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Variation of leaf-level gas exchange rates and leaf functional traits of dominant trees across three successional stages in a Southeast Asian tropical forest

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ABSTRACT

Deforestation has created heterogeneous patches of old-growth and secondary forests throughout Southeast Asia, posing challenges for understanding the hydrological and carbon cycles. In addition to changes in species composition, environmental conditions differ across successional stages which in turn can influence forest water use and productivity. Here, we investigated leaf-level area-based photosynthesis (A_{area}) and stomatal conductance (g_s) of 11 tree species dominating an old-growth (OF; >200 years), an intermediate (IF; ~44 years), and a young forest (YF; ~4 years) in Thailand during both the wet and dry season. Specifically, we compared A_{area} and g_s and assessed the sensitivity of g_s to vapor pressure deficit (VPD). We also examined relationships between gas exchange parameters and key functional leaf traits, including leaf mass per area (LMA), nitrogen (N), phosphorus (P), and chlorophyll concentration. All three forests showed comparable A_{area} and g_s in the wet season, whereas significantly lower values were observed in IF during the dry season. All forest stages displayed similar sensitivity of g_s to VPD. Among the leaf functional traits considered, LMA, N and P were significantly higher in YF compared to the other two successional stages. Our results suggested that forest succession may not influence gas exchange, rather, canopy development associated with forest stage produced the main effect. Furthermore, the young forest was the most active in resource acquisition with its high LMA and leaf nutrient concentrations, which could result in high photosynthetic rates. However, low soil water availability in YF possibly limit the gas exchange rates thereby making them similar to those in the old-growth forest. These findings highlight the potential effects of canopy characteristics inherent in successional forests on water and carbon exchanges between trees and the atmosphere and their sensitivity to atmospheric drought. These results call for the need for further studies to identify the main factors influencing forest productivity during secondary succession in the tropics, particularly in the Southeast Asian region where such information is lacking.

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1. Introduction

Tropical forests play an important role in the biosphere, especially in global water and carbon cycles. Transpiration represents *ca.* 40–90% of the total amount of water emitted to the atmosphere (e.g., Miralles et al., 2011; Jasechko et al., 2013; Wang-Erlandsson et al., 2014; Good et al., 2015) and thus strongly influences hydrology and energy partitioning in terrestrial ecosystems (Bonan, 2008). Tropical forests sequester *ca.* 0.28–1.26 Pg C each year (Hubau et al., 2020) and thus play a critical role in mitigating rising atmospheric carbon dioxide and related climate change impacts. However, widespread deforestation and land use change are rapidly transforming these ecosystems, with over 80 million hectares of natural, old-growth tropical forests being lost since 1990 (FAO and UNEP, 2020). Deforestation and land use change is especially pervasive across Southeast Asia (Zeng et al., 2018; FAO and UNEP, 2020), where large-scale agricultural production and commercial tree plantations have been the main drivers of forest loss (Curtis et al., 2018). However, many of these large-scale operations have been abandoned because of unsustainable practices, leading to the regeneration of secondary forests either through natural or aided processes. Consequently, forests in Southeast Asia are characterized by a patchy mosaic of primary, old-growth forests, and forests at different stages of secondary succession.

Structural attributes, such as canopy height and tree density, vary considerably among forests which in turn can strongly influence the microclimate (Rambo and North, 2009; Jucker et al., 2018) as well as the carbon and water balance in old growth, primary forests, and forests at different stages of secondary succession (Powers and Marín-Spiotta, 2017). Old-growth forests usually contain larger trees and heterogeneous canopy layers, and lower stem density, compared to secondary forests (Chazdon, 2014; Chanthorn et al., 2016, 2017; Jucker et al., 2018). Conversely, the intermediate successional stage, namely the “stem exclusion” stage, has a relatively homogeneous canopy and high stem density (Chazdon, 2014; Chanthorn et al., 2016, 2017). Variation in canopy height can lead to differences in the convective boundary layer which is responsible for transport of energy and gases from plant surfaces to the atmosphere. Smaller convective boundary layers over early successional forest (stand initiation stage), which are characterized by low canopy height, result in a hotter and drier microclimate, especially during the dry season (Fisch et al., 2004). Additionally, early successional forests have greater variability in their physical environments, including water and light conditions, compared to later successional and old growth forests (Culf et al., 1996). Consequently, species acclimated to early-successional stages tend to have higher gas exchange rates, and higher stomatal conductance and photosynthesis (Hölscher et al., 2006; Vargas and Cordero, 2013; Mujawamariya et al., 2018). In contrast, the canopy is more homogeneous and shaded in the intermediate, stem exclusion stage (Chazdon, 2014; Chanthorn et al., 2016, 2017), which constrains gas exchange, especially leaf transpiration (Hardwick et al., 2015).

Environmental gradients during secondary succession can impact the strategies trees use to acquire resources and ultimately lead to differences in tree species richness and composition among different successional forests (Zhang et al., 2012; Chazdon, 2014, Chanthorn et al., 2016, 2017). Previous studies in humid tropical forests have shown that decreasing light penetration during secondary succession results in changes of leaf traits (Lohbeck et al., 2013, 2015). Most trees in early successional forests are fast-growing species and, according to the leaf economic spectrum (Wright et al., 2004), have leaf traits promoting quick returns on investment in nutrients and carbon (i.e., high specific leaf area and nutrient levels, short lifespan and high metabolic rates). In contrast, trees in old growth forests tend to exhibit conservative strategies (Lohbeck et al., 2013, 2015) with high investments in leaf carbon structures (i.e., high leaf dry matter content). However, in dry tropical forests, the light gradient during succession is less pronounced and these forests are often more water-limited and have higher temperatures which may be stronger factors driving changes in plant communities (Lebrija-Trejos et al., 2010, 2011). In general, trees growing in more xeric conditions tend to exhibit leaf traits with slow returns on resource investment, i.e., have conservative strategies (Reich, 2014). Yet, we still know little about how leaf traits vary during secondary succession in dry tropical forests and how variation in leaf traits and microclimate conditions affect leaf gas exchange measurements (i.e., photosynthesis and transpiration) and ultimately, the growth and productivity of these forests.

In this study, we measured leaf-level gas exchange and plant functional traits of the dominant tree species in a seasonal evergreen forest in Thailand. Measurements were made during both the wet (May–October) and dry (November–April) season as well as within forests representing different stages of succession: a young forest (YF, ~4 years), an intermediate forest (IF, ~44 years) and an old-growth forest (OF, >200 years). Specifically, our study addressed the following questions: (Q1) Does leaf-level gas exchange (photosynthesis and stomatal conductance) differ across successional forests and between seasons? (Q2) Does the sensitivity of stomatal conductance to changes in atmospheric demand vary across different stages of forest succession? (Q3) How do different leaf functional traits relate to leaf gas exchange parameters, and do these relationships change depending on forest stage? Results from this study will improve our understanding of the underlying mechanisms governing water and carbon fluxes in different successional forests as well as assessing how these forests may respond to a hotter, drier future.

2. Materials and methods

2.1. Site description

The study was carried out in Khao Yai National Park (KYNP), a seasonal evergreen forest in Nakhon Ratchasima Province, Thailand (14°26′31″ N, 101°22′55″ E, 700–800 m asl; Fig. 1). Based on 1994–2018 data, mean annual temperature and precipitation at the site are about 22.4 °C and 2100 mm, respectively. The wet season usually covers the months from May to October while the dry season ranges from November to April, when monthly precipitation is less than 100 mm (Brockelman et al., 2017). KYNP contains a mosaic of different forest types including old-growth (primary) forests and secondary forests of different ages that have regenerated from old fields within the past 42 years (Jha et al., 2020). In this study, we selected three plots representing different successional stages. The first plot was within the 30-ha Mo Singto forest dynamic plot (Brockelman et al., 2017), a ForestGEO plot in the network of the Centre for Tropical Forest Science (CTFS), Smithsonian Tropical Research Institute. These plots were established using a uniform methodology (Condit, 1998) in which every woody stem $\geq$ 1 cm DBH is identified, mapped, and measured every five years. This plot represented an old-growth stage (hereafter OF), with the age of at least *ca.* 200 years. The OF’s main canopy height was 20–30 m with some emergent trees being higher than 50 m, a leaf area index (LAI) of 5 and stem density of 1112 trees ha^{-1} (Chanthorn et al., 2016; Brockelman et al., 2017). Adjacent to the northern edge of this plot, a 1-ha plot in a secondary forest was established in 2003, using the same CTFS methods. This plot (hereafter IF) was in an intermediate successional stage at about 44 years of age and classified as stem exclusion stage. The forest canopy of IF was more homogenous and denser compared to that of OF and had a mean canopy height of 25 m, an LAI of 6, and stem density of 2052 trees ha^{-1} (Chanthorn et al., 2016). Approximately 3 km away from the OF plot, we established a 2-ha plot in a 4-year-old, early successional forest (hereafter YF). Its mean canopy height was 15 m and stem density of 1226 trees ha^{-1}. Despite the lack of LAI data, the YF canopy was distinctly sparse compared to the other stages based on visual observation. The IF and YF were classified as “stem exclusion” and “stand initiation” stages, respectively (Chazdon, 2014; Chanthorn et al., 2016, 2017). The soil type of these forests was gray, brown ultisol, but the soils under the IF and YF were degraded by

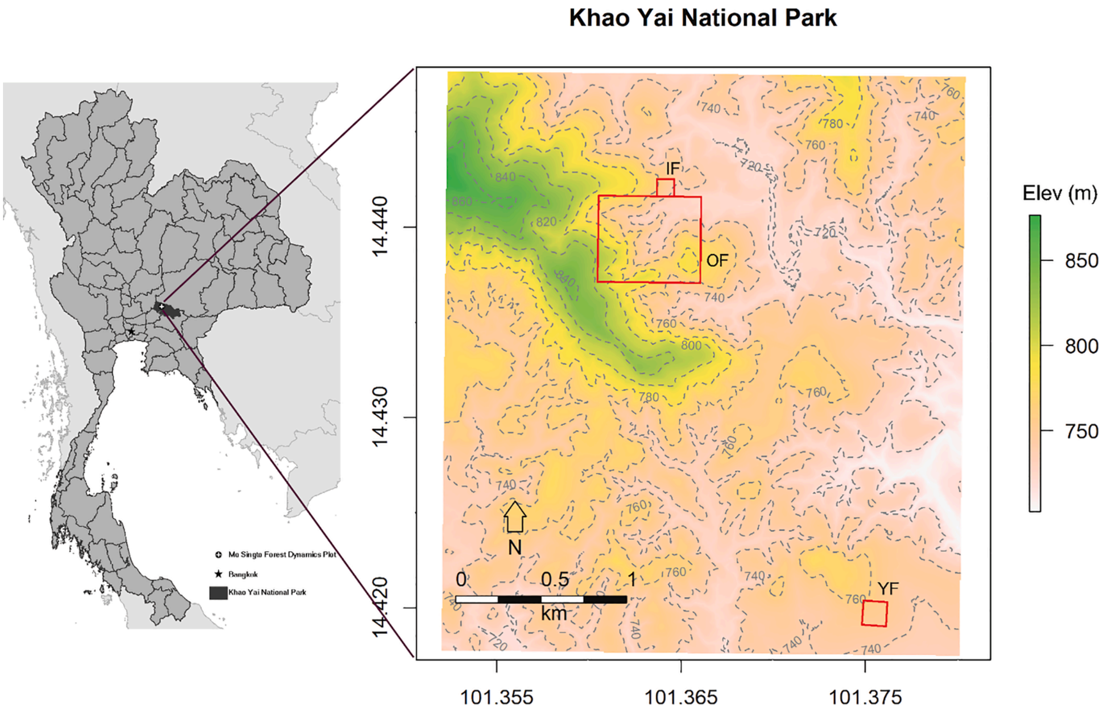

Fig. 1. Study sites include a young (YF), an intermediate (IF) and an old growth (OF) forest in Khao Yai National Park, Thailand.

shifting agriculture and burning prior to regeneration (Chanthorn et al., 2016, 2017).

2.2. Plant materials and measurements

In each plot, we selected five dominant tree species, based on basal area ranking within the site. The selection resulted in 11 species in total with three species occurring in more than one forest stage: *Syzygium nervosum* in IF and YF, *Schima wallichii* in OF and IF, and *Symplocos cochinchinensis* in all stages. Table 1 summarizes the selected dominant species in each study site.

For each species, five trees of similar stem size (diameter at breast height averaged 13.83 ± 2.74 cm (standard deviation); Table S1 in Supplementary Information) were randomly selected for gas exchange measurements and leaf sample collection. For each tree, we randomly chose three mature and fully expanded leaves with good exposure to sunlight from the lower and outside branches (Kröber et al., 2015). For sampling in the intermediate and old-growth forests, we particularly selected leaves that were always present in light gaps within each canopy to ensure that the leaves received full or substantial sunlight (Fan et al., 2011; Markesteijn et al., 2011; Zhu et al., 2013). Since the canopy could not be accessed directly due to the unavailability of towers or canopy cranes, we had to perform the measurements on cut branches containing the sun-exposed leaves with the stems submerged in a container filled with water. Prior to gas exchange measurements, the stems of individual branches were recut underwater to allow the restoration of the xylem water column (Dang et al., 1997). Within 5 min after re-cutting, we placed a leaf in the cuvette for gas exchange measurement to minimize excision-induced effects (Santiago and Mulkey, 2003). Then, we waited for at least 2–3 min to allow the leaf to reach small changes in gas exchange over time before logging the data after observing stable gas exchange parameters. Leaf gas exchange measurements were made using a portable photosynthesis system (TARGAS-1, PP Systems, Amesbury, MA, USA). All leaves covered the entire window area of the cuvette which was equal to 4.5 cm^2. Area-based photosynthetic rate (A_{area}; μmol m^{-2} s^{-1}) and stomatal conductance (g_s; mmol m^{-2} s^{-1}) were recorded for each leaf and reported per unit area. All measurements were conducted between 0900 and 1600 h (Marenco et al., 2001). We realized that the measurement period was longer than that often used for gas exchange measurement to avoid stomatal closure which is usually 1–2 h before and after midday (Brodribb and Holbrook, 2004; Bianco and Avellone, 2014; Urban et al., 2014). However, because of logistical issues, we utilized sunny conditions between the periods for gas exchange measurements. Nevertheless, we compared both A_{area} and g_s values that were recorded after 1400 h with those recorded during midday (1000–1400 h) on the same day and found no statistical differences (Fig. S1; $p \geq 0.064$). The flow rate was set to 250 ml min^{-1} (TARGAS-1 Portable Photosynthesis System Operation Manual Version 1.04 2018). Photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}) inside the cuvette was set to 1700 μmol m^{-2} s^{-1}, which corresponded to the light saturation point (data not shown; Hölscher et al., 2006; Zhu et al., 2013). Temperature, relative humidity and CO_2 concentration were not controlled and thus tracking ambient conditions. Because no previous publications reporting gas exchange measurements from this model of portable photosynthesis system were found, we compared our measured values to others made in tropical forests (Table S2) by plotting photosynthesis against stomatal conductance (Fig. S2). Although our values are mostly concentrated in the low ranges of photosynthesis and stomatal conductance, they fall within the ranges of values measured by other techniques. We realized that this comparison may not fully justify our measurements, but our main goal was to study the variations among forest stages rather than attempting to quantify absolute gas exchange rates.

Table 1
Dominant tree species selected for measurements in each forest stage in Khao Yai National Park, Thailand.

Old growth (OF)	Intermediate (IF)	Young (YF)
Dipterocarpus gracilis	*Syzygium nervosum*	*Adinandra integerrima*
Ilex chevalieri	*Eurya acuminata*	*Cratoxylum cochinchinensis*
Schima wallichii	*Machilus gamblei*	*Syzygium nervosum*
Sloanea sigun	*Schima wallichii*	*Syzygium antisepticum*
Symplocos cochinchinensis	*Symplocos cochinchinensis*	*Symplocos cochinchinensis*

Leaf-to-air vapor pressure deficit (VPD; kPa) was recorded for each measurement and used in the sensitivity analysis. Leaf-level gas exchange measurements were performed in both the dry (March 2019, total monthly precipitation = 0.8 mm) and the wet (July 2019, total monthly precipitation = 141.7 mm) seasons. During the wet season campaign, we also collected the leaves on which gas exchange measurements were made to measure leaf functional traits. Leaf functional traits used in this study included leaf mass per area (LMA; g m^{-2}), area-based nitrogen (N; g cm^{-2}) and phosphorus (P; g cm^{-2}) concentration, and chlorophyll concentration (Chl; μg cm^{-2}). LMA was calculated as the ratio of leaf dry mass and leaf area (Poorter et al., 2009), measured by ImageJ (Schneider et al., 2012). For chemical analyses of total N and P concentrations, three leaves from each tree were pooled to obtain enough samples (at least 0.1 g) for laboratory analyses. Total N was determined using the Kjeldahl method (Kammerer et al., 1967) and the colorimetric method was used to determine total P (Gales et al., 1966). Chlorophyll concentration was estimated from SPAD values (range 34.3–75.8) which were measured using the SPAD-502 chlorophyll meter (Konica Minolta, Tokyo, Japan). We converted SPAD into Chl using the relationship derived from 13 Neotropical species ($Chl = \frac{117.1 \times SPAD}{148.84 - SPAD}$, $r^2 = 0.89$, SPAD value ≤ 80; Coste et al., 2010).

2.3. Statistical analyses

To test for significant differences in A_{area} and g_s among forest stages and seasons (Q1), we used a General Linear Mixed Model with forest stage and season as fixed factors and species as a random factor. A Tukey's test was applied for post hoc analysis. We conducted regression analyses using exponential decay and logarithmic functions to analyze the sensitivity of g_s to VPD. To compare the sensitivity across forest stages (Q2), we performed the analysis with pooled data from all species within each stage and then analyze the data from species that existed in multiple stages (i.e., *Syzygium nervosum* (IF, YF), *Schima wallichii* (OF, IF) and *Symplocos cochinchinensis* (all stages)). We applied an *F*-test to compare the regression curves among stages. In these analyses, the sample size was 15 per species, resulting in 75 samples for each stage. We performed a one-way Analysis of Variance (ANOVA) to compare leaf traits, which were only measured in the wet season, across forest stages. We did regression analysis to evaluate the relationships between A_{area} and g_s and the leaf traits and used an Analysis of Covariance (ANCOVA) to assess variations of significant relationships across forest stages. All analyses of comparisons were done in SPSS (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY, USA) and regression analyses were performed in SigmaPlot (version 12.0, Systat Software, Inc., San Jose, CA, USA). In all statistical analyses, we used the significance level of 0.01.

3. Results

3.1. Does leaf-level gas exchange differ across successional forests and between seasons?

In general, species in all forest stages had higher A_{area} and g_s in the wet than in the dry season ($p \leq 0.0001$). When combining data from both the wet and dry season, there was no significant difference in A_{area} and g_s among successional forest stages ($p \geq 0.184$). However, when comparing dry-season measurements, there were significant differences in A_{area} and g_s among the forest stages ($p \leq 0.0006$; Fig. 2 brown bars), whereas there were no differences in the wet season ($p \geq 0.03$; Fig. 2 yellow bars). In the dry season, trees in OF and YF had comparable A_{area} and g_s but higher values than trees in IF (Fig. 2).

For *Schima wallichii* and *Symplocos cochinchinensis*, tree species found in multiple sites, there was no significant difference in A_{area} and g_s among forest stages during the wet season ($p \geq 0.659$; Fig. 3A, B, D, E; yellow bars). However, during the dry season these two species had significantly higher gas exchange rates in OF compared to the younger sites ($p \leq 0.004$, 3A, B, D, E; brown bars). For *Syzygium nervosum,* which was found in the intermediate and early successional forests, A_{area} and g_s were similar across stages regardless of season (Fig. 3C, F; $p \geq 0.631$).

3.2. Does the sensitivity of stomatal conductance to changes in atmospheric demand vary across forest succession?

We tested the relationship between g_s and VPD in all tree species using data from both seasons. Various equations have been proposed to explain such relationship, including linear (McCaughey and Iacobelli, 1994), exponential (Dye and Olbrich, 1993) and logarithmic (Oren et al., 1999). We employed these equations in our regression analysis for each species in each stage and found significant results with exponential ($y = a \times exp(-bx) + c$) and logarithmic ($y = b \times \ln(x) + c$) forms in 10 out of 11 species, which is consistent with previous studies of various tree species (Oren et al., 1999; Mielke et al., 2005; Motzer et al., 2005). No equation could explain the relationship in *Machilus gamblei*. First, we examined the relationship between g_s

and VPD in all dominant species within each site. We found that g_s exponentially decreased with VPD in all forests ($p < 0.0001$, $r^2 \geq 0.66$) with no difference among successional stages (Fig. 4A, $F2_{,447} = 1.25$, $p = 0.287$). Next, we further considered the species that occurred in multiple forest stages. A logarithmic decline was the best fit between g_s and VPD for *Syzygium antisepticum*, whereas for *Schima wallichii* and *Symplocos cochinchinensis,* an exponentially decaying function was the best fit (Fig. 4B-D; $p \leq 0.01$). When compared among sites, the relationships between g_s and VPD for these species were similar across forest stages ($p \geq 0.136$). Summary statistics for regression and comparative analyses are shown in Table S3.

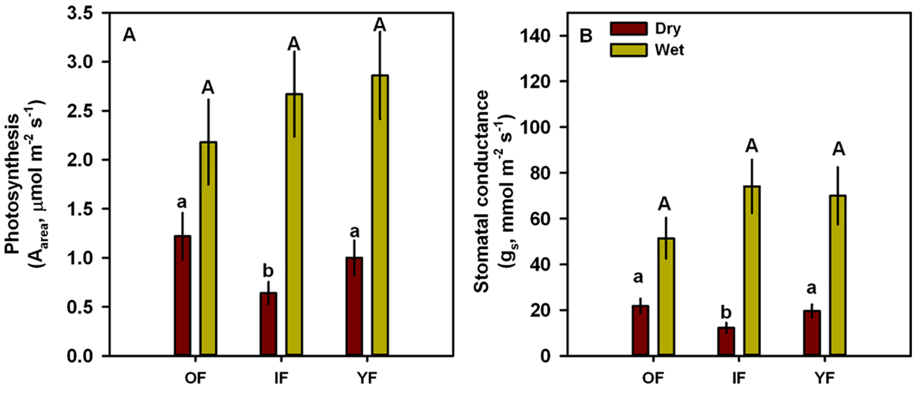

Fig. 2. Overall mean (±1 SE) leaf-level (A) photosynthesis (A_{area}; μmol m^{-2} s^{-1}) and (B) stomatal conductance (g_s; mmol m^{-2} s^{-1}) in young (YF), intermediate (IF) and old-growth forests (OF) within Khao Yai National Park, Thailand. Measurements were taken in the dry (brown bars) and the wet (yellow bars) season. Different lowercase (uppercase) letters indicate significant difference among forest stages during the dry (wet) season. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

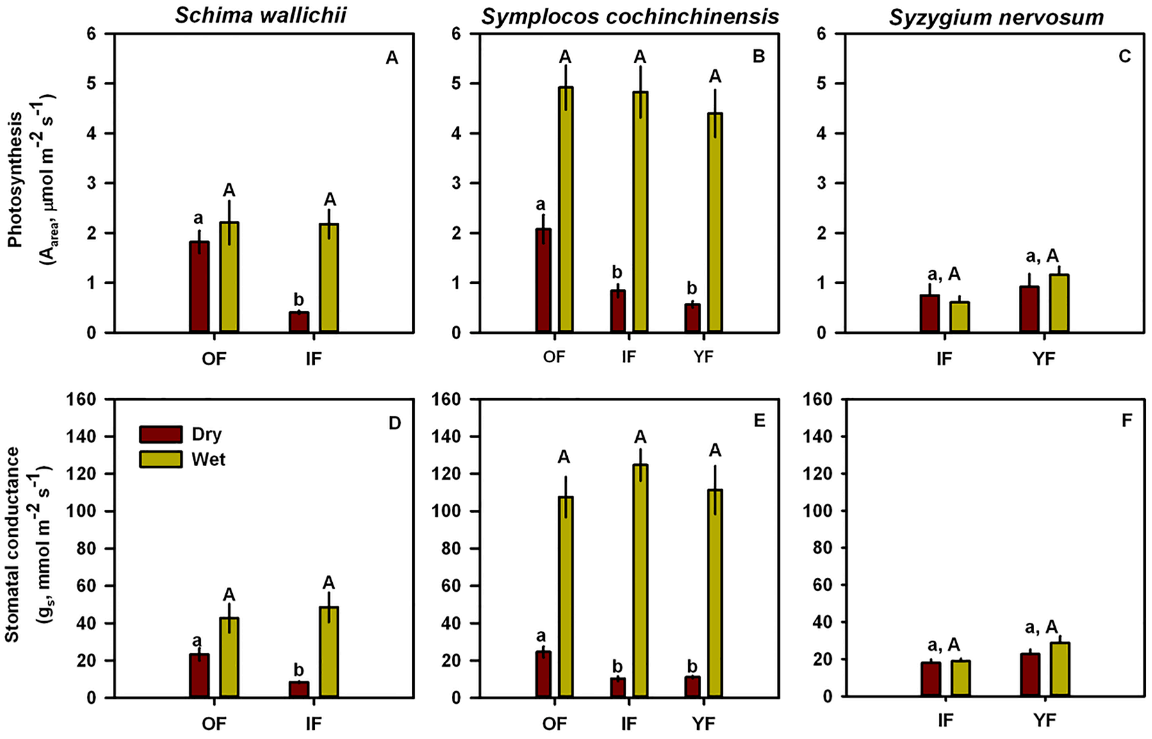

Fig. 3. Mean (±1 SE) leaf-level (A–C) photosynthesis (A_{area}; μmol m^{-2} s^{-1}) and (D–F) stomatal conductance (g_s; mmol m^{-2} s^{-1}) of species that occurred in multiple forest stages in Khao Yai National Park. Measurements were made during the dry (brown bars) and wet (yellow bars) season. Different lowercase (uppercase) letters indicate significant difference among forest stages during the dry (wet) season. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

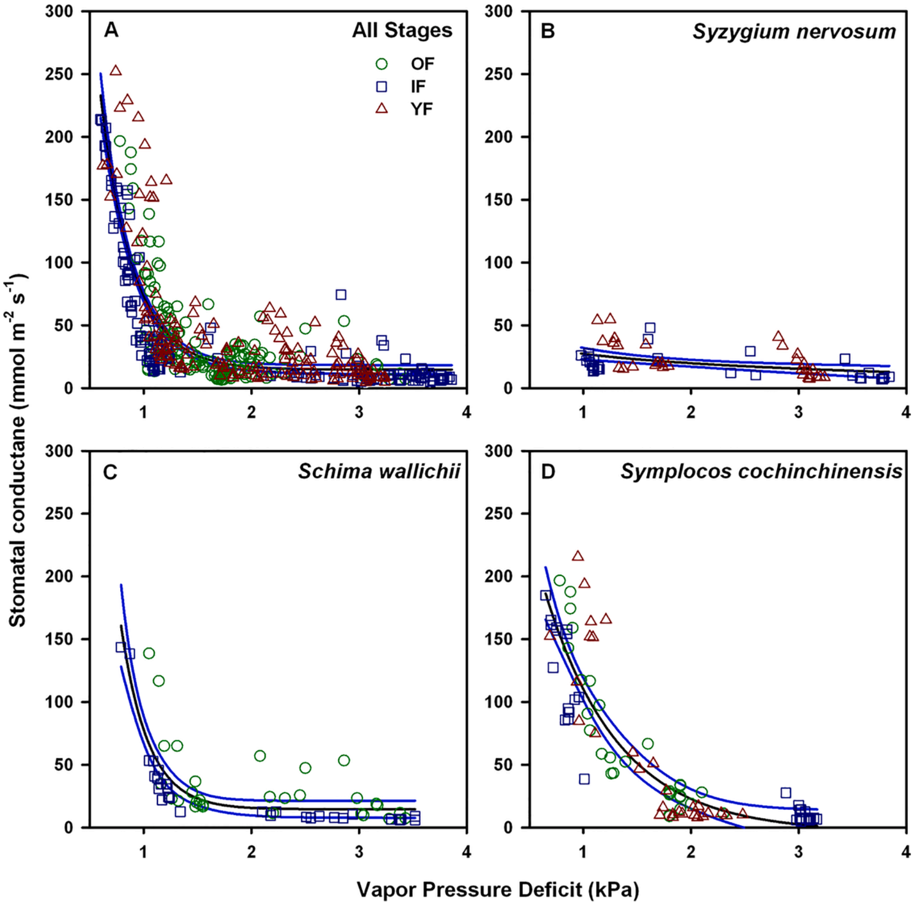

Fig. 4. Relationships between leaf-level stomatal conductance (g_s; mmol m^{-2} s^{-1}) and leaf-to-air vapor pressure deficit (VPD; kPa) for (A) all forest stages (B) *Syzygium nervosum*, (C) *Schima wallichii*, and (D) *Symplocos cochinchinensis*. Measurements were made in an old-growth forest (OF, green circles), an intermediate forest (IF, blue squares), and a young forest (YF, red triangles). Black solid lines show the best fits with 95% confidence intervals (blue lines) for pooled data after finding no difference among different stages. Regression statistics are presented in Table S3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. How do different leaf functional traits relate to leaf gas exchange parameters and do these relationships change depending on forest stage?

For this research question, we focused on the wet season only due to the availability of data. Across the three forest stages, average LMA, P and N values were higher in YF compared to the two older forests (Fig. 5A–C; $p < 0.0001$). In contrast, there was no significant difference in Chl among the successional forests (Fig. 5D; $p = 0.067$). Next, we explored the relationships between gas exchange parameters and the leaf traits. Of all considered traits, only LMA and N were significantly related with A_{area} and g_s in IF and OF ($p \leq 0.01$). We further compared the relationships between both gas exchange parameters and LMA and N in OF and IF and found no difference between the stages ($p \geq 0.024$). Fig. 6 shows the significant relationships for the pooled data from both OF and IF (black solid lines; regression statistics are listed in Table S3).

4. Discussion

Seasonal variations in both gas exchange parameters were observed at the forest level and at species level. Generally, both A_{area} and g_s were higher in the wet than in the dry season. For all studied species, lower A_{area} and g_s in the dry season corresponded to higher VPD (Table S1) which is consistent with plants closing their stomata in response to increasing atmospheric drought (Cunningham, 2004; Chen et al., 2016). These results suggested that productivity of these successional stages may differ, especially during the dry season when both atmospheric and soil humidity are usually limiting (Harper et al., 2013). However, we found no significant difference in the gas exchange parameters across our successional forests during the wet season. Instead, a significant decrease in the parameters was observed in the intermediate forest (IF) with the highest stem density (2052 trees ha^{-1} vs. 1112 trees ha^{-1} and 1226 trees ha^{-1} in OF and YF, respectively), in the dry season. Such high density induces shading in the canopy with lower variability in LAI (Chazdon, 2014; Chanthorn et al., 2016, 2017) and may limit the gas exchange as previously observed in shade-acclimated trees (Chazdon et al., 1996; Gerardin et al., 2018; Yang et al., 2019). Based on observations, the indifference of gas exchange parameters across stages in the wet season may result from the higher canopy leaves in OF and YF compared to those in the dry season. In other words, the shaded canopy in IF maintained throughout seasons while the canopy in OF and YF varied seasonally, with the greatest difference between seasons in YF. Further measurements of canopy leaf areas should be performed to confirm this point. Overall, our results suggest that the gas exchange rates did not differ across forest succession but were affected by different microclimates induced by different canopy density. Nevertheless, previous reports on gas exchange measurements in various tropical tree species have shown inconclusive evidence on the effects of forest succession on leaf gas exchange rates (Hogan et al., 1995, Coste et al., 2005; Hölscher et al., 2006).

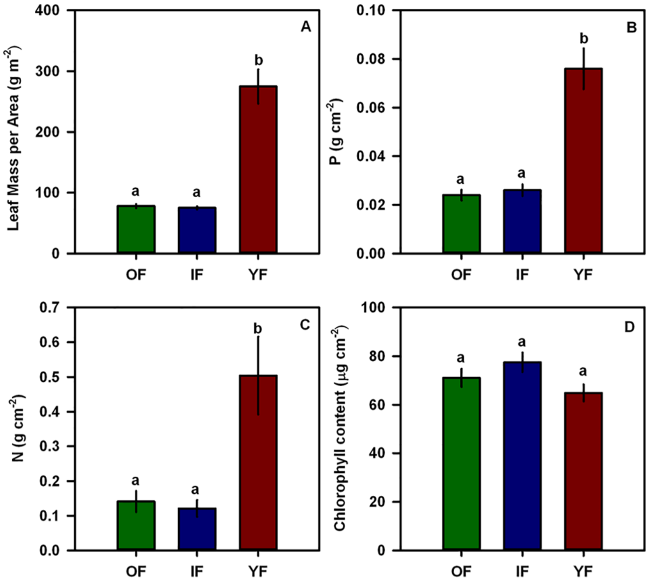

Fig. 5. Mean (±SE) (A) leaf mass per area (LMA; g m^{-2}), (B) phosphorus concentration (P; g cm^{-2}), (C) total nitrogen concentration (N; g cm^{-2}) and (D) chlorophyll concentration (Chl; µg cm^{-2}) among the old-growth (OF; green bars), intermediate (IF, blue bars), and young (YF, red bars) forest stages. Lower case letters indicate significant differences among forest stages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Next, we examined species that grew in multiple successional stages to further investigate the effect of forest succession on gas exchange rates. There were no differences in gas exchange for *Syzygium nervosum* among the forest stages regardless of season. In contrast, *Schima wallichii* and *Symplocos cochinchinensis* exhibited higher gas exchange rates in the old growth forest compared to the two young successional forests during the dry season. The lack of difference in the gas exchange rates of *Syzygium nervosum* may be supported by similar stomatal density ($p = 0.22$, data not shown) across seasons, showing unchanged number of sites available for gas exchange per unit leaf area (Wu et al., 2018). Compared to the rates in the primary forest, lower rates of *Schima wallichii* and *Symplocos cochinchinensis* in the intermediate forest agreed with site-level results of limited gas exchange under shaded canopy while lower rates in the young forest may be attributed to its drier soil (average soil moisture = 23.85 ± 5.34% in YF vs. 44.54 ± 8.46% and 38.11 ± 6.73% in OF and IF, respectively). Nevertheless, further investigations on physiological responses such as tree hydraulic conductivity and architecture should be performed to confirm these results.

Sensitivity of g_s to VPD provides insight into how trees respond to increasing atmospheric drought (i.e., higher temperature combined with low humidity). Trees with greater sensitivity of g_s to VPD, closing stomata more rapidly when air dries, acclimate better to increasing atmospheric drought compared to those with lower sensitivity. Nevertheless, trees in our successional forests did not show distinct sensitivity of g_s to VPD when considering both the forest level and species level. Most studies investigating the sensitivity of stomatal conductance to VPD in tree species found differences in the relationships across various factors besides species, such as crown height and wood anatomy (Woodruff et al., 2009; Tsuji et al., 2020). However, our data showed similar sensitivities of stomatal conductance to changing vapor pressure deficit across our successional forests, suggesting similar responses of the dominant trees to varying atmospheric humidity throughout the year. This finding may support the observed similarity in the gas exchange rates between the two contrasting forest stages (OF and YF), despite the widely reported results that early successional species usually have greater maximum gas change rates than late-successional ones (Hölscher et al., 2006; Zhu et al., 2013). Regarding the response of stomatal conductance to atmospheric conditions, we further examined the slope parameter in the unified stomatal optimization model (USO; Medlyn et al., 2011; Fig. S3, S4) which represents a measure of intrinsic plant water-use efficiency. Wu et al. (2019) showed that the slope parameter significantly varied with leaf mass per area in tropical forests. However, we tested this finding with our data and found an insignificant result ($p = 0.998$, Fig. S5), suggesting similar intrinsic water-use efficiency among the dominant trees regardless of LMA. Furthermore, we found no difference in slope parameters across successional forests in the case of species existing in multiple sites (Fig. S4, $p \geq 0.66$). Nevertheless, further studies on canopy fluxes should be conducted to confirm such findings because results from leaf-level measurements can obscure those from the canopy level (Tor-ngern et al., 2015).

While similar chlorophyll concentration was observed across all forest stages, LMA, leaf N and P were significantly higher in YF compared to other forest stages. Previous studies indicated that nutrient-

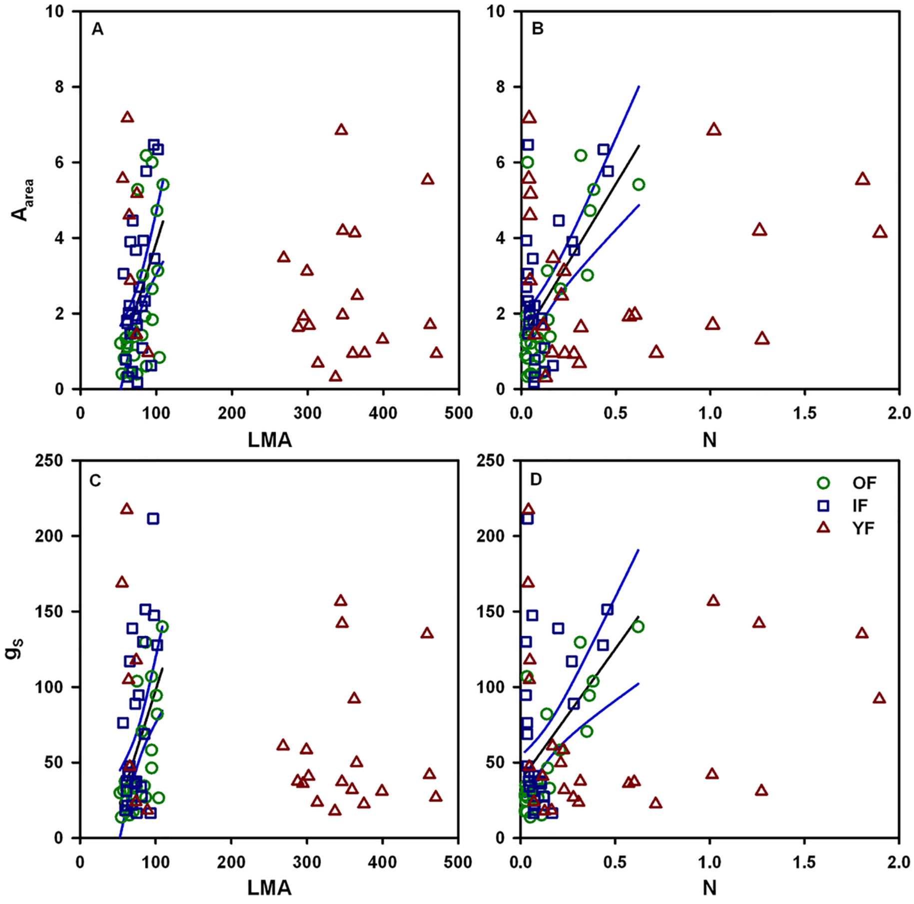

Fig. 6. Linear relationships between photosynthesis (A_{area}; μmol m^{-2} s^{-1}) and stomatal conductance (g_s; mmol m^{-2} s^{-1}) and leaf mass per area (LMA; g m^{-2}) and total nitrogen concentration (N; g cm^{-2}). Measurements were made in an old-growth forest (OF, green circles), an intermediate forest (IF, blue squares), and a young forest (YF, red triangles). Black solid lines show the best fits with 95% confidence intervals (blue lines) for pooled data of OF and IF after finding no difference among between the stages. Note that no significant relationships were found in YF. Regression statistics are presented in Table S3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

poor soils may induce larger allocation of leaf nitrogen into cell walls, increasing LMA but decreasing maximum photosynthesis (Takashima et al., 2004; Hikada and Kitayama, 2009). However, we found no significant difference in soil N and P among the forest stages ($p \geq 0.21$; data not shown), suggesting that the soil condition in YF was not nutrient poor compared to the others. Other studies have shown that species with high LMA usually occur in areas with low rainfall and high light and temperature (Niinemets, 2001; Villar and Merino, 2001; Lamont et al., 2002; Wright et al., 2004). This supports our result because trees in YF experience more xeric conditions and higher radiation due to their sparse canopy cover. Higher LMA may be associated with greater accumulation of nutrients in leaves (Kimura et al., 1998) as observed in our data, allowing high photosynthesis under adverse growing conditions, such as low soil moisture as often observed in sparse canopy forests with low leaf area indices (Von Arx et al., 2013). Nevertheless, our results did not show such high photosynthesis in YF which may be limited by the low soil water availability of this site compared to the others.

To gain insight into which leaf traits were linked to tree growth, we explored the relationships between leaf functional traits and gas exchange parameters (A_{area} and g_s) within the different successional forests. Maximum net photosynthesis is usually affected by various leaf traits, such as LMA (Field and Mooney, 1986; Reich et al., 1999; Poorter et al., 2009), and leaf nutrient concentrations (Evans, 1989; Reich et al., 1999; Wright et al., 2004). Several studies have reported significantly positive correlations between maximum photosynthesis rate and LMA (Reich et al., 1997; Wright et al., 2004; Quero et al., 2006), leaf N (Reich et al., 1994; Ellsworth and Reich, 1996; Kull and Niinemets, 1998; Gulías et al., 2003; Hölscher et al., 2006) and P (Hölscher et al., 2006; Zhang et al., 2018). Our results showed that LMA and leaf N were significantly related to the gas exchange rates in IF and OF, although we found no relationships between the rates and leaf P. Comparing the linear dependence of A_{area} and g_s on LMA and N between OF and IF, we found no differences between the trends, which is in contrast to a recent study that showed a lower slope between A_{area} and N in climax species (Zhang et al., 2018). However, the study argued that such difference was relevant to different soil phosphorus concentrations between successional stages, which was not the case for our sites. Interestingly, we observed no significant relationships between maximum gas exchange parameters and any leaf traits in YF. High variations of species-specific data may contribute to the insignificant relationship as seen in clearly separated clusters of data, corresponding to different species within YF. This finding suggests that trees in the young forest (YF) may be more active in resource acquisition, as shown by the large variation in leaf nutrients, and in morphological acclimation through the increased LMA for greater nutrient accumulation. Such acclimation should facilitate high gas exchange rates; however, the different soil water availability may have limited the rates in the young forest. Nevertheless, findings from this study warrant further investigations from different perspectives, including other physiological parameters, such as tree hydraulics and canopy-level measurements, to arrive at firm conclusions.

5. Conclusions

Varying environmental conditions among different successional forests present a challenge for estimating forest water use and productivity in tropical forests. Such heterogeneity in environmental conditions can strongly influence water and carbon exchanges between the forest canopy and the atmosphere. Our results show that, in general, gas exchange rates between the tree canopy and the atmosphere did not vary across forest stages yet differed among them in the dry season, as a result of changes in canopy density during secondary succession. The similar rates were further supported by similar sensitivity of stomatal conductance to changing atmospheric humidity across forest stages. Our data also suggest that the young forest was highly active in acquiring resources, but such high resource acquisition did not allow high gas exchange rates because of limiting soil water availability. These findings highlight the potential effects of inherent canopy characteristics of successional forests on water and carbon exchanges between trees and the atmosphere. Nevertheless, further studies on canopy level are needed to confirm such findings.

CRediT authorship contribution statement

Pantana Tor-ngern: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Chidsanuphong Chart-asa:** Formal analysis. **Wirong Chanthorn:** Writing - review & editing. **Chadtip Rodtassana:** Writing - review & editing. **Siriphong Yampum:** Project administration. **Weerapong Unawong:** Visualization, Project administration. **Anuttara Nathalang:** Project administration. **Warren Brockelman:** Writing - review & editing. **Kanchit Srinoppawan:** Resources. **Yajun Chen:** Writing - review & editing. **Niles J. Hasselquist:** Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119101.

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