

Supplementary material

Sapwood allocation in tropical trees: a test of hypotheses

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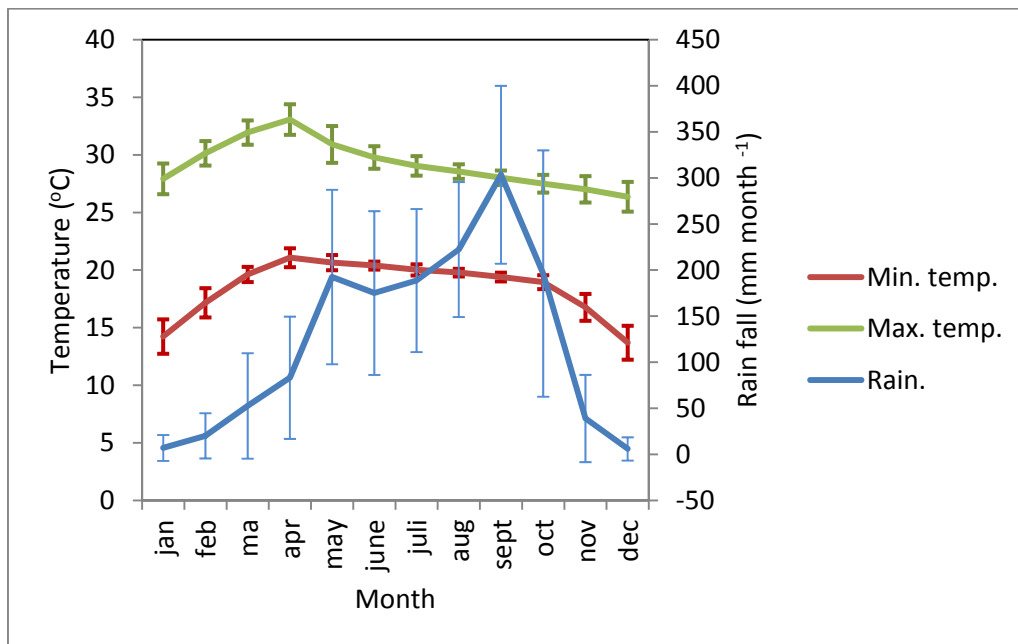


Fig. S1. Estimated mean rain fall maximum and minimum temperature of Huai Kha Khaeng (HKK) wild life sanctuary located in the west-central Thailand, approximately 250 km north west of Bangkok (15°60' N 99°20' E) at an altitude between 490 and 650 m. Error bars represent ± 1 s.d. The HKK data were obtained using long-term monthly maximum and minimum temperatures and rainfall of the Nakhon Sawan meteorological station (15°80' N 100°20' E), located 107 km east of the research site, at an altitude of 28 m. We adjust these meteorological data to match a 13 year meteorological data recorded at HKK (Bunyavejchewin, LaFrankie *et al.* 2009)

Table S1. Table of parameters used in the model

Symbol	Unit	Description	Value	Obtained ¹	Source
Photosynthesis					
k	m ² ground m ⁻² leaf	Extinction coefficient of the canopy	0.61	V	(Maass, 1995)
LUE	(kg CO ₂ Mj PAR ⁻¹)	Light use efficiency at optimal conditions at Ca of 350ppm (C3 species)	0.007	V	(Schippers, 2001)
Km	ppm	The Michaelis Menten constant for the carboxylation	404	V	(Lambers, 1998)
C_{ai}	(-)	Ratio between internal and external CO ₂ concentration	0.7	V	(Grant, 2001)
C_c	ppm	Compensation point of the carboxylation process	37	V	(Tuzet, 2003)
Respiration					
R_l	(kgCH ₂ O kgDM ⁻¹ d ⁻¹)	Respiration rate of leaves	0.032	E	from leaf N and (Poorter, 2006)
R_s	(kgCH ₂ O kgDM ⁻¹ d ⁻¹)	Respiration rate of total sapwood	0.0008	V	(Sterck, 2011)
R_r	(kgCH ₂ O kgDM ⁻¹ d ⁻¹)	Respiration rate of root	0.015	V	(Penningdevries, 1975)
R_{rs}	(kgCH ₂ O kgDM ⁻¹ d ⁻¹)	Respiration rate of reserves	0.0008	V	(Sterck, 2011)
CVF_l	(kg DM/kg carbohydrates ⁻¹)	Conversion factor of leaves	0.68	V	(Penningdevries, 1974)
CVF_s	(kg DM/kg carbohydrates ⁻¹)	Conversion factor of sapwood	0.63	V	(Penningdevries, 1974)
CVF_r	(kg DM/kg carbohydrates ⁻¹)	Conversion factor of root	0.68	V	(Penningdevries, 1974)
CVF_{rs}	(kg DM/kg carbohydrates ⁻¹)	Conversion factor of reserves	1	V	(Penningdevries, 1974)
T_{ref}	(°C)	Reference temperature at which respiration is measured	25	V	(Penningdevries, 1975)
T_{dbl}	(°C)	Temperature increase at which the respiration doubles	10	V	(Goudriaan, 1994)
Architecture					
SLA	(m ² kg ⁻¹)	Specific leaf area	13.6	S	(Ares, 2000)
B_s	(m ² kg ⁻¹)	Ratio between sapwood cross sectional area and leaf weight	0.0054	F	estimated from field values and (Poorter, 2006)
B_r	(-)	Mass ratio between root and leaves	1.4	E	(Malhi, 2011;Sanz-Perez, 2009)
$B_{r/s}$	(-)	Mass ratio between reserves and sapwood	0.2	V	(Veneklaas, 2005; VanNieuwstadt, 2002)
WD	(kg m ⁻³)	Wood density	450	S	(Nock CA 2009)
a	(-)	Scaling parameter of height-DBH relation	2.71	F	estimated from field values and (Poorter, 2006)
b	(-)	Scaling parameter of height-DBH relation	0.564	F	estimated from field values and (Poorter, 2006)
c	(-)	Scaling parameter of crown area-DBH relation	1.3	E	estimated from (Poorter 2006)
Turnover of organs					
M_l	year ⁻¹	Leaf turnover	1.04	F	from deciduous period of <i>Toona</i>
M_s	year ⁻¹	Sapwood turnover	0.08	F	measured from tree ring records of <i>Toona</i>
M_r	year ⁻¹	Root turnover	0.59	V	(Finer, 2011)
Extra mortality and regrowth of leaves as a results of the difference between optimal an actual LAI					
M_e	(d ⁻¹)	Fraction of leaf surplus that is dying	0.05	C	optimized to follow optimal LAI curve
F_r	(d ⁻¹)	Fraction of leaf shortage that regrowth at the cost of reserves	0.05	C	optimized to follow optimal LAI curve
Water relations					
H_w	(mm mm ⁻¹)	Relative soil moisture content at wilting point	0.15	E	(Bunyavejchewin, 2000; Saxton, 1986)
H_c	(mm mm ⁻¹)	Critical relative soil moisture content below which stomata are closed	0.23	E	(Bunyavejchewin, 2000; Saxton, 1986)
H_{fc}	(mm mm ⁻¹)	The water content of the soil at field capacity	0.32	E	(Bunyavejchewin, 2000; Saxton, 1986)
$R_{H2O,CO2}$	(-)	Ratio between water diffusivity and CO ₂ diffusivity molar based	1.6	V	(Sterck, 2011)

F= measured in the field locally, C= calibrated value, V= value from reference, E= estimated value from reference

ESM model description IBTREE -----

Introduction. IBTREE (Individual Based Tree Ring Expansion Estimator) is a mechanistic tree growth model that simulates an individual canopy tree. The model's state variables are leaf biomass, sapwood biomass, fine root biomass expressed in kg dry matter per tree and reserve biomass expressed in kg carbohydrates per tree (Fig. 1). In this model the sapwood biomass represents all living tissue connecting leaves and fine roots, i.e. including branches and coarse roots. The growth limiting factors include: light, CO₂, temperature and water. Processes that are highly variable on a daily basis like photosynthesis, respiration and transpiration are calculated on an hourly basis, whereas other processes, that are less dynamic, are calculated on a daily basis. The model is especially designed to simulate tree biomass and diameter growth that can be compared to tree ring measurements.

Growth of dry matter. The changes of leaf biomass (W_l), the sapwood biomass (W_s), the root biomass (W_r), and the reserves (W_{rs}) can be described as the change in the individual plant organ weight, W_o , (kg DM tree⁻¹, DM = dry matter):

$$\frac{dW_o}{dt} = (A - R_m) \cdot F_o \cdot CVF_o - W_o \cdot M_o \quad (1)$$

Where A is the assimilation rate (kg CH₂O tree⁻¹ d⁻¹, CH₂O = carbohydrates), R_m is the maintenance respiration rate of the tree (kg CH₂O tree⁻¹ d⁻¹), F_o is allocation factor to organs that comes from the allocation module, CVF_o is conversion factor between dry matter and carbohydrates and biomass (kg DM kg CH₂O⁻¹) and M_o is the turnover of the plant part (d⁻¹).

The assimilation rate A depends on the amount of absorbed radiation and the light use efficiency (Haxeltine and Prentice 1996; Hickler, Smith *et al.* 2004; Makela, Pulkkinen *et al.* 2008; Pepper, McMurtrie *et al.* 2008):

$$A = 30/44 \cdot Area \cdot LUE_{(T,C_i)} \cdot I \cdot \left(1 - e^{\left(\frac{-k \cdot W_l \cdot SLA}{Area}\right)}\right) \quad (2)$$

where I is the amount radiation on top of the canopy (MJ PAR m⁻² d⁻¹), $LUE_{(T,C_i)}$ is the light use efficiency dependent on temperature and internal CO₂ concentration (C_i) (kg CO₂ MJ PAR⁻¹), k is the light extinction coefficient of the canopy (m² ground area/m² leaf area), SLA is the specific leaf area (m² kg⁻¹), $Area$ is the total crown area (m²), and 30/44 is the molar ratio between carbohydrates (CH₂O) and CO₂.

The maintenance respiration of the tree R_m (kg CH₂O tree⁻¹ d⁻¹) is dependent on the dry matter weight of living tree organs and the actual temperature T . We assume that the maintenance respiration doubles with a 10°C (Q₁₀=2) temperature increase (Atkinson, Hellicar *et al.* 2007; Ryan, Hubbard *et al.* 1994; Schippers and Kropff 2001):

$$R_m = (W_l \cdot R_l + W_s \cdot R_s + W_r \cdot R_r + W_{rs} \cdot R_{rs}) 2^{(T-T_r)/10} \quad (3)$$

where the respiration coefficients of the plant organs are leaf (R_l), sapwood (R_s), fine roots (R_r) and reserves (R_{rs}) (kg CH₂O kg DM⁻¹ d⁻¹); T is the actual temperature (°C) and T_r is a reference temperature at which respiration coefficient are measured (°C).

Light use efficiency. The light use efficiency (equation 2) is dependent on both temperature (F_T) and internal CO₂ concentration C_i (F_{C_i} , ppm) (Pepper, McMurtrie *et al.*

2008; Schippers, Vermaat *et al.* 2004):

$$LUE_{(T,C_i)} = LUE_m \cdot F_T \cdot F_{C_i} \quad (4)$$

LUE_m is the maximum light use efficiency under optimal conditions (kg CO₂ MJ PAR⁻¹), i.e. optimal temperature and at saturating water supply and CO₂ levels (PAR= photosynthetically active radiation). The (air) temperature T (°C) effect on C₃ photosynthesis is ruled by the equation:

$$F_T = -0.0022 T^2 + 0.1111 T - 0.39. \quad (5)$$

This equation has a maximum value of one at 25°C, a photosynthetic rate that is halved at 10 °C and 40 °C and fitted temperature published response curves very well (Leakey, Press *et al.* 2003; Yamori, Suzuki *et al.* 2006). Since the model uses monthly average maximum and minima data. These data are linearly interpolated to obtain daily maximum and minimum temperatures. The minimum temperature is assumed to be at dawn whereas the time of the maximum temperature can be chosen (e.g. 14.00 hours). The model fits an increasing sinusoid function between minimum temperature at dawn and the maximum temperature at the maximum temperature time. It also fits a decreasing sinusoid between the maximum temperature and the minimum temperature at dawn the next day. Note that this are two separate fits because the heating up time is much shorter than the cooling dawn time. Alternatively the model has a procedure to generate temperature data based on the day of the year and time of the day. The air temperature follows a daily curve, which is driven by the daily radiation and by seasonal change. This can be modelled by Schippers, *et al.* 2004:

$$T = T_a + A_y \cdot \sin(2\pi \cdot (d - d_r)/365) + A_d \cdot \sin(2\pi \cdot (h'-6)/24) \quad (6)$$

Where:

T_a is the average air temperature of the year °C, A_y is the year amplitude maximal long-term deviation from the average temperature, d is the day NR of the year (1-365), d_r is the reference day in spring where the temperature equals the average temperature, A_d is the daily amplitude (maximum-minimum temperature)/2, h' = transposed time frame to account for short warming and longer cooling period during the day, $h' = f(h_{min}, h_{max})$, h_{min} is the time at sunrise and h_{max} is the hottest time of the day (hour)

Water relations. Since water availability determines the stomatal conductance, it is also crucial in determining the internal CO₂ concentration (C_i). For CO₂ limitation we use a Michaelis Menten reduction based on the internal CO₂ concentration of the leaves C_i (ppm) (Farquhar, Buckley *et al.* 2002; Sterck and Schieving 2011):

$$F_{C_i} = \frac{C_i - C_c}{C_i + Km_C} \quad (7)$$

Here, C_i is the CO₂ concentration in the leaves (ppm), C_c is the CO₂ compensation concentration (ppm), and Km_C is the Michaelis Menten constant for the carboxylation process (ppm). We use C_i as a fraction C_{ai} of C_a , the atmospheric CO₂ concentration (ppm), in the absence of water stress. We use the value 0.7 for C_{ai} (Grant, Goulden *et al.*

2001; Liu, Dang *et al.* 2006; Tricker, Trewin *et al.* 2005).

The next step is to relate water availability to stomatal conductivity that in turn determines C_i and F_{C_i} . We use a simple bucket soil water model (Fig. 1). The relative stomatal conductance (F_w) is reduced when the water in the soil gets below a certain critical level H_c . (Goudriaan and Van Laar 1994; Pepper, McMurtrie *et al.* 2008)

$$F_w = \frac{H_a - H_w}{H_c - H_w} \text{ and } 0 \leq F_w \leq 1 \quad (8)$$

where H_a is the actual relative soil moisture content ($\text{m}^3 \text{ water}/\text{m}^3 \text{ soil}$), H_w is the relative soil moisture content at wilting point ($\text{m}^3 \text{ water}/\text{m}^3 \text{ soil}$), and H_c is the critical relative soil moisture content below which the stomata are starting to close and F_w becomes smaller than one ($\text{m}^3 \text{ water } \text{m}^{-3} \text{ soil}$).

The stomatal conductance for CO_2 affected by water stress is:

$$G_{S_{C,W}} = G_{S_C} * F_w = \frac{A_{T,I} * F_{C_i}}{(C_a - C_i)} \quad (9)$$

where G_{S_C} is the stomatal conductance without water limitation ($\text{kg } \text{CO}_2 \text{ ppm}^{-1} \text{ tree}^{-1} \text{ day}^{-1}$), as determined by light and CO_2 , $A_{T,I}$ is the assimilation limited by light and temperature without water stress. Since G_{S_C} , F_w , $A_{T,I}$ and C_a are known in the model and F_{C_i} can be substituted by equation 7 we can solve C_i from this equation and thus the water effect on C_i and growth.

The transpiration is calculated assuming that the stomatal conductance of water on a molar basis is 1.6 times larger than that of CO_2 ($G_{S_{C,W}}$) (Sterck and Schieving 2007). But transpiration is also determined by the humidity of the air. However, as we do not have data on air humidity at our study site. We assumed that the air vapour pressure at dawn is saturated and kept this pressure constant over the rest of the day (Kirschbaum 1999). This approach leads to lower air saturation values later on the day due to higher temperatures. This method is probably valid for relative wet conditions, but not during the dry season when lower values of air humidity can be expected. Hence, we use the soil water content as a predictor for the dawn relative air humidity. The soil water content determines evaporation and transpiration and so air humidity. We model this by introducing a critical soil water content H_{ca} that determines the level of water in soil above which the dawn air humidity is 100%. If H_{ca} drops below this values, we assume dawn air saturation to decline linearly with soil water content (H_a):

$$E_{dawn} = 100 \frac{H_a}{H_{ca}} \text{ and } 0 < E_{dawn} < 100. \quad (10)$$

The actual relative soil moisture content ($\text{m}^3 \text{ water } \text{m}^{-3} \text{ soil}$) is:

$$H_a = \frac{H_s}{C \cdot D} \quad (11)$$

D is the depth of the relevant soil layer (m). C is the crown area (m^2), H_s is the water

content in the relevant soil layer (m^3).

We assume a simple bucket model to model the amount of water in the relevant soil layer:

$$\frac{dH_s}{dt} = \frac{R \cdot C}{1000} - H_T - H_E - H_P \quad (12)$$

P is the percolation ($\text{m}^3 \text{H}_2\text{O d}^{-1}$), R is rainfall ($\text{mm H}_2\text{O d}^{-1}$), H_t is the transpiration of tree ($\text{m}^3 \text{H}_2\text{O d}^{-1}$). The percolation (P) is simply the surplus of water above the field capacity H_{fc} .

H_T , the flux of water transpired through the stomata is proportional to the difference between the water pressure in the leaf and that in the atmosphere. When we assume that the H_2O partial pressure in the leaf is saturated the H_2O flux from the leaf can be modelled as:

$$H_T = \frac{R_{HC} \cdot G_{S_{HC}} \cdot H_D}{1000} \quad (13)$$

where $G_{S_{HC}}$ = stomatal conductivity for CO_2 affected by water ($\text{kg CO}_2 \text{ tree}^{-1} \text{ day}^{-1} \text{ ppm}^{-1}$), R_{HC} = ratio between water diffusivity and CO_2 diffusivity on a mass base ($=1.6 \times 18/44=0.655 \text{ kg H}_2\text{O kg CO}_2^{-1}$), H_D = the deficit between water pressure at saturation and the actual water pressure of the air (in ppm) at the actual temperature:

$$H_D = e_{sat}(T) - e_{act}(T) \quad (14)$$

If the atmospheric water pressure is not known from data we may estimate the atmospheric water pressure deficit from maximum and minimum temperature of the day assuming that at the minimum temperature the air is completely saturated. Then the deficit H_D can be calculated as (Kirschbaum 1999):

$$H_D = e_{sat}(T) - e_{sat}(T_{dawn}) \quad (15)$$

where $e_{sat}(T)$ is the saturated water pressure at an actual temperature (T) during the day (ppm), $e_{sat}(T_{dawn})$ is the saturated water pressure at the minimum temperature of the day at dawn (ppm).

The soil evaporation (H_E) is strongly linked to the transpiration and the LAI and can be described by the function (Wang and Liu 2007):

$$H_E = \frac{H_T \cdot e^{-k \cdot LAI}}{1 - e^{-k \cdot LAI}} \quad (16)$$

Growth and tree dimensions

Individual trees in the model also grow in dimensions like height crown area and basal area of sapwood and heart wood. We assume simple relations between diameter at breast height DBH (cm) and height (H in m) according to (Poorter, Bongers *et al.* 2006):

$$H = a \cdot DBH^b \quad (17)$$

Where a and b are scaling parameters.

For the relation between DBH (cm) and crown area CA (m^2) we can write (Poorter, Bongers *et al.* 2006):

$$CA = c \cdot DBH \quad (18)$$

Note that (Poorter, Bongers *et al.* 2006) used more complex relations, however these can be replaced by these simpler without any loss of accuracy.

Using the height-DBH relation we can write using the biomass equation (20):

$$DBH = \sqrt[2+b]{\frac{\frac{W_s+W_h}{WD}}{a \cdot 2.5 \cdot 10^{-5} \cdot \pi \cdot F}} \quad (19)$$

Where: W_s = sapwood weight of the tree (kg), W_h = heart wood weight of the tree (kg), WD wood density ($kg\ m^{-3}$), a and b are scaling parameter of height equation, F is form factor of biomass equation (0.45). Note that $2.5 \cdot 10^{-5}$ comes from the cm to meter conversion in the biomass equation:

$$W_s + W_h = WD \cdot H \cdot F \cdot \pi \cdot \left(\frac{DBH}{200}\right)^2 \quad (20)$$

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Derivation of optimal LAI equation -----

We derive the optimal *LAI* equation from equation 1 2 and 3 of the manuscript:

$$\frac{dW_o}{dt} = (A - R_m) \cdot F_o \cdot CVF_o - W_o \cdot M_o \quad (1)$$

$$A = 30/44 \cdot CA \cdot LUE_{(T,ci)} \cdot I \cdot \left(1 - e^{\left(\frac{-k \cdot W_l \cdot SLA}{Area}\right)}\right) \quad (2)$$

$$R_m = (W_l \cdot R_l + W_s \cdot R_s + W_r \cdot R_r + W_{rs} \cdot R_{rs}) Q_{10}^{(T-Tr)/10} \quad (3)$$

We assume that the optimal *LAI* (leaf area index) is reached when the export of assimilates from leaves corrected for the maintenance and replacement costs of leaves and supporting fine roots is maximized. The export of the leaves A_l can be estimated as:

A_l = gross assimilation – respiration losses of leaves and supporting roots – replacement costs of leaves and supporting roots.

Following equation 1 and 3 and substituting q for $Q_{10}^{(T-Tr)/10}$ we can write for the export of leaves:

$$A_l = A - qW_lR_l - qW_rR_r - \frac{W_l \cdot M_l}{CVF_l} - \frac{W_r \cdot M_r}{CVF_r} \quad (4)$$

Per m^2 is the leaf weight $W_l = LAI/SLA$ (SLA = specific leaf area) and the root weight is linearly related to the leaf weight in the model $W_r = c_1 \cdot W_l$. Incorporation this in equation 4 we get:

$$A_l = A - \frac{LAI}{SLA} \left(qR_l + c_1 qR_r + \frac{M_l}{CVF_l} + \frac{c_1 M_r}{CVF_r} \right) \quad (5)$$

From equation 2 we can write the gross assimilation A per m^2 , replacing $30/44 \cdot LUE_{(T,ci)} \cdot I$ by p to be:

$$A = p \left(1 - e^{(-k \cdot LAI)}\right) \quad (6)$$

Merging equation 5 and 6 yield:

$$A_l = p \left(1 - e^{(-k \cdot LAI)}\right) - \frac{LAI}{SLA} \left(c_1 R_l + c_1 c_2 R_r + \frac{M_l}{CVF_l} + \frac{c_2 M_r}{CVF_r} \right) \quad (7)$$

The respiration losses per m^2 leaves are: $r = (qR_l + c_1 qR_r)/SLA$ and the replacement costs per m^2 leaves are: $l = (M_l/CVF_l + c_1 M_r/CVF_r)/SLA$. Using this, we can rewrite equation 7 into:

$$A_l = p \left(1 - e^{(-k \cdot LAI)}\right) - LAI(r + l) \quad (8)$$

To estimate the maximum of A_l we calculate the derivative of equation 8 which is:

$$A'_l = kpe^{-k \cdot LAI} - (r + l) \quad (9)$$

To estimate the optimal LAI (LAI_{opt}) we set A'_l to zero yielding:

$$kpe^{-k \cdot LAI_{opt}} = (r + l) \quad (10)$$

If we rearrange equation 10 we get:

$$LAI_{opt} = -\left(\ln \frac{r+l}{p \cdot k}\right) / k \quad (11)$$