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Vertical changes in leaf ecophysiological traits in diverse tropical rainforest tree species in Lambir Hills National Park in Sarawak

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Abstract Information about vertical changes in morphological and physiological leaf traits with forest height are essential for quantifying carbon and water fluxes of forest ecosystems. We examined changes in leaf traits with forest height in diverse tree species and their role in environmental acclimation in a mixed dipterocarp forest in Lambir Hills National Park in Sarawak that does not experience dry spells. The mean canopy height in the forest was about 30–40 m; some emergent trees reached 50 m in height. The upper canopy layer is dominated by many dipterocarp trees, such as *Dryobalanops* and *Shorea* spp. Vertical changes in the leaf traits [e.g., maximum photosynthetic rate (A_{max}), stomatal conductance (gs), dark respiration rate (Rd), carbon isotope ratio (δ^{13}C), nitrogen (N) content, and leaf mass per area (LMA)] from understory to emergent trees were investigated in 104 species in 29 families. We used an 85-m canopy crane to conduct all physiological measurements. We found that many leaf area-based gas exchange traits (e.g., $A_{\mathrm{max\text{-}area}}$, Rd, gs), N, δ^{13}C, and LMA increased linearly with tree height, whereas leaf mass-based physiological traits (e.g., $A_{\mathrm{max\text{-}mass}}$) only increased slightly. These patterns differed from those of other biomes such as temperate and tropical dry forests, where trees usually show decreased photosynthetic capacity (e.g., $A_{\mathrm{max\text{-}area}}$, $A_{\mathrm{max\text{-}mass}}$) with height. Increases in photosynthetic capacity, LMA, and δ^{13}C are favored under bright and dry upper canopy conditions with higher photosynthetic productivity and drought tolerance, whereas lower Rd and LMA may improve shade tolerance in lower canopy trees. The rapid recovery of leaf midday water potential to theoretical gravity potential during the night supports the idea that the majority of trees do not suffer from strong drought stress. Overall, leaf area-based photosynthetic traits were associated with tree height and the degree of leaf drought stress, even in diverse tropical rain forest trees.

Keywords Hydraulic limitation, Leaf water potential, LMA, Respiration, Sarawak

Introduction

Forest microenvironments, which strongly affect leaf morphophysiological traits, differ significantly from the understory to canopy (Kumagai et al. 2001; Lloyd et al. 2010; Ichie et al. 2016). Leaves that develop in the upper canopy layer in the forest are exposed to higher irradiances, air temperatures, and wind speeds, and must cope with microclimatic conditions that potentially lead to desiccation, while leaves from the lower stratum canopy experience milder conditions, such as lower irradiance, constant temperature, and higher humidity (Kumagai et al. 2001). In addition, the increased path length that water must travel to reach transpiring leaves from soil and increased gravitational potential can increase drought stress in the upper canopy (Koch et al. 2004; Woodruff et al. 2004; Ryan et al. 2006). Leaves acclimate to this vertical environmental gradient by changing their morphological and biochemical properties. Leaf nitrogen (N) and leaf mass per area (LMA) are the primary driving factors for leaf photosynthetic acclimation and drought tolerance, respectively (Niinemets 2002). Traditionally, this acclimation was considered o be explainable by sun- versus shade-leaf adaptation: leaves under canopy conditions with high light intensity show higher photosynthetic capacity and drought tolerance due to the high allocation of leaf N and larger LMA, whereas leaves under lower light conditions show reduced LMA and N with decreased respiration rates (*Rd* values) to maintain low light compensation points (Larcher 2003).

However, previous studies on leaf photosynthesis, morphology, and biochemistry across a wide range of tree heights (which have mainly been performed in tall temperate trees) revealed that leaf photosynthetic capacity and N content are usually lower at the upper canopy, while LMA increases linearly with tree height (Niinemets 2002; Koch et al. 2004; Ryan et al. 2006; Steppe et al. 2011). This reduction in leaf photosynthesis and increase in LMA is thought to be a response to increased leaf drought stress (i.e., more negative leaf water potentials) imposed by increased hydraulic constraints, and is affected by leaf morphophysiological traits rather than changes in the light intensity with height (Koch et al. 2004; Burgess and Dawson 2007). In addition to temperate trees, trees growing on semiarid land and in tropical dry forests, which experience severe seasonal drought and/or cold stresses, showed decreasing photosynthetic capacity with increasing tree height (Kenzo et al. 2012; Su et al. 2013). In contrast, trees in a tropical rain forest that do not experience extended dry and cold spells showed an increased capacity with height, even in emergent trees over 50 m tall (Rijkers et al. 2000; Kenzo et al. 2006, 2015; Kosugi et al. 2012). Differences in height-related changes between forest types may reflect the degree of environmental stress such as drought and cold among forest types. These environmental stresses may accelerate the reduction in photosynthetic capacity due to stomatal closure and hydraulic constraints with tree height.

In this study, we explored the effect of tree height on leaf gas exchange properties, LMA, and N to derive a general relationship between these variables for diverse tree species in the tropical rain forest of Borneo, which is located in the wettest area in Southeast Asia (Kume et al. 2011). We examined specimens including more than 100 species ranging from understory trees grown on the dark forest floor to emergent or canopy trees under strong light conditions (Kenzo et al. 2006, 2015).

Materials and methods

Study site and plant materials

Our study was performed at the Crane Plot (4 ha) in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4º20'N, 113º50'E; 150–250 m a.s.l.). The mean height of the canopy in the stand was about 30–40 m, and some emergent trees reached 50 m in height. The annual precipitation at the study site averaged 2600 mm from 2000 to 2009, and the average annual temperature from 2000 to 2009 was 25.8 °C (Kume et al. 2011). We selected 104 species in 59 genera and 28 families for a total of 204 individuals from the understory to emergent trees. All trees were evergreens with different mature tree heights such as emergent, canopy, subcanopy, and understory trees. The measurement points ranged from 0.5 to 53 m above the ground, and we measured a total of 220 points from 204 individuals. Most measurement points were at the top of the crown.

Measurements of light condition, gas exchange and leaf water potential

We measured the relative active photosynthetic photon flux density (PPFD) at different forest heights (about 1–53 m) and the top of the canopy crane (~75 m) using a quantum sensor with ultrasmall memory (MDS-MkV/L; Alec, Kobe, Japan). A portable photosynthesis apparatus (LI-6400; Li-Cor, Lincoln, NE) was used to measure the leaf gas exchange rate. For the maximum photosynthetic rate at light saturation (A_{max}) for all trees, conditions inside the chamber were controlled to maintain leaf temperature at 30 °C, relative humidity at about 60 %, CO_2 concentration of 360 ppm, and saturating levels of active PPFD (800 µmol photon m^{-2} s^{-1} for understory trees and 1700 µmol photon m^{-2} s^{-1} for mid- and top-canopy trees). Light intensity was controlled using an internal light-emitting diode (LED) light source (Li-640B; Li-Cor). We also measured the stomatal conductance and transpiration rate (*T*r) at A_{max}. We measured leaf *Rd* under full darkness at 30°C. Following the gas exchange measurements, leaves were collected to measure N and LMA. Stable carbon isotope composition was also measured for 153 individuals from 92 species. The leaf water potential at predawn (Ψ_{pd}) and midday (Ψ_{mid}) was measured using a pressure chamber (model 1002; PMS Instrument Co., Albany, OR).

Results

Leaf traits and tree height

Both area- and mass-based A_{max} and *Rd* increased significantly with tree height (Fig. 1a-d), although the regression coefficients of mass-based values were lower than those of area-based values. Many seedlings and saplings of canopy trees and understory trees showed a low $A_{\mathrm{max\text{-}area}}$ (about < 5 µmol CO_2 m^{-2} s^{-1}). The leaf A_{max}/Rd ratio decreased slightly with increasing tree height, although the slope of the regression line was nearly zero ($A_{\mathrm{max}}/Rd = -0.05\mathrm{height} + 10.96$, $r^2 = 0.06$, $P < 0.05$, $n = 118$; data not shown). The *gs* and T_{r} increased linearly with tree height (Fig. 1e, 1f), although relatively large variation in the values was observed under the canopy condition. The LMA increased significantly with tree height (Fig. 2a). The N content per unit area (N_{area})

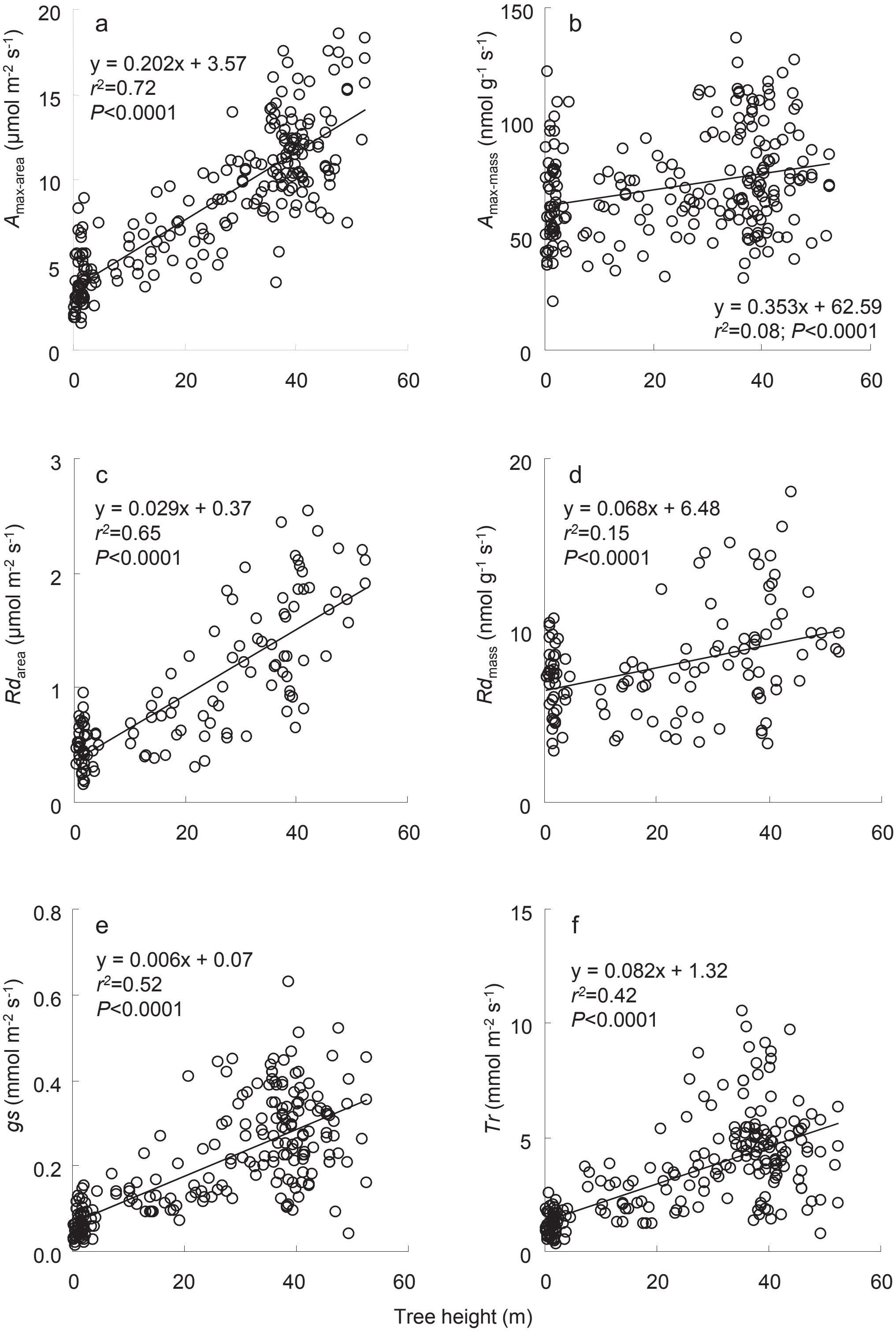

Fig. 1 Relationship between tree height and light-saturated area- and mass-based photosynthetic rate [(a) $A_{\text{max-area}}$ and (b) $A_{\text{max-mass}}$], area- and mass-based dark respiration [(c) R_{darea} (d) and R_{dmass}], maximum stomatal conductance [(e) gs], and maximum transpiration rate [(F) T_{r}]. Values represent the means for each measurement point across all replicate leaves.

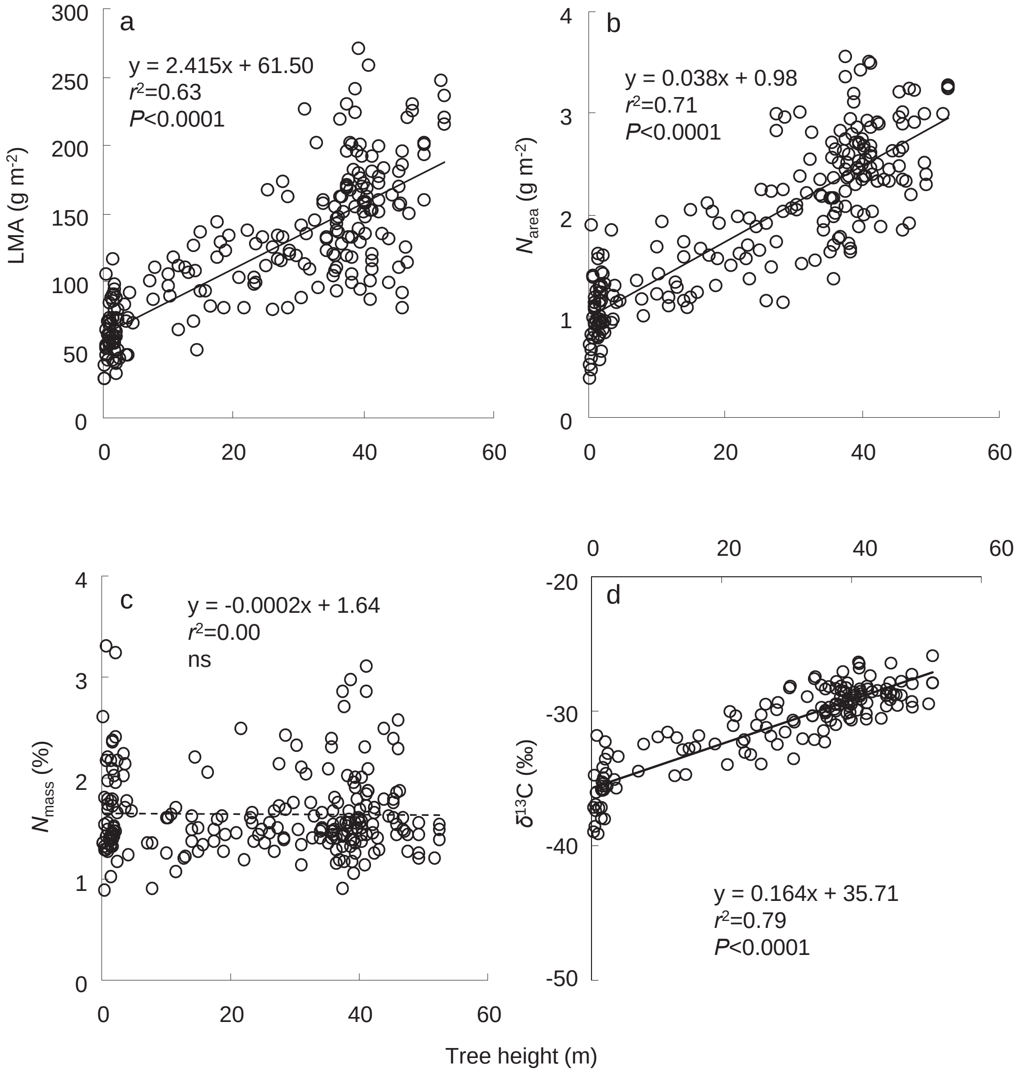

Fig. 2 Changes in leaf mass per area [(a) LMA], leaf area-based nitrogen [(b) N_{area}] content, mass-based nitrogen [(c) N_{mass}] content, and carbon isotope ratio [(d) δ^{13}C] with tree height. Values represent the means of each measurement point across all replicate leaves.

increased linearly with tree height (Fig. 2b), although the N content per unit leaf dry mass did not change with tree height (Fig. 2c). The leaf δ^{13}C also significantly increased with tree height (Fig. 2d).

Photosynthetic rate, LMA, and N content in relation to the light environment

The relationship between leaf area-based photosynthetic rate ($A_{\mathrm{max\text{-}area}}$) and relative photosynthetic photon flux density (RPPFD) was more accurately approximated using a simple allometric function of the form $y = ax^b$ than a linear regression (Fig. 3a). LMA and N_{area} also showed similar patterns as $A_{\mathrm{max\text{-}area}}$ (Fig. 3c, d). In contrast, the leaf mass-based photosynthetic rate did not have a significant relationship with RPPFD (Fig. 3b).

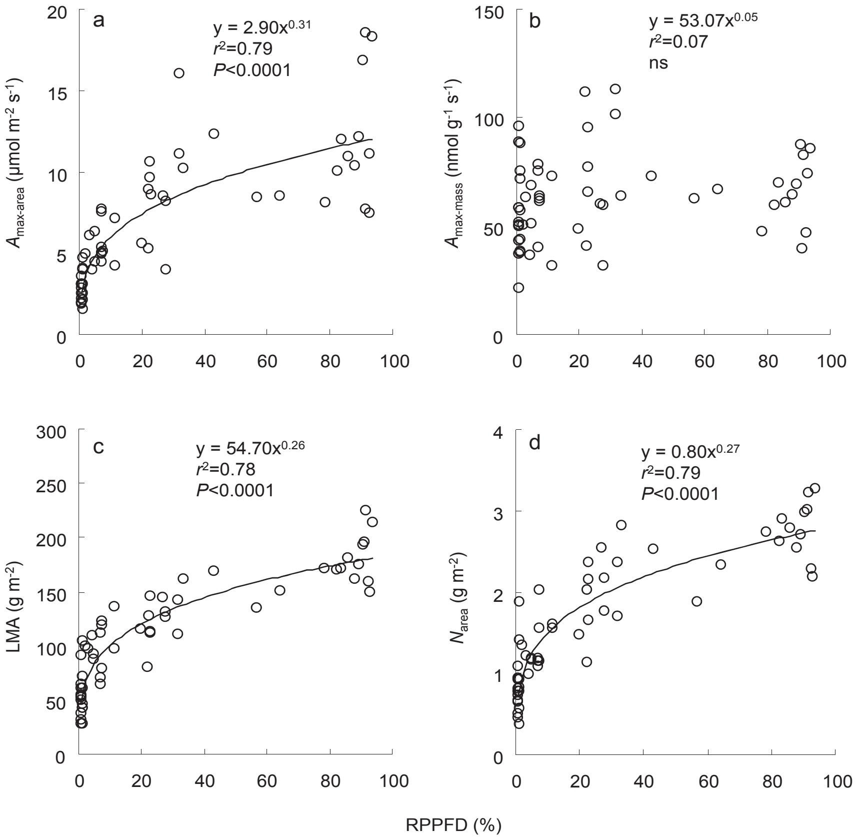

Fig. 3 Changes in leaf area-and mass-based photosynthetic rate [(a) $A_{\text{max-area}}$ and (b) $A_{\text{max-mass}}$], (c) LMA, and (d) leaf area-based nitrogen content along with relative photosynthetic photon flux density (RPPFD). Values represent the means for each measurement point across all replicate leaves.

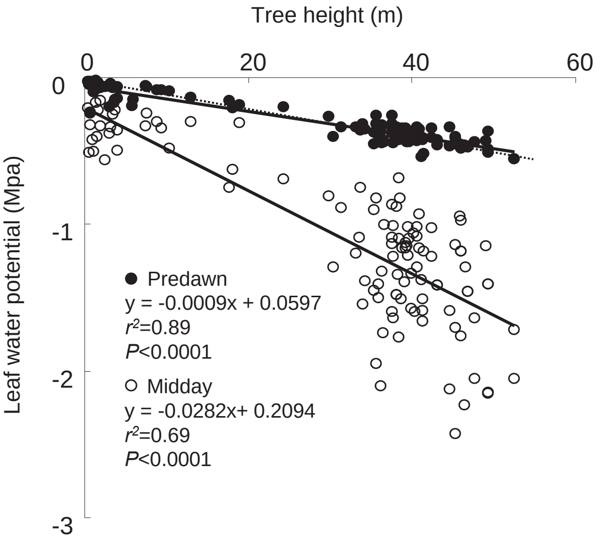

Fig. 4 changes in leaf predawn and midday water potential with tree height. The dotted line represents the theoretical hydrostatic gradient of the leaf predawn potential (–0.0098 MPa m^{-1}). Values represent the means for each measurement point across all replicate leaves.

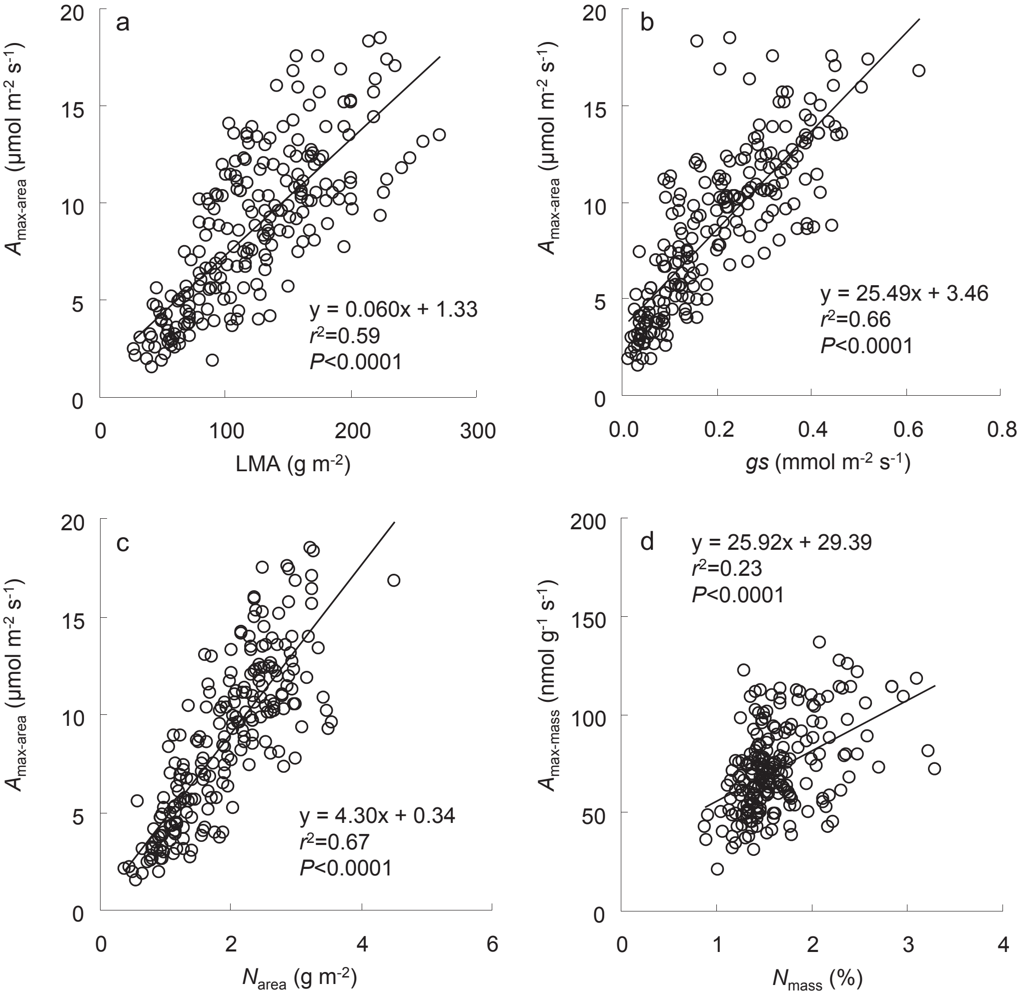

Fig. 5 Relationships of (a) leaf area-based photosynthetic rate with LMA, (b) leaf area-based photosynthetic rate with stomatal conductance, (c) leaf area-based photosynthetic rate with area-based nitrogen content, and (d) mass-based photosynthetic rate with mass-based nitrogen content. Values represent the means for each measurement point across all replicate leaves.

Predawn and midday leaf water potential in relation to tree height

The predawn (Ψ_{pd}) and midday (Ψ_{mid}) leaf water potential decreased linearly with tree height (Fig. 4). The rate of decrease of Ψ_{pd} was similar to the theoretical value associated with the gravitational potential (–0.098 Mpa/10 m). In contrast, midday leaf water potential (Ψ_{mid}) showed a much greater decrease with increasing height than Ψ_{pd} (ANCOVA, $P < 0.05$).

Relationship between A_{max} and leaf characteristics

A significant correlation was found between $A_{max\text{-}area}$ and LMA (Fig. 5a), between $A_{max\text{-}area}$ and gs (Fig. 5b; $r^2 = 0.66$, $P < 0.001$), and between $A_{max\text{-}area}$ and N_{area} (Fig. 5c). In contrast, no significant relationship was detected between $A_{max\text{-}area}$ and N_{mass} ($r^2 = 0.00$, $P > 0.05$; data not shown). $A_{max\text{-}mass}$ and N_{mass} also showed positive relationships, although the regression coefficients were lower than area-based regression coefficients (Fig. 5d).

Discussion

Changes in photosynthetic capacity and respiration rate with tree height

A simple linear increase in area-based photosynthetic capacity ($A_{\text{max-area}}$) with height was observed in tropical rain forest trees, indicating that trees maintained their physiological activity such as photosynthesis and growth through large amounts of seasonal rainfall without cold stress. In contrast, decreases and plateaus in $A_{\text{max-area}}$ with tree height or diameter were usually observed in temperate, semiarid, and dry tropical forests (Thomas 2010; Kenzo et al. 2012; Sendall and Reich 2013; Su et al. 2013). The majority of studies in tropical rain forests showed a significant linear increase in $A_{\text{max-area}}$ with tree height, including for upper canopy trees over 40 m tall (Rijkers et al. 2000; Kenzo et al. 2006). Even the $A_{\text{max-area}}$ of saplings of canopy trees grown in a gap with direct sunlight (canopy openness of 18.2 ± 1.0 %) was ~50 % lower than that of canopy and emergent trees. In addition, the mass-based photosynthetic rate ($A_{\text{max-mass}}$) also increased weakly with tree height. This is not consistent with previous studies on tall canopy trees in other biomes, which showed a significant reduction with increasing tree height (Koch et al. 2004; Steppe et al. 2011; Kenzo et al. 2012). The causes of the difference remain unclear, but the relatively low soil moisture deficits due to year-round rainfall in tropical rain forests (rainfall exceeded 100 mm/month) compared with temperate and tropical dry forests (Kume et al. 2011) may explain the increase of the photosynthetic capacity in the upper canopy. In fact, the nearly zero predawn water potential in understory trees implies that substantial soil water exists in this forest. Modeling approachs also support the idea that trees maintaining high photosynthesis with less stomatal closure (anisohydric plants) are more successful under the moist conditions in the Bornean tropical rain forest (where little risk of hydraulic failure exists) than trees that regulate transpiration through sensitive stomatal closure to maintain a constant midday leaf water potential (isohydric plants, Kumagai and Porporato 2012). On the other hand, the relatively large variation of leaf midday water potential among canopy trees (tree height > 27.5 m, Kenzo et al. 2007) compared with subcanopy and understory trees may suggest that there is different leaf water use by different stomatal regulations, such as isohydric and anisohydic behavior, among the canopy species (Kumagai and Porporato 2012). In fact, Hiromi et al. (2012) and Inoue et al. (2015) reported a large difference of leaf midday water potential caused by different stomatal regulations between canopy and shorter trees in the same forest stand. They also suggested that leaf and xylem structure are related to different leaf water uses. We also found that canopy trees with high LMA showed significantly lower midday water potential than those with low LMA, though the correlation coefficient was low ($P < 0.05$, $r^2 = 0.06$, n = 81). The higher stomatal conductance and T_r of taller trees compared with shorter trees indicated that the water supply from deeper root systems of large trees may be adequate for a high photosynthetic capacity in the forest (Sendall and Reich 2013). The rapid recovery of leaf midday water potential to theoretical gravity potential at night in the majority of canopy trees supports the notion that large canopy trees did not suffer from strong drought stress in this region, although they consume a large amount of water through their high transpiration activity (Fig. 4; Hiromi et al. 2012). However, midday photosynthetic depression occurs in canopy trees on sunny days (Kenzo et al. 2003). We did not conduct the gas exchange measurement in the afternoon, and there are no data on midday photosynthetic depression with tree height gradient, but larger depression in canopy trees than in shorter trees may have weakened the linear relationship between tree $A_{\text{max-area}}$ and height.

The leaf respiration rate is more strongly associated with tree height when expressed on a leaf area basis than a leaf mass basis, likely as a result of strong linear increase of LMA with tree height (Cavaleri et al. 2008). Higher leaf *Rd* values in the upper canopy may be a result of higher leaf physiological activities such as photosynthesis, carbohydrate export, and photoprotection from high light intensity (Solt et al. 2013). In general, the photosynthetic rate is positively associated with the leaf respiration rate in plant species, including tropical trees (Kosugi et al. 2012; Solt et al. 2013), and this is consistent with the present study. Many tropical forest trees also showed similar increases in the respiration rate with tree height (Cavaleri et al. 2008), although the rate decreased with tree size in several temperate trees (Sendall and Reich 2013). The high leaf respiration rate in the canopy layer also contributes to the high gross photosynthetic production (GPP) in tropical rain forests because total leaf respiration accounts for almost half of the total aboveground respiration in tropical rain forests of Malaysia (Yoda 1983). The simple linear increases in leaf respiration and photosynthetic capacity we observed indicate that the relationship is useful to estimate the community GPP in tropical rain forests even if they consist of diverse tree species (Cavaleri et al. 2008).

Leaf photosynthetic capacity in relation to LMA and N content

LMA is a key leaf morphological variable, since variations in the area-based photosynthetic rate ($A_{\text{max-area}}$) and N content could be traced back to variations in LMA with tree height (Rijkers et al. 2000). $A_{\text{max-area}}$ is known to be strongly affected by various leaf characteristics, such as LMA (Niinemets 2002), leaf mesophyll structure [surface area of mesophyll cells per unit leaf area ($A^{\text{mes}}/A_{\text{a}}$)], leaf vein structure (Sack and Holbrook 2006), and N content (Niinemets 2002; Niinemets et al. 2015). Differences in $A_{\text{max-area}}$ with height in this study were positively correlated with the LMA and area-based N content (Fig. 5). In general, height-dependent decreases in both mass- and area-based leaf N content reduce the photosynthetic capacity in temperate and tropical dry forest trees, even when the LMA increases under tall canopy conditions (Niinemets 2002; Kenzo et al. 2012). However, we found that mass-based N content does not change with tree height, and that this results in an increase of the LMA and a resultant increase of leaf area-based N content with tree height. This increase may be the result of high allocation of leaf N to photosynthetic enzymes, such as Rubisco, rather than light capture components such as chlorophyll–protein complexes under canopy conditions (Koike et al. 2001). In fact, the chlorophyll/N ratio decreased with tree height in several canopy species in the study site (Kenzo et al. 2006). A larger LMA usually facilitates the construction of leaf photosynthetic apparatus structures such as a thicker mesophyll structure with well-developed layers of palisade parenchyma and increased surface area of mesophyll cells per unit leaf area (Terashima et al. 2001). The developed mesophyll structure facilitates CO_2 diffusion in the leaves and may enhance the photosynthetic capacity in canopy leaves with larger LMA (Kenzo et al. 2004). In fact, leaves in canopy trees showed highly developed mesophyll structures with high LMA and high photosynthetic capacity in Bornean tropical rain forests (Kenzo et al. 2006).

Leaf hydrostatic conditions and environmental adaptation with height gradient

The large transpiration demand associated with high photosynthetic rates due to high stomatal conductance in canopy leaves decreases the leaf water potential at midday, and induces drought stress (low water potential) in tall trees at midday. More than a twofold increase in the T_{r} was observed in canopy leaves compared with understory trees (Fig. 1), indicative of a larger water transport demand from soil to leaf because of the large difference in water potential along with tree height. The theoretical hydrostatic gradient of the leaf predawn potential (–0.0098 MPa m^{-1}) confirmed that strong drought stress was unusual in the studied tropical rain forest trees, even in the upper canopy. However, the leaf water potential in all trees decreased significantly at midday; e.g., in canopy trees (height > 40 m) MPa varied from –1.0 to –2.0 (Fig. 4). Moreover, the degree of the reduction was steeper in tall upper canopy trees with high T_r values compared with lower understory trees, which indicated that canopy trees and trees grown in other tropical and temperate regions may suffer drought stress at midday; e.g., the variation in midday potential was in the range of previous studies with similar tree heights (–1.0 to –2.5 Mpa; Koch et al. 2004; Woodruff et al. 2004; Burgess and Dawson 2007).

The high LMA under canopy conditions may allow a decreased midday leaf water potential with tree height because the large LMA may increase tolerance to collapse caused by a low water potential (Niinemets 2002; Koch et al. 2004; Woodruff et al. 2004). Wind exposure and physical abrasion likely increase with tree height, favoring more robust leaves with a higher LMA in the upper canopy (Sendall and Reich 2013). In fact, a positive relation between LMA and leaf toughness is observed in many tree species (Kenzo et al. 2012, 2016). In contrast, the saturated relationship between LMA and relative PPFD in our study revealed that light intensity did not linearly affect LMA, $A_{\text{max-area}}$, or N_{area}. These observations indicate that leaf drought and physical stress with tree height are more important factors for leaf morphological and physiological functions through changes in LMA than light intensity in tropical rain forests (Steppe et al. 2011). In contrast, lower LMA in the lower canopy contributes to high shade tolerance through reduction in the leaf respiration rate (Kosugi et al. 2012; Slot et al. 2013).

A linear increase in δ^{13}C with tree height is consistent with height-dependent drought stress tolerance, because it is likely to reflect improvement of long-term leaf photosynthetic water use efficiency (*WUE*) with tree height (Domingues et al. 2005). The combination of high light intensity and high photosynthetic rate with tree height results in a low leaf internal CO_2 concentration (C_i) and higher δ^{13}C and *WUE*. However, the index of δ^{13}C for long-term *WUE* may include error due to variations in the leaf C_i from different light conditions (Kumagai et al. 2001). Leaf δ^{13}C (–38 to –25 ‰) values in trees in this forest are similar to those of many tropical rain forest tree species (Domingues et al. 2005; Holtum and Winter 2005), although these values are significantly lower than those of arid and semiarid tree species, even in canopy leaves (Tanaka-Oda et al. 2010). The relatively low leaf δ^{13}C in the forest studied here may indicate that stomatal limitation or sensitivity to drought stress (i.e., low leaf water potential) is weaker than that in arid land trees.

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References

Cavaleri MA, Oberbauer SF, Ryan MG (2008) Foliar and ecosystem respiration in an old-growth tropical rain forest. Plant Cell Environ 31:473–483

Domingues TF, Berry JA, Martinelli LA, Ometto JP, Ehleringer JR (2005) Parameterization of canopy structure and leaf-level gas exchange for an eastarn Amazonian tropical rain forest (Tapajós national forest, Pará, Brazil). Earth Interactions 9:1–23

Hiromi H, Ichie T, Kenzo T, Ninomiya I (2012) Interspecific variation in leaf water use associated with drought tolerance in four emergent dipterocarp species of a tropical rain forest in Borneo. J For Res 17:369–377

Holtum JA, Winter K (2005) Carbon isotope composition of canopy leaves in a tropical forest in Panama throughout a seasonal cycle. Trees 19:545–551

Ichie T, Inoue Y, Takahashi N, Kamiya K, Kenzo T. (2016) Ecological distribution of leaf stomata and trichomes among tree species in a Malaysian lowland tropical rain forest. J Plant Res, in press

Inoue Y, Kenzo T, Tanaka-Oda A, Yoneyama A, Ichie T (2015) Leaf water use in heterobaric and homobaric leafed canopy tree species in a Malaysian tropical rain forest. Photosynthetica 53:177–186

Kenzo T, Ichie T, Ninomiya I, Koike T (2003) Photosynthetic activity in seed wings of Dipterocarpaceae in a masting year: Does wing photosynthesis contribute to reproduction? Photosynthetica 41:551–557

Kenzo T, Ichie T, Yoneda R, Kitahashi Y, Watanabe Y, Ninomiya I, Koike T (2004) Interspecific variation of photosynthesis and leaf characteristics in five canopy trees of Dipterocarpaceae in a tropical rain forest. Tree Physiol 24:1187–1192

Kenzo T, Ichie T, Yoneda R, Watanabe Y, Ninomiya I, Koike T (2006) Changes in photosynthesis and leaf characteristics with height from seedlings to mature canopy trees in five dipterocarp species in a tropical rain forest. Tree Physiol 26:865–873

Kenzo T, Ichie T, Watanabe Y, Hiromi T (2007) Ecological distribution of homobaric and heterobaric leaves in tree species of Malaysian lowland tropical rainforest. Am J Bot 94:764–775

Kenzo T, Yoneda R, Sano M, Araki M, Shimizu A, Tanaka-Oda A, Chann S (2012) Variations in leaf photosynthetic and morphological traits with tree height in various tree species in a Cambodian tropical dry evergreen forest. JARQ 46:167–180

Kenzo T, Inoue Y, Yoshimura M, Yamashita M, Tanaka-Oda A, Ichie, T (2015) Height-related changes in leaf photosynthetic traits in diverse Bornean tropical rain forest trees. Oecologia 177:191–202

Kenzo T, Tanaka-Oda A, Matsuura Y, Hinzman LD (2016) Morphological and physicochemical traits of leaves of different life forms of various broadleaf woody plants in interior Alaska. Can J For Res, in press

Koch GW, Sillett SC, Jennings GM, Davis SD (2004) The limits to tree height. Nature 428:851–854

Koike T. Kitao M, Maruyama Y, Mori S, Lei TT (2001) Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profiles. Tree Physiol 21:951–958

Kosugi Y, Takanashi S, Yokoyama N, Philip E, Kamakura M (2012) Vertical variation in leaf gas exchange parameters for a Southeast Asian tropical rainforest in Peninsular Malaysia. J Plant Res 125:735–748

Kumagai T, Kuraji K, Noguchi H, Tanaka Y, Tanaka K, Suzuki M (2001) Vertical profiles of environmental factors within tropical rainforest, Lambir Hills National Park, Sarawak, Malaysia. J For Res 6:257–264

Kumagai T, Porporato A (2012) Strategies of a Bornean tropical rainforest water use as a function of rainfall regime: isohydric or anisohydric? Plant Cell Environ 35:61–71

Kume T, Tanaka N, Kuraji K, Komatsu H, Yoshifuji N, Saitoh TM, Suzuki M, Kumagai T (2011) Ten-year evapotranspiration estimates in a Bornean tropical rainforest. Agric For Meteorol 151:1183–1192

Larcher W (2003) Physiological Plant Ecology. 4th Edn. Springer-Verlag, New York

Lloyd J, Patiño S, Paiva RQ, Nardoto GB, Quesada CA, Santos AJB, Baker TR, Brand WA, Hilke I, Gielmann H, Raessler M, Luizão FJ, Martinelli LA, Mercado LM (2010) Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar for Amazon forest trees. Biogeoscience 7:1833–1859

Niinemets Ü (2002) Stomatal conductance alone does not explain the decline in foliar photosynthetic rate with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. Tree Physiol 22:515–535

Niinemets Ü, Kenan TF, Hallik L (2015) A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. New Phytol 205:973–993

Rijkers T, Pons TL, Bongers F (2000) The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. Funct Ecol 14:77–86

Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. Plant Cell Environ 29:367–381

Sack L, Holbrook NM (2006) Leaf hydraulics. Annu Rev Plant Biol 57:361–381

Sendall KM, Reich PB (2013) Variation in leaf and twig CO_2 flux as a function of plant size: a comparison of seedlings, saplings and trees. Tree Physiol 33:1338–1353

Slot M, Wright SJ, Kitajima K (2013) Foliar respiration and its temperature sensitivity in trees and lianas: in situ measurements in the upper canopy of a tropical forest. Tree Physiol 33:505–515

Steppe K, Niinemets Ü, Teskey RO (2011) Tree size-and age-related changes in leaf physiology and their influence on carbon gain. In: Meinzer FC, Lachenbruch B, Dawson TE (eds) Tree Physiology (4): Size- and age-related changes in tree structure and function. Springer, New York, pp 235–253

Su H, Li Y, Liu W, Xu H, Sun OJ (2013) Changes in water use with growth in *Ulmus pumila* in semiarid sandy land of northern China. Trees 28:41–52

Tanaka-Oda A, Kenzo T, Koretsune S, Sasaki H, Fukuda K (2010) Ontogenetic changes in water-use efficiency ($\delta^{13}C$) and leaf traits differ among tree species growing in a semiarid region of the Loess Plateau, China. For Ecol Manage 259:953–957

Terashima I, Miyazawa S, Hanba TY (2001) Why are sun leaves thicker than shade leaves? Consideration based on analyses of CO_2 diffusion in the leaf. J Plant Res 114:93–105

Thomas SC (2010) Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. Tree Physiol 30:555–573

Woodruff DR, Bond BJ, Meinzer FC (2004) Does turgor limit growth in tall trees? Plant Cell Environ 27:229–236

Yoda K (1983) Community respiration in a lowland rain forest in Pasoh, Peninsular Malaysia. Jpn J Ecol 33:183–197