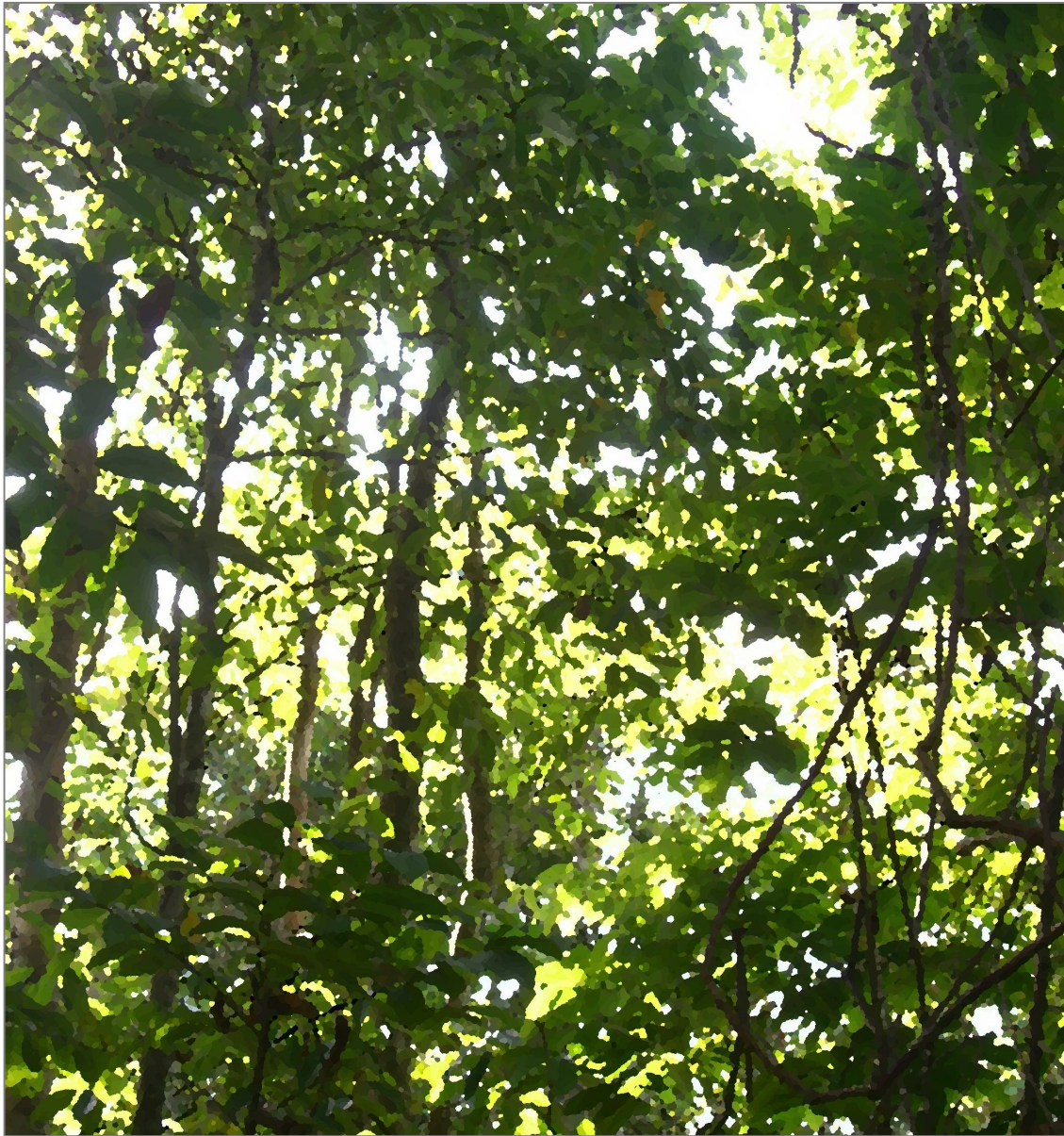


Understory microclimate of tropical secondary forests in Panama



Béatrice M. M. Wedeux
AV 2010 - 39

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Béatrice Maité Myrtille Wedeux

AV 2010 - 39

Supervisors

prof. dr. F. Bongers - Wageningen University and Research Center

dr ir. M. van Breugel - Smithsonian Tropical Research Institute

dr. ir. C. Smit - Utrecht University



Universiteit Utrecht



Acknowledgements

In first place, I want to thank my supervisors Frans Bongers, Michiel van Breugel and Chris Smit for their guidance and for giving me the opportunity to conduct this research. Jefferson Hall and Michiel van Breugel are acknowledged for providing structure and soil water content data. My sincere gratitude goes to Dylan Craven for his support, putting his equipment at my disposal, and for being so helpful in any kind of situations. Daniela Weber and Frederico Davis are gratefully acknowledged for their help in the coordination of my project as well as Carlos for his help with fieldwork. I thank my friends of the Agua Salud technical staff, Yuriza, Anabel, Mario, Fernando and Guillermo for their kindness and hospitality. ¡Gracias muchachos, fue un placer conocerles! A particular thought goes to Dani for being a great friend and companion during our stay in Panama. Finally, I would like to thank my parents and Jean-Luc for their support during the more and less exotic parts of this project. Frans Bongers, Michiel van Breugel, Chris Smit and anonymous reviewers are acknowledged for their useful comments and suggestions on previous versions of the manuscript.

This project is part of the Agua Salud Project led by the Smithsonian Tropical Research Institute. The Agua Salud Project is a collaboration between STRI the Panama Canal Authority (ACP) and the national environmental authority of Panama (ANAM) and financially supported by the HSBC climate partnership, with additional funding from STRI, (ACP), the Frank Levinson family foundation and the Motta family foundation.

Summary

Few studies have addressed the understory microclimate in regenerating secondary tropical forests. While the area of secondary forests is increasing at fast pace in the tropics and succession is driven by changing environmental conditions, a study of the most ecologically relevant environmental drivers light, temperature and moisture is needed. Research has mainly focused on describing the microclimate in closed forests and open areas, and it stays unknown how the microclimate changes between these two extremes across a succession gradient, and especially in early succession when changes in forest structure and biomass are fast. The aim of this study conducted in Panama was therefore to study microclimatic changes over the first 20 years of succession and to identify the structural characteristics of the forest that determine them. Furthermore, the study was performed during the dry season spanning from mid-December to April and its effect on soil moisture and soil evaporation across the succession gradient was addressed. Measurements of light, air and soil temperature and relative humidity were conducted across eleven forest sites aged between 2 and 17 years. Moreover, soil water content was monitored during a five month period spanning the dry season and mini-lysimeters were used to determine soil evaporation. The understory environment became darker, cooler and moister with succession and was increasingly buffered in regard to daily variability. Tree basal area, as an indicator for biomass, was the best structural determinant of the microclimate succession trend but canopy closure showed relevant too. The dry season was short and an equal decrease in soil water content could be observed in all sites, while sites older than 10 years were the wettest over the whole monitoring period and the pastures were the driest. The evaporation experiment revealed that evaporation over a rainless week led to soil moisture loss in all forest sites but was more pronounced in the pasture and the youngest forest site in which the experiment was performed (4 years). Therefore, it can be deduced that soil moisture decrease during the dry months is chiefly determined by evaporation due to high solar irradiance in open spaces while vegetation uptake leads to soil water loss in sites with a well-developed vegetation cover. Nevertheless, soil moisture is enhanced as forests grow older, which improves water regulation at landscape level. Young succession sites were chiefly determined by high light levels, air temperature and vapor pressure deficits, which constitute important filters for germination and establishment of plant species. Nevertheless, the understory environment reached stabilized values 10 years after disturbance only and was close to understory conditions in old-growth forests, which suggests that the climatic driver in succession is limited to the first 10 years after disturbance. Secondary tropical forests in Panama hence seem to recover quickly in terms of understory microclimate.

Key-words

Secondary forest, succession, understory, microclimate, Panama, chronosequence, dry season, environmental driver

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Abbreviations

BA	Basal area [m ² /ha]
DBH	Diameter at breast height [cm]
PAR	Photosynthetically active radiation [μ moles photons/m ² /s]
PCA	Principal component analysis
PPFD	Photosynthetically active photon flux density [μ moles/m ² /s]
RH	(air) Relative humidity [%]
SEM	Standard error of the mean
SWC	(gravimetric) Soil water content [%]
VPD	Vapor pressure deficit [kPa]

Introduction

Tropical secondary forests result from regeneration after environmental disturbance (*e.g.* natural fires, landslides) or human-initiated disturbance (*e.g.* slash and burn, cattle ranging, urbanization) on former forest lands (Bazzaz and Pickett 1980, Brown and Lugo 1990). Most of the world's secondary forests however result from human impact (Chazdon 2008). Secondary forests are nowadays an intricate part of tropical landscapes and their area is increasing at the cost of primary forests. Indeed, the total area of secondary and degraded forests in tropical countries was estimated to 850 million ha in 2002; that is 60% of the area classified as forest in the tropics (ITTO 2002). Such extended areas of transformed forest are of great concern but should not be underestimated in their potential to provide environmental functions such as watershed regulation, carbon capture and storage and erosion control. Furthermore, secondary forests can offer hubs for biodiversity conservation in fragmented landscapes and the economic exploitation of their timber and non-timber products could possibly mitigate the pressure on old-growth forests (ITTO 2002). Consequently, their rehabilitation and sustainable management are crucial to assure their well-functioning (Brown and Lugo 1990, ITTO 2002).

Local environmental conditions are considered to be important drivers of forest regeneration. Light (Denslow and Guzman 2000), temperature and water conditions (Comita and Engelbrecht 2009, Daws *et al.* 2002, Engelbrecht *et al.* 2007), determine the success of establishment of tree seedlings and hence the forest composition (Bazzaz and Pickett 1980). In turn, establishing young forests shape the microclimatic environment in their understory (Lugo and Lowe 1995). Structural characteristics have been shown to change rapidly in early succession (van Breugel *et al.* 2006, Lebrija-Trejos *et al.* 2010) and hence quick climatic changes should simultaneously take place in the understory, determining subsequent succession stages. Moreover, seasonality, and more particularly the presence of a dry season, may induce important changes at microclimatic level and consequently deeply influence forest dynamics (Comita and Engelbrecht 2009, Condit 1998). Few studies concentrate on the abiotic environment across a succession gradient, especially over the first years following disturbance. Often, single variables are of interest, *e.g.* light in seedling recruitment studies, and studies on microclimate address forest gaps and clearings rather than different stages of secondary forest succession. This study therefore aims at describing the relations between ecologically determining environmental variables and the effects of regrowth and of the dry season on the understory microclimate of secondary moist tropical forests in Panama during the first 20 years of succession.

Composition and structure changes of a forest community after disturbance have shown to be dynamic and probabilistic rather than linear and deterministic (climax vegetation) (Bazzaz and Pickett 1980, Chazdon *et al.* 2007). The nature and rate of succession is influenced by the duration, frequency and intensity of disturbance of sites (Brown and Lugo 1990, Chazdon 2008) as well as by the residual vegetation (Chazdon *et al.* 2007, Uhl *et al.* 1988). The return of the tree composition from the primary forest may be extremely slow (Bazzaz and Pickett 1980, Ewel 1980) or it might never recover (Chazdon *et al.* 2007). Secondary forests are characterized by the following related trends: (1) high total stem density but low density of trees of DBH > 10 cm (diameter at breast height), (2) low BA (basal area, cross sectional area at breast height in m²/ha) and (3) low woody volume (Brown

and Lugo 1990). The changing structure of secondary forests influences the local abiotic environment, or microclimate, beneath the canopy (Denslow and Guzman 2000, Lebrija-Trejos *et al.* 2010). In this study, forest structure is described by canopy openness, tree density and BA, three characteristics that showed to be determinant for understory microclimatic conditions (Chazdon *et al.* 2007).

Across a succession gradient, understory light levels are expected to decline with forest age (Denslow and Guzman 2000) as biomass accumulates and the canopy closes. In particular, the canopy openness and the forest density showed to influence the understory light regime (Kabakoff and Chazdon 1996, Montgomery and Chazdon 2001). During the dry season, the light environment might be altered as tree leaves are shed due to water stress (Longman and Jeník 1987). The energy-rich, short-wave solar radiation between wavebands of 400 and 700 nm, called photosynthetic active radiation (PAR), is relevant for plants, and more particularly the photon energy perceived per area unit (photosynthetic photon flux density, PPFD). Light absorption, reflection and transmission by and through the canopy dictate the temperature and moisture environments in the understory (Bazzaz 1996, Brown 1993, Kabakoff and Chazdon 1996).

Air temperature below the canopy is accordingly thought to decrease with succession, following closely light decline. In fact, higher temperatures were recorded in exposed clearings and gaps than in closed forest understory (Ashton 1992, Fetcher *et al.* 1985). In turn, air relative humidity, defined as the available percentage of the saturated vapor pressure of water at a certain temperature, is usually low in open sites and during the dry season but is known to increase considerably under closing understories and during the wet season (Bazzaz and Pickett 1980). It is thus considered to increase with succession.

The soil environment, and more precisely its moisture and temperature, is also influenced by succession (Bazzaz 1996). The amount of water stored in the soil was shown to increase with vegetation cover (Ashton 1992, Camargo and Kapos 1995). In open areas (*e.g.* large gaps), soil dries from evaporation due to direct solar radiation (Marthews *et al.* 2008). In the understory in contrast, soil moisture is mainly determined by water extraction by roots. Additionally, soil water content was shown to be strongly influenced by topographic position (*i.e.* position on slope) (Ashton 1992, Becker *et al.* 1988, Daws *et al.* 2002, Ediriweera *et al.* 2008, Markesteijn *et al.* 2010) and to decrease strongly over the dry season (Ashton 1992, Markesteijn *et al.* 2010). On the other hand, the behavior of soil temperature over succession is uncertain. High evaporation in open areas has a cooling effect on the soil but direct solar radiation heats it (Marthews *et al.* 2008), leading often to soil temperature exceeding air temperature (Bazzaz and Pickett 1980). In the understory however, soil temperature is chiefly influenced by air temperature. The presence of a litter layer, blocking evaporation and radiation, proved beneficial to soil moisture especially in young forest stands, but was found to have opposite effects on soil temperature in different studies (warming effect due to blocking of evaporation opposed to cooling effect due to barrier to direct radiation) (Bazzaz 1996, Camargo and Kapos 1995, Marthews *et al.* 2008, Molofsky and Augspurger 1992).

Given the shortcomings of knowledge on micro-climatic changes in early succession in tropical moist forests, the present study asks the following research questions: 1) how do light, temperature, and water regime change with succession?, 2) which forest structural properties (BA, canopy openness, tree density and leaf litter layer) are determinant of the

understory microclimate and 3) are understory soil moisture and light influenced by the dry season?

The hypotheses are that 1) the understory environment becomes darker, cooler and moister with succession, 2) BA determines best the understory microclimate as it is strongly related to above-ground biomass but canopy openness is also relevant 3) the dry season has a positive effect on light in the understory by canopy opening and a drying effect on soil.

Methodology

Study site

The Agua Salud research area is located adjacent to Soberania National Park in the watershed of Río Agua Salud and Río Mendoza, part of the larger Panama Canal watershed (approximately 9°13' N and 79°47' W). It is a hilly region with narrow interfluves, short and steep slopes and narrow or no valley floors. The area is seasonally wet with a dry season from mid December through April. Rainfall amounts to 2300 mm/year with a cumulative rainfall of about 700 mm during the dry season (Pyke *et al.* 2002). The mean daily temperature is 27 °C and varies only little throughout the year (Windsor 1990). Soils in the area have a homogeneous texture (silty clay to clay), with pH values ranging from 4.4 to 5.8 (Hall *et al.* unpublished data).

Most common land uses in the region are pasture lands for extensive livestock farming (< 1/ha) and small scale shifting cultivation agriculture. The current vegetation cover is a mosaic of pastures and agricultural fields, secondary forest as well as islets of old growth moist tropical forest (Ibañez *et al.* 2002, Martínez *et al.* 2006, Smithsonian Institution 2008). The last decade, an increasing part of the population has been seeking employment in the two nearby cities of Colón and Panamá (Ibañez *et al.* 2002), resulting in increasing land abandonment and growing area under secondary forest cover (ANAM-ACP 2005, CICH).

The Agua Salud Project, led by the Smithsonian Tropical Research Institute monitors 54 sites of secondary forest distributed across an agricultural area of approximately 15 km². Each site includes an upper slope and a lower slope transect of 20 x 50 m each, laid out parallel to the main slope direction. In each transect, stems of ≥ 1 cm DBH (diameter at breast height) are censused annually in two of four adjacent 5x50 m strips, while the two other strips are censused for stems of ≥ 5 cm DBH (Appendix). The time since abandonment of the sites was estimated through interviews with former land owners and other members of the local population.

For the present study on understory microclimate across a succession gradient, a subset of sites was selected according to their age, homogeneous succession history and accessibility (Table 1). Data sampling took place from January to April 2010 in 11 sites with vegetation aged between 2 and 17 years. Additionally, reference data for open conditions were collected by a meteorological tower and in a nearby fully open pasture (distance to selected sites ranged from 100 m to 3000 m). A chronosequence approach is adopted and validated by the similarity of soil characteristics across the study site (Johnson and Miyanishi 2008).

Data collection

Collection of data on microclimatic conditions included instantaneous light measurements (2 campaigns) and two-day monitoring of light, air and soil temperature and relative humidity (RH). The number of sites varied between 5 and 11, depending on the type of measurements (Table 1). A soil evaporation experiment with mini-lysimeters was conducted in a subset of 5 sites (Table 1). Additionally, leaf litter was collected in 6 sites (Table 1).

Table 1 Overview of the 11 selected sites and collected data: (#) light, air temperature, soil temperature and RH logging over 2 days; (+) mini-lysimeter experiment and 1st campaign of instantaneous light measurements; (\$) 2nd campaign of instantaneous light measurements (*) leaf litter collection. The BA and density of transects (van Breugel and Hall, unpublished data) in which climate data was logged were selected to characterize the sites (average of upper and lower transect BA and density if logging took place in both transects).

Age class	Age (yrs)	BA (m ² /ha)	Tree density (ind/ha)	Collected data
Young (≤ 5 yrs)	2	0,01	80,0	(#, \$)
	4	3,4	11970,0	(#, +, \$, *)
	5	2,0	21998,7	(#, \$, *)
Intermediate (6-9 yrs)	6	6,8	18720,0	(#, +, \$, *)
	8	8,5	13480,0	(#, \$)
	8	16,6	8460,0	(#, \$)
Old (≥ 10 yrs)	10	16,0	8155,0	(#, +, \$, *)
	14	16,6	8460,0	(#, \$)
	14	21,2	8205,0	(#, +, \$, *)
	14	15,1	6520,0	(#, +, \$, *)
	17	16,0	8155,0	(#, \$)

Light

Instantaneous PAR (photosynthetic active radiation) measures were collected with the AccuPAR PAR/LAI ceptometer LP-80 of Decagon Devices, Inc. The ceptometer offers a 100 cm long probe with 80 sensors spaced 1 cm. Instantaneous PAR measures were collected between 10:00 and 13:00 in order to assure maximum direct incoming light through the canopy. The PAR value for one sampling point results from the average of 4 measures in 4 directions following the transect orientation around the sampling point. Two different instantaneous light measuring campaigns were conducted. The first campaign was linked to the mini-lysimeter study (see section "Soil evaporation" below and Appendix). In five secondary forest sites (Table 1), a preliminary round served to identify sampling points with similar light conditions (7 points per transect, 14 sampling points per site) (Appendix). Subsequently, these sampling points at 10-15 m intervals were visited six times between 16 February and 15 April. A second campaign took place between 15 March and 9 April in all sites (Table 1). Five sampling points were located at 10 m intervals along the central 50 m line in each transect and five sampling points at 10 m intervals along the upper slope (upper slope transect) or lower slope (lower slope transect) border (Appendix). Sampling points along the upper and lower transect border corresponded to soil sampling points for SWC (see section "Soil water content" below). All sites were visited 3 times.

In addition to the instantaneous measurements, short-term light measurements were collected using 2 to 3 LICOR LI-190 Quantum PAR Sensors. Light was measured every 10 s and logged as 5 min averages over 2 full days. Short-term light monitoring previously showed to be very representative of light conditions over longer periods (9 months) (Engelbrecht and Herz 2001). In each site, two sampling points were randomly selected from the ceptometer sampling points.

Above canopy PAR was recorded in 5 min intervals on a meteorological tower. Due to device failure, recordings are missing from 19th February to 25th March 2010. The percentage of PAR that crosses the canopy and reaches the forest ground is given by relative PAR, $\%PAR = (PAR_{\text{below canopy}} / PAR_{\text{above canopy}}) \times 100$. The time of ceptometer measurements for single sample points did not coincide exactly with the 5-minute light recordings of the meteorological tower. Hence, the time spent in one transect was identified and an average of above canopy PAR over the same period of time was used to express %PAR at each sample point in the understory. Logged understory PAR values were relativized with simultaneous above canopy PAR measures.

Per measurement period of two days, data from each sensor was averaged to produce a full-day (00:00 to 00:00) pattern of understory PAR availability. Per site, a single averaged daily pattern at five-minute resolution was calculated by averaging the daily patterns of the two PAR measurement periods. The total PPFD intercepted in each site was calculated by trapezoidal integration of the resulting site curve. Subsequently, the sites were grouped in three age classes (young: ≤ 5 years, intermediate: 6-9 years and old: ≥ 10 years) (Table 1), and for each age class an average daily curve with 95% confidence intervals was calculated. The same steps were followed to obtain daily curves per site and per age class of the other logged microclimatic variables. To present smooth curves, thirty minutes averages were used, except in the case of soil temperature, which was logged at three hour intervals.

In line with literature, absolute photon irradiance reaching the understory is determined as PPFD (photosynthetically active photon flux density) [$\mu\text{moles}/\text{m}^2/\text{s}$], while relative radiation in the understory as compared to above canopy is given in relative PAR (photosynthetically active radiation, noted %PAR) [%].

Temperature

Air and soil temperature were recorded at the same points as – and simultaneously to – short-term light measurements. Air temperature was recorded twice over two full days. It was measured every 10 s, once with a shielded ONSET HOBO Pro RH and Temperature Data Logger and once with a shielded ONSET 12-bit Temperature Smart sensor, and averages were logged every 5 min. Soil temperature was recorded once in each site over two full days. It was measured with two LI-COR soil temperature sensors 1400-103 buried vertically in the upper 10 cm of the soil profile, and was recorded at 3 h intervals. Soil temperature data for the youngest site (2 years) are not available due to device failure.

Air humidity

Air relative humidity (RH) was recorded once in every site over two full days in parallel to short-term light measurements. RH was measured by a shielded ONSET HOBO Pro RH and Temperature Data Logger and logged at 5 min intervals, averaging measurements taken every 10 s. Another measure for air moisture is the vapor pressure deficit (VPD), the

difference between the amount of water vapor in the air and the amount it can hold being saturated at the same temperature (Prenger and Ling 2010). A high VPD indicates that the air has a low humidity (low RH). VPD [kPa] was calculated for each site using simultaneous air temperature and relative humidity measures according to the following equations: $VPD = e_s - e_a$ with e_s the saturation vapor pressure [kPa] and e_a the actual vapor pressure of the air [kPa]. Further, $e_s = 0.6018 \times \exp(17.27 \times T / (T + 273.3))$ with T the air temperature [°C] and $e_a = (e_s \times RH)/100$, with RH the relative humidity [%] (Prenger and Ling 2010, Stewart and Howell 2003).

Soil water content

The gravimetric soil water content (SWC) was monitored by the Agua Salud staff from December 2009 through May 2010, including the entire dry season span. Five soil cores from 0-10 cm depth were collected at 10 m intervals along the upper border of upper slope transects and along the lower border of lower slope transects (10 sampling points per site), wrapped in aluminium, put in zip-locked bags and stored and transported in coolers to avoid water loss. Sites were visited at approximately 2 weeks' intervals. All samples were weighed within two days after collection with a high precision balance and subsequently dried at 110 °C during 48 h in a ventilated oven and re-weighed. The gravimetric water content Θ [%] of the soil sample is the mass of water (difference between soil mass before and after drying) in a unit mass of dry soil, $\Theta = (M_{\text{water}} / M_{\text{dry soil}}) \times 100$ (adjusted from Percy *et al.* 1991). Averages per site per census were calculated for SWC and the sites were grouped in age classes.

Soil evaporation

Evaporation from the soil was studied with mini-lysimeters. The use of mini-lysimeters is based on the assumption that the mass loss of an amount of soil isolated from its environment is solely due to evaporation (Trambouze *et al.* 1998) under absence of rainfall. Hence, if the initial weights of soil and water inside an impermeable mini-lysimeter are known, weight loss over a rainless period equals to water loss by evaporation. The mini-lysimeters were built of plastic plant pots (internal diameter 16 cm, length 12 cm). Soil for mini-lysimeters was collected from one location, sun-dried, sieved (2 mm mesh), filled in resistant plastic bags and placed into the pots at a soil density of 0.95 g/ml. This density value corresponds to the average soil density found across the study area (Neumann-Cosel *et al.* in press). Mini-lysimeters were placed in adjusted holes in the ground in 5 sites (Table 1). In each site, seven points were selected around both transects (Appendix) and two mini-lysimeters, spaced at 50 cm were placed at each sample point. Additionally, 14 mini-lysimeter points were established in a pasture. Once all mini-lysimeters had received a comparable amount of water, weight loss by evaporation was recorded twice over a period of 6-7 days. Mini-lysimeters were weighted in the field. Only very short and light rain events took place during this experiment (0.8 mm rainfall), so that it can be assumed that weight gain by rain can be disregarded. Previous to data analysis, data from all mini-lysimeters that had experienced weight loss other than by evaporation (hole in bag, excavation by animals) were discarded (3 to 7 out of 28 mini-lysimeters per site). SWC average by site and sampling day was calculated.

Leaf litter

Leaf litter was collected in 6 sites (Table 1). Samples of 30 x 30 cm were collected on 10 random points around the upper and lower transects (Appendix), summing up to a total of 20 leaf litter samples per site. Only leaf litter that was detached from the ground was collected and woody litter was eliminated. Leaves crossing the 30 x 30 cm boundary were collected if at least half of their surface was inside the square. Samples were dried in paper bags at 70 °C during 72 h in a ventilated oven and weighed thereafter. The weight of the dry leaf litter samples was expressed in g/m² and the average of all samples of one site was calculated.

Data analysis

UNDERSTORY MICROCLIMATE CHANGE WITH SUCCESSION

Soil water content

In order to test for significant differences of SWC between age classes over the SWC monitoring period, a repeated-measures ANOVA followed by Gabriel's (adjusting for different sample sizes) or Tukey's post-hoc tests, was performed. To detect the effect of topography on SWC, the difference between upper and lower transects was assessed by one-way ANOVA.

Soil evaporation

Significant decrease of SWC by evaporation during the mini-lysimeter experiment was tested by repeated-measures ANOVA. The difference between final SWC values in mini-lysimeters was tested by ANOVA adjusted for heteroscedasticity followed by Gabriel's post-hoc tests.

A PCA was performed using Canoco (Canoco for Windows 4.5) in order to relate microclimatic variables to each other and reveal their associations and similarities the studied forest sites. Given that the variables had different scales, they were first centered and standardized (mean = 0 and variance = 1).

UNDESTORY MICROCLIMATE AND FOREST STRUCTURE

In order to reveal structural trends over the succession gradient, the relation between average structural properties (BA, stem density and %PAR as an indication of canopy openness) and leaf litter of each site and its age were tested by linear and non-linear regression. Simple models, known to fit biological responses well (linear, power, logarithmic, exponential, polynomial) (Ratkowsky 1990) were fitted and the best model was selected according to the R² and F values. The latter evaluates the fit of the model balancing it with the number of parameters it includes.

Stepwise backward multiple regression analyses were performed in order to assess which of the predictor variables (age, BA and %PAR) is the most important in the distribution of each climatic variable. The backward approach is the most robust in stepwise multiple regression as it is less likely to exclude a predictor that does predict the outcome (Field 2009) and it permits to identify sets of variables that have predictive capability even though single variables do not. In order to get linear relations between average structure

data and average microclimate data (from day time only, 06:30 to 18:30) at site level, data was transformed (natural logarithm). %PAR was not included as a predictor in the analysis for total PPFD given that it was directly calculated from it.

The direct relationship between each environmental variable and the predictor variables that were selected in the multiple regression analysis was studied by nonlinear regression on non-transformed data and the statistical acceptability of the model was tested by the F-test.

DRY SEASON EFFECTS

Light

To assess first whether instantaneous light measurements corresponded to logged light values, instantaneous light measurements at site and at census level were compared to average short-term light measures from 06:30 to 18:30 and from 10:00 to 13:00 (time slot of ceptometer measurements) by repeated-measures ANOVA. Spearman's r was calculated to assess the correlation between the two methods at site level.

Thereafter, differences in light levels between sites at census level and between censuses for different sites were assessed by one-way ANOVAs and Tukey's post-hoc tests.

Soil water content

The negative effect of the dry season on SWC in all age classes was tested with a paired t-test to compare two censuses separated by a period without rain.

Results

UNDERSTORY MICROCLIMATE CHANGE WITH SUCCESSION

Light

The day curves for absolute photosynthetically active photon flux density (PPFD) and relative photosynthetically active radiation (%PAR) coming through the canopy show that the understory of young sites (≤ 5 yrs) receive much higher levels of light during one day than the understory of older sites. In these young forest sites, more than 500 $\mu\text{moles photons/m}^2/\text{s}$ were intercepted during a large part of the day while light intensity stayed mostly below 200 $\mu\text{moles photons/m}^2/\text{s}$ in the intermediate age class (6-9 years) and below 10 $\mu\text{moles photons/m}^2/\text{s}$ in the old sites (≥ 10 years) (Figure 1 A). The percentage of PAR coming through the canopy in young sites fluctuates around 50% while it strongly drops to around 20% and 10% for the intermediate and old age class respectively (Figure 1 B), indicating a gradual closure of the canopy already after 5 years. The fluctuations of the %PAR curve are probably due to temporal and spatial variability in cloud cover between the logging location and the meteorological tower. Total PPFD per day (\pm SEM) was of 342.7 (± 128.8) moles/m² in the young age class; 98.3 (± 34.2) moles/m² in the intermediate age class and 23.0 (± 4.5) moles/m² in the old age class. The frequency distribution of PPFD in the different age classes shifts from a predominance of intense radiation in the young and

intermediate age class (40% of radiation in sites younger than 10 years have an intensity of 500-1000 $\mu\text{moles photons/m}^2/\text{s}$) to predominantly low intensity radiation in the old age class (37% of radiation have an intensity of 0-10 $\mu\text{moles photons/m}^2/\text{s}$) (Figure 2).

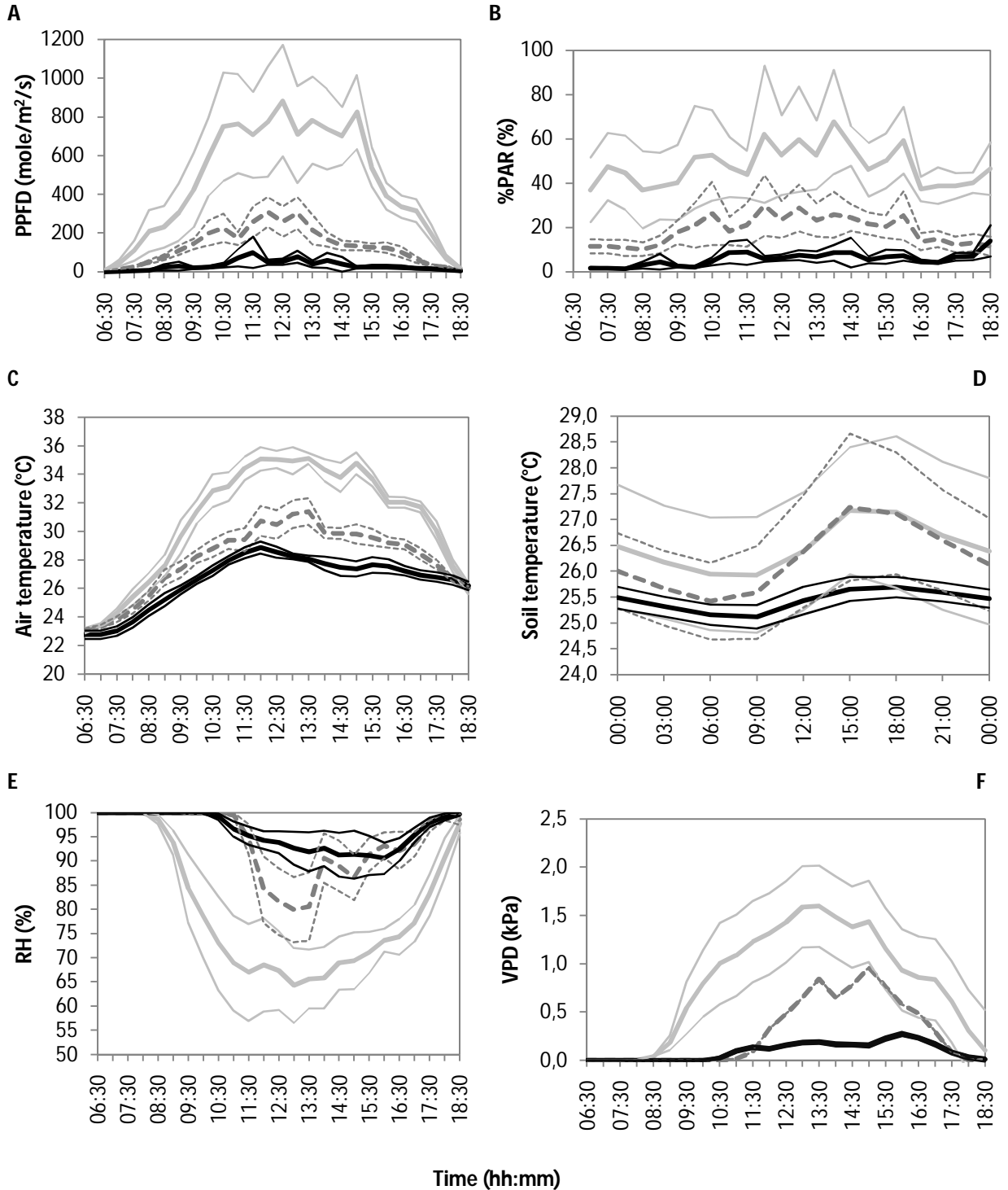


Figure 1 Day curves of environmental conditions for three age classes of forest. Each thick line represents measurements of two whole days shown in 30 min averages for 3 or 5 sites grouped per age class. Grey continuous = young (≤ 5 years), $n = 3$; grey slashed = intermediate (6-9 years), $n = 3$; black = old (≥ 10 years), $n = 5$. Thin lines show 95% confidence intervals of each age class.

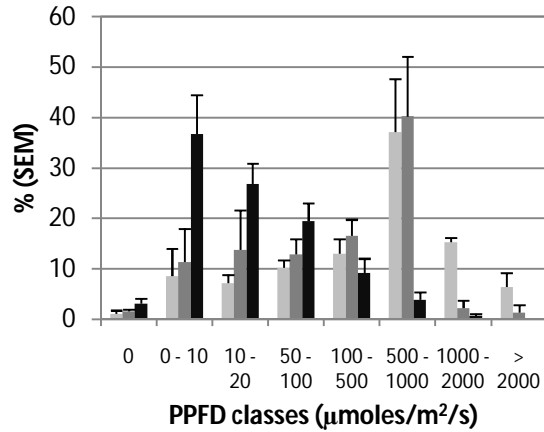


Figure 2 Frequency distribution of photosynthetic photon flux density (PPFD) classes during day time (06:30 to 18:30) for three age classes plotted with SEM (light grey = young (≤ 5 years), grey = intermediate (6-9 years), black = old (≥ 10 years)).

Temperature

Air temperature has a similar value in all age classes during night time (about 23 °C) but differs considerably between age classes during day time (Figure 1 C). The young sites (≤ 5 years) experience an important increase from early morning hours until reaching a maximum of about 35 °C around the midday hours. In the intermediate age class (6-9 years), the maximum value reached around noon is 31 °C, while in the oldest age class (≥ 10 years) the maximum barely reaches 29 °C (Figure 1 C). Soil temperature shows a time delay in comparison to air temperature, as maximum values are only reached around 16:30. During night time the soil temperature of the different age classes varies between 25.5 and 26.5 °C. These values are approximately 3 °C higher than the measured night air temperatures. During daylight hours however, soil temperature stays below air temperature and increases only of about 1 °C in comparison to night soil temperatures. The young and intermediate age classes show an increase in soil temperature over the day while the oldest age class is barely fluctuating (Figure 1 D).

Air humidity

Air relative humidity (RH) reaches 100% in all sites during the night, while vapor pressure deficit (VPD) drops to 0 kPa, indicating a state of complete water vapor saturation of the air during night time (Figure 4 E and F). During day time however, RH drops early and fast, especially in young sites (≤ 5 years) to reach minimum values of 65% around noon. In the intermediate (6-9 years) and old (≥ 10 years) age classes, the decrease in RH starts later in the day but minimal values are also reached around the midday hours: RH at midday is 80% in the intermediate age class and decreases to 90% in the oldest age class (Figure 1 E). The VPD increases from 0 kPa during night time in all cases towards maximal values of 1.6 kPa for the young sites, 0.8 kPa for the intermediate sites and only 0.2 kPa for the oldest age class (Figure 1 F).

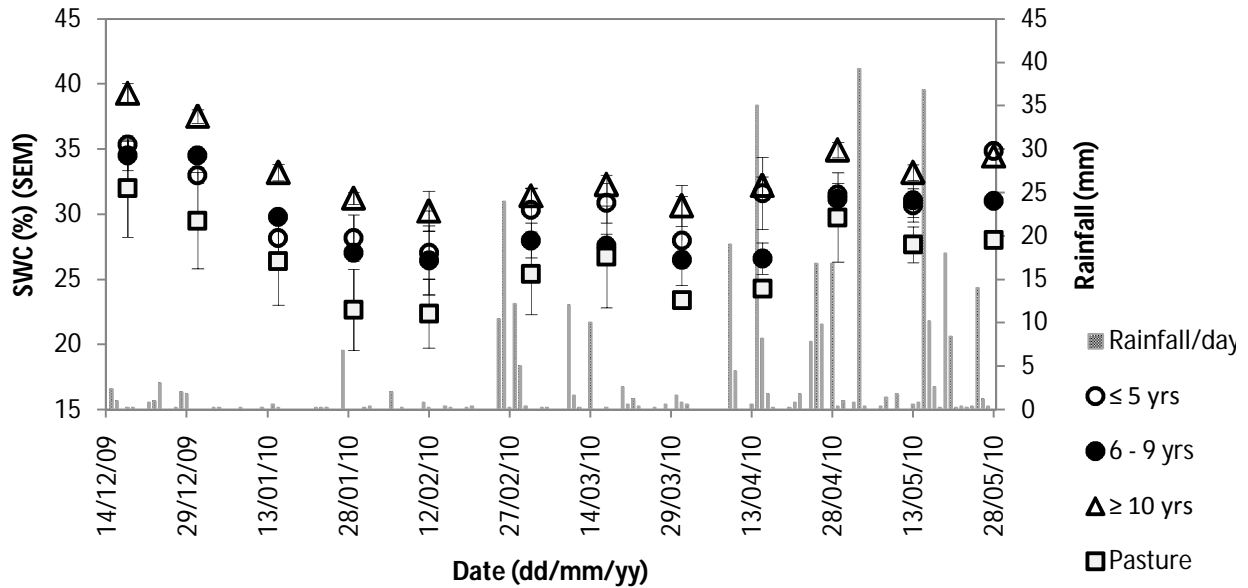


Figure 3 Soil water content (SWC) monitoring in selected sites grouped in age classes, over a span of 4 months. The dry season was shorter as usual and spanned from mid-December to the end of February. Daily rainfall is plotted along with the age class SWC averages of 9 censuses spaced approximately 2 weeks (averages are plotted at the end date of the census). Different marker shapes represent significant differences between the curves.

Soil water content

Gravimetric SWC fluctuated considerably over the monitoring period as rainfall events occurred (Figure 3). Nevertheless, the SWC curve of the old sites (≥ 10 yrs) stayed always above the curves of other sites (repeated measures ANOVA: $F_3 = 42.63$, p -value < 0.001 ; Gabriel's post-hoc: p -value < 0.001), indicating that the oldest sites were the moister ones. Open pastures in contrast showed to have the driest soil conditions (p -value < 0.001), while the curves for the two other age classes were very similar. The lowest SWC value per age class was accordingly recorded in pastures, and the highest minimal value was found for the oldest age class; both values were recorded at the beginning of February (Table 2), 1.5 months after the monitoring start. Finally, upper transects were significantly drier than lower slope transects in all age classes (one-way ANOVA, $F = 4.63$, p -value < 0.01) indicating an effect of topography on SWC.

Soil evaporation

The evaporation experiment performed with mini-lysimeters shows that the SWC decreases significantly (repeated measures ANOVA, $F_5 = 267.12$, p -value < 0.001) in all sites during a 7-day dry period. After the 7-day period, the soil was significantly drier in the pasture and in the 4-year-old site than in the other sites (repeated measures ANOVA, $F_5 = 288.246$, $p < 0.001$, Gabriel's post hoc: $p < 0.001$) (Figure 4), suggesting that canopy closure during succession may result in a decreasing loss of soil water due to evaporation. However, the mini-lysimeter experiment does not test for further sources of water loss such as extraction by roots or loss to deeper soil layers.

Table 2 Minimal average SWC per age class over a 5 months' monitoring period in selected sites. All minimal soil water content values were measured at the beginning of February. The lowest value was recorded in pastures. The young (≤ 5 years) and intermediate (6-9 years) age classes had no significantly different minimal SWC. The oldest age class showed the highest minimal SWC.

Age class	Min SWC average/census (SEM) [%]	Dates of sample collection (dd/mm)
Pasture	22.38 (3.12)	01/02 and 08/02
≤ 5 yrs	27.07 (1.79)	03/02 and 12/02
6-9 yrs	26.47 (0.24)	01/02 – 05/02
≥ 10 yrs	30.25 (0.46)	04/02 and 05/02

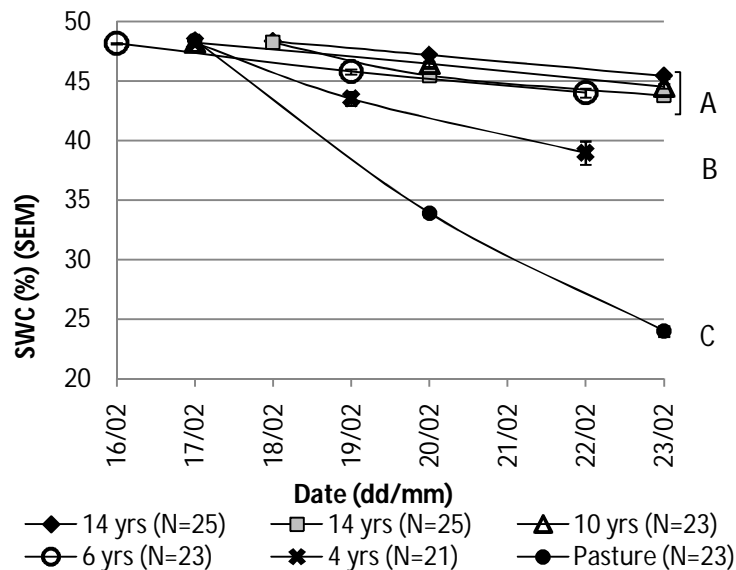


Figure 4 Soil water content (SWC) decrease due to evaporation, recorded using mini-lysimeters. Significant differences between the SWC site averages of the last census are designated by letters in the graph.

The PCA of the environmental conditions in the understory of the selected sites represented 63.4% of the variation on its first axis and 20.6% on its second axis, summing up to 84.0% of the variation (Figure 5). The environmental variables' vectors indicate that VPD, total PPFD, %PAR and air temperature are strongly correlated, while they are opposite to high RH and minimum SWC and soil temperature. Sites older than 10 years (with the exception of one 14-year-old site) were clustered and thus have similar environmental conditions. Those are determined by high SWC and soil temperature and low VPD, light and air temperature. Sites younger than 10 years were widely scattered, suggesting that they differ more in their understory climatic conditions than older sites.

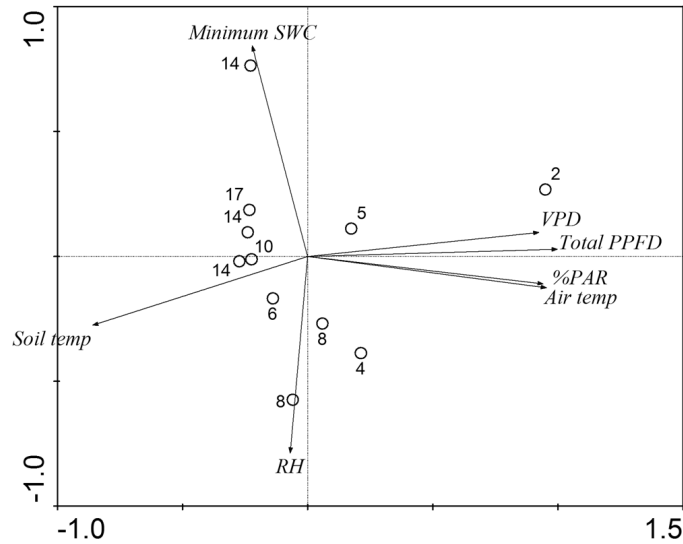


Figure 5 PCA of 7 environmental variables in the understory of the 11 selected forest sites. Numbers next to the circles indicate forest age.

UNDERSTORY MICROCLIMATE AND FOREST STRUCTURE

Basal area (BA) increases linearly with forest stand age ($p < 0.001$) (Figure 6), even though some variation between stands of similar age is available; for example the three 14-year-old sites ($15.1 \text{ m}^2/\text{ha}$, $16.6 \text{ m}^2/\text{ha}$ and $21.2 \text{ m}^2/\text{ha}$), and the two 8-year-old sites ($4.8 \text{ m}^2/\text{ha}$ and $8.5 \text{ m}^2/\text{ha}$). %PAR decreases exponentially with age until reaching a stable level around 5% between 10 and 17 years ($p < 0.01$) (Figure 7). Hence, quick canopy closure takes place during succession. The density of forest appears to reach a maximum around 5 to 10 years and to decrease afterwards, but the trend is statistically not significant (not shown). Given that stem density is not related to age and its pattern consequently does not reflect a succession trend, its relation with microclimate is not analyzed further. Leaf litter weight shows a hump-backed relation with age, suggesting an accumulation of litter during the first 10 years of succession, followed by a decrease in older sites (Figure 8).

Results of the multiple regression analysis on environmental variables show that BA, *i.e.* biomass, is the most important predictor variable, followed by %PAR, *i.e.* canopy openness. BA was chosen as the only predictor variable for total PPFD per day (standardized $\beta = -0.92^{***}$, $R^2 = 0.84$) and RH (standardized $\beta = 0.86^{**}$, $R^2 = 0.76$). BA and %PAR were selected to predict air temperature (standardized $\beta_{\text{BA}} = -0.79^{**}$, standardized $\beta_{\% \text{PAR}} = 0.24^*$, $R^2 = 0.75$) and VPD (standardized $\beta_{\text{BA}} = -1.23^{**}$, standardized $\beta_{\% \text{PAR}} = 0.55 \text{ n.s.}$, $R^2 = 0.80$). The model best predicting soil temperature included %PAR, BA and age (standardized $\beta_{\% \text{PAR}} = -0.93^*$, $R^2 = 0.69$, standardized $\beta_{\text{BA}} = -0.87 \text{ n.s.}$, standardized $\beta_{\text{age}} = -0.36 \text{ n.s.}$). Minimal SWC was best predicted by age but the model had a poor fit (standardized $\beta = 0.62 \text{ n.s.}$, $R^2 = 0.38$). It can be observed that BA was the most represented predictor variables in the models, and had a larger influence (size of standardized β) than %PAR to explain average environmental conditions across secondary forest sites.

The relations between environmental variables and BA show that the environmental conditions undergo quick changes (negative or positive) in sites with low BA but tend

towards a stabilization as BA reaches 15 m²/ha. Meanwhile, they follow a linear trend along the %PAR gradient. An exponential fit was chosen to represent the relation between the environmental variables and BA. Total PPFD, air temperature and VPD decrease until reaching stable levels of 31 moles/m²/s, 26 °C and 0.1 kPa (Figure 9 A, C, E). RH increases with BA and stabilizes at around 95% (Figure 9 B). BA being an indicator for biomass, these results reveal that the understory becomes darker, cooler and moister as trees grow and accumulate biomass. Air temperature and VPD decreased linearly with canopy closure (Figure 9 D, F) which indicates that the air is hotter and drier when the canopy is missing or very open and becomes cooler and moister as the canopy closes and bears shade to the understory. Soil temperature showed non-significant relations with age, BA and %PAR (not shown) and the minimal SWC reached over the monitoring period in each of the selected sites was not significantly related to age (not shown).

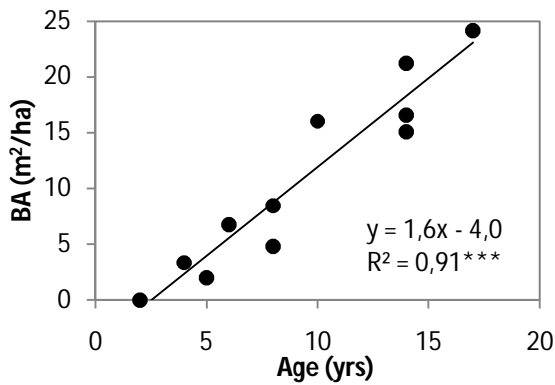


Figure 6 Increase of basal area (BA) with forest age in selected sites. BA, the surface covered in tree stems per ha, increases linearly with age of the forest during the 20 first years of succession (***) = $p < 0.001$).

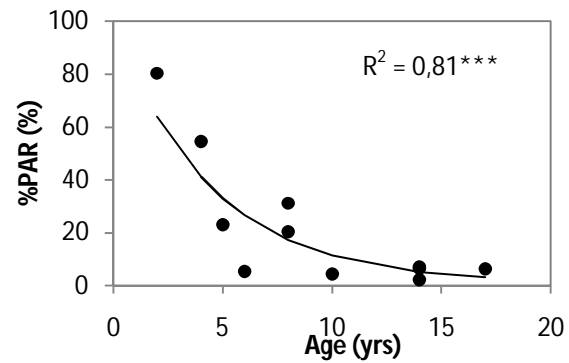


Figure 7 Exponential decrease of mean daytime (06:30 to 18:30) %PAR with forest age (***) = $p < 0.001$).

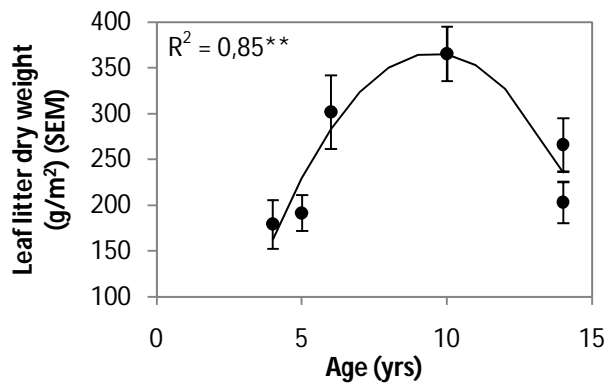


Figure 8 Distribution of leaf litter dry weight across selected sites of different ages. The quadratic hump-shaped model had the highest R² but was not significantly better than a horizontal line through the average (** = $p < 0.01$).

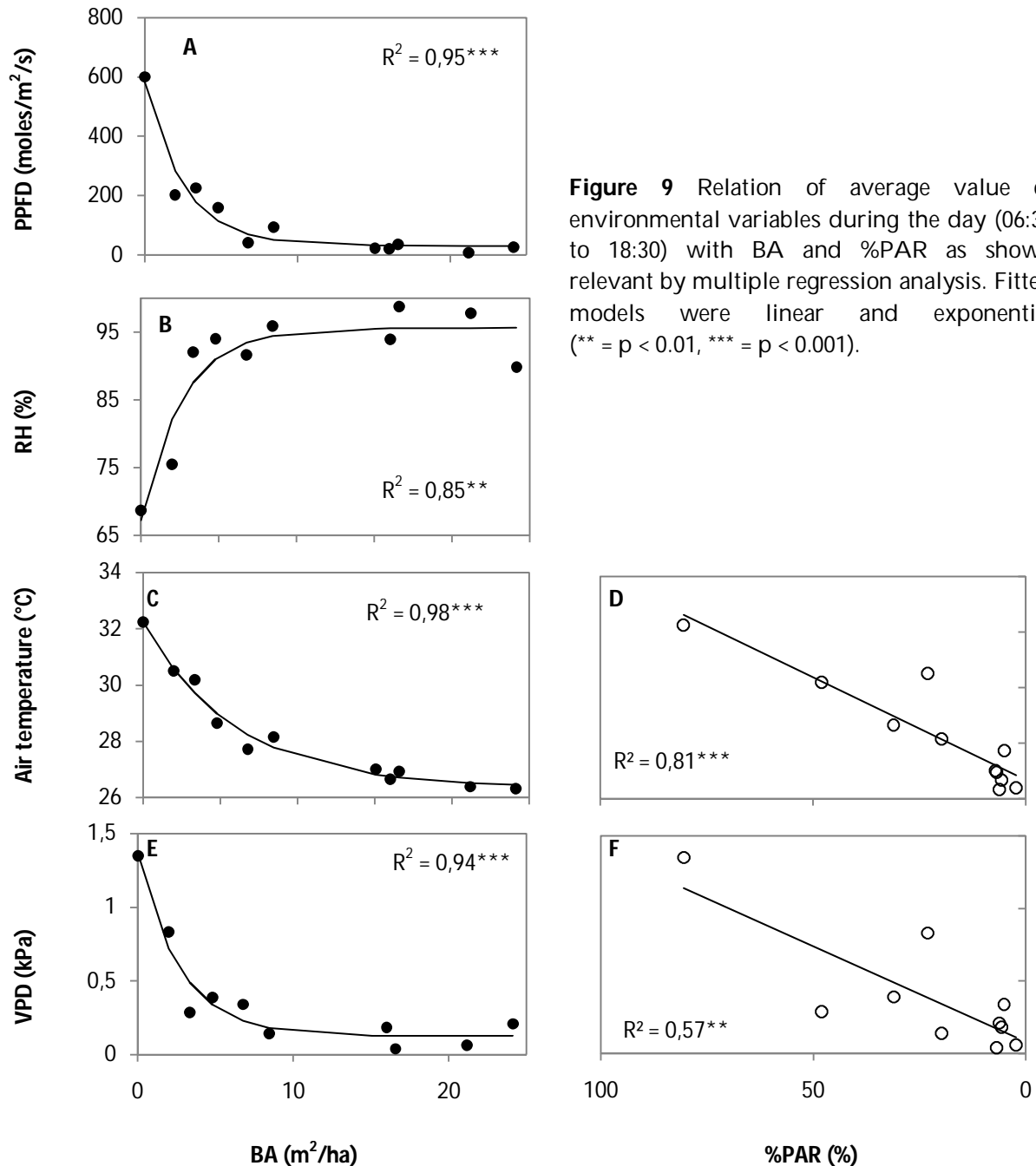


Figure 9 Relation of average value of environmental variables during the day (06:30 to 18:30) with BA and %PAR as shown relevant by multiple regression analysis. Fitted models were linear and exponential (** = $p < 0.01$, *** = $p < 0.001$).

DRY SEASON EFFECTS

Light

At site level and averaging all the censuses in time, light data from instantaneous and short-term measures were not significantly different, for both ceptometer campaigns (Figure 10). Site averages for single censuses were however overall significantly different from logged light data ($F = 28.78$, $p < 0.001$), especially due to accumulation of variance in young sites. No significant pattern could be detected between the sites and the different censuses as variability within and between censuses of one site was very high.

Soil water content

SWC decreased significantly ($p < 0.05$) of about 10% in all the age classes during the first two dry months. The differences in SWC between age classes persist over the whole monitoring period (curves are approximately parallel) spanning the short dry season as well as the beginning of the wet season. This suggests that old sites are the wettest and pastures are the driest sites over the whole year. SWC loss was equal in all age classes during a dry period without major rain event between 2 censuses (censuses 2 and 3 in January).

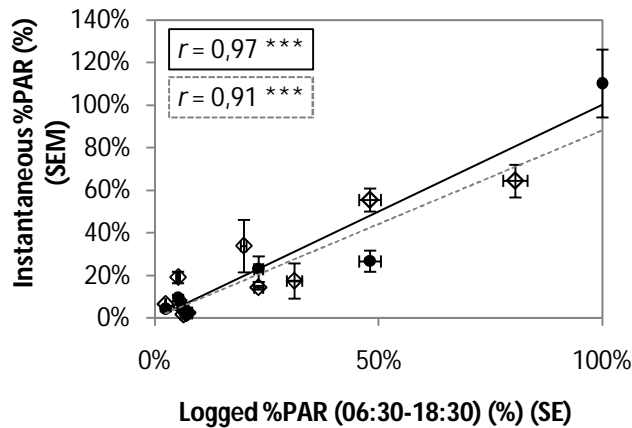


Figure 10 Correlation between instantaneous %PAR measures of the ceptometer (all censuses averaged at site level) and the daytime average logged %PAR: black circles = ceptometer campaign on mini-lysimeter points (5 censuses over 3 months); white rhombs = ceptometer campaign on SWC points (2 censuses over one month) (r = Pearson's r , *** = $p < 0.001$).

Discussion

The objectives of this study were to evaluate the interrelations of environmental variables in the understory of secondary tropical moist forests across an early succession gradient. In particular, attention was paid to identifying structural changes of the vegetation influencing the understory microclimate as well as to the effect of the dry season. The dominant climatic conditions at different succession stages, often related to as environmental “filters” or “drivers” of succession (Finegan 1996, Lebrija-Trejos *et al.* 2010), are discussed in relation to their implication for plant species composition. Finally, the limitations of the study are critically addressed. As literature is scarce on microclimate in secondary forests, the results are compared to studies on forest gaps. Secondary forests in agricultural landscapes may be compared to large gaps but differ from gaps by their isolation from old-growth forests (Denslow and Guzman 2000).

UNDERSTORY MICROCLIMATE CHANGE WITH SUCCESSION

Notable changes in the understory microclimate are already visible within the first 17 years of succession. As expected, forest age, or time after disturbance, combining all recovery processes (biomass accumulation, leaf area increase, canopy closure, growth in height *etc.*), had a negative effect on light and temperature and a positive effect on air and soil moisture measured in the understory (Figure 1, Figure 3) which stands in accordance with previous literature (Bazzaz 1996, Fetcher *et al.* 1985). Moreover, the amplitude of daily oscillations of the environmental variables decreased with age (Figure 1), indicating a buffering of the microclimate in the understory in regard to oscillating external climatic conditions on a daily basis. Similar decreasing daily variations were observed between clearings, forest gaps and closed understory (Ashton 1992, Bazzaz and Pickett 1980, Chazdon and Fetcher 1984, Fetcher *et al.* 1985).

Light reaching the understory of secondary forests decreased drastically over the studied succession gradient (Figure 1A and B). Relative light measured in the intermediate age class (6-9 yrs) was comparable to relative light levels in large gaps (20%) in Costa Rica, while relative light in the older sites (≥ 10 yrs) was already comparable to relative light measured in small gaps (9%). In Costa Rica, 1 - 2 % relative light was measured in mature forest, a level not yet reached in the studied secondary forests (Chazdon and Fetcher 1984).

Air temperature decreased with succession (Figure 1C), a finding that is qualitatively in line with previously recorded decreasing temperatures between clearings, gaps and understory (Fetcher *et al.* 1985, Schulz 1960). Nevertheless, understory temperatures measured in this study were higher, supposedly due to high sun exposure in the opener landscape. Soil temperature was only slightly influenced by succession (Figure 1D) even though previous studies could observe declining soil temperatures between open clearings and understory (Schulz 1960). As in Ashton (1992), night time soil temperature was higher than air temperature, independent of succession stage, pointing out the heat storage capacity of the soil. During day time however, air temperature was higher than soil temperature in all three age classes, showing heat buffering by the soil. This is not in line with previous studies in which higher soil than air temperatures were recorded in open areas (Bazzaz and Pickett 1980). Given the moist conditions at the moment of logging the data, soil might have been kept cooler than air during the day due to evaporation but different soil compositions and sampling depths might also play a role.

The observed increase of RH with succession (Figure 1E) is in accordance with RH increase between clearings and closed understory (Grubb and Whitmore 1966). Mean RH minima measured in clearings were close to minima measured in the young age class (68% and 65%). RH measured under closed understory in previous studies (75% in Grubb and Whitmore (1966) and 60% in Bazzaz and Pickett (1980)) are lower than the minima recorded in the two oldest age classes (80% and 90%), probably an effect of frequent rainfall. VPD decreased with succession (Figure 1F) and average values measured in the intermediate (6-9 yrs; 0.30 kPa) and old age class (≥ 10 yrs; 0.12 kPa) were lower as VPD in closed understory (0.35 kPa), while the youngest sites had a similar VPD (≤ 5 yrs; 0.8 kPa) as measured in a clearing (0.7 kPa) in Costa Rica (Fetcher *et al.* 1985).

Finally, SWC increased with succession (Figure 3) which proves to be qualitatively in accordance with Ashton's (1992) observations in gaps and understory but in discordance to

Ediriweera *et al.* (2008) who found no differences between gaps and understory and Becker *et al.* (1988) who measured decreasing soil moisture from gap to understory. Differences might be caused by different soil types, sampling at different depths but especially different vegetation structure and abundance. Indeed soil moisture might be high in gaps due to higher rain input and low water extraction by roots, but might be lower than in the understory due to higher evaporation (Marthews *et al.* 2008). As a matter of fact, in this study, soil evaporation was most pronounced in pastures and a young secondary forest site where vegetation cover is lacking or sparse (Figure 4). Water loss due to transpiration by vegetation increases with increasing biomass (Calder 1998) and hence will follow an opposite pattern as soil evaporation and increase with succession. Nevertheless, net gain between transpiration and moisture storage guarantees highest air and soil moisture in the oldest sites. Finally, landscape topography showed to influence the distribution of SWC as down slope areas showed to be wetter than upslope areas and ridges due to downwards water flow along hillsides (Becker *et al.* 1988, Daws *et al.* 2002, Ediriweera *et al.* 2008, Markesteijn *et al.* 2010).

Altogether, high light levels, air temperature and VPDs showed to be highly correlated and to determine understory microclimate in young and intermediate sites (Figure 5). Microclimatic conditions were more heterogeneous in the understory of young and intermediate sites than in old sites (seen both in errors on curves and in the PCA (Figure 1 and Figure 5)). This outcome points out that the factors determining microclimate are more heterogeneous between different young secondary forest sites than between older ones (*e.g.* forest structure), and that young forests are possibly more sensitive to spatial landscape variability creating local microclimatic changes (*e.g.* sun exposure depending on aspect of the slope). Old sites in turn, were rather determined by high air and soil moisture and showed to have very similar understory environmental conditions (Figure 5) by effective buffering of external climatic variations.

UNDERSTORY MICROCLIMATE AND FOREST STRUCTURE

Forest structure showed well-defined trends along the studied succession gradient, especially BA, an indicator for biomass, and canopy openness. The structural succession trends found in this study are in accordance with previous literature whereas direct connection of structure and understory environment is scarce in literature (but see Lebrija-Trejos *et al.* 2010 for a study in a tropical dry forest).

The linear increase of BA over the studied chronosequence (Figure 6) hints towards accumulation of above-ground biomass and crown diameter increase (van Breugel *et al.* 2006) and is in accordance with studies that identified similar BA trends in early succession (van Breugel *et al.* 2006, Chazdon *et al.* 2007, Peña-Claros 2003). Moreover, it implies that forest structure recovery is linear and predictable over the first 20 years of succession in the studied area. Consequently, forest age could be approximated by measuring the BA of present trees if time since abandonment is unknown. Furthermore, the chronosequence approach is supported as the considered succession time gradient is closely underlined by a structural trend. Later in succession however, productivity is expected to slow down and BA stabilizes as fewer but larger trees subsist (Panama: BA peak at 37 m²/ha at 70 years after disturbance (Denslow and Guzman 2000); Bolivia: 70% of BA of mature

forests reached after 25 yrs (Peña-Claros 2003)). Succession was accompanied by canopy closure by biomass accumulation, as relative light decreased exponentially (Figure 7). As previously observed (van Breugel *et al.* 2006, Denslow and Guzman 2000, Peña-Claros 2003), tree density was not significantly related to age as it might vary considerably among sites depending on their species composition and land-use history. Furthermore, BA and density were calculated from individuals of DBH ≥ 1 cm, so that especially BA and density of young sites with young sprouting trees could be underestimated.

Leaf litter accumulation was highest at 10 years after disturbance (Figure 8) suggesting that productivity is most important at that stage or that more leaves are shed due to the composition of the forest (*e.g.* young pioneers at the end of their lives (Finegan 1996)). In previous literature, accumulation of leaf litter was found to closely follow the accumulation of biomass over the first 15 years of succession (Molofsky and Augspurger 1992). Even if precautions were taken to prevent the effect of spatial variability in species composition by collecting many samples, the litter accumulation due to differential deciduousness of tree species during the dry season, as well as leaf size could have influenced the outcome. Indeed, spatial and temporal litter distributions proved to be highly heterogeneous in tropical forests (Molofsky and Augspurger 1992).

As hypothesized, BA proved to be the best determinant for understory microclimate, which implies that it chiefly drives the observed trend towards darker, cooler and moister understories with succession. Nevertheless canopy openness showed to be also an important determinant of air temperature and VPD. Soil temperature and moisture in turn were influenced by multiple factors rather than solely by BA or %PAR.

BA was chosen as a single (PPFD, RH) or partial (air temperature, VPD, soil temperature) predictor for understory microclimate. BA being a good indicator for above ground biomass, the growth of trees and their accumulation of leaf area are consequently the most influential factors determining microclimate in the understory (Lebrija-Trejos 2009) and driving its changes across succession. Changes in microclimate were fast in early succession (low BA) but a stabilization is observed as soon as BA reaches approximately 15 m²/ha (Figure 9A, B, C, E), corresponding to about ten years after disturbance. This finding implies that after only 10 years, secondary forests reach stabilized microclimatic conditions which are very close to understory conditions in older forests. Consequently, restoration of microclimatic conditions in secondary forests happened surprisingly fast in the studied area.

Canopy openness was also selected as a predictor for air temperature and VPD. Air temperature and VPD decreased as the canopy closed (Figure 9D and F) and less light and heat penetrated the understory. Indeed, light is increasingly reflected by the canopy and heat stored by biomass (Uhl *et al.* 1988), leading to a cooling effect on the air. Similar observations were made by Bazzaz (1996), Brown (1993), Kabakoff and Chazdon (1996).

In previous studies, soil temperature showed to be determined by a complex assembly of factors: leaf litter (especially in young sites), biomass accumulation, soil organic material, root density, *etc.* (Marthews *et al.* 2008). Accordingly no singledeterminant could be detected and the association of factors %PAR, BA, canopy openness and leaf litter predicted soil temperature in this study, even though no clear relation could be identified between soil temperature and any of these three predictor variables when considered individually.

Forest age was selected to predict minimum SWC, even though no clear relations could be established between the two variables. This could indicate that soil moisture is dictated by changes occurring with succession other than BA increase or canopy closure. These could be *e.g.* soil organic matter increase, decomposition rate and accumulation of below-ground biomass.

DRY SEASON EFFECTS

Instantaneous light measurements showed to represent daily light averages (06:30 to 18:30 and 10:00 to 13:00) well when various repetitions in time and in space are carried out (Figure 10). The ceptometer campaign on mini-lysimeter points had more censuses in time and showed a better correlation to logged light measures and smaller errors. The ceptometer campaign on SWC sampling points had few censuses in time but its good correlation with logged light can certainly be explained by the fact that it took place during the same month as light logging. Nevertheless, the expected increase of understory light levels during the dry season could not be detected on basis of the instantaneous light measurements. Between and within census variability in one site suggests that the lack of clear pattern during the dry season is rather due to poor resolution of instantaneous light measurements as to absence of effect by leaf deciduousness. Leaf loss by trees could however have been slowed down due to the frequent rainfalls. Limited resolution of the ceptometer approach is possibly due to the fact that measurements were made both on sunny and overcast days due to great variability of the cloud cover during the study, while much literature advises to make measurements on overcast days or cloud-free days only (Messier and Puttonen 1995).

SWC patterns between age classes seemed to persist during dry and wet periods, and no differences in SWC loss could be observed during the longest dry period. These results first suggest that the oldest secondary forest sites are wetter over the whole year (Figure 3) proving increased soil moisture storage capacity with succession and tree development. The regulating function of water storage by forests through the dry season was observed in previous studies and is of great local interest in regard to the maintenance of the Panama Canal, a major world trade gateway and important source of income for Panama's economy (Ibañez *et al.* 2002). Between mid-December and mid-February, SWC decreased significantly. Nevertheless, soil water content decreased evenly in all age classes while evaporation showed to be highest in the pasture and in a young forest site. The comparison of these findings implies that a factor compensated for the larger SWC loss by evaporation in open sites, *e.g.* higher moisture gain by rain given the absence of vegetation. Unfortunately, the frequent rains occurring from the end of February on did not permit further understanding of SWC patterns after a longer dry season. Furthermore, it is impossible to assess whether the age differences would remain constant under harsher drought. All in all, the dry season was less pronounced than in other years and the microclimatic conditions measured are probably less extreme than during other dry seasons.

IMPLICATIONS FOR PLANT SPECIES

The microclimate was shown to undergo important changes along the studied succession gradient and consequently, different species are expected to dominate the different succession phases. Tree species are classified according to their life strategies and to their apparition in succession: 1) light-demanding short-lived pioneer species, 2) long-

lived pioneer or intermediate species and 3) shade-tolerant understory species. However, in reality, a continuum of physiological adaptations exists (Denslow 1980, Chazdon and Fetcher 1984, Finegan 1996). Generally, preferential survival and growth of species adapted to a particular microclimate (Bekker *et al.* 1988, Brown 1993, Engelbrecht *et al.* 2006) is observed while low adaptation results in high mortality rates (Denslow 1980).

Young secondary forests experience high light levels (40% of daily radiation between 500-1000 $\mu\text{moles}/\text{m}^2/\text{s}$) (Figure 2), air temperatures (35°C at midday) and important VPDs (up to 1.6 kPa) (Figure 5), which represent stressful environments for plants, especially at the seedling stage. However, seeds of early succession species require high light intensities and temperatures to germinate, guaranteeing the successful colonization of open spaces by trees. Furthermore, short-lived trees grow fast to the canopy and produce many large leaves to compete for light resources (Poorter and Bongers 2006). Trees exposed to high light levels and VPDs experience high transpirational demand (Stewart and Howell 2003) but their photosynthesis is less affected by transpiration than for other species (Fetcher *et al.* 1985,) as they have a better control of stomata closure to avoid *e.g.* low water potentials at noon (Bazzaz and Pickett 1980, Poorter and Bongers 2006). So-called early pioneer tree species form the first cohort, but are short-lived and will be replaced after 10 to 30 years (Finegan 1996).

In the meanwhile, the forming canopy offers high moisture conditions but emerging seedlings have to cope with low light levels (Figure 5) (37% of radiation between 0-10 $\mu\text{moles}/\text{m}^2/\text{s}$) (Figure 2). Intermediate or long-lived pioneer species are able to germinate in the shade. They stay in the understory until a gap opens and then grow to the canopy to eventually replace the first pioneer cohort. This phase of succession may take between 75 and 150 years (Finegan 1996). The shift in dominance between short-lived and long-lived pioneer species is probably taking place in the studied succession gradient as light levels were already considerably low in the intermediate and old age classes. Moisture demanding species are moreover expected to be found at the bottom of slopes (Daws *et al.* 2002) as SWC showed to accumulate there.

As soon as dominant pioneer species form a canopy, shade-tolerant understory species are able to germinate and colonize the shady understory (Chazdon and Fetcher 1984, Denslow 1980, Finegan 1996). These species are adapted to shade by the fact that even very low light levels in the understory may produce large photosynthetic responses (Chazdon and Fetcher 1984, Ellis *et al.* 2000, Niinemets 2006).

LIMITATIONS

Results were generally consistent with each other and with literature. Nevertheless, short-comings and limitations of this study are discussed and possible improvements for further research are suggested.

First of all, the present study was conducted during a limited time frame and is consequently only partly representative of the understory microclimatic conditions over a whole year. In particular, the studied dry season turned out to be extraordinarily short and thus not indicative of other dry seasons. Hence, understory microclimate should be followed over a few consecutive dry seasons in order to capture representative microclimatic conditions and their seasonal fluctuations (Chazdon and Fetcher 1984). The present study

moreover omits the spatial variability of microclimate while microsites with *e.g.* high light (gap partitioning) (Denslow 1980) or soil moisture (Comita and Engelbrecht 2009, Daws *et al.* 2002, Engelbrecht *et al.* 2006), proved to be of great importance for tree regeneration and spatial composition of forests (Denslow 1980).

Kursar *et al.* (2005) observed that gravimetric SWC did not coincide with soil water availability in tropical moist forests in Panama. In general, tropical forest soils can reach low water potentials at high water contents (especially aggregated soil types as clay, the soil type present in the study area), thus possibly giving a misleading idea of favorable conditions for vegetation if only SWC is measured. They therefore suggest available water capacity to be measured in addition to SWC.

Finally, the use of more robust and smaller mini-lysimeters is recommended as the poor mechanical resistance of the used mini-lysimeters lead to water loss. Consequently, a considerable number of mini-lysimeters had to be excluded from the study while a high amount of repetitions still guaranteed sufficient measurements after discarding. Furthermore, their use is only adapted to short rainless periods.

Conclusions

The understory microclimate of moist tropical secondary forests was expected to become darker, cooler and moister over succession. Indeed, light levels and temperature decrease while air and soil moisture increase over the first 20 years of succession. Over this time span, tree basal area increases quickly and is a good explanatory variable for understory microclimate trends with succession. Furthermore, canopy closure was also an important determinant of understory microclimate. In the present study, the microclimate stabilizes already 10 years after disturbance, and the oldest forest sites show to be more buffered in regard to daily variations than the youngest sites. These results indicate that 1) secondary forests play an important role in the regulation of light, temperature and water regime in a tropical landscape, 2) the recovery of understory microclimate towards old-growth conditions may happen fast and 3) the regenerating trees need to cope with quickly changing conditions. Consequently, the changing understory environment will drive succession by filtering successful species according to their adaptations, but the effect is limited to the first 10 years of succession after which microclimate stabilizes. Altogether, the present study offers a framework for future studies of the ecophysiology of secondary tropical forests.

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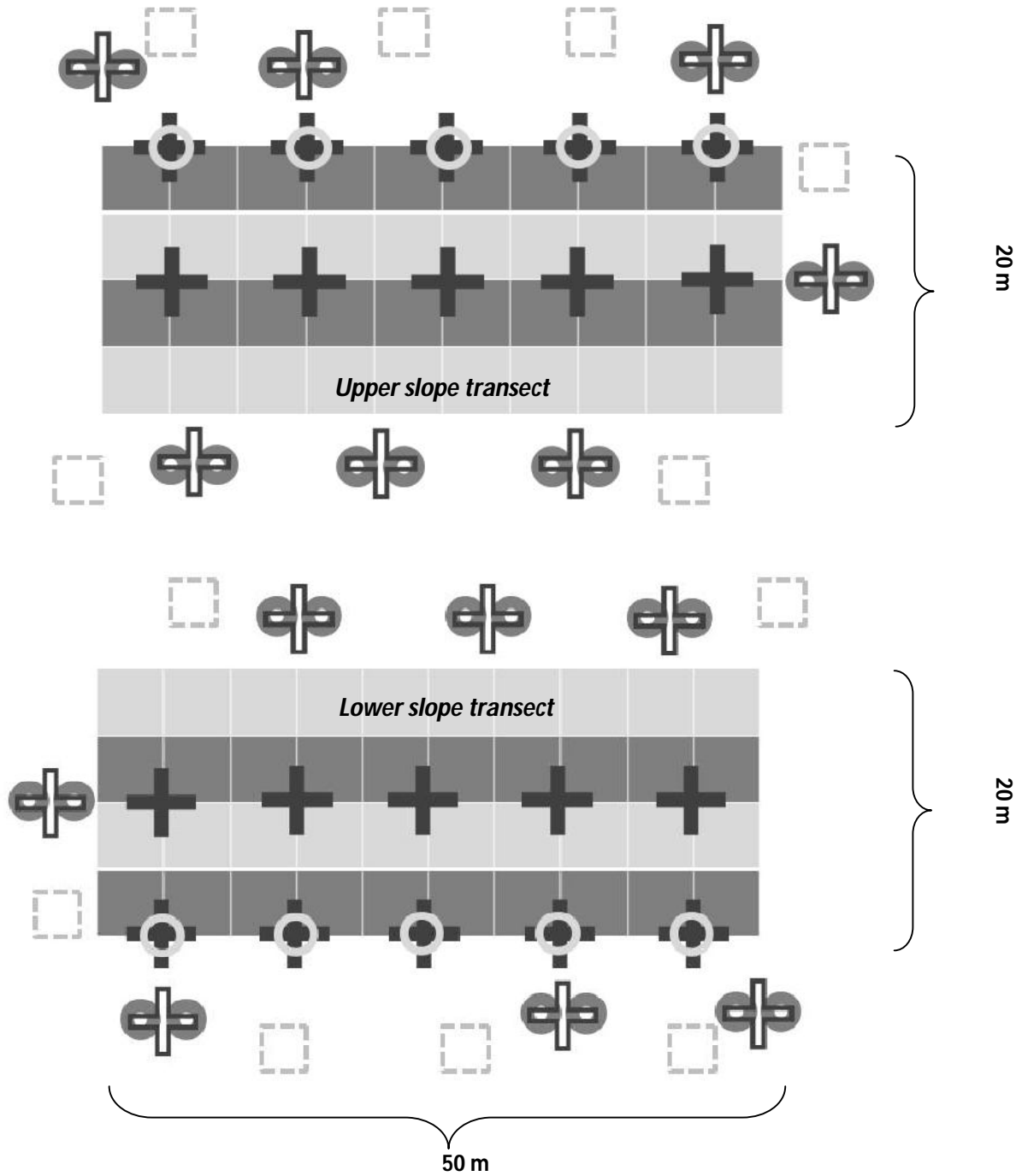
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Appendix – SITE SAMPLING OVERVIEW



- Legend**
-  Ceptometer campaign (mini-lysimeter)
 -  DBH ≥ 1 cm
 -  Mini-lysimeter points (random)
 -  DBH ≥ 5 cm
 -  Leaf litter sampling points (random)
 -  SWC sampling point
 -  Ceptometer campaign (SWC)