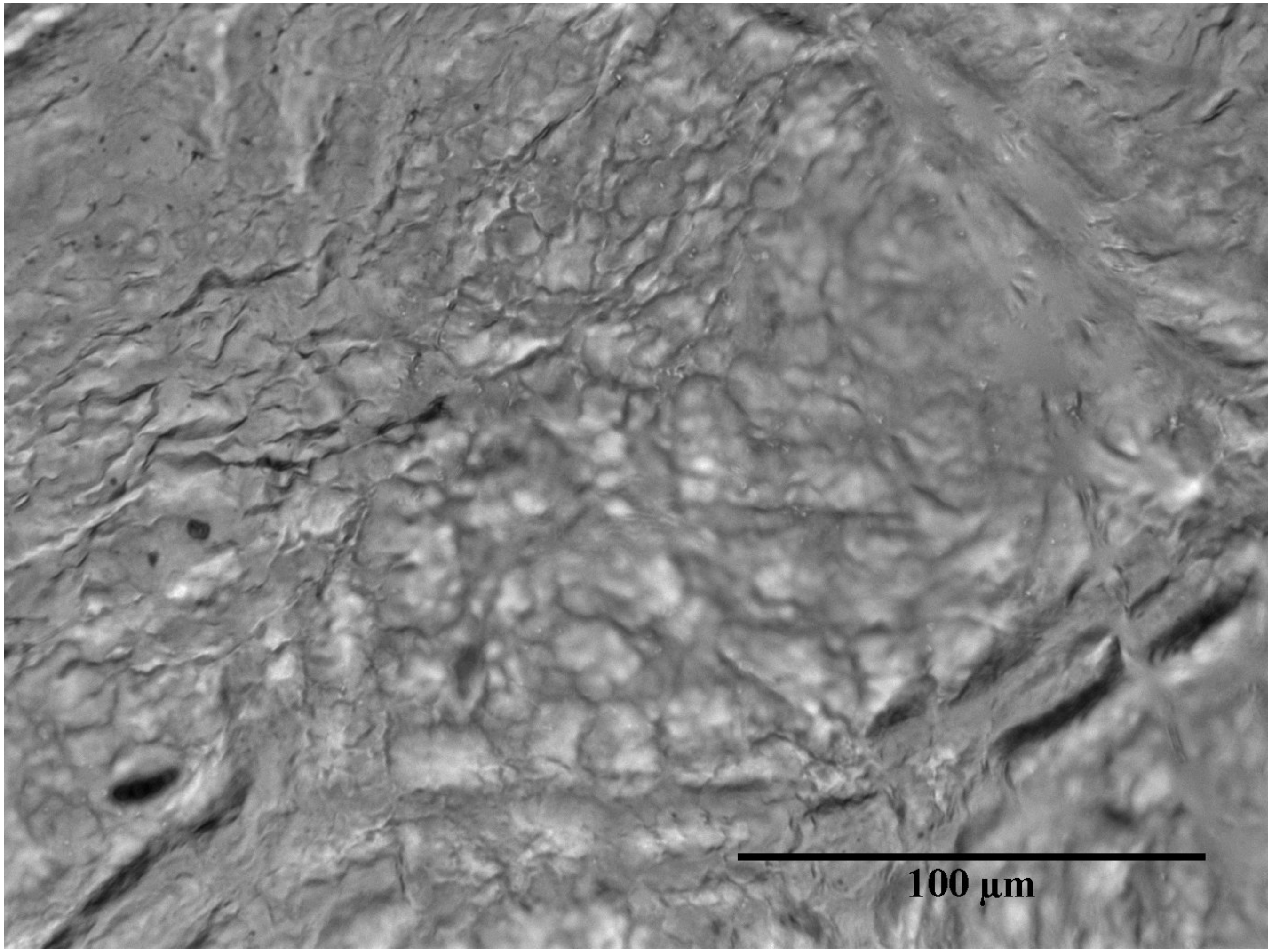

Figure 24-A. Adaxial leaf surface photomicrograph at 20× resolution of *Quercus meuhlenbergii* Engelm. (CO).

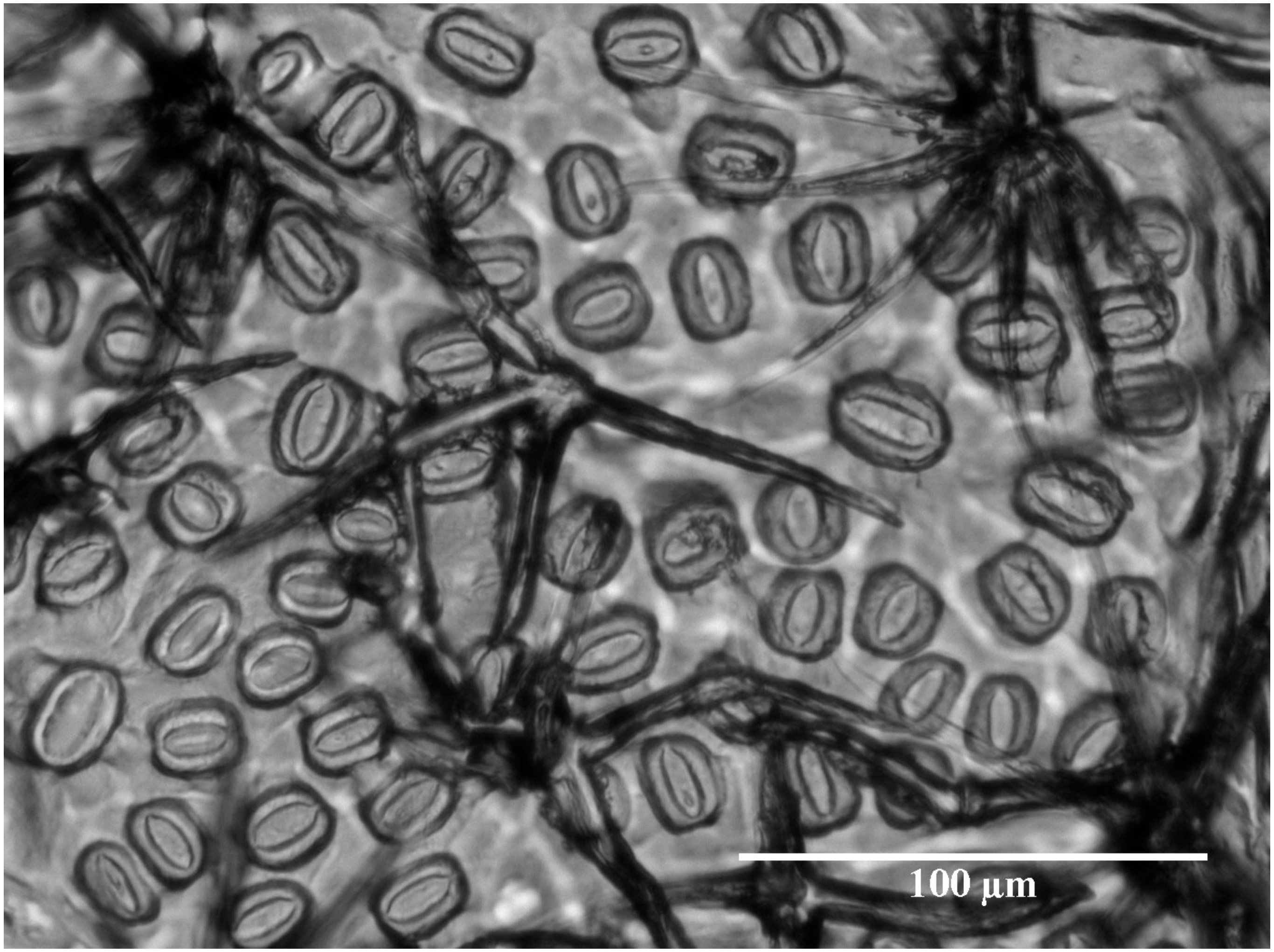

Figure 25-A. Abaxial leaf surface photomicrograph at 20× resolution of *Quercus muehlenbergii* Engelm. (CO).

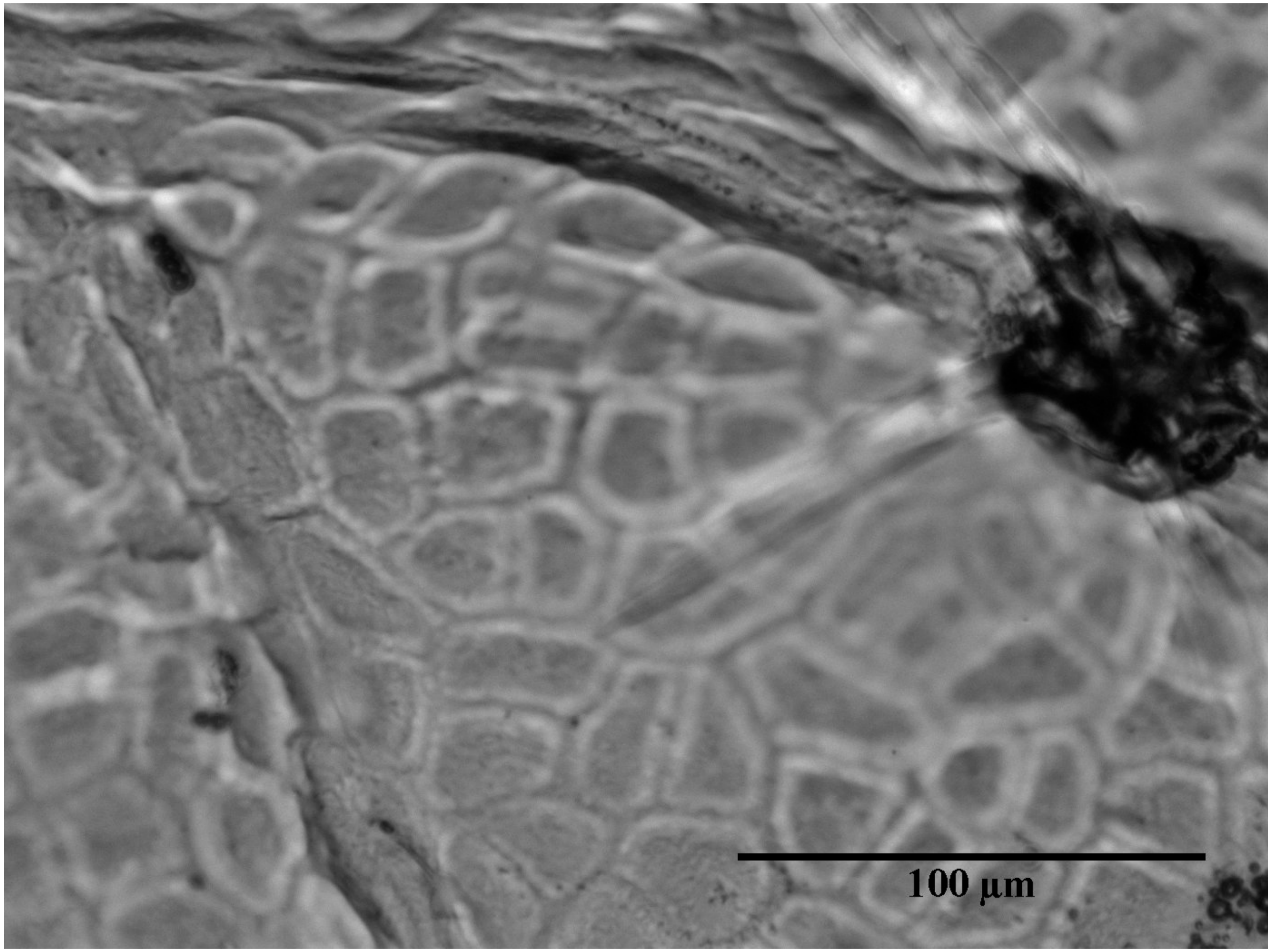

Figure 26-A. Adaxial leaf surface photomicrograph at 20× resolution of *Quercus stellata* Wangenh. (PO).

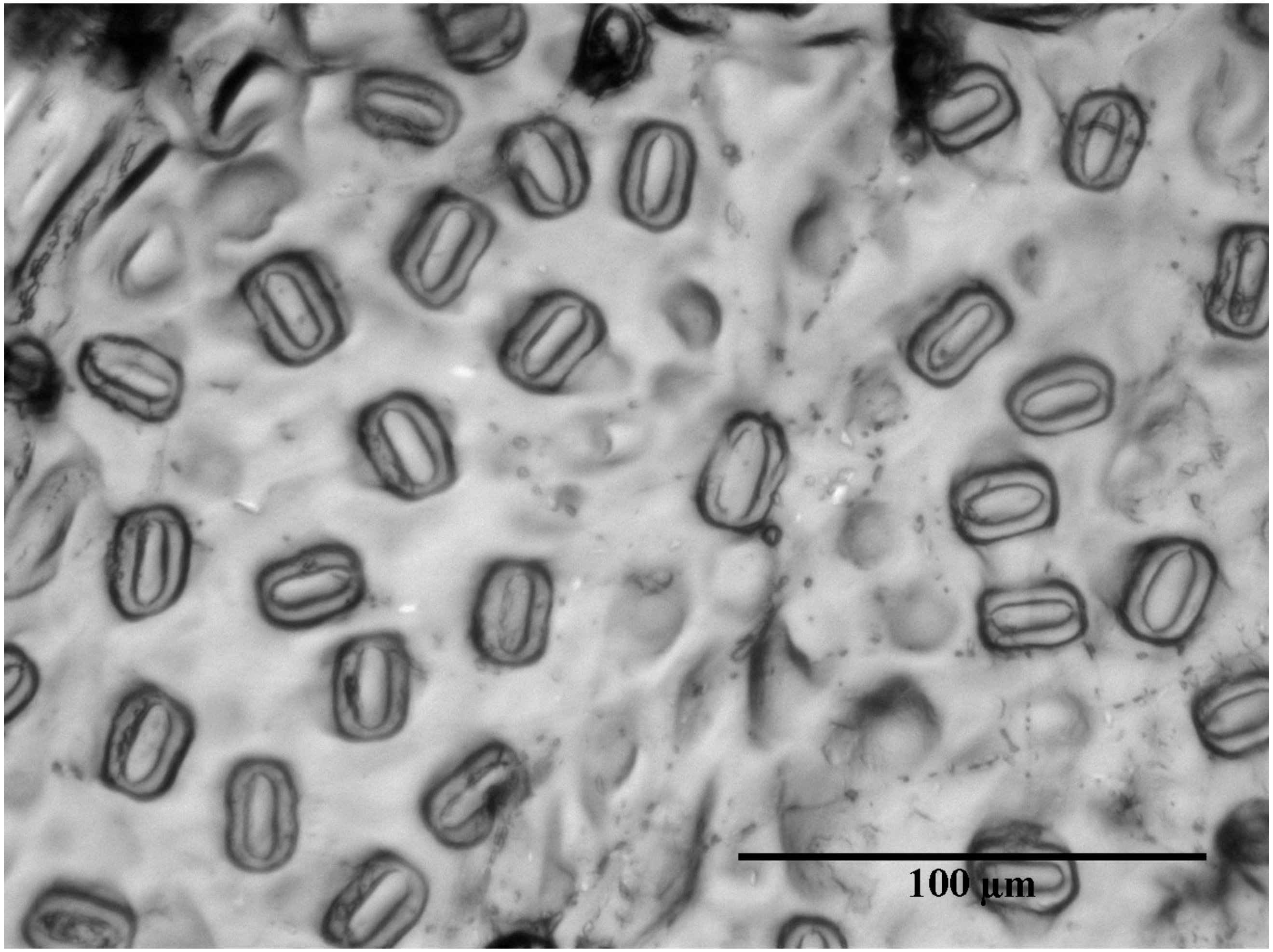

Figure 27-A. Abaxial leaf surface photomicrograph at 20× resolution of *Quercus stellata* Wangenh. (PO).

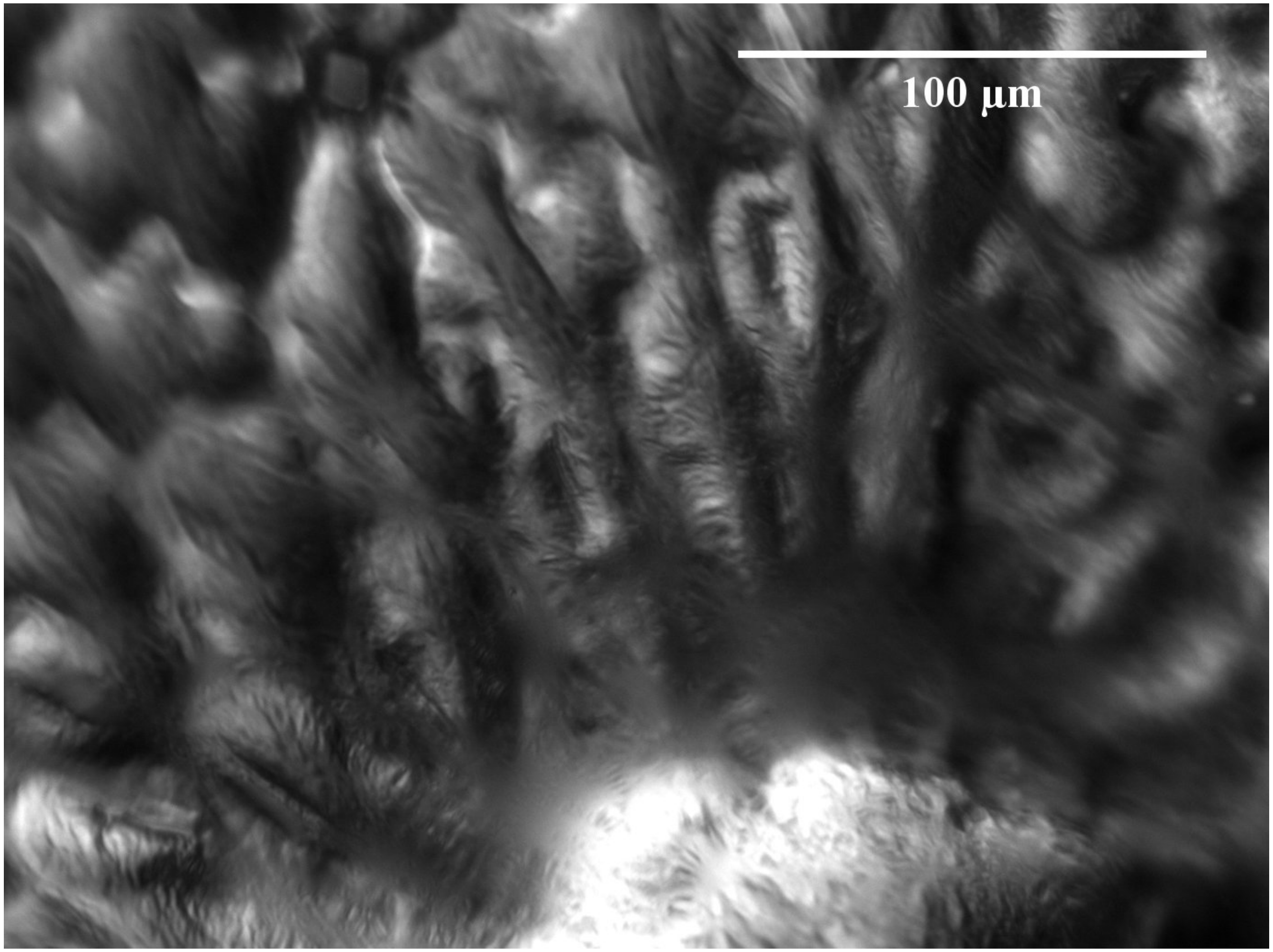

Figure 28-A. Adaxial leaf surface photomicrograph at 20× resolution of *Stachytarpheta jamaicensis* (L.) Vahl (SJA).

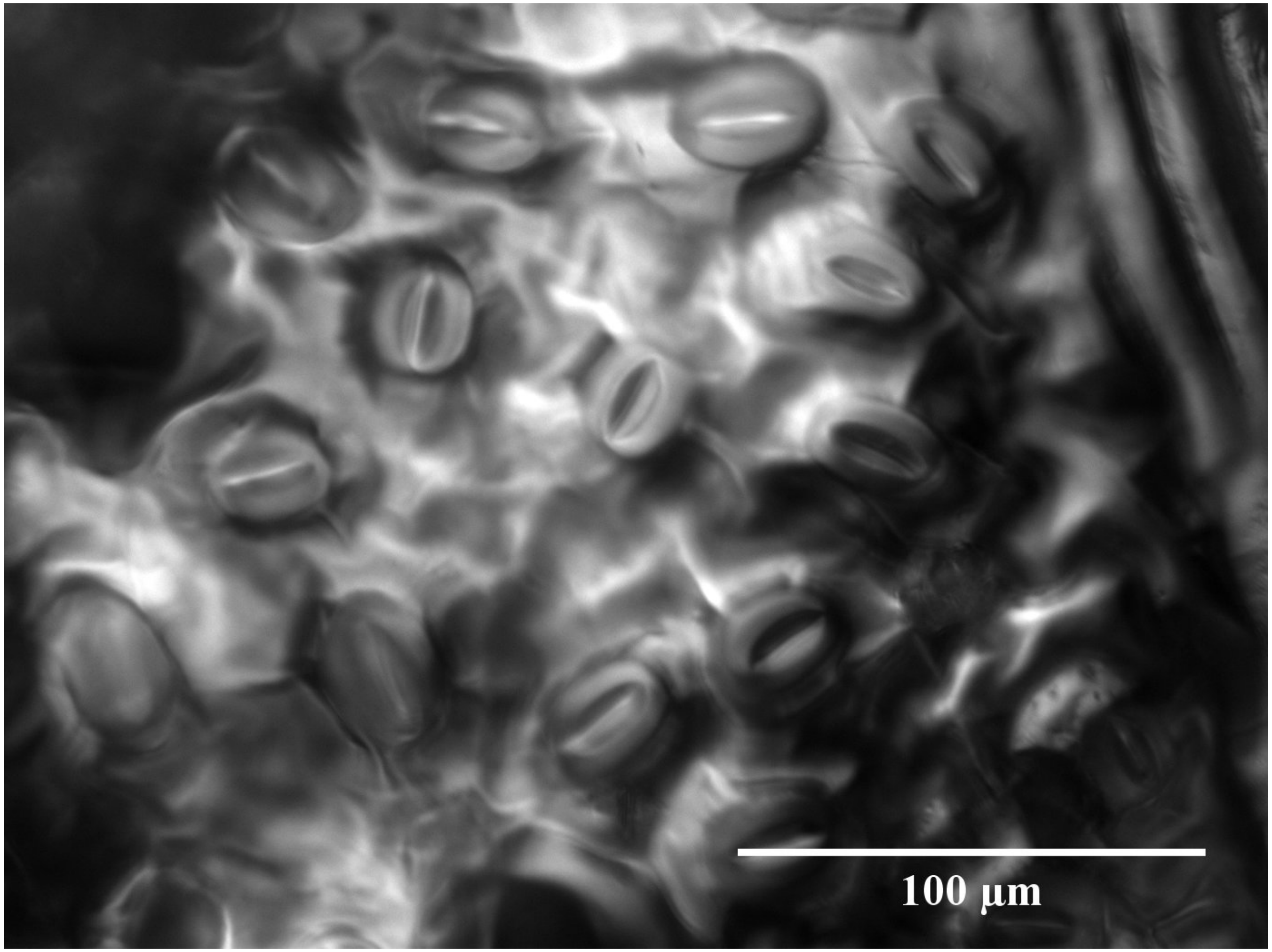

Figure 29-A. Abaxial leaf surface photomicrograph at 20× resolution of *Stachytarpheta jamaicensis* (L.) Vahl (SJA).

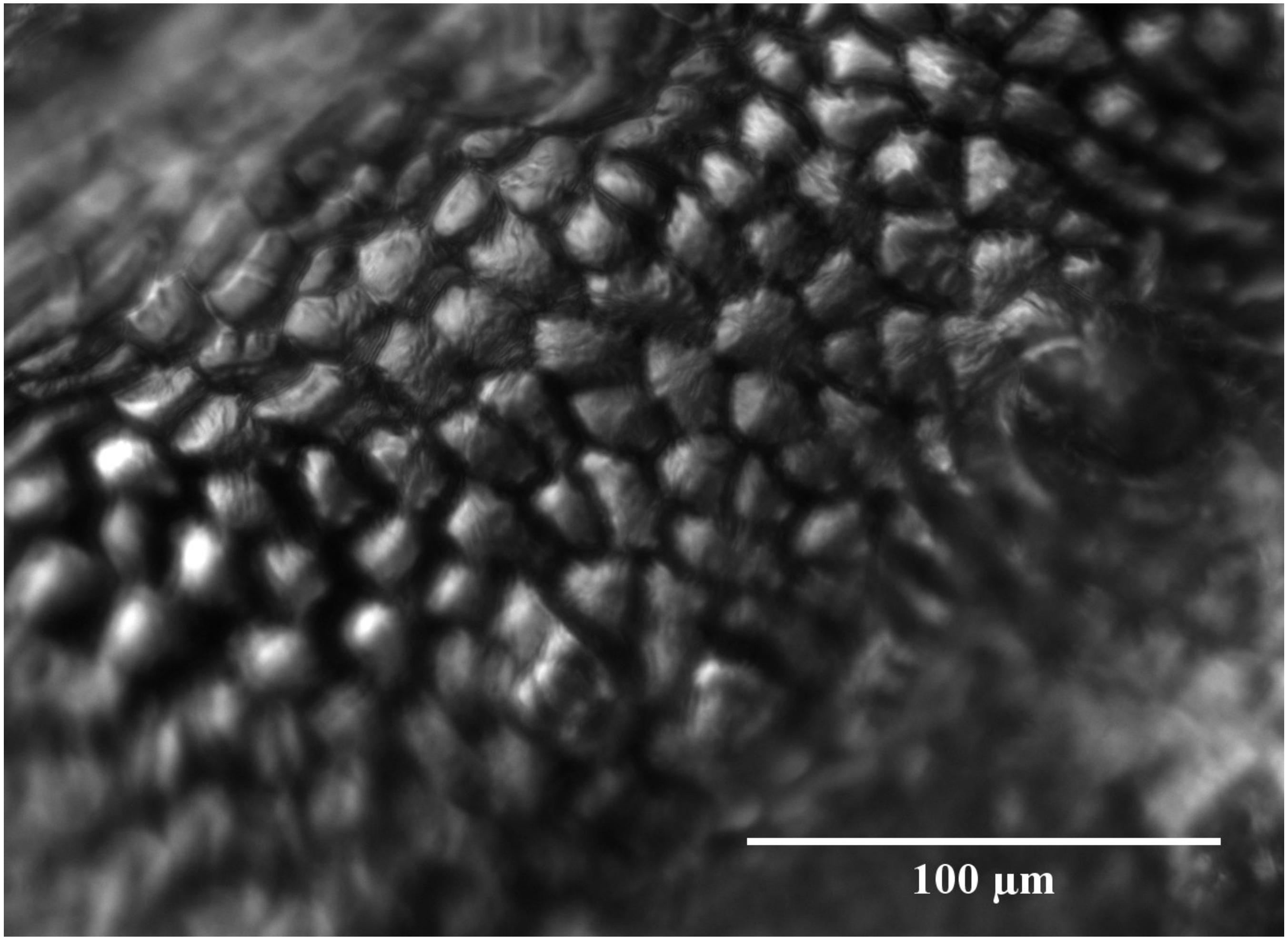

Figure 30-A. Adaxial leaf surface photomicrograph at 20× resolution of *Tibouchina heteromalla* Cogn. (THE).

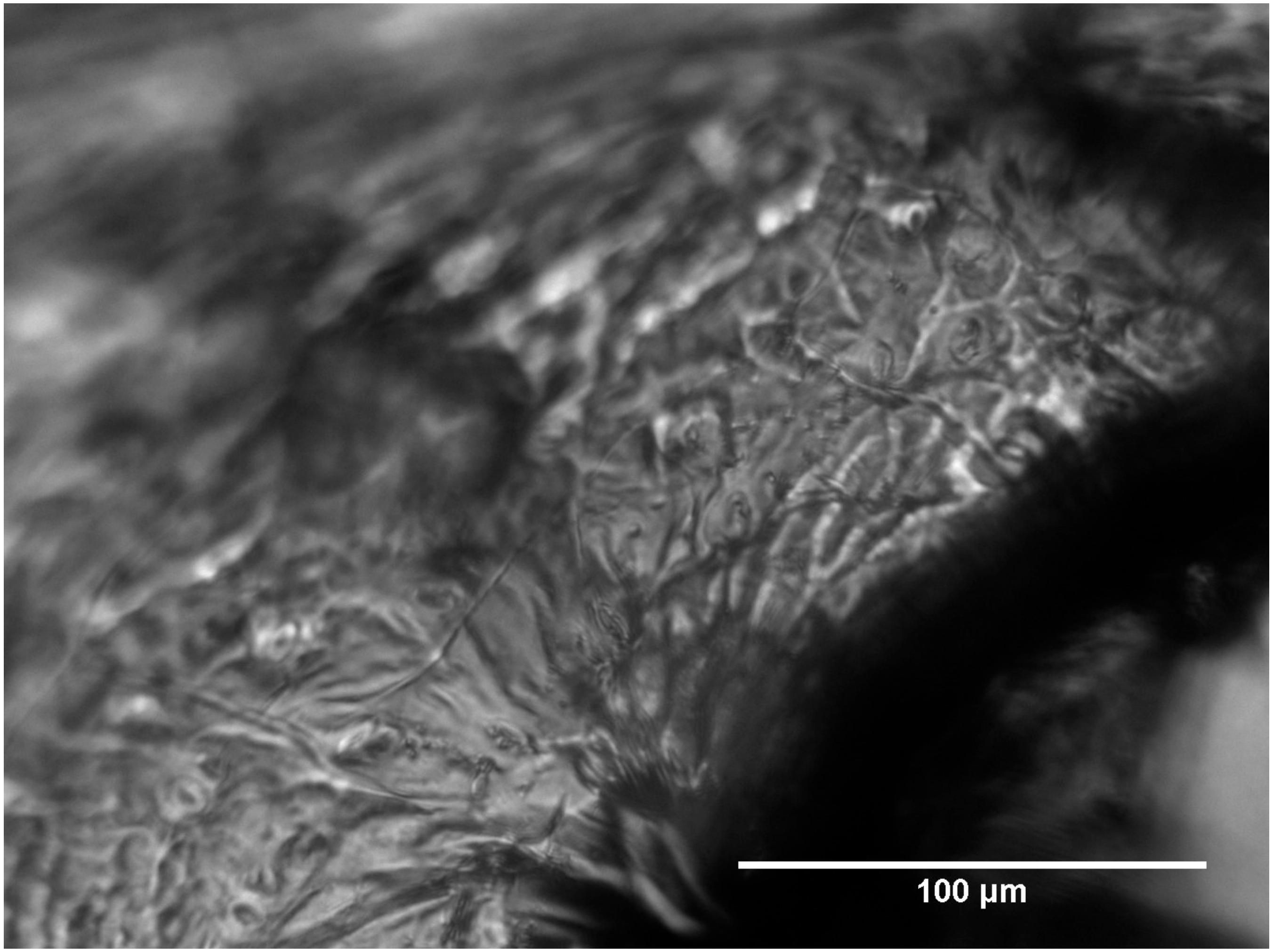

Figure 31-A. Abaxial leaf surface photomicrograph at 20× resolution of *Tibouchina heteromalla* Cogn. (THE).

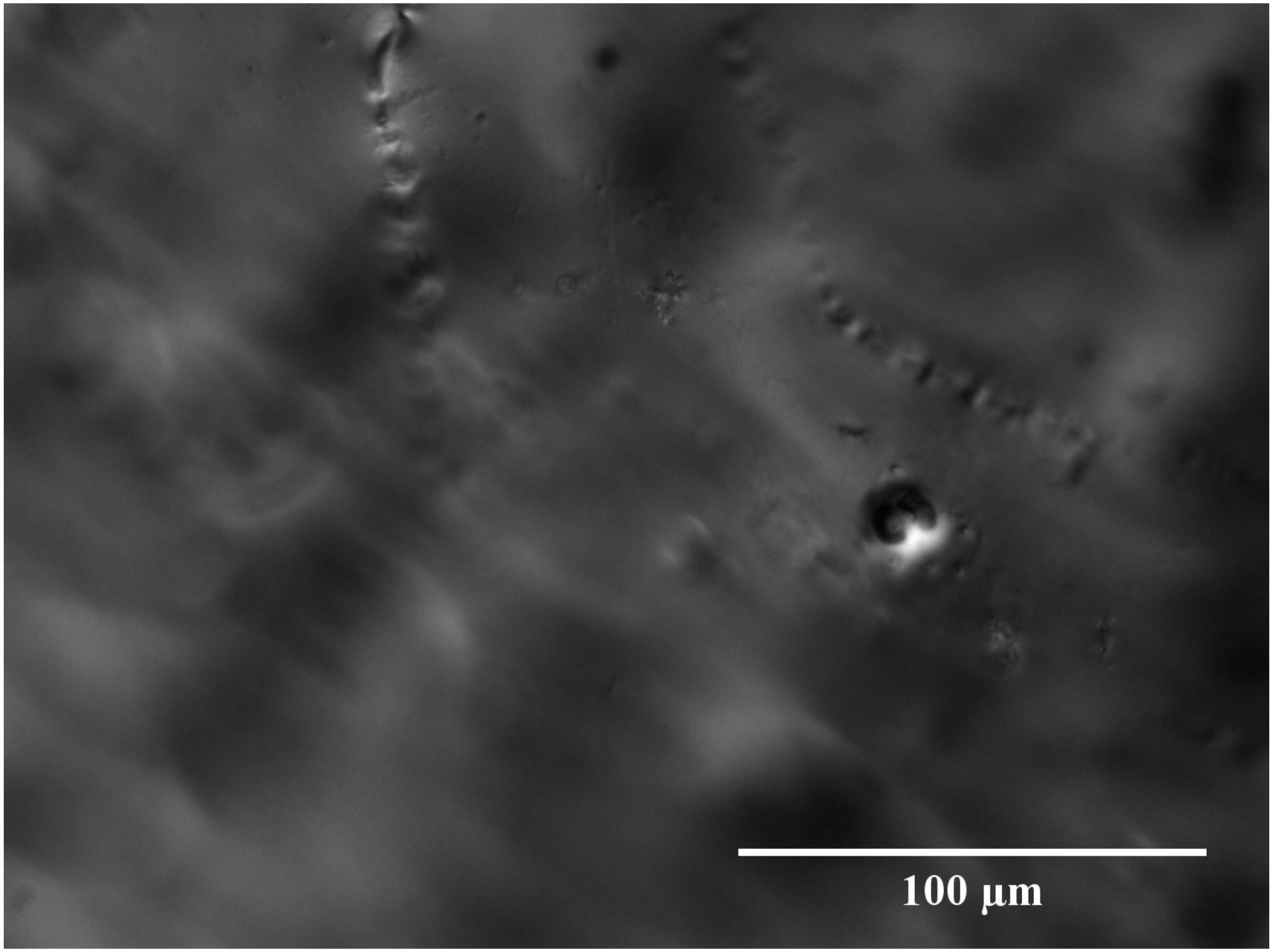

Figure 32-A. Adaxial leaf surface photomicrograph at 20× resolution of *Zamia skinneri* Warsz. Ex. A. Dietr. (ZSK).

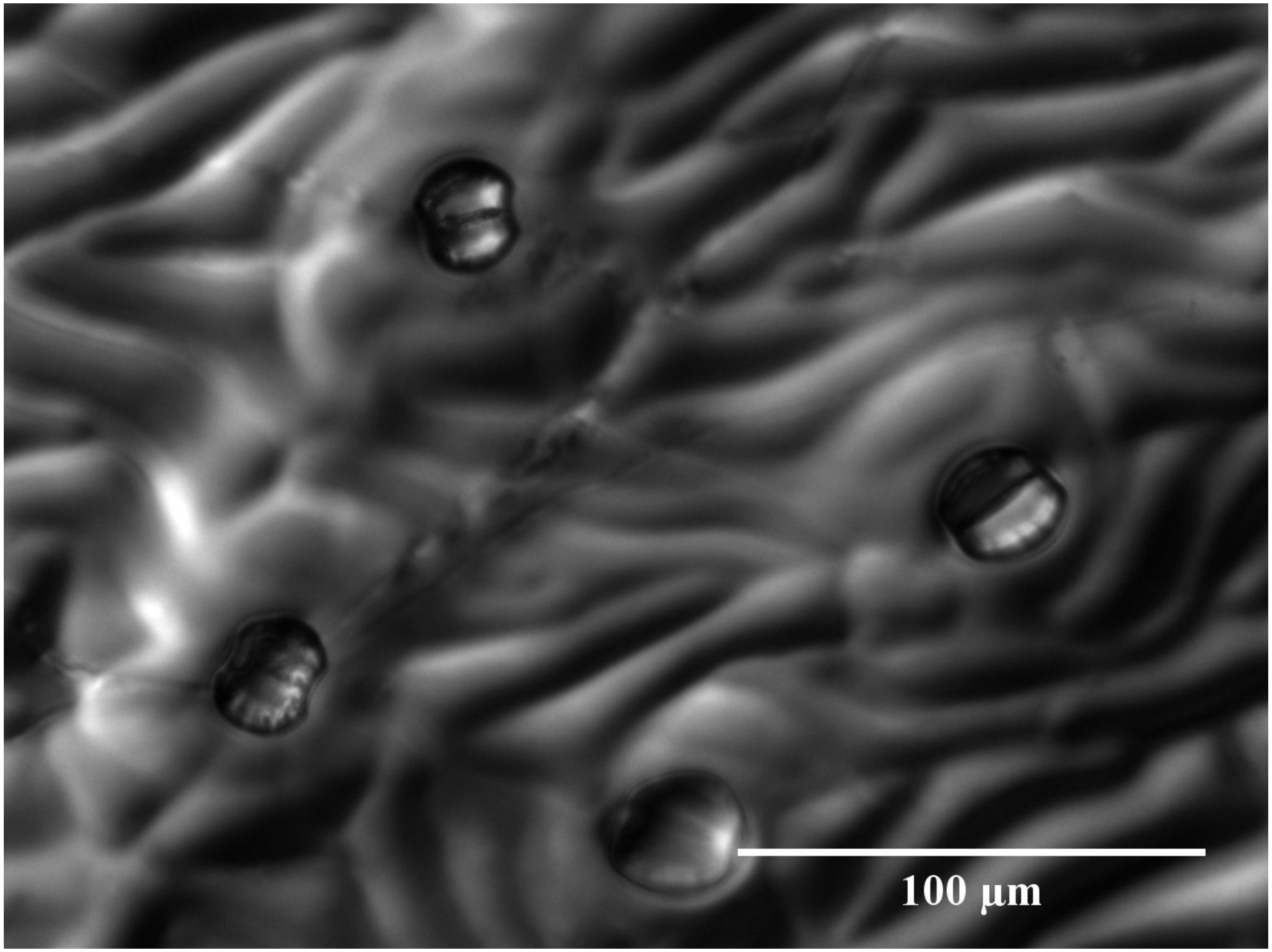

Figure 33-A. Abaxial leaf surface photomicrograph at 20× resolution of *Zamia skinneri* Warsz. Ex. A. Dietr. (ZSK).

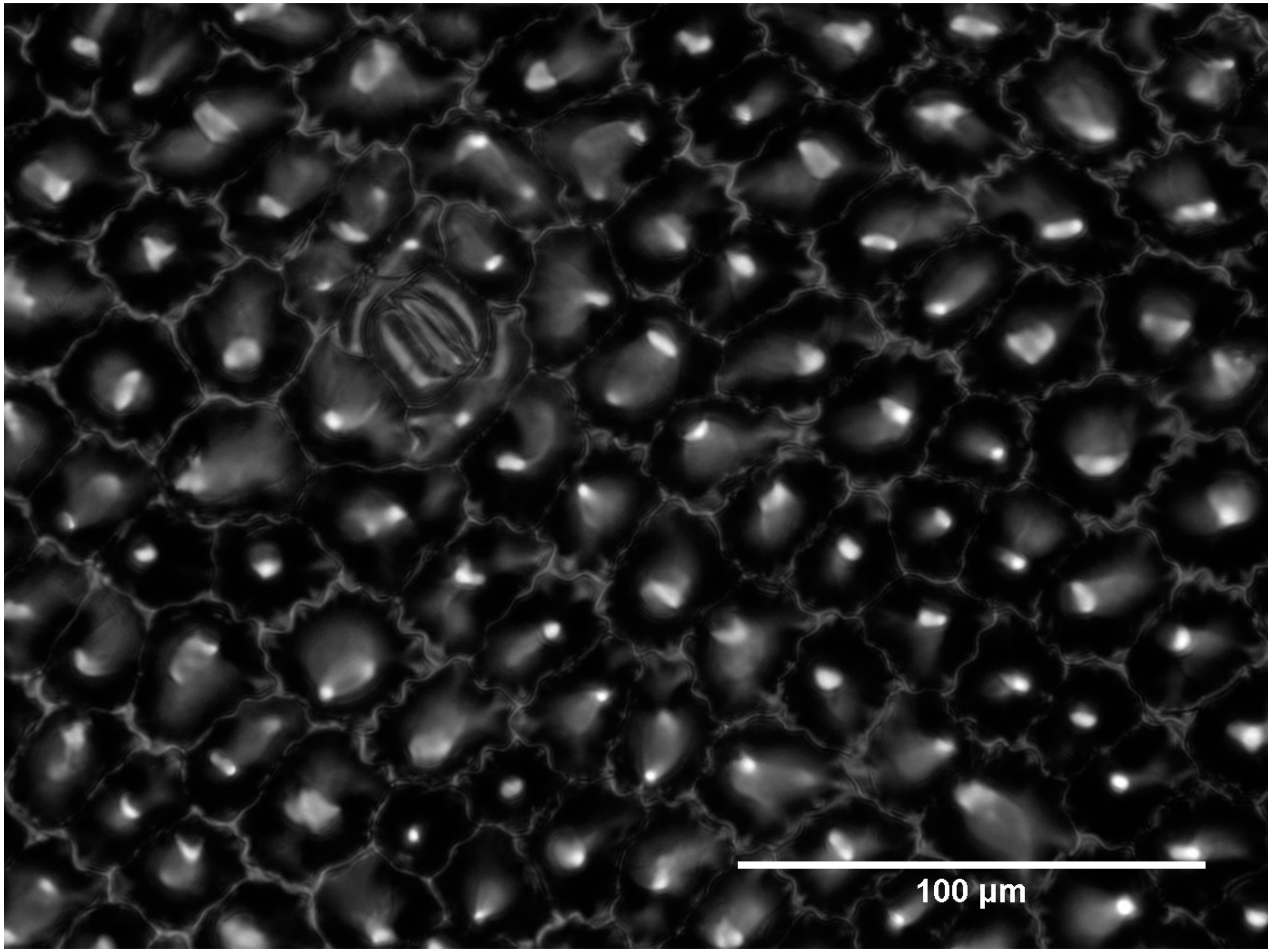

Figure 34-A. Adaxial leaf surface photomicrograph at 20× resolution of *Calathea crotalifera* S. Watson (CCR).

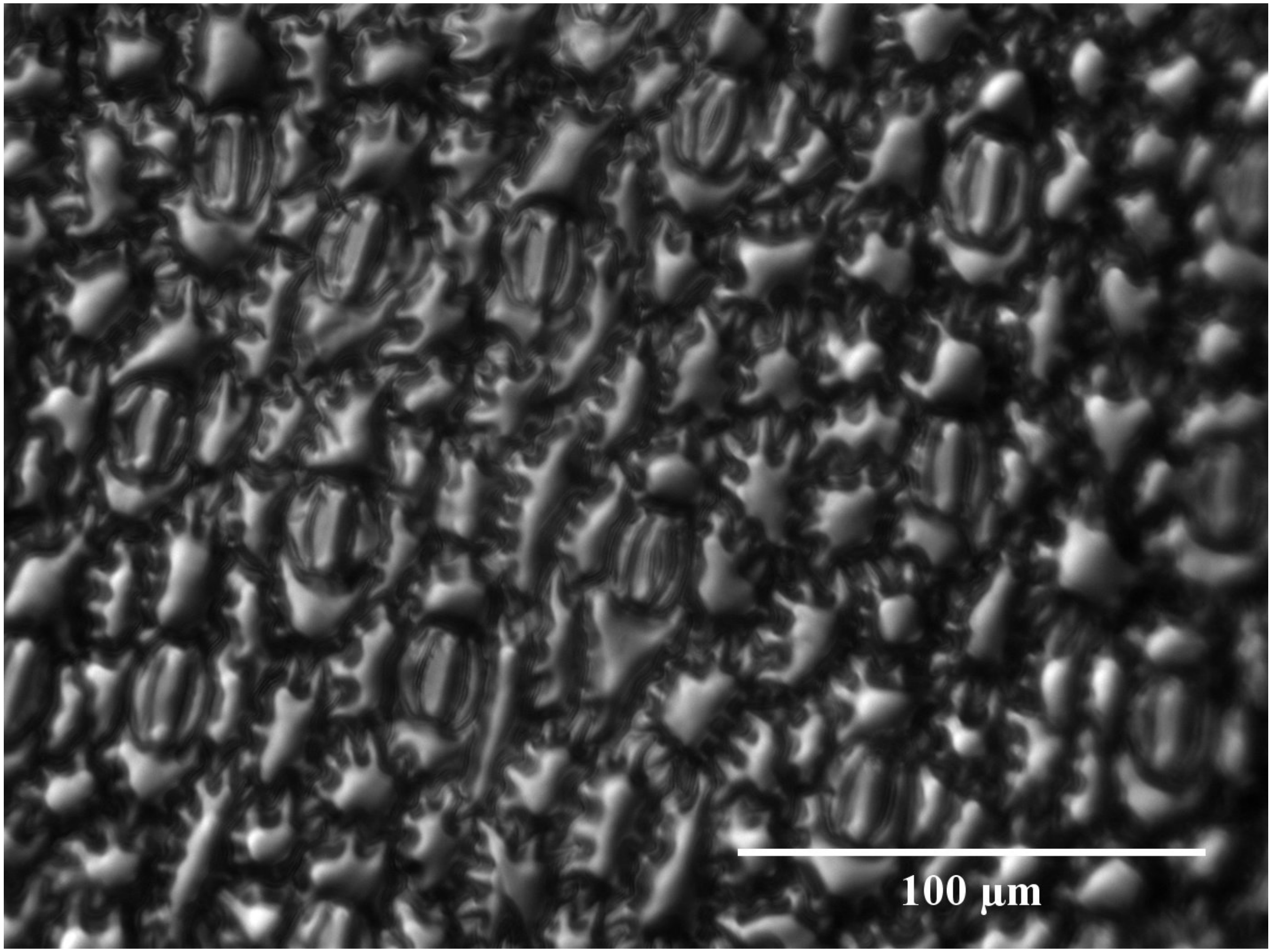

Figure 35-A. Abaxial leaf surface photomicrograph at 20× resolution of *Calathea crotalifera* S. Watson (CCR).

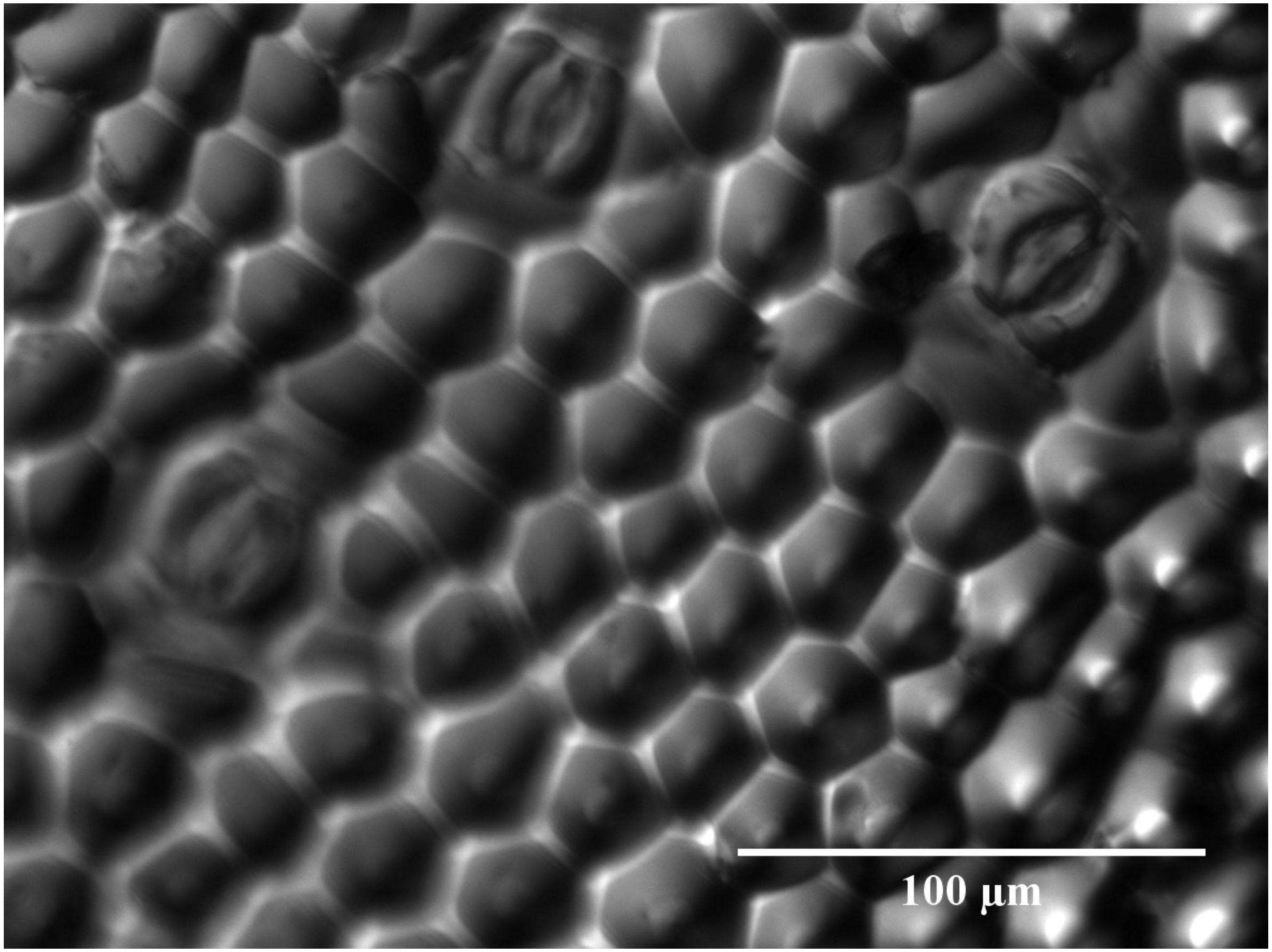

Figure 36-A. Adaxial leaf surface photomicrograph at 20× resolution of *Costus laevis* Ruiz & Pav. (CLA).

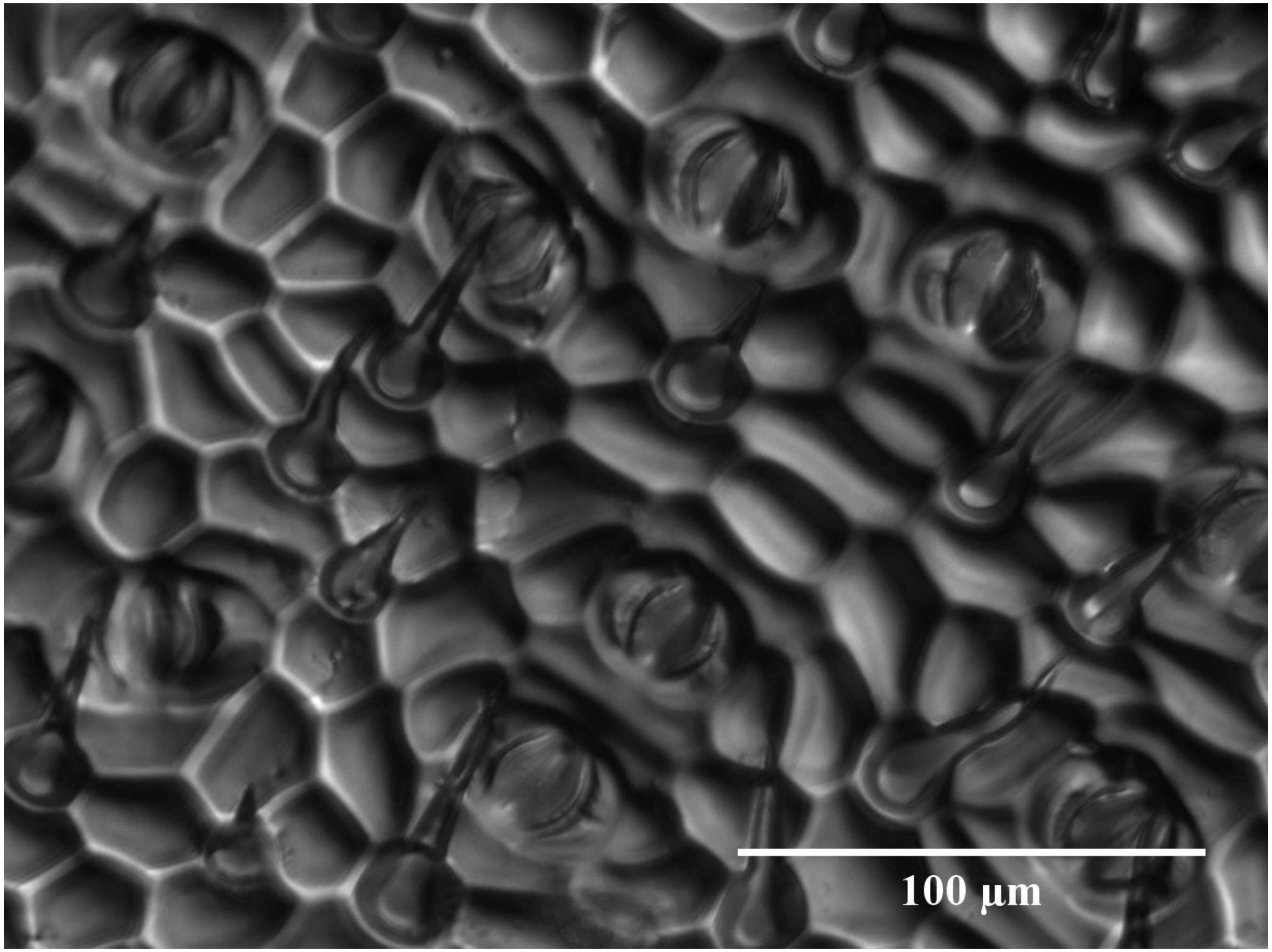

Figure 37-A. Abaxial leaf surface photomicrograph at 20× resolution of *Costus laevis* Ruiz & Pav. (CLA).

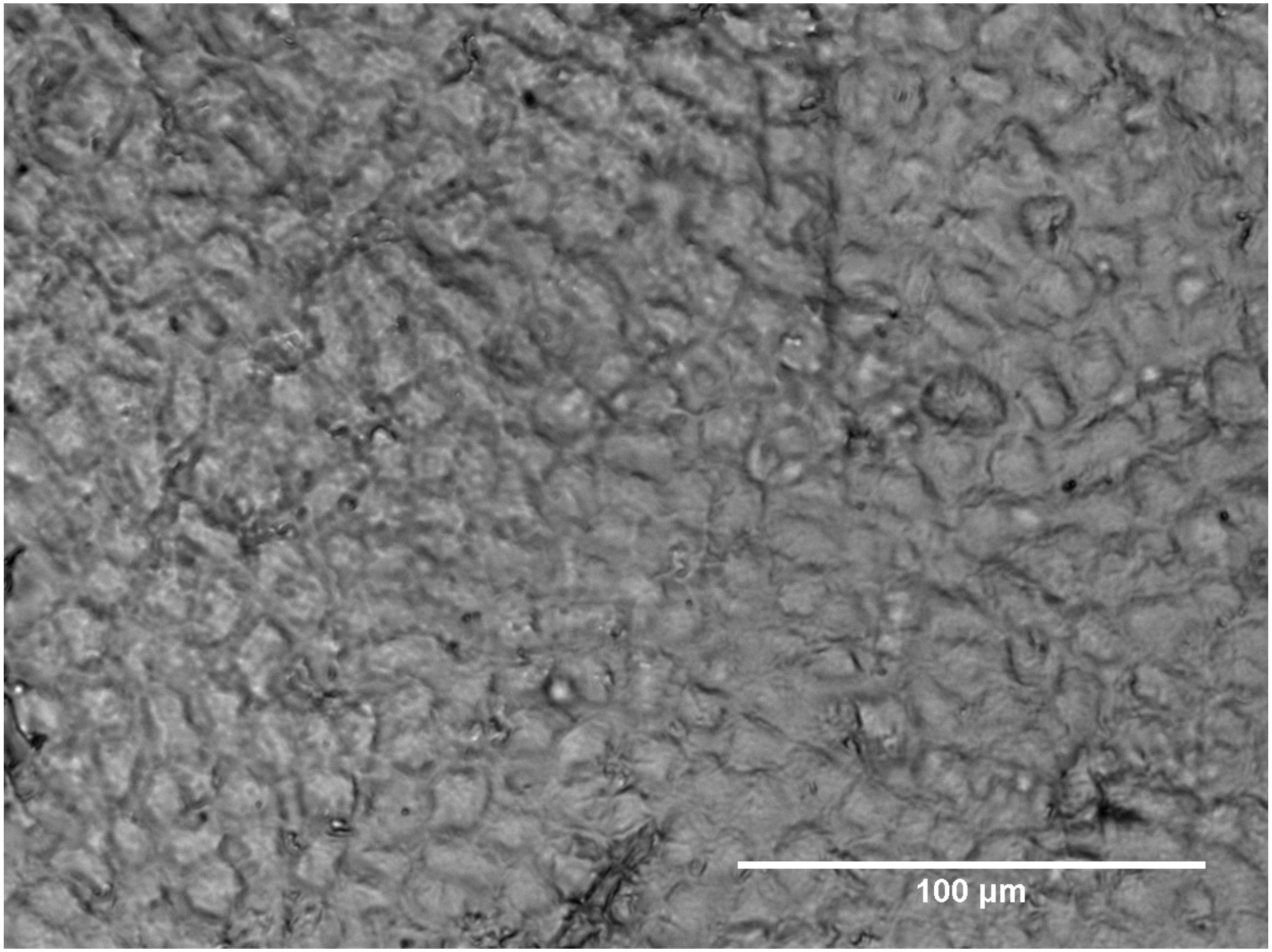

Figure 38-A. Adaxial leaf surface photomicrograph at 20× resolution of *Carapa guianensis* Aublet. (CGU).

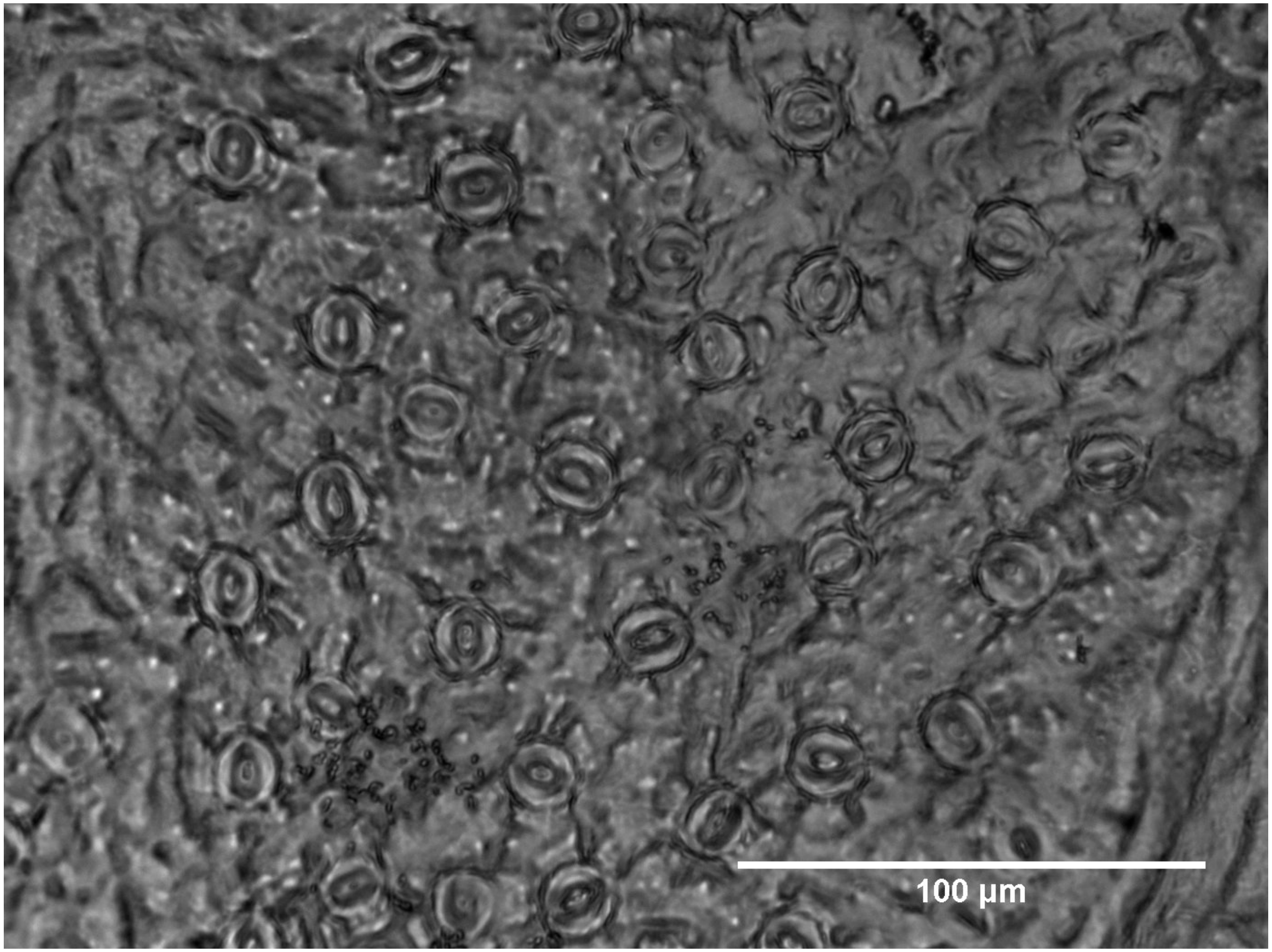

Figure 39-A. Abaxial leaf surface photomicrograph at 20× resolution of *Carapa guianensis* Aublet. (CGU).

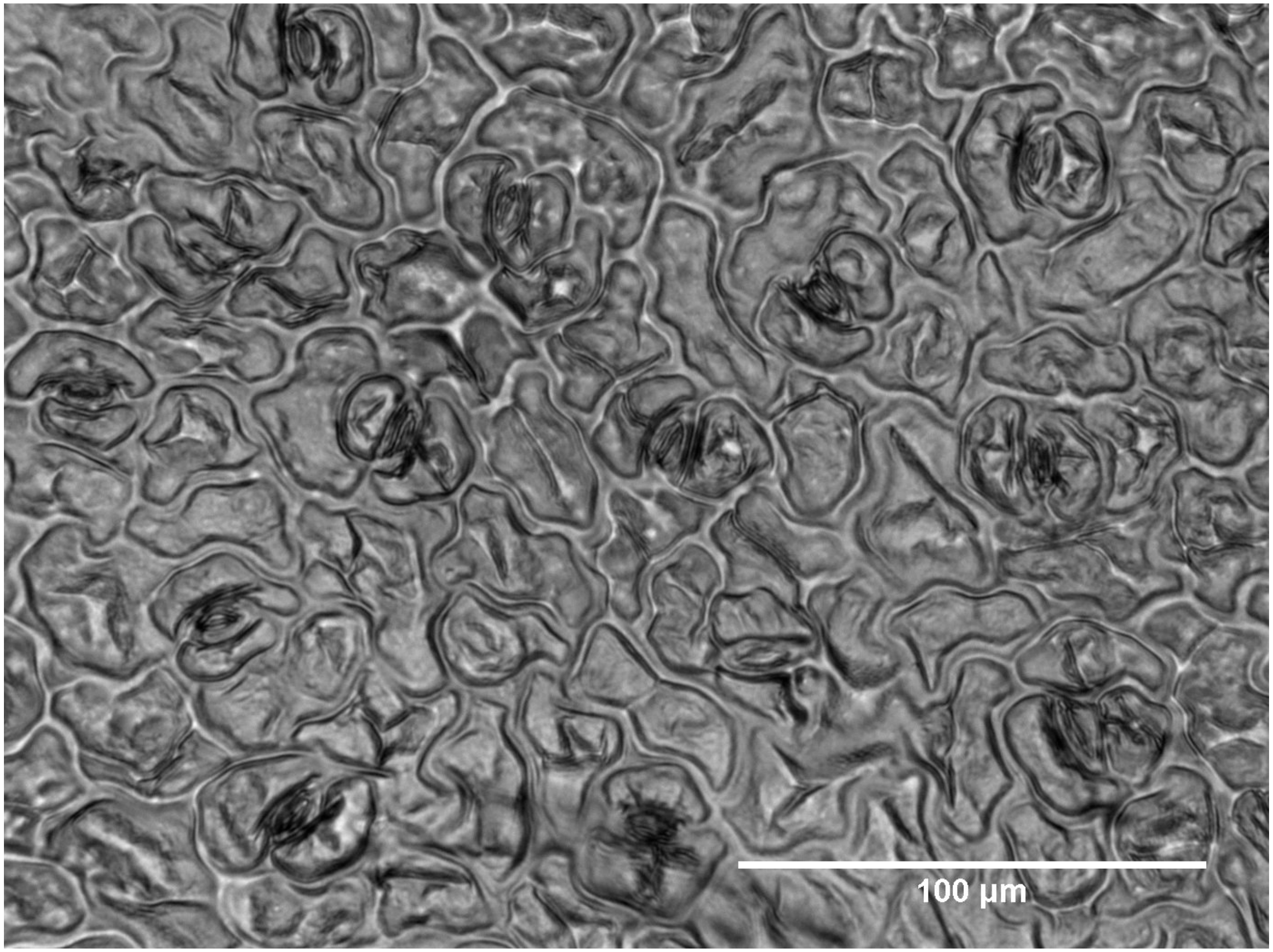

Figure 40-A. Adaxial leaf surface photomicrograph at 20× resolution of *Senna alata* (L.) Roxb. (SLA).

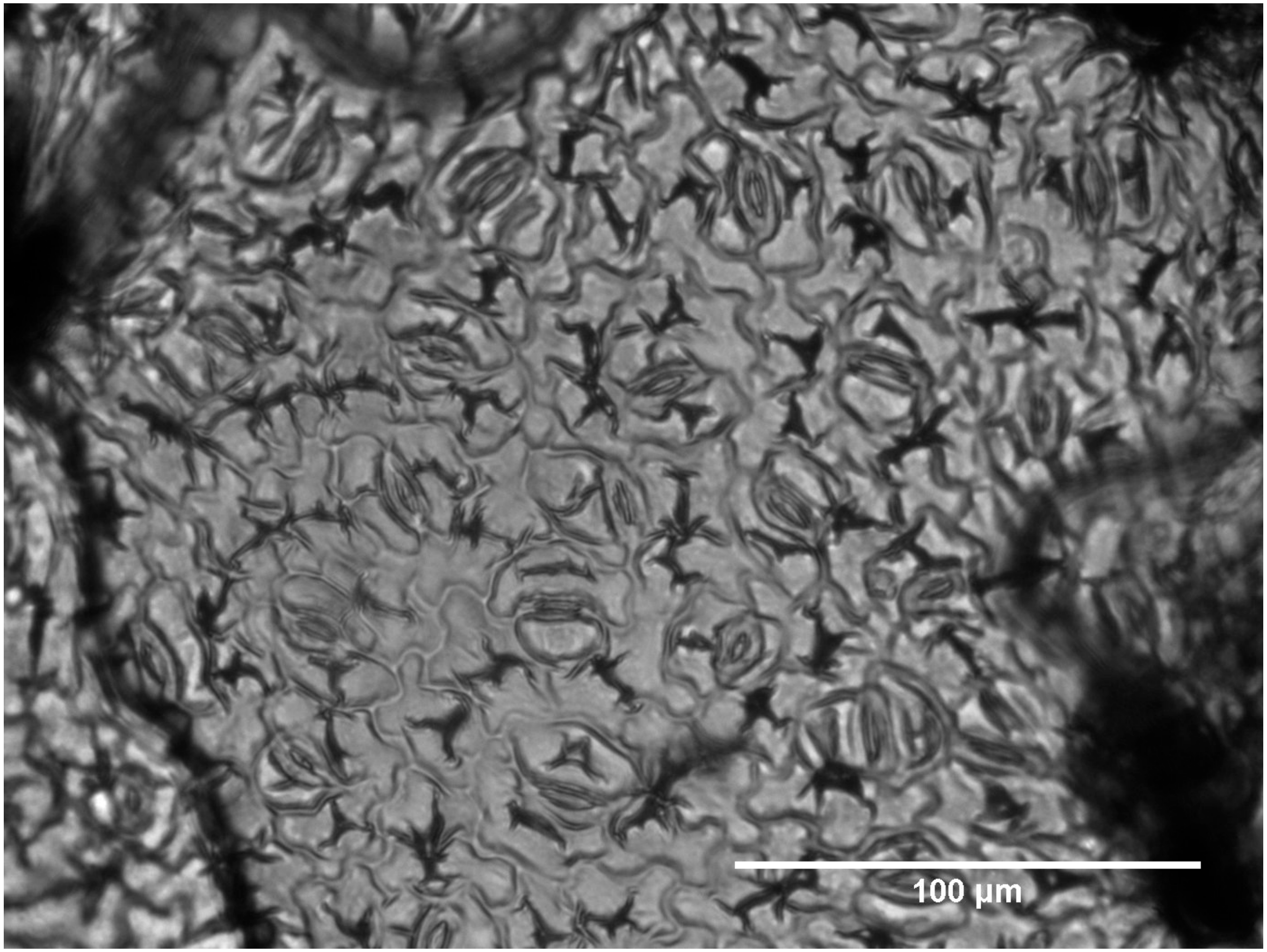

Figure 41-A. Abaxial leaf surface photomicrograph at 20× resolution of *Senna alata* (L.) Roxb. (SLA).

APPENDIX B

SUPPLEMENTARY INFORMATION AND ANALYSES FOR CHAPTER V

Transpiration can be modelled through robust models like Penman-Monteith (Monteith and Unsworth 1990) and Priestley-Taylor (Priestley and Taylor 1972). The Priestley-Taylor model was originally based on the heating effects on evaporation of free water surfaces (e.g., lakes and sea) or saturated lands, but the researchers acknowledged that adaptations were needed for it to be applied to vegetated surfaces (e.g. type and amount) (Priestley and Taylor 1972). This model relies solely on energy flux parameters, such as net radiation, ground heat flux and Bowen ratio (represented by α). The authors based their model's choice of parameters based on Swinbank and Dyer (1967) and Dyer (1967), which stated that specific humidity and temperature vary little over the land, and eddy turbulences are small at the lower levels of the atmospheric boundary layer. Assuming that net radiation mostly dominates the aerodynamic term (Priestley-Taylor) (Flint and Childs 1991) may lead to large estimation errors in tropical forests with highly diverse canopy structures and wetness gradients.

To assess the usage of an empirical estimation of canopy estimation in the humid tropics, I also estimated E_c through the Priestley-Taylor (PT) transpiration equation (Flint and Childs 1991, Pereira 2004, Loescher et al. 2005) (eq. 13).

$$E_c = \alpha \frac{\Delta(R_{net}-G)}{(\Delta+\gamma)\cdot\lambda} \qquad \text{(eq. 13)}$$

where, R_{net} is net radiation (W m^{-2}), G is ground heat flux (W m^{-2}), α is an empirical correction based on Bowen ratio proposed by Priestley and Taylor (1972) (= 1.26), Δ is the rate of change of saturation of water vapor pressure with temperature (kPa K^{-1}) and γ is the psychometric constant (kPa K^{-1}). Δ and γ were calculated according to Zotarelli et al. (2010).

Canopy transpiration derived from sap flux measurements totaled 540 mm $year^{-1}$, with a daily average of 1.4 ± 0.6 mm day^{-1}, while Priestley-Taylor daily estimates averaged 1.5 ± 0.6 mm day^{-1}. After accounting for the unavailable net radiation data when instrumentation failed (~20%), the Priestley-Taylor model (E_c-PT) resulted in 13% higher estimates than sap flux derived transpiration (E_c-SF). Although tightly correlated ($R^2_{adj} = 0.75$, $P<0.001$), Figure 42-B also shows how variable these rates are from each other ($P<0.001$). The maximum E_c-SF rate for the entire period was 45% lower than the E_c-PT estimates. When assessing daily total transpiration rates for each wetness condition, E_c-PT was also overestimated in every condition, but at different magnitudes. Semi-dry days had the largest difference among estimates, as it was 17% higher ($P<0.001$) than E_c-SF rates. The smallest difference of 2% was seen during wet days ($P=0.91$), while net radiation was significantly lower than dry (-50%) and semi-dry days (-33%).

Not only were annual and daily transpiration rates divergent, diurnal patterns were drastically different. While E_c-SF mainly peaked between 12PM and 1PM, with the exception of when leaves were wet, as discussed on Chapter II, E_c-PT peaked, on average, before midday for every wetness condition (dry = 10:30AM; semi-dry = 10AM;

wet = 11 AM) (Figure 42-B). Additionally, E_c-PT estimates usually started around 5AM and declines around 5PM, coinciding with the sun rise and sun set, respectively (Figure 43-B). Yet, E_c-SF peaked later similarly to vapor pressure deficit and leaf temperature (Figure 16). Since the PT model is mainly composed of heat fluxes, net radiation induces transpiration to strictly cease at this timeframe (Figure 43-B). Since air and leaf temperature and vapor pressure deficit are closely associated with humidity, they may lead E_c-SF to continue on for a slightly more extended period. E_c-PT not only depicted the stomatal aperture inaccurately when other climatic variables did not follow net radiation trends, but it also failed to model nighttime transpiration that may occur and, ultimately, neglect another output of the water balance (Figure 43-B).

Although climatic parameters altered the conductance peak, the elevated E_c-PT estimates were not obscured by the other climatic parameters embedded in the models. Within the g_s estimates (using shaded leaf temperature) with different sources of transpiration, the $g_{s\text{-MU}}$ was estimated to be 44% higher than $g_{s\text{-J\_PT}}$ and 49% higher for $g_{s\text{-J\_SF}}$.

Canopy conductance estimates were the most similar within models. Sap flux based estimates differed on average only 15% between McNaughton & Jarvis (g_c-MJ) and Penman-Monteith ($g_{c\text{-PM}}$), while Priestley-Taylor based conductances were 20% higher. However, both transpiration sources had higher estimates through the MJ model that does not consider aerodynamic parameters (i.e. wind speed and canopy roughness). On average, $g_{c\text{-PT}}$ and $g_{c\text{-SF}}$ differed 34% from each other. The largest difference between PT and SF was during dry days (+36%) and smallest during wet days (+14%).

Meanwhile, semi-dry days increased 28%, showing that although ambient conditions are somewhat wet, if net radiation is still high, the Priestley-Taylor equation will continue to estimate high transpiration values, neglecting water storage in the atmosphere and the flattening of the leaf water potential gradient. Thus, considering all the overestimations while using Priestley-Taylor estimations in the conductance equations, I decided to only analyze environmental control over conductance using sap flux-based measurements.

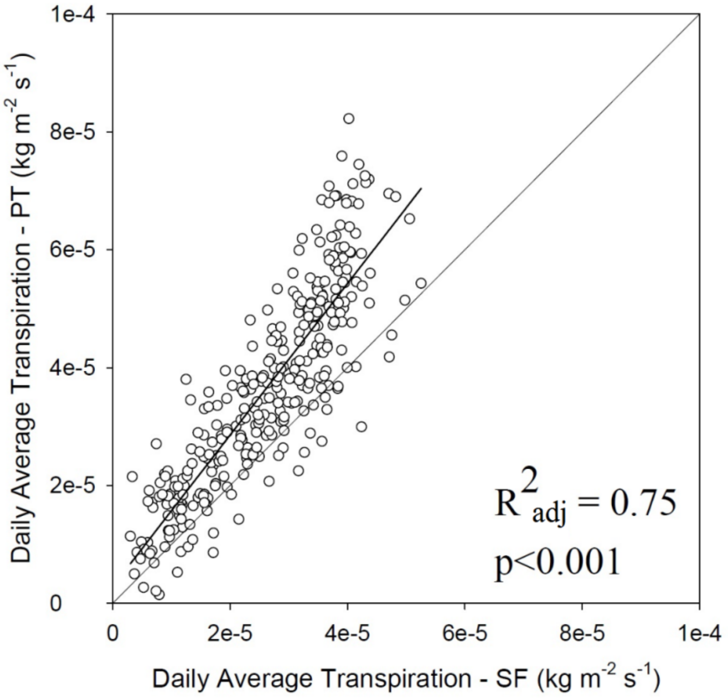

Figure 42-B. Cross-validation between daytime daily averages of transpiration derived from actual sap flux measurements and Priestley-Taylor derived estimates.

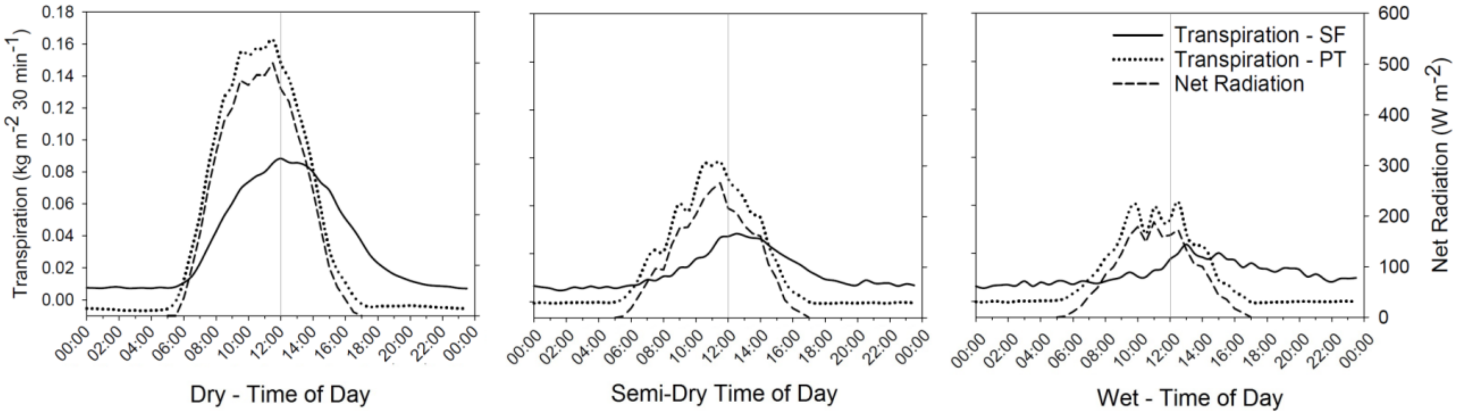

Figure 43-B. Diurnal trends of transpiration rates (kg m^{-2} 30 min^{-1}) derived from sap flux measurements (E_c-SF– solid line), Priestley-Taylor equation (E_c-PT – dotted line) and net radiation (W m^{-2} – dashed line) across wetness conditions (From left to right: dry, semi-dry and wet)

Net radiation was a poor predictor of transpiration, g_s and g_c, even though the study site is considered energy-limited, since vapor pressure deficit was relatively low ($\delta e<1$ kPa) and leaf boundary layer was always thick ($\Omega>0.90$). Even when considering vapor pressure deficit in the models, most models over-predicted g_s and g_c (in comparison to $g_{s\text{-J\_SF}}$ and $g_{c\text{-PM\_SF}}$ that depicted best the E_c_SF trends) independently of wetness conditions. Clearly, Priestley-Taylor is unfit to be used in an environment that does not follow the daily course of solar radiation and does not account for other suppressing climatic parameters, such as vapor pressure deficit. The almost 2-hour long gap between net radiation and air temperature in dry days resulted in a reduced period of conductance that may lead to daily underestimations of water fluxes, while diurnal variations of vapor pressure deficit and wind speed on semi-dry and wet days are somewhat apparent due to the transpiration input in the model.

Priestley-Taylor has been recommended for evapotranspiration measurements in various ecosystems (Jarvis and McNaughton 1986, Pereira 2004, Sumner and Jacobs 2005, Weiss and Menzel 2008) for its parameter simplicity (number and instrumentation, Gunston and Batchelor 1983), yet few studies evaluated its accuracy or cross-validated the estimates with actual transpiration measurements (Herbst et al. 2008, Amani et al. 2013). Although energy is an important variable in wet tropical ecosystems, estimates of transpiration in humid environments based solely on net radiation may be biased. Loescher et al. (2005), with a study site also located in Costa Rica reached similar conclusions. Their study acknowledged that overall Priestley-Taylor had good estimates during wet conditions, but that the model tended to overestimate water fluxes during dry conditions and net radiation was below 500 Wm^{-2} due to hyperbolic changes in canopy and boundary layer conductance variation throughout the day. Although performing better under wet canopy conditions, most of the days at our site are considered atmospherically dry (e.g., $\delta e \sim 1.0$ kPa, $T_{air} \sim 24$ ^{o}C), while canopies may still be wet from nighttime rainfall. Hence, the model will not depict the physical suppression on stomatal conductance of leaves that take longer to dry. Although useful, this model needs to be improved so it can incorporate seasonal and daily variations of wind, atmospheric humidity and canopy wetness to actually be applied appropriately to wet tropical forests.