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Article

Physiological Responses of Species to Microclimate Help explain Population Dynamics along Succession in a Tropical Dry Forest of Yucatan, Mexico

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Abstract: We investigated relationships between population dynamics and microclimate, physiology, and the degree of mycorrhizal colonization, for three species (*Piscidia piscipula* L.(Sarg.) (Fabaceae), *Bunchosia swartziana* Griseb. (Malpighiaceae) and *Psidium sartorianum* (Bergius) Nied. (Myrtaceae)) of a tropical sub deciduous forest in Yucatan, Mexico that were growing in plots of different successional ages. We hypothesized that abundance and persistence were related to increased plasticity in CO₂ assimilation. We found that *Piscidia piscipula* had greater abundance in intermediate plots (18 to 21 years), presented higher levels of plasticity in CO₂ assimilation (greater variability among individuals, plots, and seasons), presented the highest CO₂ assimilation rates, and presented greater drought resistance (higher water potentials and capacitance). Conversely, *Psidium sartorianum* had greater abundance in older plots (more than 50 years of secondary succession), lower assimilation rates, and low levels of plasticity in CO₂ assimilation. *Bunchosia* had intermediate values. Locally, the degree of mycorrhizal colonization was consistent with abundance across plots. Regionally (but not locally), plasticity in CO₂ assimilation was consistent with abundance. We found differences in microclimates among plots and within plots among species. Physiological adjustments appeared to play an important role in the capacity to regenerate and in the successional persistence of these species in this tropical dry forest.

Keywords: *Bunchosia swartziana*; *Piscidia piscipula*; *Psidium sartorianum*; CO₂ assimilation; ecological succession; fluorescence; photosynthesis; tropical dry forest; microclimate; population dynamics

1. Introduction

Over 90% of existing tropical dry forests are at risk, and although pressures differ among regions, for tropical dry forests in the Americas, climate change has been found to be one of the major threats [1]. Given their ecological and economic importance, there is an urgent need for more information on these systems, especially during stressful periods such as droughts [2].

Tropical dry and sub deciduous forests present considerable variability in the timing, intensity, and amount of annual rainfall they experience [2], and forecasts of global change indicate this variability will only become more extreme [3]. In these forests, water availability plays a strong role in ecosystem functions [2,4,5], and seasonal drought is a common factor. The Yucatan Peninsula of Mexico presents

a gradient in precipitation increasing from northwest at the coast, towards the southeast inland. This gradient is followed by a corresponding variation in vegetation types, from microphyll desert, matorral, and low deciduous forests toward the coast, to medium semi-perennial forests further inland [6]. The Yucatan Peninsula is an important ecoregion with unique flora and fauna, and high (~10%) levels of endemism [7,8].

During the last 3500 years, the Yucatan Peninsula of Mexico has been subject to variation in wet/dry periods with exceptionally dry periods coinciding with the fall of the Classic Maya civilization [9]. As in other tropical dry forests [5], plants in the Yucatan should therefore possess a wide variety of strategies to withstand drought.

In addition to fluctuations in water availability, the Yucatan Peninsula is also subject to frequent disturbance from hurricanes and fires, as well as a centuries-long practice of slash and burn agriculture by the Maya population [10]. Large expanses of the peninsula are the result of, or are in the process of, secondary succession. Alvarez Añorve et al. (2012) [11] have proposed that, as communities change, so do plant functional types, and that although regional level studies provide a powerful tool for the understanding of tropical dry forest dynamics, a finer scale understanding is also needed.

Although the number of studies looking at regeneration in tropical dry forests is increasing [12–14], still few have looked at functional processes behind regeneration (but see [15]). Fewer still have attempted to associate differences in microclimate that occur during ecological succession to changes in the physiology of plants and to their population dynamics. This paper is a first attempt to look at associations among microclimate and physiology, and differences in abundance of forest age classes at the population level for different species.

Although ecological succession implies species replacement over time, some species persist and one may find these species in plots of several different successional ages. We propose that persistence despite successional change may imply a suite of adaptations or a degree of plasticity that enables some species to survive and reproduce under changing conditions.

In this study we examined three species, in three families: *Piscidia piscipula* L.(Sarg.), Fabaceae; *Bunchosia swartziana* Griseb., Malpighiaceae; and *Psidium sartorianum* (Bergius) Nied., Myrtaceae (see summary characteristics of species, Table 1). Two of the species (*Piscidia* and *Bunchosia*) are reported at various stages of succession in a previous study in Northern Yucatan [16], and all three species, including *Psidium sartorianum*, are relatively common at our study site and appear to persist through out several stages of ecological succession, as reported in a previous study [13].

Table 1. Summary characteristics of three species studied in the tropical subdeciduous forest of the Biocultural Reserve of Kaxil Kiuic in the Yucatan Peninsula, Mexico.

Family	Species	Growth form	Leaf phenology	Fruit
Fabaceae	<i>Piscidia piscipula</i> L.(Sarg.)	Canopy species, reaches 12 to 15 m tall.	Brevi deciduous	Bean like pod with papery wings
Malpighiaceae	<i>Bunchosia schwartziana</i> Griseb.	Understory species, small tree 2 to 3 m tall.	Evergreen	Berry
Myrtaceae	<i>Psidium sartorianum</i> (Bergius) Nied	Canopy species, reaches up to 15 m tall.	Evergreen or deciduous ¹	Fleshy berry

¹ Delgado-Vargas, F., Díaz-Camacho, S.P., Salazar-Zamora, G., Uribe-Beltrán, M.J. and Vega-Aviña, R. 2005. *Psidium sartorianum* (O. Berg) Nied., an Indigenous Plant to Mexico, from Biology to Biological Activity. In *Search for Natural Drugs*. Vol. 13, Recent Progress in Medicinal Plants, Eds. Govil JN, Singh VK & Arunachalam C, pp. 81–114. Houston, TX: Studium Press LLC [17].

We used a chronosequence, which, although presents limitations (e.g., [18]); have been used successfully to infer mechanisms and processes behind successional change by comparing sites within an area that are known to differ in time since a disturbance [12,13,16,19,20].

We hypothesized the following:

- (1) Levels of plasticity, measured as variation in photosynthetic rates within and among individuals of a given species, would be positively related to species abundance.
- (2) Species would differ in their abundance of individuals of different size among plots (size classes were used instead of age categories—for example, saplings, juveniles, and adults—because of the difficulty of assigning developmental stage). Additionally, these differences would be associated with physiological and morphological traits of the species; in particular, successful species in young plots would also have higher photosynthetic rates, higher light saturation values, and higher incidence of mycorrhizal structures, when compared with species with lower abundance and regeneration capacity in young plots. Success, in this case, would be categorized as being present as adults (large size classes), and regenerating (producing saplings and juveniles of smaller size classes).
- (3) Microclimatic conditions at the leaf level would differ among plots with different time since disturbance (higher light and temperature would be observed in the younger plot, compared with the older one), but, because all plants were of a similar size (height and diameter) and growing in the understory, microclimate would not differ among species in a given plot.
- (4) As a result of differences in microclimate and soil conditions among plots (higher light and lower nitrogen in younger plots), we hypothesized that when plants of the same species were compared across plots, individuals growing in the younger plots would present higher photosynthetic rates, lower water potentials, lower specific leaf area (SLA), lower percent N, higher percent C, and higher incidence of mycorrhizal colonization when compared with individuals of the same species growing in older plots.

To address the above hypotheses, we collected climate data for our study area and investigated aspects of population dynamics (juvenile recruitment and mortality over a three-year period) for the three species growing in plots of different time since disturbance (young: 10 to 13 years; intermediate: 18 to 21 years; and old: more than 50 years of secondary succession). We associated differences in abundance (population dynamics) to select physiological (CO₂ assimilation rates, chlorophyll fluorescence, and water relations) and morphological (specific leaf area, percent N and C, and mycorrhizal associations) traits of each species, and to microclimatic conditions at the leaf level of individuals of each species growing in two (intermediate and old) of the three aforementioned plots during the wet season. Also, to further investigate microclimate differences among plots of different age of the chronosequence, we examined microclimate at a coarse level at four sites within each of the aforementioned plots (young: 10 to 13 years; intermediate: 18 to 21 years; and old: more than 50 years of secondary succession) during the dry season.

2. Materials and Methods

2.1. Study Site, Climate, and Microclimate

The study took place in the tropical sub deciduous forest of the Biocultural Reserve of Kaxil Kiuic located toward the center of the Yucatan Peninsula (20°04' N, 89°35' W) in Mexico. The forest is characterized by trees 12 to 15 m high, mean annual temperature of 26 °C, mean annual rainfall between 1078 and 1220 mm, and a marked dry season during which 50–75% of the trees lose their leaves [21]. The dry season is frequently interrupted by a season referred to as *Nortes* (January to February) during which time short episodes of rainfall may occur (2–3 days) and temperatures are relatively low (down to ~5 °C).

A meteorological station was set up at the field site and climate data over the study period (2007 to 2011) are summarized in Figure 1. The species examined in this study included two canopy *Piscidia piscipula* L.(Sarg.) (Fabaceae) and *Psidium sartorianum* (Bergius) Nied. (Myrtaceae), and one understory species, *Bunchosia swartziana* Griseb. (Malpighiaceae). Summary characteristics of species are included in Table 1.

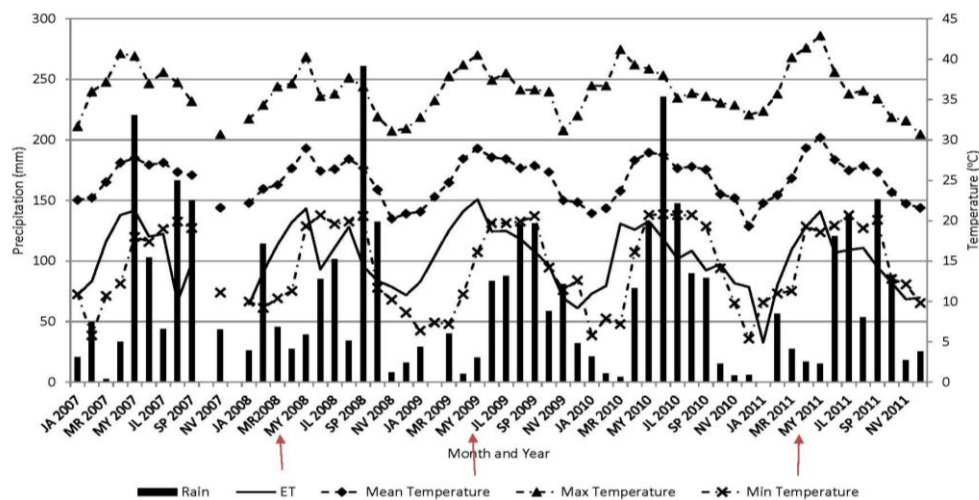


Figure 1. Precipitation (mm) and temperature ($^{\circ}\text{C}$) measured at the study site of the Biocultural Reserve of Kaxil Kiuic, Yucatan, Mexico (2007–2009). Total monthly rainfall (solid bars), evapotranspiration (ET) (solid line); and mean (diamonds), minimum (exes) and maximum (triangles) temperatures for each month. Arrows on the bottom indicate sampling times for the dry (May 2008), wet (July 2009) and dry (2011) seasons.

Nine permanent plots (three plots in each age class; 50×20 m: 1000 m^2 each) of different time since disturbance (10–13 young, 18 to 21 intermediate, and more than 50 years since disturbance, old) were used to study changes in the abundance of each species over three years (2007 to 2009). Three size classes were used as surrogates for plant age. Saplings: individuals less than 1 cm stem diameter (measured at 1.3 m), surveyed every four months to coincide with the wet, *Nortes*, and dry seasons, in 30 sub-plots of 2×1.5 m; juveniles: 1–5 cm stem diameter; surveyed every six months (wet and dry seasons) in sub-plots of 6×5 m; and adults: >5 cm diameter; surveyed every six months (wet and dry seasons) in 10×10 m sub-plots. Mortality and recruitment were determined for each size class and species in each of the plots of different successional age.

Two of the $50 \text{ m} \times 20 \text{ m}$ plots of different age (intermediate and old) were used for the determination of microclimate and for physiological measurements. Microclimate was determined at each plot in the wet season of 2009. For this, photosynthetic photon flux density (PPFD) was measured with gallium arsenide phosphide photodiodes (Hamamatsu Corporation, Bridgewater, NJ, USA; [22]) placed 1 cm above selected leaves of three individuals of each species within each plot. Also, leaf temperature was measured with copper-constantan thermocouples 0.2 mm in diameter for two leaves of three individuals of each species. Individuals were of similar characteristics (height and size) and in relative vicinity of those used in physiological measurements (with restrictions given by cable lengths). Individuals were chosen growing at microsites qualitatively representative of plot characteristics. Data were recorded every 15 s in a data logger (CR21X, Campbell Scientific Inc., Logan, UT, USA), equipped with a 32-channel multiplexer (AM416, Campbell Scientific Inc., Logan, UT, USA), and 10-min means were stored in a solid-state storage module (SM192, Campbell Scientific Inc., Logan, UT, USA). Microclimate was also determined at a coarse level. Four sites representative of plot heterogeneity were chosen per plot, and daily courses of relative humidity (RH; Compact Whirling Hygrometer, Ertcro, UK), light (Traceable Light Meter, Fisher Scientific, Pittsburgh, PA, USA; measurements were taken in Lux and converted to $\mu\text{mol m}^{-2}\text{s}^{-1}$ using $1000 \text{ lux} = 1 \text{ klux} = 19.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$; [23]), and temperature (infra-red –IR- gun thermometer, Minitemp, Raytek, Santa Cruz, CA, USA) were recorded every hour over the course of one day (dry season 2011). A single measurement of relative humidity, four measurements of photosynthetic photon flux density (PPFD; taken at breast height and facing in each of the four cardinal directions), and four measurements of leaf litter temperature and leaf temperature (in each of the four cardinal directions) were recorded. For leaf

litter, the IR gun was pointed down at the leaf litter in each cardinal direction and for leaf temperature the IR gun was pointed outward at the first leaf on a plant in each cardinal direction.

2.2. Physiological Measurements

For the determination of CO₂ assimilation rates (photosynthetic rates), light curves were measured with an infrared gas analyzer (LI-6400, LI-COR, Lincoln, NE, USA) both in the dry (May 2008) and in the wet (July 2009) season. For maximum apparent photosynthetic electron transport rate (ETR_{max}), effective yield of photosystem II (quantum yield in light; $F_m' - F/F_m'$), and PSII efficiency (quantum yield of photosynthesis; F_v/F_m) light curves were determined with a Mini PAM (Heinz Walz GmbH, Effeltrich, Germany) fluorometer in the wet season (July 2009). Measurements were taken each morning over three days (both seasons Licor 6400, wet season only, Mini PAM) on a single leaf of each of 4–5 individuals per species per plot. For the determination of leaf traits (specific leaf area: SLA; leaf area (cm)/leaf dry weight (g)), and percent nitrogen and carbon content, one leaf per individual (4–5 individuals), species, and plot was collected at the end of the wet season 2009. Predawn and mid-day leaf water potentials were measured in both the wet and dry seasons in both plots. Leaf water potential measurements (Ψ) were determined using psychrometric chambers (C-30, Wescor Inc., Logan, UT, USA) and a micro voltmeter (HR33, Wescor Inc., Logan, UT, USA). In the dry season, relative capacitance of foliar tissue for each of the three species was obtained from curves of Ψ and relative water content (RWC). RWC was determined as follows: (fresh weight – dry weight)/(saturated weight – dry weight) of the samples [24]. Water potential (Ψ) measurements of water saturated tissue samples were followed by Ψ measurements of air dried samples (for 1–2 min) using a vapor pressure osmometer (Vapro 5520, Wescor Inc., Logan, UT, USA).

To check for the presence of mycorrhizal associations, root tips from ten individuals per species and plot were sampled. The stem of each individual was followed (excavated) underground and young non suberized adventitious roots were sampled. Root samples were kept refrigerated and surveyed for presence/absence of mycorrhizal structures by clarifying with 10% KOH in a water bath at 90 °C for about 20 min; rinsing, and acidifying roots in 2.5% HCl. After acidification roots were stained with 0.05% trypan blue and examined under the microscope (procedure modified from Koske and Gemma, 1989 [25] with suggestions from S. Greipsson).

2.3. Statistical Analyses

Repeated measures analyses of variance (ANOVAR, SPSS 15 or 18, Chicago, IL, USA) were used to compare light curves (Licor 6400) among species, plots and seasons. For these, if Mauchly's test of sphericity was not met and epsilon values were $\ll 1$, then multivariate analyses of variance (MANOVAR, SPSS 15 or 18, Chicago, IL, USA) were used (as per [26]). Factorial analyses of variance (fluorescence) and standard univariate analyses of variance (mycorrhizae) and/or *t*-tests (mean maximum assimilation rates, minimum water potentials) were used for comparisons of means (SPSS or Excel). For comparisons involving small sample sizes, additional non-parametric Mann Whitney *U* tests (SPSS 18, Chicago, IL, USA) were performed.

3. Results

3.1. Climate

Climatological data for Kaxil Kiuic indicated an average cumulative rainfall per year of 795 mm and was higher in the first two years of the study (2007 and 2008: 834.8 and 893.4 mm respectively). The wet season extended roughly from May/June to September/October (Figure 1). Mean annual temperature was 25.1 ± 0.4 °C ($X \pm SEM$), with a mean maximum of 36.1 ± 0.4 °C, and a mean minimum of 14.4 ± 0.7 °C. The highest temperatures were in the 40 °C range (40.2–42.9 °C) and generally occurred in May, whereas lowest temperatures occurred December through February. The lowest value registered was 5.8 °C in February 2007 and again in January 2010 (Figure 1).

3.2. Population

Population data from 2007 to 2009 showed marked differences among species in their relative abundance of saplings, juveniles, and adults among plots of different age (young 10 to 13 years, intermediate 18 to 21, and old more than 50 years of secondary succession, Figure 2). *Piscidia piscipula* had few saplings across the three plot ages (eight total), and the mean number of juveniles and adults for this species was highest in the youngest plot (Figure 2a). All *P. piscipula* saplings were found in plots of less than 22 years of secondary succession (designated as young and intermediate in this study). Over a three-year period no recruitment of saplings was observed, but there was sapling mortality, suggesting that recruitment may be very low and limited to areas of relatively early succession. Furthermore, juveniles were more abundant in younger areas (quadrats of less than 22 years; in some of which they grew to adults) than in older ones (those of more than 50 years of secondary succession). Adults of the species were found in all three categories of successional age (plots), but only had recruitment (growth of juveniles) in plots of less than 22 years, and mortality was only registered in older plots (more than 50 years).

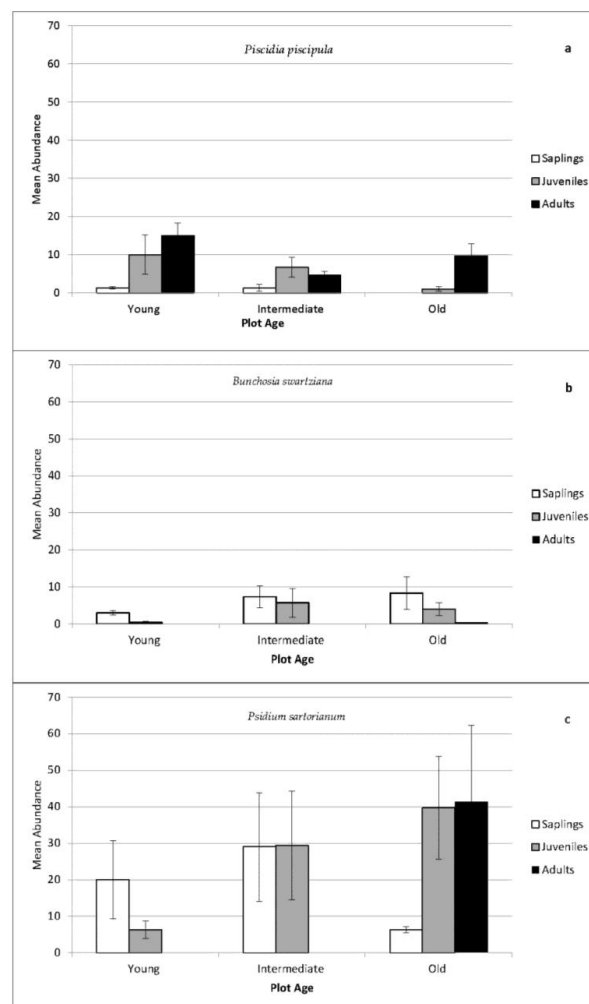


Figure 2. Population data (mean number of saplings, juveniles and adults) for three species: *Piscidia piscipula*, (a) *Bunchosia swartziana*, (b) and *Psidium sartorianum* (c) For population data, saplings were individuals less than 1 cm stem diameter (measured at 1.3 m); juveniles: 1–5 cm stem diameter; and adults: >5 cm diameter. Data were collected in plots of different time since disturbance (10 to 13 young, 18 to 21 intermediate, and more than 50 years since disturbance, old) over three years at the Biocultural Reserve of Kaxil Kiuic, Yucatan, Mexico. (See Materials and Methods section for additional sampling details).

Bunchosia swartziana had relatively low numbers of individuals across all plots, had a greater number of saplings (compared with juveniles or adults) in all plots, and the number of saplings increased with plot age (Figure 2b). However, *B. swartziana* only had one adult at one plot, and the results from sapling dynamics showed an almost neutral balance between recruitment and mortality, with a slightly greater mortality. Of the three species, *Psidium sartorianum* had the highest abundance across plots, and sapling abundance was greatest in the young and intermediate plots (less than 22 years since disturbance) and lowest in the old plot (more than 50 years of secondary succession; Figure 2c). Mean number of juveniles for *P. sartorianum* was greatest in the older plots and adults were only found in older plots (Figure 2c). Overall, *B. swartziana* had the lowest and *P. sartorianum* had the greatest abundance among the three species across plots (Figure 2a–c).

3.3. Microclimate and Fluorescence:

Large differences were seen in fine scale microclimate data in light (PPFD $\mu\text{mol m}^{-2} \text{s}^{-1}$) and temperature ($^{\circ}\text{C}$) among plots (Figure 3a–d), and within the *intermediate* plot among species (Figure 3a,c; wet season 2009). Light was higher in the *intermediate* plot compared with the old (Figure 3a,b), and in the intermediate plot, individuals of *Piscidia piscipula* received higher light and had higher temperatures at noon compared with the other two species (Figure 3a,c).

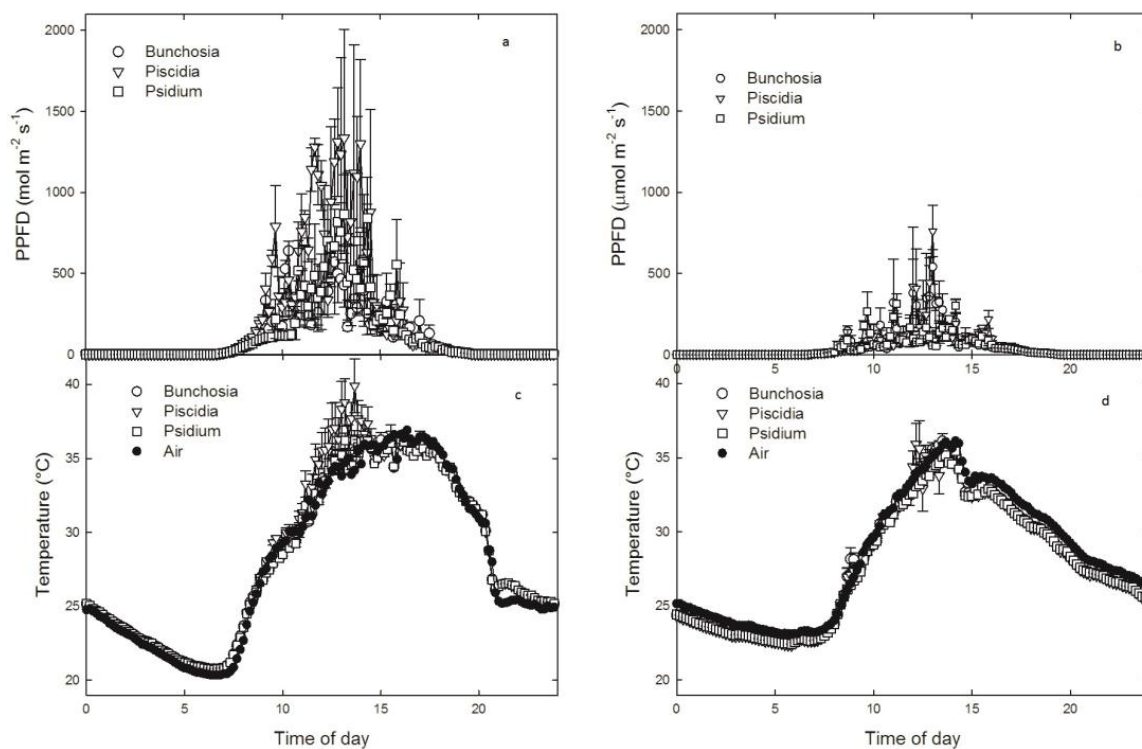


Figure 3. Fine scale microclimate measurements for individuals growing in the understory of an *intermediate* (18 to 21 years; **a, c**) and old (>50 years of secondary succession; **b, d**) plot at Biocultural Reserve of Kaxil Kiuic, Yucatan Mexico (rainy season 2009). Photosynthetic photon flux density (PPFD) was measured with gallium arsenide phosphide photodiodes placed 1 cm above selected leaves of three individuals of each species within each plot. Leaf temperature was measured with copper-constantan thermocouples for two leaves of three individuals of each species. Data were recorded every 15 s in a data logger and 10-min means were stored in a solid-state storage module.

All species had a greater mean maximum electron transfer rate (ETR_{max}) in the *intermediate* plot in the morning, and rates declined progressively for noon and afternoon mean values (Table 2). This was not the case for the old plot, where mean ETR_{max} values were highest at noon for all three species (Table 2). A factorial analysis of variance indicated significant effects of plot ($F_{(1)} = 6.120$; $p = 0.018$), time of day (morning, noon, or afternoon, $F_{(2)} = 5.698$; $p = 0.007$), and for the plot*time* interaction on ETR_{max} ($F_{(2)} = 6.950$; $p = 0.003$), but not a significant effect of species for an α of 0.05. Among species, the greatest ETR_{max} registered was for *P. piscipula* ($160 + 23 \mu\text{mol m}^{-2} \text{s}^{-1}$ intermediate plot, morning values). Maximum quantum photosynthetic efficiency (F_v/F_m) registered for *P. piscipula* (0.80 and 0.81; Table 2) and *Bunchosia swartziana* (0.81 for both plots) reached the expected optimum values. However, F_v/F_m values for *Psidium sartorianum* (0.78, intermediate and 0.79, old plot) were somewhat below the 0.80 optimum level (Table 2).

Table 2. Mean maximum electron transport rate (ETR_{max}), photosynthetic photon flux density at saturation (PPFD $\mu\text{mol}/\text{m}^2/\text{s}^1$), effective quantum yield of photosystem II (PSII) in light ($(F_m' - F)/F_m'$); quantum yield of PSII (F_v/F_m); for measurements in leaves taken at different times of day (Hour) for each species and plot (intermediate: approximately 18 to 21 years; and old: >50 years of secondary succession). Data represent mean values for four to six individuals ($n = 4-6$; $\pm\text{SE}$), collected in the wet season (July 2009) at the Biocultural Preserve of Kaxil Kiuic in the Yucatan Peninsula, Mexico.

Species	Hour	ETR_{max}^1		PPFD _{sat}		$(F_m' - F)/F_m'$		F_v/F_m	
		Interm.	Old	Interm.	Old	Interm.	Old	Interm.	Old
<i>Piscidia piscipula</i>	07:00	-	-	-	-	-	-	0.80 \pm 0.008	0.81 \pm 0.001
	09:00	160 \pm 23	86.7 \pm 12	1190 \pm 199	817 \pm 20.3	0.74 \pm 0.02	0.78 \pm 0.003	-	-
	12:00	106.7 \pm 10	105.3 \pm 14	1133 \pm 249	1283 \pm 301	0.48 \pm 0.15	0.51 \pm 0.12	-	-
	17:00	78.7 \pm 1	103.3 \pm 4	607 \pm 3	1127 \pm 73	0.72 \pm 0.01	0.74 \pm 0.009	-	-
<i>Bunchosia schwartziana</i>	07:00	-	-	-	-	-	-	0.81 \pm 0.005	0.81 \pm 0.006
	09:00	135 \pm 12	82 \pm 9	773 \pm 93	983 \pm 44	0.72 \pm 0.03	0.78 \pm 0.013	-	-
	12:00	129 \pm 16	108 \pm 6	870 \pm 65	710 \pm 56	0.64 \pm 0.09	0.59 \pm 0.15	-	-
	17:00	86 \pm 6	89 \pm 8	806 \pm 248	697 \pm 32	0.75 \pm 0.004	0.75 \pm 0.017	-	-
<i>Psidium sartorianum</i>	07:00	-	-	-	-	-	-	0.78 \pm 0.009	0.79 \pm 0.009
	09:00	157 \pm 23	83 \pm 9	1123 \pm 113	680 \pm 20	0.71 \pm 0.08	0.80 \pm 0.003	-	-
	12:00	140 \pm 44	148 \pm 39	1050 \pm 76	713 \pm 95	0.48 \pm 0.15	0.63 \pm 0.02	-	-
	17:00	93 \pm 9	86 \pm 18	683 \pm 60	670 \pm 43	0.73 \pm 0.03	0.77 \pm 0.003	-	-

¹ For ETR_{max} a factorial analysis of variance indicated significant effects of plot ($F_{(df=1)} = 6.120$; $p = 0.018$), time of day (morning, noon, or afternoon, $F_{(df=2)} = 5.698$; $p = 0.007$), and for the plot*time* interaction on ETR_{max} ($F_{(df=2)} = 6.950$; $p = 0.003$), but not a significant effect of species for an α of 0.05.

At a coarse level, in the dry season (2011) the intermediate plot had higher mean light levels and higher maximum light in the afternoon compared with the old plot (Figure 4), and measurements indicated temperatures for leaves on plants were more than 10 °C lower than ground level leaf litter (Figure 4). Afternoon leaf temperatures among forest species were frequently at or above 40 °C in all plots (one measurement of 50 °C for leaf in the youngest plot, 10 to 13 years since disturbance, was recorded; data not shown); and most plants exhibited outward signs of water stress with the notable exception of *Piscidia piscipula* (that in the dry season of 2011 exhibited turgid, upright leaves).

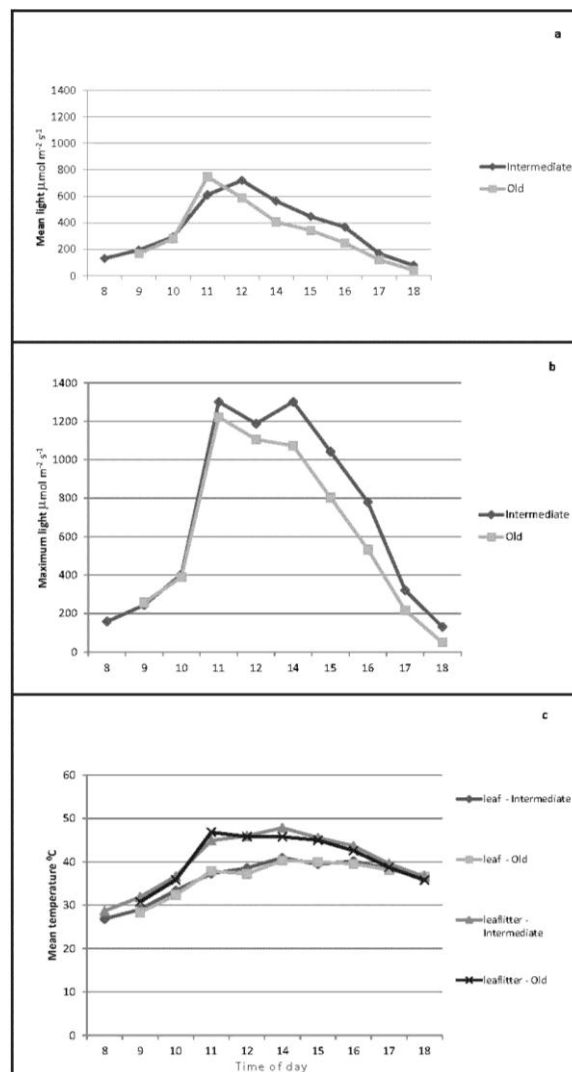


Figure 4. Coarse scale microclimate measurements of mean light (a), maximum light (b), and mean temperature of leaves or leaf-litter (c) for plots of different time since disturbance. Intermediate (~18 to 21 years; dark line with diamonds; a,b) and old (>50 years; gray line with squares, a,b). Four sites representative of plot heterogeneity were chosen per plot, and daily courses of light (Traceable Light Meter, Fisher Scientific, Pittsburgh, PA, USA; taken in Lux and converted to $\mu\text{mol m}^{-2} \text{s}^{-1}$ using $1000 \text{ lux} = 1 \text{ klux} = 19.5 \mu\text{mol m}^{-2} \text{s}^{-1}$; [22]), and temperature (infra-red –IR- gun thermometer, Minitemp, Raytek, Santa Cruz, CA, USA) were recorded every hour over the course of one day (dry season 2011). Four measurements of light (taken at breast height and facing in each of the four cardinal directions), and four measurements of leaf litter temperature (gray line with triangles intermediate; dark-line with exes old) and leaf temperature (line with diamonds, intermediate; gray line with squares, old) were recorded (c). For leaf litter, the IR gun was pointed down at the leaf litter in each cardinal direction and for leaf temperature the IR gun was pointed outward at the first leaf on a plant in each cardinal direction.

3.4. Seasonal and Plot Differences in CO_2 Assimilation:

Multivariate analyses of variance with repeated measures indicated significant effects of season ($F = 7.883$; $p = 0.008$) and species ($F = 7.068$; $p = 0.011$) on CO_2 assimilation light response curves, but no significant overall effect of plot ($F = 3.586$; $p = 0.066$) (Figure 5). With the exception of the old plot in the

wet season where *Bunchosia* had the highest response curve, *Piscidia piscipula* had the highest response curves in all other instances.

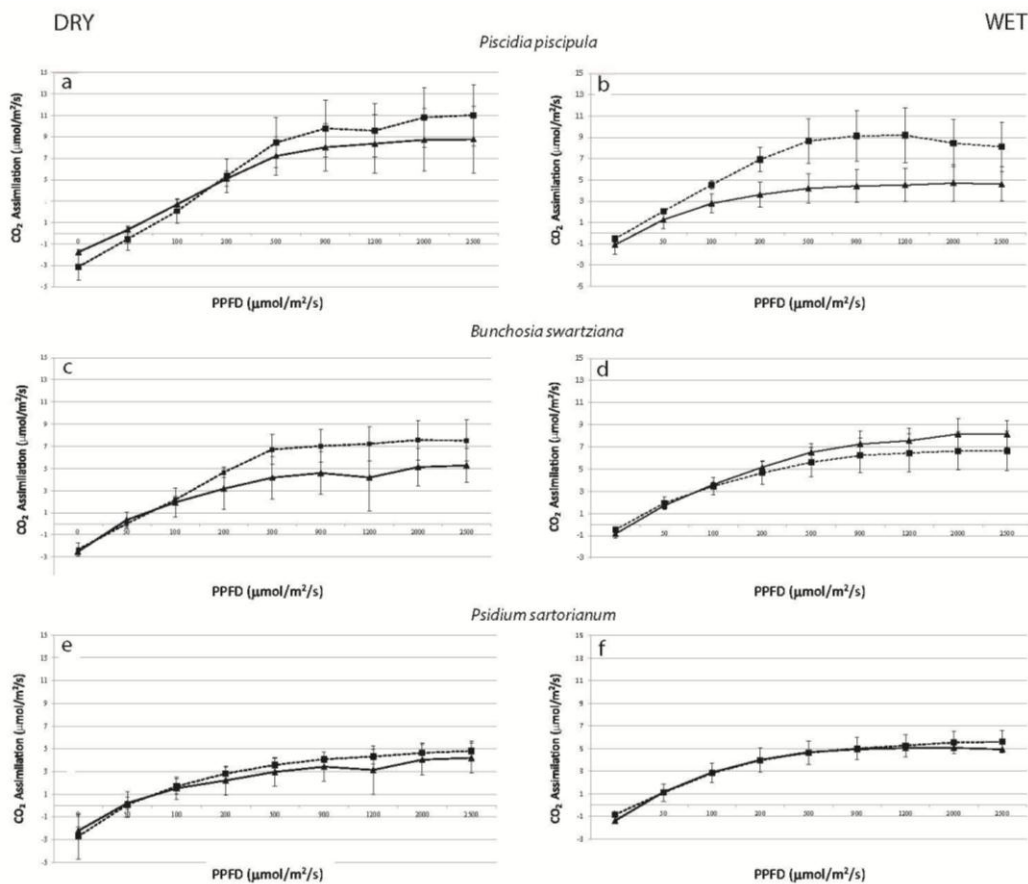


Figure 5. Comparison light response curves (CO_2 uptake in $\mu\text{mol m}^{-2} \text{s}^{-1}$; Licor 6400) for study species collected in plots of different time of secondary succession (*intermediate*, ~18 to 21 years, dashed line with squares; and old >50 years, straight line with triangles) in the dry (May 2008) and wet (July 2009) seasons at the Biocultural Preserve of Kaxik Kiuic, Yucatan, Mexico.

Between seasons, the largest difference in CO_2 assimilation curves was for *Piscidia* in the old plot (Figure 5). For *P. piscipula* (Table 3 and Figure 5), the mean maximum assimilation rate (A_{max}) was almost two times greater in the old plot during the dry season compared with the same plot during the wet season (8.2 ± 1.35 versus $4.9 \pm 0.81 \mu\text{mol m}^{-2} \text{s}^{-1}$; Table 3). In addition, *P. piscipula* was the only species that showed a significant difference among plots in A_{max} . In the wet season *P. piscipula* had a significantly greater A_{max} in the *intermediate* plot compared with the old plot (9.4 ± 1.3 versus $4.9 \pm 0.81 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively. t -test $p < 0.05$; Table 3).

Table 3. Mean maximum CO₂ assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) \pm SE in leaves for each species. Data were collected for each species, plot (intermediate: approximately 18 to 21 years; and old >50 years of secondary succession) and season (DRY and WET) from light curves generated each morning over three days. Data represent mean values for four to six individuals ($n = 4-6$), collected in the dry (May 2008) and wet season (July 2009) at the Biocultural Preserve of Kaxil Kiuic in the Yucatan Peninsula, Mexico. Significant differences among plots are indicated by * (t -test for mean maximum assimilation rate comparison $p < 0.05$).

Species	Dry		Wet	
	CO ₂ Assimilation		CO ₂ Assimilation	
	Intermediate	Old	Intermediate	Old
<i>Piscidia piscipula</i>	10.5 \pm 1.2	8.2 \pm 1.35	9.4 \pm 1.13 *	4.9 \pm 0.81
<i>Bunchosia schwartziana</i>	8.0 \pm 0.72	6.9 \pm 0.98	6.8 \pm 0.77	8.2 \pm 0.60
<i>Psidium sartorianum</i>	3.3 \pm 0.77	3.2 \pm 1.6	5.6 \pm 0.46	4.6 \pm 0.44

3.5. C, N, Water Relations, and Mycorrhizae

Percent C and N showed no consistent patterns among plots, and the difference was only significant for percent N in leaves of *P. sartorianum* that had significantly greater %N in the older plot (one tailed t -test $p = 0.04$; $df = 7$; Table 4). For all species, the mean specific leaf area was greater in the older plot, however differences between plots were not statistically significant (t -test $p > 0.05$).

Table 4. Mean percent C and N (dry weight), SLA (Specific Leaf Area = leaf area (cm)/dry mass (gr)) + SE in leaves for each species and plot (intermediate: approximately 18 to 21 years, and old: > 50 years of secondary succession). Data represent mean values for four to six individuals ($n = 4-6$) collected in the wet season (July 2009) at the Biocultural Preserve of Kaxil Kiuic in the Yucatan Peninsula, Mexico. Significant differences between plots are indicated by an asterisk * (t -test $p < 0.05$).

Species	% C		%N		SLA	
	Interm.	Old	Interm.	Old	Interm.	Old
<i>Piscidia piscipula</i>	40.96 \pm 0.45	41.47 \pm 0.8	2.54 \pm 0.18	2.47 \pm 0.17	149.9 \pm 12.12	176.9 \pm 18.40
<i>Bunchosia schwartziana</i>	45.05 \pm 2.33	41.90 \pm 0.8	3.35 \pm 0.25	3.30 \pm 0.27	121.2 \pm 14.76	145.2 \pm 9.95
<i>Psidium sartorianum</i>	44.76 \pm 1.1	46.4 \pm 0.62	1.98 \pm 0.14 *	2.36 \pm 0.13 *	163.5 \pm 15.39	172.3 \pm 26.38

* One tailed t -test $p = 0.04$; $df = 7$.

For plant water relations, maximum (pre-dawn) and minimum (midday) water potentials showed significant differences among seasons and species but not among plots. All species had lower minimum leaf water potentials in the dry season (t -test $p < 0.05$, Figure 6). Among the three species, *B. swartziana* had significantly lower mean minimum leaf water potentials ($\Psi = -8.0$ MPa; Figure 6) and significantly lower leaf osmotic potentials compared with the other two species (Figure 6; t -test $p < 0.05$ for each). For mean leaf water and osmotic potentials, values for *B. swartziana* were followed by values for *P. sartorianum* ($\Psi = -6.0$ MPa), and leaves of *P. piscipula* had the greatest Ψ values (-2.0 MPa; Figure 6), and also showed the greatest levels of relative leaf capacitance (Figure 7).

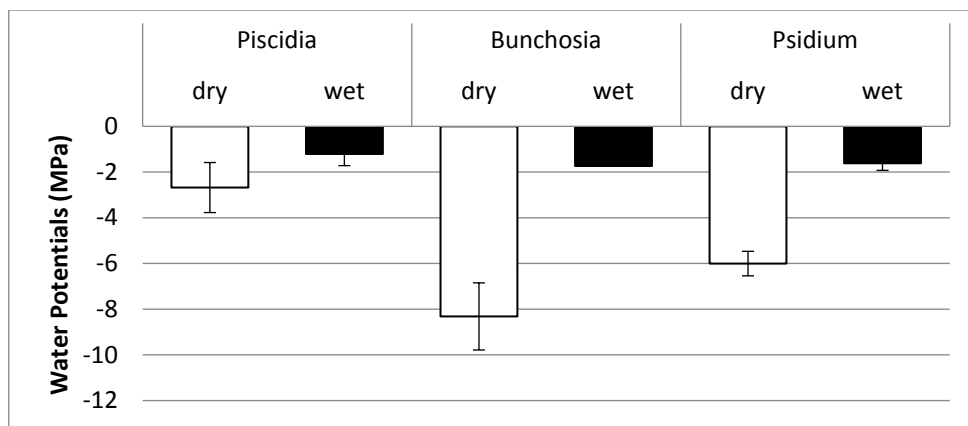


Figure 6. Mean minimum water potentials (MPa; \pm SE) for the species: *Piscidia piscipula*, *Bunchosia swartziana*, and *Psidium sartorianum* collected during the dry (May 2008) and the wet seasons (July 2009) at the Biocultural Preserve of Kaxil Kiuic, Yucatan, Mexico. Differences between plots (see methods) were not statistically significant, differences between seasons were significant (t -test $p < 0.05$).

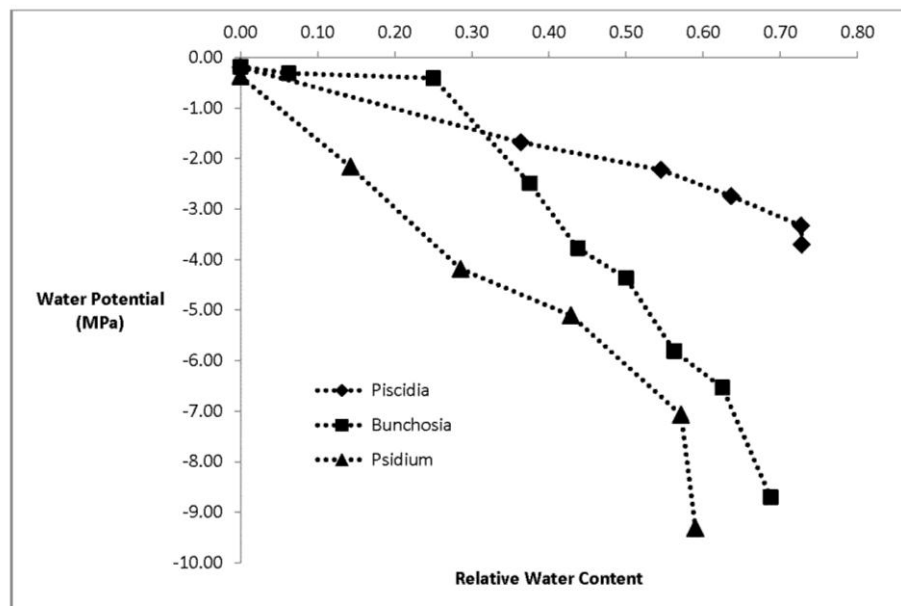


Figure 7. Curves of water potential (MPa) and relative water content (RWC) for the determination of relative capacitance of the study species. RWC was determined as: (fresh weight – dry weight)/(saturated weight – dry weight) of the samples. Measurements of water saturated tissue samples were followed by measurements of air dried samples (for 1–2 min) using a vapor pressure osmometer (Wescor Inc., Logan, UT, USA).

The percent incidence of mycorrhizae per species and plot (from youngest to oldest plot, i.e., young, intermediate, old) was, for *P. piscipula* 100, 58, and 50 percent; for *B. swartziana* 90, 80, and 90 percent; and for *P. sartorianum* 60, 67, and 100 percent. There appeared to be a slight effect of plot and species on mycorrhizal presence/absence. Univariate analyses of variance suggested a species*plot interaction $p = 0.057$ and showed a difference in mean mycorrhizae presence among plots t -test $p = 0.045$.

4. Discussion

The three species studied exhibited within species variation in abundance along the successional gradient. *Piscidia piscipula* had more individuals in the young successional sites, *Psidium sartorianum* in the old successional sites, and *Bunchosia swartziana* was present at low abundance at all sites. All of the species were subjected to drought stress irrespective of the forest age, because a prolonged dry season with high air temperatures was ubiquitous to all the plots. Nevertheless, because of differences in canopy cover, microclimatic differences between plots of different ages were found. Light readings recorded above understory individuals of the three species followed predictions and were significantly higher in the intermediate plot compared with the *old* plot, with *P. piscipula* being more prevalent in the more exposed sites within those plots. In agreement with these microenvironmental differences and the differential distribution among plots of different ages, *P. piscipula* presented a series of physiological traits related to higher light and water stress tolerance, while *P. sartorianum* had traits to deal with shade tolerance and *B. swartziana* showed intermediate traits.

We had hypothesized that levels of plasticity, measured as variation in photosynthetic rates within and among individuals of a given species, would be positively related to species abundance (H1) and that species would differ in their abundance of individuals of different size among plots (e.g., saplings, juveniles, and adults), and that these differences would be associated with physiological and morphological traits of the species (H2). Species distribution among plots supported our second hypothesis and prediction for *P. sartorianum*, which based on physiological traits, was expected to present a greater abundance in older plots. Dupuy et al. (2012) [13] also found that *P. sartorianum* was among the dominant species in plots older than 15 years on flat areas, but not in younger plots or plots located on hills. Our results may also suggest a density dependent mortality for this species as juveniles in young plots had greater recruitment than mortality, but the opposite trend was found in older plots. The site with the highest density of adults (>50-year-old site; old) was also the one with the highest juvenile mortality. The low abundance of *Bunchosia* across plots was not expected (H1; but see below). *B. swartziana* presented the lowest overall abundance, whereas *P. sartorianum* presented the greatest abundance. In northern Yucatan where conditions are drier, González-Iturbe et al. (2002) [16] found that although its presence varied by location, *B. swartziana* was present in plots of all ages (which for that study comprised ages of 10 years, 15 years, and more than 20 years of secondary succession). Their results also indicated that *Bunchosia* was among the species that contributed 45 to 50% of the importance value in “intermediate” (~15 years) and “advanced” (much more than 20 years) successional plots and all sites. However, other studies in our same study area have found that *B. swartziana* was present in different forest age classes, but at low abundances (J M. Dupuy pers. obs.) In northern Yucatan adults of *P. piscipula* (≥ 3 cm DBH) were present in sites of all successional ages [16], as it was in ours, but at our site abundance of all stages was highest in the young plot. Dupuy et al. (2012) [13] also report *P. piscipula* among the ten most dominant species across different forest age classes.

Differences in microclimate among plots followed predictions (H3), with the younger plots exhibiting higher light and temperature. However contrary to our predictions (H3, second part; that because all plants were of similar size (height and diameter) and growing in the understory, microclimate would not differ among species in a given plot), differences in the microclimatic conditions of the three species in a given plot were also observed, with individuals of *P. piscipula* receiving higher light and leaves exhibiting higher temperatures than individuals of the other two species. These differences at the individual level may have resulted by chance (sampling error) or from a combination of physiological differences and differences in survival of seedlings under different microclimate (temperature, light, leaf-litter cover, etc.). These results suggest the need for a more detailed study of microclimate variability within plots and its potential effect on seedlings.

Differences in leaf temperature may have resulted from differences in cooling at the leaf level (e.g., Flexas et al., 1999 [27] studying grapevines, found higher leaf temperatures in plants subjected to drought, presumably as a result of stomatal closure). Leaf size and microenvironment influence

leaf energy balance and growth [28,29] and, despite *P. piscipula* potentially having the deepest roots among the three species (see below), it also had the largest leaf area, thus being in the most exposed microenvironment can be advantageous for this species during the rainy season, but not in the dry season.

Microhabitat conditions have been found to play an important role in seed germination and survival [30–32]. In this study, significant differences were found in microclimate at a coarse level both between plots (higher mean and maximum light in the intermediate-18–21-year-old-plot compared with the old ≥ 50 year old-plot during the dry season of 2011) and within plots at different sites. Ground level leaf litter temperature reached quite high maximum values (61 °C in the young plot: 10 to 13 years old (data not shown), and 56 and 52 °C in intermediate and old plots respectively), posing quite strenuous conditions at the leaf litter surface, and suggesting that leaf litter cover may be a strong buffer to high temperatures at the ground level, especially during the dry season, in this forest.

We predicted that differences in abundance across plots would be associated to functional traits of each species (H2, H4). Differences in light use among the species were evident in the light response curves performed, and consistent with results from population dynamics. Carbon dioxide assimilation values were greater in *P. piscipula*, whose population dynamics also included a higher number of juveniles and adults in the young plot. Carbon dioxide assimilation was lower in *P. sartorium*, the old plot species, and *B. swartziana* had intermediate values across plots.

Regarding the association between persistence and plasticity (H1), this hypothesis did not seem to be supported at the local level, but did seem to be consistent with the regional distribution and abundance of species. Light curves for CO₂ assimilation in *P. piscipula* showed the highest variation among individuals, plots and seasons. This high degree of plasticity is consistent with its designation as dominant species in central Yucatan [7] and it being found across the Peninsula. On the other hand, light curves for *P. sartorianum* a species with a more restricted regional distribution (but highest abundance at our site), showed the least variation among individuals, plots, and seasons. Carbon dioxide assimilation in *B. swartziana* showed greater plasticity and higher overall rates than *P. sartorianum*.

Although there was a significant effect of season (and species) on CO₂ assimilation light response curves (MANOVA $p < 0.05$); contrary to what has been found in other studies (e.g., [33]), the season effect did not translate into consistent increases in mean maximum assimilation rates for the wet season. Because relatively small levels of water stress may result in decreased CO₂ assimilation [34] and given that stomatal responses have been found linked to chemical signals from the roots when soil dries [35,36], we expected to find increased CO₂ assimilation rates in the wet season (or, conversely; lower rates in the dry season). Only *P. sartorianum* had higher mean maxima in the wet season. Furthermore, for *P. piscipula* assimilation rates were higher in the dry season. This lack of an increase in assimilation rates across species in the wet season however, may have been the result of the relatively low rainfall of 2009, which had the lowest recorded rainfall for a wet season over the five-year study period.

Differences in microclimates between plots may have affected maximum electron transport rates (ETR_{max}). For all species in the intermediate plot ETR_{max} values were higher in the morning and declined progressively for noon and afternoon values, whereas in the *old* plot, where microclimate conditions were milder, the higher ETR_{max} values were seen at noon. Intermediate plot ETR_{max} responses were probably a result of a combination of light (highest at noon) and vapor pressure deficit (higher at noon and in the afternoon; data not shown), leading to a lack of recovery of morning ETR_{max} values. Old plot ETR_{max} with high noon values were probably influenced by the lower light environment of the morning and afternoon hours in the old plot. Our data are consistent with that of Ribeiro et al., 2005 [37]. They looked at photosynthesis in tropical species under different irradiance and found that under high light conditions, pioneer species exhibited higher ETR at mid-morning and afternoon, but under milder light (34% of full sunlight) they exhibited higher ETR values at noon.

The differences between the three species in photosynthetic capacity shown by the assimilation light response curves were not evident in the ETR_{max} values. This may be because ETR_{max}

measurements were instantaneous and are not representative of the full spectrum of responses to light, better represented in the light response curves. Alternatively, higher than expected ETR rates in *P. sartorianum*, (which exhibited low CO₂ assimilation rates), may have been the result of other light driven processes that increase ETR but do not translate into assimilation (e.g., O₂ reduction; [38]).

Given that drought first affects stomatal closure, and that internal leaf metabolic processes are frequently not affected until leaf relative water content decreases below ~70%, decreases in F_v/F_m are usually not linked to water stress, but may indicate other stressors such as heat or photoinhibition [34]. Predawn values of F_v/F_m (quantum yield of photosynthesis) registered for *P. piscipula* (0.80 and 0.81) and *B. swartziana* (0.81 for both plots) were probably indicative of some level of overnight repair of potential photo-damage. For *P. sartorianum* F_v/F_m values remained close to, but slightly below the 0.80 optimum level (0.78, intermediate and 0.79, old plot; Table 2), which could point towards high light levels having a stronger effect on *P. sartorianum* and/or the species being more susceptible to heat. Brestic et al. (2012) [39] applied heat treatments in the dark to winter wheat (*Triticum aestivum* L.) and found that a dark heat treatment at 40 °C brought about a decrease in F_v/F_m . The same authors also found that plants could exhibit acclimation effects on photosystem II (PSII) photochemical efficiency. These effects were associated with an enhanced PSII thermostability induced by increases in daily temperature maxima above 30 °C [39]. Other authors have also found significant differences in the levels of heat susceptibility and extent of thermotolerance among species, and within species based on habitat of provenance or genetic variety [40,41]. In addition, plant species frequently have large capacities for plastic acclimation of photosynthetic thermotolerance, with the magnitude of plasticity within species sometimes exceeding that of differences among congeners [40]. Because of the high temperatures registered at our field sites, the potential strong impact of heat on photosynthesis [34], and because periodic extreme leaf temperatures may induce higher temperature photosynthetic acclimation [39–41]; we would expect species in this environment to present mechanisms to cope with heat either through acclimation or species specific adaptations.

Although PSII is thought to be quite drought resistant; in drought susceptible groups prolonged drought may lead to damage in PSII photochemistry [42] and the interactive effects of heat and drought may impinge strongly on plant physiology. Common garden experiments done with European beech (*Fagus sylvatica* L.) from populations that differed in altitude of origin found very small differences in gas exchange parameters among populations, but strong differences in PSII photochemistry. The authors propose that these differences may represent adaptations and acclimations related to photoprotective functions. Future experiments should investigate potential differences in heat and light acclimation and adaptation between *P. sartorianum* and *P. piscipula*, the two species that appear to follow opposing strategies in our study.

Regarding water use, species and seasons had a significant effect on water potentials, but differences among plots were not statistically significant. As expected, all species presented strategies to deal with limited water availability. However, each of the three species had different strategies. *P. piscipula*, which was more abundant in the young plots and presented light use traits of a pioneer species, was also the species with the greatest apparent drought tolerance. *P. piscipula* had the highest water potentials and capacitance; deep roots, and in young plots, high levels of mycorrhizal colonization. The mycorrhizal association may contribute both to high nutrient acquisition needed to maintain the observed high CO₂ assimilation rates, and to additional water supply [43]. A study by Tamayo-Chim et al. (2011) [44] found that *Piscidia piscipula* presented a high degree of plasticity in its response to drought, potentially increasing water storage in the stem (as evidenced by an increase in stem diameter) during drought and modifying root length with water availability.

From digging for mycorrhizae, a potential relationship between rooting depth and plant age (stem diameter) was apparent in *Piscidia piscipula*. Stems of smaller (presumably younger) individuals of *P. piscipula* continued deep underground before roots were found, whereas larger individuals presented more superficial roots, to the extent that we were only able to obtain samples for mycorrhizae analysis from larger individuals. A similar relationship between tree size and (in that study) depth of water use;

with larger trees preferentially tapping into more shallow water sources was found by Meinzer et al. (1999) [45] in Panama. A study by Estrada-Medina et al. (2013) [46] analyzed source water use by *Piscidia piscipula* in Northern Yucatan and found that this species appeared to use primarily shallow water sources. In that study however, only “trees” were sampled. Potential differences in source water use with respect to tree size require further investigation in this species.

Bunchosia swartziana followed *P. piscipula* in drought tolerance. *Bunchosia*'s strong potential to tolerate dry conditions, degree of plasticity in assimilation rates (see above) with an ability to maintain high rates under high light (see Figure 5 b, where assimilation was consistently higher in the intermediate plot in the dry season) may combine to allow *B. swartziana* to be a better competitor under harsher conditions, such as those found in Northern Yucatan, where the species is abundant. *Psidium sartorianum* showed evidence of tolerance to low water potentials, reaching a mean minimum of -6 MPa in the dry season, but also had the lowest leaf capacitance among the three species.

Although not investigated in this study, seed traits may also reflect the different pioneer/late successional species strategies of *P. piscipula* and *P. sartorianum*. Wind dispersed seeds, such as those exhibited in *P. piscipula* are more frequent in open canopies, while as the canopy closes in the more mature sites, and wind currents diminish, seeds are more frequently dispersed by animals [5], as observed for *P. sartorianum* and *B. swartziana*.

The three species presented contrasting patterns of percent mycorrhizal colonization. The two canopy species had opposite trends. *P. piscipula* had the highest mycorrhizal colonization on individuals in young plots and *P. sartorianum* had the greatest percentage on individuals in the old plot. *Bunchosia swartziana* had high mycorrhizal colonization across all plots. Although an unexpected result, differences in colonization among species were consistent with other findings of, for example, *P. piscipula* as a pioneer, and *P. sartorianum* as a late successional species, with these species showing greater mycorrhizal colonization percentage in the plots where they were most abundant.

5. Conclusions

The combined characteristics of *Piscidia piscipula*, a deciduous species, are consistent with a pioneer species [37] or a “long lived pioneer”. This designation is also consistent with data on its population structure (Yazmín Martínez Téllez, unpublished Masters’ thesis) and population dynamics found in our study. They suggest a species whose strategy for success includes a high level of plasticity and high photosynthetic (and potentially high growth) rates, coupled with deep roots in young individuals and high mycorrhizal colonization in young plots, both of which probably aid in water uptake, maintaining a positive water balance, and high water potentials especially during the dry season.

The behavior of *Psidium sartorianum*, an evergreen with low assimilation rates, was consistent with a late successional species [37], and indicative of a potentially slow growing species that (eventually) reaches the canopy, which would be expected to be more prevalent in old growth forests.

Although *Psidium sartorianum* had the highest abundance among the three species in our study area, its absence in Northern Yucatan suggest *Psidium* may require mild conditions, as those found in the center of Yucatan, and may be precluded from the more northern drier areas of the Peninsula. The low variation in CO₂ assimilation rates for *P. sartorianum* suggests that it may have a lower capacity to modulate CO₂ uptake in response to environmental change.

Data indicating a high abundance for *Bunchosia swartziana* (an evergreen species) in Northern Yucatan, as reported by González Iturbe et al. (2002) [16], where conditions are dryer, indicate this species’ strategy for success includes a strong tolerance for drought, and as found in our study, this is potentially achieved through osmotic adjustment, coupled with an ability to withstand very low water potentials, and maintain high assimilation rates, virtually identical in the wet and dry seasons across plots.

Our study points toward a need to investigate the extent of large differences in temperature and light over small spatial scales (microclimate effects) and their potential effects on seedling establishment and survivorship.

For all three species physiology seemed to play a strong role in the capacity to regenerate and the ability to prevail in the understory of this tropical dry forest.

Author Contributions: P.C.J. constructed and wrote the first draft of the manuscript; J.L.A., P.C.J., C.R.-G., T.M. and J.M.D. conceived and designed the experiments; T.M. led the collection of mycorrhizae and analyzed mycorrhizal data. J.M.D. collected and analyzed population data. O. H.-G. led the collection of fluorescence data and performed preliminary analyses of fluorescence; C.R.-G. and P.C.J. led the collection and analyses of CO₂ assimilation data and performed preliminary analyses of coarse microclimate data; J.L.A. led the collection of and analyses of fine microclimate data; R.U.-S., and J.L.S. identified study sites and species and aided in the collection of field data; J.L.A., collected and analyzed data on water potentials and capacitance. P.C.J. organized data, performed additional statistical analyses, and wrote the first draft and final paper after receiving comments and contributions from coauthors.

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