

Acclimatization of Tropical Palm Species Associated with Leaf Morpho-Physiological Traits to the Understorey Environment of *Hevea* Rubber Farms

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ABSTRACT

Hevea rubber farm is viable for agroforestry systems since its canopy lessens extreme weather conditions and contributes to the adaptation of shade-tolerant plants. However, some limitations in the availability of soil water and shades vary with the age of rubber trees and affect the understorey plants' acclimatization. Tropical palms are potentially associated plants for the rubber-based agroforestry systems because they are rainforest species adaptable to understorey environments. Two rubber farms, ages 12 and 25 years, intercropped with tropical palms were selected to investigate the acclimatization of the palms to the seasonal abiotic variations in the mature rubber farms. The studied palm species were *Chrysalidocarpus lutescens* and *Rhapis excelsa* in the 12-year-old rubber farm and *Livistona speciosa* and *Licuala spinosa* in the 25-year-old rubber farm, respectively. Leaf area, stomatal conductance, photosynthesis pigments, and leaf nitrogen content were identified as the palms' morpho-physiological traits. The 12-year-old rubber farm had a marked soil water deficit in all soil depths at the beginning of the rainy season,

reaching around 200 kPa at the 80 cm soil depth, while the 25-year-old rubber farm received greater light transmissions, ranging between 37 and 46% in the late dry season. All palms adjusted leaf area to balance the photosynthetic capacity. The *Rhapis* palm had greater acclimatization with significant responses of stomatal conductance. Other than the *Licuala* palm, all palms exhibited the allocation of chlorophyll pigments and nitrogen content significantly in their leaves

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in response to the different intensities of abiotic stresses in the understory of the rubber farms.

Keywords: Agroforestry, Arecaceae, ecophysiological adaptation, *Hevea brasiliensis*, tropical palm species

INTRODUCTION

Natural rubber (*Hevea brasiliensis*) is a forest tree that naturally grows and thrives together with other forest species in its origin, the Amazon rainforest. However, it has been planted traditionally as a monocrop for many years in Southeast Asian countries where commercial plantings developed. Most commercial expansions have invaded tropical forests in the regions, resulting in environmental costs accumulated, such as loss of biodiversity, soil fertility, carbon stock, and forest ecosystem services (Ahrends et al., 2015; Fox & Castella, 2013; Sun et al., 2017). To recover these costs, agroforestry, a created forest ecosystem in which biodiversity could be restored with the interactions of tree and agricultural components ensuring ecological and economic sustainability (Leakey, 2017), is the most recommended option (Langenberger et al., 2017; Somboonsuke et al., 2011; Wu et al., 2016).

The understory environment of rubber farms is viable for an agroforestry system since the overstorey lessens extreme weather conditions, such as high temperature and light intensity, and contributes to biodiversity enhancement complementing forestry ecosystem services in agricultural farms (Rappaport & Montagnini, 2014).

Furthermore, with low irradiance and better light interception, greater light distribution under multi-layered canopy structures like the understory environment of rubber-based agroforestry enhances the efficient light energy capture of the understory plants, thus improving the photosynthetic rate in the system (Powles, 1984).

Typically, in smallholder rubber production, mature rubber farms aged between 10 and 20 deliver the highest yield, while the overaged rubber farms aged over 20 years start yield decreasing due to the high-frequency tapping system conventionally practiced by the farmers (Munasinghe & Rodrigo, 2017; Zaw et al., 2017). These different production potentials also implicate the above- and below-ground ecosystem components, such as seasonal variations of overstorey canopy and soil water conditions that tend to affect the ecophysiological adaptation of understory plants. Unlike other crops, *Hevea* rubber is regularly exploited secondary metabolite, rubber latex, throughout the year (d'Auzac et al., 1997), which could lead to higher soil water consumption, particularly during high productive years (Tan et al., 2011). In addition, during the dry season, the rubber tree typically does not provide canopy shades to the understory environment due to its deciduous nature (Premakumari & Saraswathyamma, 2000). Such changes in light intensity are interrelated to the above- and below-ground water availabilities of the understory environment (Galhidy et al., 2005). These factors could be key considerations that affect the adaptability

performance of understorey plants in a rubber-based agroforestry system and vary with the age of the overstorey rubber trees (Pathiratna, 2006).

Therefore, acclimatization of the understorey plants to these factors is vital to facilitate interdependence among the component of the agroforestry system. Furthermore, since leaves play an important role in photosynthesis, closely influenced by environmental variations and stresses, tree acclimatization could be based on changes in leaves' morphological and physiological traits (Givnish et al., 1988; Valladares et al., 2016).

Although most plant species typically improve photosynthesis with higher vegetative growth under an optimal light intensity (Feng et al., 2019), shade-tolerant plants exhibit greater acclimatization to a light deficit condition with a higher resource allocation to leaves, thus increasing in total leaf area to achieve maximum exposure to irradiance for a greater light-harvesting capacity (Givnish, 1988; Poorter, 1999). However, typical adaptable plants reduce leaf surface area under a water deficit condition or extreme light intensity to improve water conservation in the plant (Chaves et al., 2003). As a vital mechanism to balance gas exchange between the plant and the adjacent atmosphere, stomatal traits such as its apertures and density are leaf anatomical responses closely associated with plant-water relationships (Aasamaa et al., 2001) and photosynthetic capacity (Farquhar & Sharkey, 1982). Photosynthetic pigments—chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl

b), and carotenoids (Car), and their ratios, notably Chl *a/b* and Chl/Car, reflect the physiological status of photosynthetic mechanism (Houborg et al., 2015) and adaptability to environmental stresses (Hendry & Price, 1993). The chlorophyll contents are positively associated with leaf nitrogen content that varies with the light availability (Evans, 1989). A plant with greater acclimatization allocates higher nitrogen concentration to leaves, thus higher chlorophyll pigments with larger leaf areas ensuring improved light harvesting under stress (Field & Mooney, 1986; Givnish, 1988).

Many studies confirmed that shade-tolerant plants like coffee, tea, cocoa, bamboo, and ginger could thrive with higher adaptability in the understorey environment of mature rubber farms and deliver sustainable benefits to the agroforestry ecosystem (Langenberger et al., 2017; Wu et al., 2016). Like these shade-tolerant plants, tropical palms belong to the Arecaceae (Palmae) family and are potentially associated plants for the rubber-based agroforestry system because most palms in rubber-growing regions are tropical rainforest species and are highly adaptable to understorey environments (Dransfield et al., 2004; Johnson, 2011). The distribution of tropical palm species is greatly concentrated in the equatorial regions of Southeast Asia, notably southern Thailand, the Malay Peninsula, and Indonesian islands (Dransfield et al., 2004; Saw et al., 2003), where the *Hevea* rubber has been planted extensively, and around 60% of the world's

total rubber growing area exists, producing over 50% of the world's total supply (Association of Natural Rubber Producing Countries [ANRPC], 2021). In addition, some palm species naturally grow and are cultivated traditionally as understorey plants in some smallholder rubber farms, supplying household subsistence for small rubber farmers (Jongrungrot et al., 2014; Supapvanich et al., 2014). For example, Jongrungrot et al. (2014) reported that tropical palm species like *Livistona* spp., *Licuala* spp., and *Chrysalidocarpus* spp. were commonly found in smallholder rubber farms in southern Thailand, providing not only household uses of non-timber forest products, such as food, decoration, and building materials but also greater on-farm economic performances. Thus, conserving these tropical palm species under smallholder rubber farming would deliver ecological and economic benefits and improve farmers' resilience. To ensure these benefits, the ecophysiological adaptation of tropical palm species to the rubber farm understorey environment is crucially important.

Scientific research studies on the combination of palms in rubber-based agroforestry systems are limited. Hence, an on-farm study was carried out to investigate the acclimatization of the common tropical palm species to the seasonal abiotic variations of the understorey environment in mature rubber farms. The study also identified the palm species ecologically compatible with the different ages of mature rubber farms.

MATERIALS AND METHODS

Experimental Location and Planting Materials

The study was conducted in the Namon district of Songkhla province, located at 6°59'30" N, 100°8'7" E in the east part of southern Thailand. The area is generally under the influence of Southwest Monsoon with a monthly rainfall of around 200 mm from June to September, and Northeast Monsoon with about 400 mm rainfall per month from October to December, resulting in a heavy rainy season, followed by a dry period with a mean temperature of around 28 °C from mid-January to mid-May (Thai Meteorological Department [TMD], 2019).

Two rubber farms, ages 12 and 25 years, intercropped with tropical palms, adjacently situated, were selected for the study. The studied palms were yellow butterfly palm (*Chrysalidocarpus lutescens* H. Wendl.) and lady palm (*Rhapis excelsa* (Thunb.) Henry) in the 12-year-old rubber farms and *Livistona* palm (*Livistona speciosa* Kurz.) and mangrove fan palm (*Licuala spinosa* Roxb.) in the 25-year-old rubber farm, respectively. All rubber trees were RRIM 600 and planted in a spacing of 3 m × 7 m, and the intercropped palms were spaced in 3 m × 7 m in the inter-rows of the rubber trees.

Abiotic Parameters

Rainfall, atmospheric temperature, and evapotranspiration data during the study period were obtained from a local agricultural meteorological station in the area. In addition, light intensities in the understorey

were measured from five different points in the farms compared with under full sun at the same time between 10:00 and 11:00 a.m. once a week using the Sun System – 748205 – photosynthesis active radiation meter (Sun System, Canada).

Soil moisture tensions at 20, 40, 60, and 80 cm depths were monitored monthly on the farms, using the WATERMARK sensor (IRROMETER Company, USA) installed horizontally from the ground between the rubber tree and the palms at 1.5 m far from them.

Changes in the farms' canopy areas were monitored by measuring the farms' leaf area index (LAI) using the hemispherical photography method (Chen et al., 1997). The canopy areas were captured using a Nikon Coolpix 8400 (Nikon, Japan) camera attached with a fish-eye lens upward positioned at 1.2 m from the ground. The photos were taken monthly from three points between the rubber trees and the palms at each farm. The photos were processed using the Gap Light Analyzer software version 2.0 (Simon Fraser University, Canada) to quantify the LAI of the farms.

Morphological Traits

Six palm leaves were sampled randomly from fully expanded fronds to quantify the understorey palm's leaf traits of leaf area (LA), leaf dry mass, and specific leaf area (SLA). An image analyzing software, the ImageJ program (National Institute of Health, USA) (Schneider et al., 2012), was used to process the leaf photos for the LA. The sample leaves were put in paper

bags and oven-dried at 70 °C for 72 hours to calculate the leaf dry mass and the SLA (Awal et al., 2004).

Quantifying the palm leaves' stomatal and guard cells were carried out monthly by the impression method (Weyers & Meidner, 1990). First, 1 cm² of leaf specimens was prepared by sampling the middle portion of the leaves collected from each palm species between 09:00 and 10:00 a.m. Next, an impression solution, formalin acetic acid alcohol, was applied to the leaf specimens for replication. Once the solution hardened, the replica was detached from the specimen, located on a microscope slide, and investigated under a compound microscope (Zeiss CP-Achromat 40× Objective) (Carl Zeiss Microscopy, USA).

Physiological Traits

For the photosynthesis pigment determination, leaf samples in 1 cm² dimension were excised from five different points of each palm species. The pigments (chlorophylls and carotenoids) were extracted with 3 ml of *N, N*-dimethylformamide solvent by the direct immersion method and kept for 24 hours at 4 °C under a dark condition (Moran & Porath, 1980). The absorbances were measured at wavelengths of 647 nm, 664 nm, and 480 nm with a UV spectrophotometer— Ultrospec 3000 UV/VIS (Pharmacia Biotech, USA) for Chl *a*, Chl *b*, total Chl and Car, respectively (Wellburn, 1994). Calculations of the pigment contents followed the simultaneous equations devised by Inskeep and Bloom (1985).

The oven-dried sample leaves were ground and sieved through a 1 mm aperture mesh for the sample preparation of the total nitrogen content determination using the micro-Kjeldahl method (Sáez-Plaza et al., 2013). Leaf nitrogen contents in mass-based (N_m) and area-based (N_a) were then calculated based on the dry weight of the leaf and SLA.

Data Collection and Statistical Analysis

The data collection was carried out from July 2016 to June 2017 and split into four seasonal periods according to the typical weather patterns in the area, the southern peninsular of Thailand: Wet I (July–September 2016), Wet II (October–December 2016), Dry I (January–March 2017), and Dry II (April–June 2017), respectively.

The collected data were analyzed using the *F*-test in one-way analysis of variance (ANOVA) for the overall significance and then followed by Duncan’s multiple range test at $P \leq 0.05$ to compare the significant data among the seasonal periods for each understorey palm species. R stat 3.6.2 software was performed for the data analysis.

RESULTS

Agroclimatic Situation of the Study Area

According to the weather data from the local meteorological station, the area received 2,560 mm of total rainfall, and it accumulated 286, 1177, 646, and 489 mm in the Wet I, Wet II, Dry I, and Dry II seasons, respectively (Figure 1). Monthly rainfall in the Wet I period was under 150 mm. It then increased

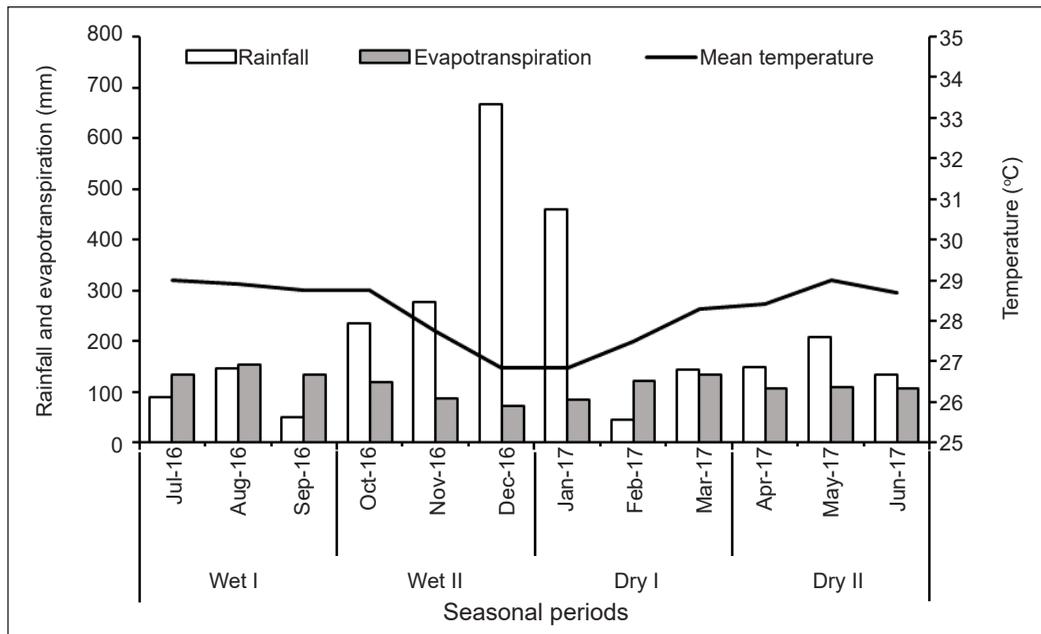


Figure 1. Monthly weather conditions: rainfall, evapotranspiration, and mean temperature of the study area (from July 2016 to June 2017)

in October from 235 to 666 mm in December during the Wet II season, a heavy rainy period. In January of the Dry I season, the rainfall decreased and reached its minimum of 44 mm in February. Then few light spots of rain started, with monthly rainfall ranging between 130 and 210 mm in the Dry II season.

It was observed that monthly evapotranspiration rates were at the highest between 130 and 155 mm during the Wet I season, followed by the Dry I and Dry II seasons. The minimum evapotranspiration rate of 72 mm per month was found in December in the Wet II season.

Soil Moisture Tensions at the Rubber Farms

Figure 2 shows the soil moisture tensions of the rubber farms during the study period. At the 12-year-old rubber farm (Figure 2A), during the Wet I season, higher soil moisture tensions were observed in all soil depths, reaching around 200 kPa at the 80 cm soil depth in September and October, and the tension reduced with the higher rainfall in the Wet II season. In the Dry II season, its soil moisture tension rose about 130 kPa at the 60 cm soil depth, while the other soil depths had relatively lower tension, less than 40 kPa.

On the other hand, the soil moisture tensions in the 25-year-old rubber farm (Figure 2B) were not as intense as those in the 12-year-old rubber farm. However, in September of the Wet I season, particularly at the 40 cm soil depth, significant tensions were observed at around 120 kPa.

LAI and Light Intensity in the Farms

Figures 3A and 3B exhibit the light transmission and the LAI of the 12-year-old and 25-year-old rubber farms, respectively, during the study period. Both farms showed the light transmissions in the farms were lower in the wet seasons and increased in the dry seasons, while conversely, higher LAI values in the wet seasons and lower values in the dry seasons. In comparing the two farms, the 25-year-old rubber farms showed lower LAI values than the 12-year-old rubber farms, particularly during the Dry II season. The LAIs of the farms reached their minimum values of less than one in February and April. Throughout the study period, the 25-year-old rubber farm received greater light transmissions than the 12-year-old rubber farm. It was observed that the light transmission in both farms increased during the Dry II season, but a marked increase in the 25-year-old rubber farm ranged between 46 and 37%.

Morpho-Physiological Traits of the Palms

Chrysalidocarpus lutescens. Significant differences were investigated in seasonal comparisons of the LA and the guard cell length (Table 1). However, other morphological traits, notably SLA, stomatal density, and guard cell width, did not vary significantly. The LAs of the palm were exposed as the smallest at 15.71 m² in the Wet I season compared to other seasons.

The guard cell lengths in the Wet II and the Dry I exhibited significantly the longest at 24.27 and 23.89 µm, respectively.

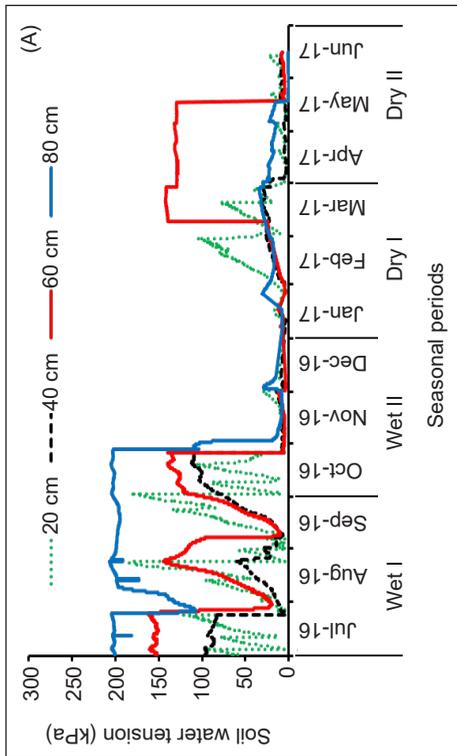
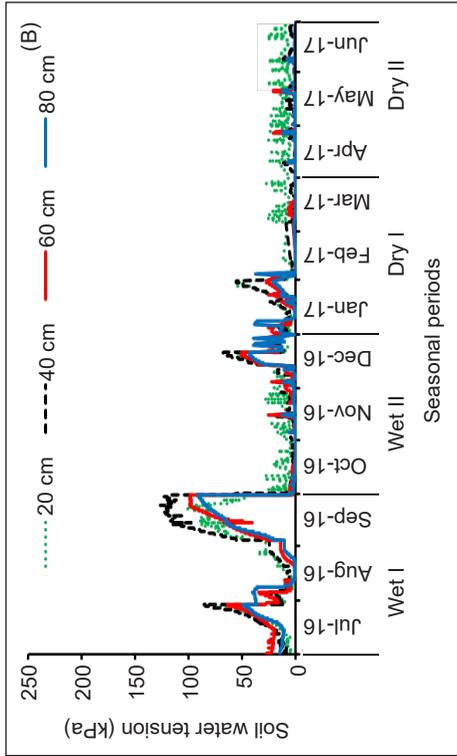


Figure 2. Monthly changes of soil water tension in (A) the 12-year-old rubber farm and (B) the 25-year-old rubber farm (from July 2016 to June 2017)

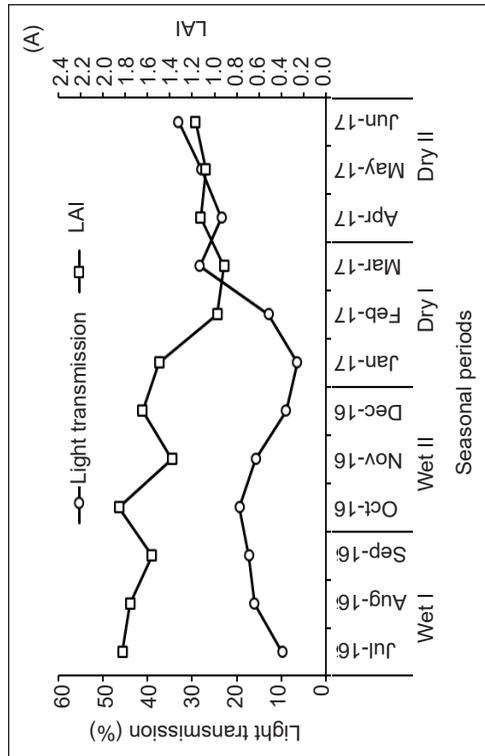
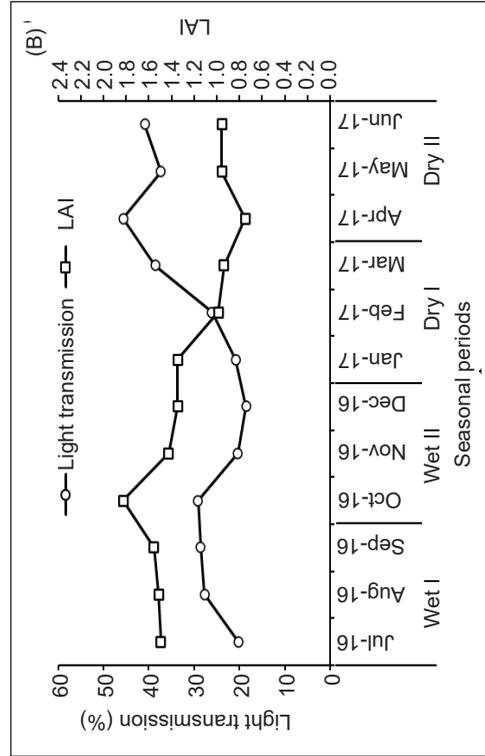


Figure 3. Monthly changes in the light transmission and LAI of (A) the 12-year-old rubber farm and (B) the 25-year-old rubber farm (from July 2016 to June 2017)

Table 1

Seasonal changes in morpho-physiological traits of the *Chrysalidocarpus lutescens* H. Wendl. leaves under the 12-year-old rubber farm

Parameters	Wet I	Wet II	Dry I	Dry II	F-test
Morphological traits					
LA (m ²)	15.71 b	23.73 a	20.21 ab	23.53 a	**
SLA (cm ² g ⁻¹)	117.76	94.71	96.82	94.71	ns
Stomatal density (stomata mm ⁻²)	44.32	45.81	44.04	44.36	ns
Guard cells width (μm)	16.43	19.26	18.87	17.59	ns
Guard cells length (μm)	22.03 ab	24.27 a	23.89 a	21.36 b	**
Physiological traits					
Chl <i>a</i> (mg cm ⁻²)	14.19 a	14.15 a	11.24 b	10.72 b	**
Chl <i>b</i> (mg cm ⁻²)	6.22 a	6.21 a	4.75 b	4.47 b	**
Total Chl (mg cm ⁻²)	20.47 a	20.41 a	16.03 b	15.22 b	**
Car (mg cm ⁻²)	2.70 a	2.70 a	2.12 b	1.98 b	**
Chl <i>a/b</i>	2.28 b	2.28 b	2.39 a	2.41 a	**
Chl/Car	7.58	7.76	7.58	7.69	ns
Total N (%)	1.81 a	1.71 ab	1.63 b	1.69 ab	*
N _m	0.24	0.33	0.40	0.35	ns
N _a	0.09	0.07	0.10	0.07	ns

Note. Wet I = from July to September 2016; Wet II = from October to December 2016; Dry I = from January to March 2017; Dry II = from April to June 2017. *, ** = Different letters in the same row indicate statistically significant differences by Duncan's multiple range test (DMRT) ($P \leq 0.05$, and $P \leq 0.01$), and ns = no significant difference

Likewise, the guard cell widths were broader in the Wet II and the Dry II than in the other seasons, but there were no statistical differences among their seasonal changes.

The major photosynthesis pigments, namely Chl *a*, Chl *b*, total Chl, and Car contents, were greater with a high significance in the wet seasons and less in the dry seasons. The higher ratios of Chl *a/b* resulted during the dry seasons, but their values in all seasons did not exceed 2.5. The highest content of total leaf nitrogen was investigated in the Wet I season.

Rhapis excelsa. During the Wet II season, the LA of the *Rhapis* palm was the biggest

at 7.26 m², while its SLAs were high values of over 79 cm² g⁻¹ in the Wet II and the Dry II seasons, respectively (Table 2). The stomatal density found in the Wet II season was also the highest at 58.25 m m⁻² among the seasons. The Wet II and the Dry I seasons resulted in the largest guard cell size, with over 21 and 25 μm in width and length, respectively.

Its seasonal changes in the Chl and Car contents were similar to those of the understorey *Chrysalidocarpus* palm growing together under the same farm. The Chl *a*, Chl *b*, total Chl, and Car contents were at the highest values in the Wet I season at 15.26, 5.67, 20.67, and 3.58 mg cm², respectively. Moreover, those contents

Table 2
Seasonal changes in morpho-physiological traits of the *Rhapis excelsa* Thunb. leaves under the 12-year-old rubber farm

Parameters	Wet I	Wet II	Dry I	Dry II	F-test
Morphological traits					
LA (m ²)	5.53 b	7.26 a	4.79 b	5.60 b	**
SLA (cm ² g ⁻¹)	70.89 ab	79.00 a	64.41 b	79.50 a	*
Stomatal density (stomata mm ⁻²)	44.93 b	58.25 a	48.64 b	50.12 ab	**
Guard cells width (μm)	14.56 b	21.21 a	22.27 a	16.55 b	**
Guard cells length (μm)	21.65 b	25.07 a	25.39 a	21.24 b	**
Physiological traits					
Chl <i>a</i> (mg cm ⁻²)	15.26 a	14.53 ab	13.38 b	10.56 c	**
Chl <i>b</i> (mg cm ⁻²)	5.67 a	5.25 ab	4.51 b	2.94 c	**
Total Chl (mg cm ⁻²)	20.67 a	19.52 ab	17.62 b	13.23 c	**
Car (mg cm ⁻²)	3.58 a	3.46 ab	3.28 b	2.82 c	**
Chl <i>a/b</i>	2.70 c	2.84 bc	3.00 b	3.60 a	**
Chl/Car	5.77 a	5.61 ab	5.36 b	4.68 c	**
Total N (%)	2.05 a	2.01 a	1.70 b	1.79 b	**
N _m	0.16 ab	0.19 a	0.10 b	0.12 ab	*
N _a	0.14 a	0.07 c	0.10 b	0.11 b	**

Note. Wet I = from July to September 2016; Wet II = from October to December 2016; Dry I = from January to March 2017; Dry II = from April to June 2017. *, ** = Different letters in the same row indicate statistically significant differences by Duncan's multiple range test (DMRT) ($P \leq 0.05$, and $P \leq 0.01$), and ns = no significant difference

gradually decreased to their smallest values in the Dry II season at 10.56, 2.94, 13.23, and 2.82 mg cm², respectively. The ratios of Chl *a* and Chl *b* were lower in the Wet seasons, with values less than three, whereas they were over three in the dry seasons. However, in contrast, the total Chl and Car ratio (Chl/Car) showed the highest value in the Wet I season at 5.77 and the lowest in the Dry II season at 4.68.

It was observed that the total nitrogen content was higher in the wet seasons than in the dry seasons. Nitrogen content per dry leaf mass (N_m) in the Wet II season was at 0.19, the highest among the seasons. On the other hand, leaf-area-based nitrogen (N_a) content was the highest in the Wet I season at

0.24, while that in the Wet II season resulted in the lowest value of 0.07.

***Livistona speciosa*.** During the Wet I season, the palm leaf area was the smallest, but later it expanded significantly in the Wet II and the dry seasons (Table 3). However, with respect to the SLA, the higher value was observed in the Wet I season, followed by a gradual decrease to the lowest value in the Dry II season.

The variations in the width and length of the guard cells were significant, and their respective lowest values were observed in the Dry II season.

All content of the major photosynthetic pigments was higher than those of other

Table 3
Seasonal changes in morpho-physiological traits of the *Livistona speciosa* Kurz. leaves under the 25-year-old rubber farm

Parameters	Wet I	Wet II	Dry I	Dry II	F-test
Morphological traits					
LA (m ²)	86.15 b	165.02 a	159.33 a	172.82 a	**
SLA (cm ² g ⁻¹)	55.59 a	49.67 ab	45.75 bc	40.48 c	**
Stomatal density (stomata mm ⁻²)	260.15	288.97	257.74	259.01	ns
Guard cells width (μm)	17.17 ab	18.83 a	16.62 ab	15.89 b	*
Guard cells length (μm)	21.28 a	21.53 a	21.65 a	18.42 b	**
Physiological traits					
Chl <i>a</i> (mg cm ⁻²)	22.30 c	22.59 bc	24.85 a	23.73 ab	**
Chl <i>b</i> (mg cm ⁻²)	10.95 c	11.15 bc	12.75 a	11.95 ab	**
Total Chl (mg cm ⁻²)	30.67 c	31.14 bc	34.85 a	33.00 ab	**
Car (mg cm ⁻²)	4.40 c	4.46 bc	4.93 a	4.70 ab	**
Chl <i>a/b</i>	2.04 a	2.03 ab	1.95 c	1.99 ab	**
Chl/Car	6.97 b	6.97 b	7.07 a	7.02 ab	**
Total N (%)	1.67 b	1.91 ab	1.95 a	1.70 ab	**
N _m	1.77 b	2.18 b	5.47 a	1.76 b	**
N _a	0.11 b	0.07 c	0.17 a	0.05 1c	**

Note. Wet I = from July to September 2016; Wet II = from October to December 2016; Dry I = from January to March 2017; Dry II = from April to June 2017. *, ** = Different letters in the same row indicate statistically significant differences by Duncan's multiple range test (DMRT) ($P \leq 0.05$, and $P \leq 0.01$), and ns = no significant difference

palms in the study. These pigments increased in the dry seasons and reduced in the wet seasons. The chlorophyll ratio (Chl *a/b*) was at the maximum of 2.04 during the Wet I season. The total Chl and Car ratio were lower in the Wet seasons and higher in the dry seasons. The total nitrogen content, N_m, and N_a were also highest, with a statistical significance at 1.95, 5.47, and 0.17, respectively, during the Dry I season.

***Licuala spinosa*.** The LA of the palm was the smallest in the Wet II season, followed by the largest in the Dry I season (Table 4). However, the SLA showed the highest in the Wet II season. The guard cells' width and length were minimal during the Dry

II season. No significant changes were observed in the photosynthesis pigments and the total nitrogen content on the palm leaves among the seasons. Nevertheless, the N_m and N_a were at the minimum during the Wet I season and peaked at 0.62 and 0.64 in the Dry II season.

DISCUSSION

Seasonal Variations in the Agroecosystem of the Mature Rubber Farms

Agroclimatic Ecology. Based on the meteorological data, the study area received a relatively higher annual rainfall during the study period. However, some months of the Wet I season did not receive the

Table 4
Seasonal changes in morpho-physiological traits of the Licuala spinosa Roxb. leaves under the 25-year-old rubber farm

Parameters	Wet I	Wet II	Dry I	Dry II	F-test
Morphological traits					
LA (m ²)	18.70 ab	11.72 c	24.39 a	20.74 ab	**
SLA (cm ² g ⁻¹)	73.76 ab	81.64 a	74.85 ab	65.67 b	*
Stomatal density (stomata mm ⁻²)	195.56	197.00	189.71	180.62	ns
Guard cells width (μm)	19.41 ab	20.78 a	19.54 ab	16.92 b	*
Guard cells length (μm)	25.01 a	24.14 a	23.52 a	18.54 b	**
Physiological traits					
Chl <i>a</i> (mg cm ⁻²)	14.48	14.42	16.03	14.13	ns
Chl <i>b</i> (mg cm ⁻²)	5.91	5.81	6.76	5.72	ns
Total Chl (mg cm ⁻²)	20.00	19.79	22.47	19.45	ns
Car (mg cm ⁻²)	2.98	2.92	3.30	2.91	ns
Chl <i>a/b</i>	2.45	4.50	2.41	2.55	ns
Chl/Car	6.11	6.76	6.80	6.61	ns
Total N (%)	1.66	1.67	1.86	1.61	ns
N _m	0.18 b	0.27 b	0.44 ab	0.62 a	**
N _a	0.23 b	0.47 ab	0.44 ab	0.64 a	**

Note. Wet I = from July to September 2016; Wet II = from October to December 2016; Dry I = from January to March 2017; Dry II = from April to June 2017. *, ** = Different letters indicate statistically significant differences by DMRT ($P \leq 0.05$, and $P \leq 0.01$), and ns = no significant difference

normal rainfall of those months. In contrast, the peak rainfall in December was higher than the average monthly rainfall normally experienced during the Wet II season. These observations indicated that although the rainfall was above average in the study period, the rain distribution was intermittent, especially at the beginning of the rainy season. However, the high monthly evapotranspiration rate experienced during the Wet I season showed that the studied area could have a good water cycle of the agroecosystem during those months.

Seasonal Abiotic Stresses. It was noticed that overcanopy developments of both rubber farms reached their highest LAIs

when the rainfall was less in the Wet I season, resulting in some extent of soil water tensions in both farms. Marked increased soil water tensions were observed in the 12-year-old rubber farm, particularly in the Wet I season, the beginning of the rainy season. However, the 25-year-old rubber farm had only slightly increased soil water tension in the Wet I season and considerably less in the dry season. Tan et al. (2011) found higher water consumption by mature rubber trees in the rainy season than in the dry season in tropical regions of China. Since the age of 25 years is normally considered the end of the economic lifespan of rubber farms (Saraswathyamma et al., 2000) because of the fewer number of productive

rubber trees that remain (Pathiratna, 2006), the soil water consumption in latex production considerably decreases with low productivity, thus less soil water deficit. Lin et al. (2011) reported that the soil water deficit decreased with the age of rubber farms because the water usage activity of overaged rubber trees gradually reduced with lesser transpiration and vegetative growth. Since the 25-year-old rubber farm had less vegetative development, the farm received a higher light transmission than the 12-year-old rubber farm throughout the year. Pathiratna (2006) reported that older rubber farms over 20 years tended to have a lesser canopy density and received a higher light transmission because of fewer trees remaining, the longer height of the trees, and the self-pruning of lower branches with age increased. Its prolonged low LAI value in the dry seasons was primarily due to the longer its deciduous period. In general, an overage rubber tree is less efficient in nutrient translocation leading to a greater duration to complete the deciduous process, which is internal nutrient storage activity for the next nutrient cycle of the deciduous tree (Jacob et al., 2018; Y. Li et al., 2016).

On the other hand, in the 12-year-old rubber farm, the soil water tension elevated slightly with the refoliation after the defoliation in the deciduous process during the Dry I season. These observations confirmed that the soil water tension markedly increased with the development of the leaf area, particularly when the water availability was limited.

Seasonal Variations of the Palm Leaf Morpho-physiological Traits under the Rubber Farms

LA and SLA. In the 12-year-old rubber farm, when the soil water tension reached the highest during the Wet I season, both understorey palms: the *Chrysalidocarpus* and the *Rhapis*, reduced their leaf areas. Plants minimize leaf area to inhibit transpiration, improving water use efficiency under certain water deficit conditions (Chaves et al., 2003; Xu & Zhou, 2005).

However, in the 25-year-old rubber farm, both understorey palms: the *Livistona* and the *Licuala*, increased the LA during the Dry I season when a greater light transmission was received because of the overstorey defoliation. In most species, optimal light intensity improves the photosynthesis process associated with biomass production with vegetative development unless considerable abiotic stress exists (Feng et al., 2019).

It was noticed that the SLA of the *Rhapis* palm was observed as the smallest in the Dry I season when the soil water tension was relatively lower than the other seasons, whereas that of the same understorey palm, the *Chrysalidocarpus*, did not vary significantly between the seasons. However, the SLAs of the understorey palms, the *Livistona* and the *Licuala*, in the 25-year-old rubber farm reduced to the smallest values in the Dry II season when there was no soil water tension but higher light transmission with dryer conditions leading to a slight water deficit in the air.

These different responses are consistent with the findings of previous studies that although a moderate drought increased the stomatal density, a severe water deficit decreased the stomatal density, which negatively correlated with the SLA (Liu et al., 2006; Meng et al., 1999; Xu & Zhou, 2005).

Stomatal Structure. The results of the stomatal density in the *Rhapis* palm also replicated the above finding of the association between the stomatal density and water stress intensity since the lowest stomatal density was found in the Wet I season when the soil water stress was significantly high. However, other palms did not significantly differ in stomatal density among the seasons.

Variation in stomatal density results from anatomical modification to balance the stomatal conductance with adaptation to prevailing environmental stresses (Casson & Hetherington, 2010) during new leaf development in which the stomatal pattern is adjusted (Hamanishi et al., 2012; Vaten & Bergmann, 2012). Stomatal pores respond instantly to weather fluctuations by regulating the aperture size by adjusting turgor pressure in adjacent guard cells (Farquhar & Sharkey, 1982; Franks & Beerling, 2009). When a plant experiences a moisture deficit, a reduction in turgor pressure decreases the guard cell size in width and length, resulting in a smaller stomatal aperture to minimize water loss (Schroeder et al., 2001). This adaptive stomatal dynamic was found significantly

in the *Rhapis* palm under the 12-year-old rubber tree as the guard cell size in both width and length enlarged, thereby the stomatal aperture, in the Wet II and the Dry I seasons when the rainfall was the highest with less soil water tension. In contrast, the guard cells become smaller in the Wet I and Dry II seasons once the moisture deficit is markedly intense.

However, the *Chrysalidocarpus* palm under the same rubber farm did not significantly alter its stomatal density and guard cell width except for the guard cell length. Thus, it indicates that the palm could not actively perform the anatomical adjustment of its stomatal traits amidst the water stresses on the farm.

On the other hand, both palms under the 25-year-old rubber farm could adjust the stomatal aperture by significantly altering the guard cell in width and length by the seasons but the stomatal densities. The significant decreases in the width and length of the guard cells of both palms in the Dry II season contributed to the reduction in the stomatal pore size to lessen the leaf transpiration under the higher light transmission. Bertolino et al. (2019) reported that dynamic responses of the stomatal aperture were significant with light intensity variation rather than soil water deficit in most rainforest species.

Photosynthetic Pigments' Contents. Under the 12-year-old rubber farm, both understorey palms exhibited higher concentrations of the majority photosynthetic pigments (Chl *a*, Chl *b*, total Chl, and Car) per unit leaf

area in both wet seasons when the light transmission was poor with higher leaf area index. Typically, the photosynthesis process becomes less efficient with some decreases in the pigments under low light conditions (Feng et al., 2019). Shade-tolerant plants, however, adapt to the low-light environment with increases in the concentration of the pigments to maintain the photosynthetic capacity (Lei & Lechowicz, 1997; Niinemets & Tenhunen, 1997; T. Li et al., 2014). Furthermore, since these plants enhance light harvesting chlorophyll-protein complexes, present in Chl *b*, to improve the light-harvest function in response to low light conditions, the value of Chl *a/b* becomes lesser with a reduction in irradiance intensity of a shady environment (Mathur et al., 2018; Terashima & Hikosaka, 1995). Thus, with the lesser values of the Chl *a/b* during the Wet seasons, both palms could approve their adaptive acclimatization to the low light condition under the rubber farm.

It was previously reported that a marked increase in the value of Chl *a/b* indicated a greater intensity of stress mainly associated with light-harvesting function in the photosynthesis process but varied with different species, development stages, nutrient levels, and environmental conditions (Kitajima & Hogan, 2003; Feng et al., 2019). Furthermore, some studies have suggested that a value of Chl *a/b* more than three was considered stress that affects the photosynthetic capacity over the threshold level (Hartmut et al., 2007; Lichtenthaler et al., 1981). Thus, the values of the Chl

a/b of the *Rhapis* palm higher than three during the dry seasons indicated that the palm experienced a stressful environment during that period.

In addition, the widest stomatal opening that continued in the Dry I season aggravated the stress more intensely in the Dry I and II seasons because of the higher transpiration rate. At the same time, the surrounding water availability was limited. However, its lesser values of the Chl/Car of 5.36 and 4.68 in the Dry I and II seasons, respectively, corresponded to the range observed in other acclimated plants under a stress condition (Hartmut et al., 2007; Sarijeva et al., 2007). The higher values of its Chl/Car ratio in the low light condition approved that the photosystem enhanced its light-harvesting complex through the significant increment of carotenoid content to balance with the light irradiance availability for the system (Hendry & Price, 1993).

On the other hand, the results of markedly higher contents of chlorophylls and carotenoid pigment in the *Livistona* palm compared to the other palms in the study agreed with the reports of Windsor-Collins et al. (2006) that palmate leaves of palms like *Livistona speciosa* were likely to change a darker color with higher concentrations of photosynthetic pigments under a low-light condition. In addition, the pigments of the palm were greater in the Dry seasons than in the Wet seasons. However, there were no significant variations of the pigments in the *Licuala* palm among the seasons.

Fan et al. (2018) and Feng et al. (2019) suggested that higher chlorophyll pigment content under a greater irradiance was related to leaf thickness associated with an increase of leaf nitrogen content per unit dry mass, which is a major source of chlorophyll pigments, contributed by optimal light intensity.

Higher values of the Chl *a/b* coupled with lower values of the Chl/Car in the Wet seasons and conversely, decreasing in the Chl *a/b* with increasing in the Chl/Car in the dry seasons reflected that the *Livistona* palm could have great adaptability to the seasonal irradiance variation in the understory environment of the 25-year-old rubber farm. In addition, according to the findings by Hartmut et al. (2007), Lichtenthaler et al. (1981), and Sarijeva et al. (2007), the Chl *a/b* of less than three and the Chl/Car ratios of greater than six approved that there were no environmental stresses affected to the palm throughout the study period.

Leaf Nitrogen Concentration. Regarding the nitrogen contents of the leaves under the 12-year-old rubber farm, it was observed that they increased in both understory palms, while the chlorophyll and carotenoid contents were at higher levels in the Wet seasons. Nitrogen-deficient leaves are normally found under stress conditions along with a marked reduction in chlorophyll pigments and leaf area together with photosynthetic capacity (Bojović & Marković, 2009). However, in contrast, a plant, which has greater acclimatization, allocates higher

nitrogen concentration to leaves, thus higher chlorophyll pigments with larger leaf area to optimize the photosynthetic capacity under abiotic stress such as low irradiance and high-water deficit (Evans, 1989; Field & Mooney, 1986; Givnish, 1988).

However, a positive relationship between the leaf nitrogen content and the SLA was observed only in the palm leaf of the *Rhapis*. This correlated variation was also reported as the acclimation response of a shade-tolerant plant to a low-light environment (Bojović & Marković, 2009; Wang et al., 2012). The *Rhapis* palm also exhibited a closed positive correlation between the leaf nitrogen content per unit dry mass and the SLA. A higher allocation of nitrogen to the photosynthetic mechanism of a shade-resilient plant enlarges light-harvesting areas, which is a main limiting factor in the photosynthetic capacity (Evans, 1989; Niinemets & Tenhunen, 1997; Terashima & Hikosaka, 1995; Wang et al., 2012). Although a greater correlation between the SLA and the leaf nitrogen content per unit area was reported in some previous studies (Cornelissen et al., 1997; Dijkstra, 1990; Meziane & Shipley, 2001), the current study did not observe a consistent relationship between them.

Under the 25-year-old rubber farm, the leaf nitrogen concentration with both mass-based and area-based varied significantly with the seasons in the *Livistona* palm and expressed their highest levels in the Dry I season when the higher light intensity with the low LAI due to the natural leaf deciduous

process. Hollinger (1989) reported that greater mass-based leaf nitrogen content was investigated in the upper layer of an evergreen forest, reflecting a positive correlation between the leaf nitrogen content per unit of dry mass and light intensity. Vincent (2001) observed that leaf nitrogen content associated with photosynthetic capacity increased with canopy openness until a threshold level that varied in different species.

It was also noted that the mass-based leaf nitrogen contents of the *Livistona* palm were markedly higher than that of other palms. Conversely, its area-based leaf nitrogen contents were smaller than the others. They were associated with the distinctive morphological traits of the *Livistona* palm. Its average LA was significantly larger, and the SLA was smaller than the other palms. Thus, the leaf could be thinner and lighter than other leaves. With the normal nitrogen content of the leaf, the thin leaf led to the higher mass-based leaf nitrogen content, while the lighter leaf caused the area-based leaf nitrogen content to be smaller. Thus, the leaves were less likely to thicken during the Dry I season. The findings on these traits are consistent with a report by Loomis (1997) that a thin leaf had a higher mass-based leaf nitrogen content resulting in greater photosynthetic capacity.

CONCLUSION

The study highlighted those significant abiotic variations with the different ages of the rubber farms primarily influenced

the morpho-physiological traits of the understorey palms. For example, the 12-year-old rubber farm had a marked soil water deficit at the beginning of the rainy season, while the 25-year-old rubber farm had a greater light transmission in the dry season.

Under these abiotic variations, all palms could adjust the leaf area in terms of the morphological traits to balance the photosynthetic capacity. However, the *Rhapis* palm had higher acclimatization with significant stomatal conductance responses than the other palms. Regarding the physiological traits, except the *Licuala* palm, all palms exhibited significant allocation of the chlorophyll pigments and nitrogen content in their leaves in response to the different intensities of the abiotic stresses in the understorey of the rubber farms.

Despite the study results showing the greater acclimatization with the adaptive morpho-physiological response of the palm leaves, it is suggested that the below-ground interactions of the system, linked with the current findings, should be further studied for a holistic understanding of their coexistence.

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