

Litterfall production and chemistry of *Koompassia malaccensis* and *Shorea uliginosa* in a tropical peat swamp forest: plant nutrient regulation and climate relationships

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Abstract

Key message This study shows that two emergent tree species growing in a nutrient-limited tropical peat swamp forest use different mechanisms for nutrient regulation.

Abstract The main aim of this study is to understand the contribution of litterfall to nutrient supply and regulation of two emergent tree species in a tropical peat swamp forest (TPSF) in Peninsular Malaysia. The questions posed by this study include: (1) Do coexisting tree species in TPSF differ in terms of litter production, physico-chemical traits and litterfall patterns? (2) How do these relate to possible nutrient regulation mechanisms of the tree species and do the strategies involved differ between a nitrogen (N) fixing legume (*Koompassia malaccensis*, Family Fabaceae) and a dipterocarp (*Shorea uliginosa*, Family Dipterocarpaceae)? (3) Is litterfall timing of the selected tree species driven by climatic variables? Litterfall was collected from litter traps placed under the selected trees in the Sungai Karang TPSF. Green leaves of the selected tree species were also collected. Both leaf litter and green leaves were assessed for their physico-chemical properties (toughness, total phenols, total tannins, proximate fibre–cellulose–lignin and a range of nutrients) and compared. Results obtained indicate that *K. malaccensis* relies on a combination of high litter

quality (higher N coupled with lower amount of tannins, fibre and cellulose) and low annual litterfall mass (388.17 g m^{-2}) for nutrient regulation while the opposite strategy is used by *S. uliginosa*, which was found to produce an annual litterfall mass of 918.14 g m^{-2} . Due to the aseasonal environment, no significant relationships were observed between climatic variables and litterfall. Therefore, litterfall characteristics in aseasonal tropical regions may depend more on species-specific physico-chemical properties than on climatic variables.

Keywords Litterfall pattern · Litter quality · Biogeochemistry · Nutrient regulation · Climate–litterfall relationship · Emergent tree species · Peat swamp

Introduction

As the first and main process that returns nutrients from above-ground living biomass to the forest floor, plant litter forms the forest organic layer, which enriches and maintains the nutrient supply in the soil (Liu et al. 2004). The timing and amount of litterfall produced exert a major control over the forest nutrient cycling process. Therefore, studies of litterfall are useful in providing information on limiting nutrients and nutrient use efficiency (NUE) in forest ecosystems. Litterfall collection is a standard non-destructive method that has been used by global researchers since the 1950s to determine forest net primary production (productivity), phenology and most importantly, turnover rates of organic and inorganic matter (nutrient cycling) (Lowman 1988; Williams-Linera and Tolome 1996; Hansen et al. 2009; Chave et al. 2010). The components of litterfall include leaves, twigs, bark and reproductive organs such as flowers and seeds, but of these, leaf

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litter contributes to the highest amount of transferrable nutrients via decomposition (Chave et al. 2010).

Over the years, the effects of litterfall on nutrient cycling have been studied extensively especially in terms of nutrient return via leaf litter decomposition. However, to further understand the underlying plant nutrient use strategies, it is also helpful to compare nutrient and physico-chemical properties between green leaves and senesced leaves (Hättenschwiler et al. 2008; Biswas and Khan 2011), but such studies are rare, particularly in the tropics (Hättenschwiler et al. 2008). Plants can use different strategies to efficiently manage their nutrients such as external cycling, which relies on mineralization of nutrients from the surrounding environment or litter decomposition and internal cycling (Hättenschwiler et al. 2008). The latter, which refers to the withdrawal or resorption of nutrients from senescing leaves, is a common strategy used by plants growing in nutrient-poor environments (Hättenschwiler et al. 2008).

Besides studies of litterfall on nutrient cycling, global research on litterfall often focusses on the effects of climatic variables on litter production, notably temperature (maximum and minimum), precipitation and seasonality (Williams-Linera and Tolome 1996; Liu et al. 2004; Chave et al. 2010), as well as forest type (varying with latitude and altitude) (Bray and Gorham 1964; Miller 1984; Campanella and Bertiller 2008). In tropical forests, patterns of litterfall have been reported to be associated with precipitation, seasonality and temperature but large variations have been obtained between sites and researchers. These differences may be due to factors such as the placement of traps, types of litter sorted, frequency of litterfall collection and duration of the study. In a recent meta-analysis conducted on litterfall studies, Chave et al. (2010) supported Proctor's (1983) claim that one year is sufficient to capture the annual litter production in a forest as they found that the inter-annual variability falls within 10 % of the mean litterfall.

In this study, we focussed on the nutrient-poor TPSF of SE Asia, where the dome-shaped topography prevents inflow of water which would otherwise supply an input of nutrients, as observed in other types of wetlands (Pahang Forestry Department 2005). Even during extreme rainfall or flooding events, nutrient input to the ecosystem is restricted to the edges or immediate riparian zones of the forest. Nutrient input in the central part of the forest is thus solely dependent upon rainfall, dusts, marine aerosols, litterfall and plant litter decomposition (Yule 2010). This may explain results obtained by Chave et al. (2010) which reported that flooded forests had the highest amount of annual litterfall as compared to other forest types. Although litterfall and its contribution to nutrient input is well

documented across various ecosystems, our knowledge of flooded, disturbed, regenerating, or nutrient-poor environments such as TPSF is still limited.

Decomposition of leaf litter in tropical peat swamps is severely limited as a result of the extreme conditions (Yule and Gomez 2009; Yule 2010) and consequently they are of global importance in carbon sequestration, storing 2–3 % of total soil carbon (Page et al. 2006). Litter builds up as peat in layers up to 25 m deep, and when these forests are disturbed through logging, draining and agricultural conversion they are extremely susceptible to fire. Regional peat fires in 1997 resulted in the highest recorded increase in global carbon dioxide (CO₂) levels since records began in the 1950s (Page et al. 2002; Aldhous 2004). Given the severe threats presently faced by these forests, further ecological research is crucial to fully understand their role in global climate change.

Two emergent tropical tree species were selected for this study, a dipterocarp *Shorea uliginosa* Foxw. (family Dipterocarpaceae) and a legume *Koompassia malaccensis* Magingay ex Benth. (family Fabaceae, subfamily Caesalpinioideae), which represent species with different adaptations to survive in such nutrient-limited environments. The commercial value of both plants is well known but little is known about their ecological importance especially in terms of effects on TPSF soil and subsequent sustainability of the forest. The most notable leaf physico-chemical properties involved in litterfall and nutrient cycling are the plant secondary compounds (especially lignin concentration), nutrient concentrations and leaf area (e.g. Campanella and Bertiller 2008).

In this study, we have examined the potential nutrient use mechanisms revolving around plant foliage and leaf litterfall that enable *Koompassia* and *Shorea* to persist in the nutrient-poor environment of the TPSF. Green leaves and leaf litter of the selected tree species were analysed with a focus on nutrient concentrations as well as physico-chemical properties. Litterfall patterns, and effects of climatic factors notably precipitation and temperature were also examined. The general working hypotheses of this study are: (1) *Koompassia* and *Shorea* will rely heavily on resorption of nutrients before litterfall as both tree species grow in a nutrient-poor environment, and (2) *Koompassia* will show greater nutrient retranslocation or resorption compared to *Shorea* as the former is a nitrogen-fixer and thus has a higher amount of nutrients in its living tissues. As a result, *Shorea* was predicted to produce lower quality, but a higher quantity of leaf litter as it was hypothesized to depend more on nutrient uptake from decomposing litter. (3) Lastly, litterfall patterns of the selected tree species were hypothesized to be affected by both leaf litter physico-chemical properties and climate.

Methods

Study area

This study was conducted in the Sungai Karang TPSF (N 3°39′30.8″E 101°19′18.4″), a protected low-lying forest reserve on the west coast of Peninsular Malaysia with an area of approximately 23,486 Ha. It is the second largest contiguous peat forest block remaining in Peninsular Malaysia after the Pekan-Nenasi peat forest on the east coast. The forest is quite diverse with 107 tree species from 27 different families recorded including *Aglaia odorata* Pannell C.M., *Camposperma coriaceum* [Jack] Hallier f., *Cryptocarya impressa* Miq., *Ixora grandiflora* Ker Gawl., *Macaranga pruinosa* Mull.Arg., *Parartocarpus venosus* [Becc.] Garrett, *Pternandra galeata* Korth., and *Shorea platycarpa* Heim. (Hahn-Schilling 1994), as well as ferns (*Stenochlaena palustris* [Burm.f.] Bedd, *Nephrolepis biserrata* [Sw.] Schott., *Asplenium longissimum* Bl., *Dicranopteris* sp.), and palms (*Pinanga* sp., *Ptychoraphis* sp., *Korthalsia* sp., *Pandanus helicopus* Kurz ex Mig.). The main soil substrate of this forest is peat (histosols) of about 5 m in depth lying above marine alluvial clay (the area was previously probably covered by mangrove forest). The forest experiences a fairly stable tropical climate throughout the year but the monsoon brings heavier rainfall to the forest from September to December. The peat substrate is permanently waterlogged and the forest floor is submerged during wet periods. The water is acidic (pH 3–4), and dark brown in colour due to high concentrations of tannins and humic acids (DOC typically 80 mg L⁻¹) (Yule and Gomez 2009). It is anaerobic because of lack of water flow. Inorganic nutrient concentrations are also low (nitrogen and phosphorus <0.1 mg L⁻¹).

At the time of the study, the forest lies adjacent to Malaysian Federal Land Development Authority's (FELDA) oil palm plantation and Integrated Agricultural Development Project's (IADP) paddy fields (rice). During the study, a large area of peat forest adjacent to the forest reserve was drained and cleared for new oil palm development. This drainage would have impacted the hydrology of the remaining forest.

Litterfall and living leaves collection

Four sites within the forest with *Koompassia* and *Shorea* were chosen for the study. At each site, four 1 × 1.5 m² litter traps were randomly established under *Koompassia* and *Shorea* canopy, respectively, with two traps per tree as placement of traps, in closed canopy relative to the cardinal directions and distance from tree trunks, does not affect the amount of leaf litter collected (Lowman 1988). The traps were made of non-degradable nylon mesh and were tied to

adjacent tree trunks 1 m above the ground using nylon ropes. Litterfall was collected monthly from March 2011 to February 2012. All litter trap samples were retrieved and brought back to the laboratory immediately to be sorted according to the litter components of *Koompassia* leaf litter, *Shorea* leaf litter, wood litter of unidentified species and residual litter (reproductive organs and leaf litter of other unidentified plant species). Large woody materials such as branches were also included in the study. They were broken into pieces and brought back to the lab to be weighed. The dry weight (g) of all the samples was obtained after oven-drying of each litter component at 60 °C for 48 h. Mature green leaves of *Koompassia* and *Shorea* were also collected from the study site. As both are emergent tree species, six smaller trees (>2 m) of each species were sampled using a tree pruner.

Chemical analysis

In the laboratory, sub-samples of living leaves and leaf litter of *Koompassia* and *Shorea* were air-dried and ground for determination of total Kjeldahl nitrogen (N) and phosphorus (P). Total N was extracted using a block digester method whereby samples were digested using sulphuric acid before being converted to ammonium cation through the use of a copper sulphate catalyst and addition of potassium sulphate. The pH of the digested sample was then altered to a known basic pH to convert the ammonium cation to ammonia. Concentration of total N was determined colorimetrically using the Lachat Quikchem[®] flow-injection analysis system after heating the buffered sample with salicylate and hypochlorite to produce a blue-coloured solution. Sodium nitroprusside was used to intensify the colour of the solution. Total P was determined by converting the sample P to orthophosphates (PO₄³⁻) via digestion in the presence of sulphuric acid and persulphate. The concentration of orthophosphates was determined colorimetrically by pH-adjusted molybdate tartrate-ascorbic acid method using the Lachat Quikchem[®] flow-injection analysis system.

Sub-samples of the air-dried and ground living leaves and litter were also analysed for sodium (Na), magnesium (Mg), potassium (K) and calcium (Ca) contents. The leaves were dried at 105 °C, weighed and converted to ash via combustion at 550 °C in a furnace for 4 h. The ash was subsequently digested in 2 N hydrochloric acid and analysed for Na, Mg, K and Ca using an acetylene-air flame atomic absorption spectrophotometer (AAS, Perkin Elmer 3100).

Total phenols, tannins as well as proximate lignin, cellulose and fibre content of litter were also quantified following the methods in Graca et al. (2005). Briefly, successive removal of tissues using acid detergent, 72 %

sulphuric acid (H_2SO_4) and ignition of samples at $550\text{ }^\circ\text{C}$ for 3 h in a muffle furnace were done. Determination of remaining tissue weight after each step was conducted to calculate the proximate lignin, cellulose and fibre content. Total phenol and tannin contents were determined following Folin–Ciocalteu's assay using 70 % acetone as extraction solution at $4\text{ }^\circ\text{C}$. For total tannin determination, polyvinylpyrrolidone (PVPP) was added to the sample to chelate the tannins before carrying out Folin–Ciocalteu's assay.

Physical analysis

To determine the leaf area, leaves were placed on a grid paper ($1\text{ mm} \times 1\text{ mm}$) and the number of squares intercepted by the leaves were counted. Leaf toughness was assessed using a penetrometer based on the protocol outlined in Graca et al. (2005).

Environmental variables

In this study, the environmental variables included monthly rainfall data, rain days and mean maximum/minimum temperatures. The data obtained from the nearest weather station—MARDI Tanjong Karang—were provided by the Malaysian Meteorological Department (MMD).

Calculation

The % nutrient retranslocation efficiency (NRE) and nutrient use efficiency (NUE) were calculated according to Finzi et al. (2001):

1. $\%NRE = [(A - B)/A] \times 100$, whereby A refers to the nutrient concentration in green leaves, while B refers to the nutrient concentration in leaf litter,
2. $NUE = \text{annual litterfall mass (g m}^{-2}\text{)}/\text{litterfall nutrient content (g m}^{-2}\text{)}$.

Data analysis

Kurtosis and skewness as well as Levene's test of homogeneity with the critical value of 0.05 was applied to evaluate the normality of the collected data. Analysis of variance (ANOVA) was then used to examine potential significant differences in litterfall components between months and the physico-chemical properties between the sample types of each tree species. ANOVA was also used to examine differences in mean monthly maximum and minimum temperature. No statistical test was conducted on annual litterfall and rainfall data because total values for the year and month were used, respectively. Tukey's post hoc test was used to determine differences between the

different treatments as stated above. The relationship between litter physico-chemical properties of each tree species were also examined using principal component analysis (PCA). For tree species ordination according to these litter traits, the loading coefficients of each species were calculated with respect to the first two principal components. Lastly, Pearson's correlation was used to evaluate the relationship between litterfall for each species and climatic variables. All statistical analyses were conducted using SPSS 16.0 and the accepted level of significance was set at 0.05.

Results

Litterfall of *Koompassia* and *Shorea* in Sungai Karang peat swamp forest, North Selangor

As shown in Fig. 1, leaf litterfall occurred throughout the year and varied across the months for both *Koompassia* ($F_{1,144} = 4.492$, $p < 0.01$) and *Shorea* ($F_{1,144} = 4.492$, $p < 0.01$). The timing of leaf litterfall differed between the two species whereby maximum leaf litter was observed in the month of June–July for *Koompassia* and December for *Shorea*. The data depicted single major leaf shedding events in the year for both tree species but the wood litter fraction did not vary much throughout the year for either tree species. The high variability observed for monthly wood litter collections was due to the inclusion of large branches collected occasionally in the litter traps. Residual litter (reproductive organs and unidentified leaf litter) collected from *Koompassia* traps recorded highest values in October and no major differences were observed throughout the remaining year. No major differences were observed for residual litter collected from the *Shorea* trap.

The total annual leaf litterfall for *Koompassia* and *Shorea* were 388.17 and 918.14 g m^{-2} , respectively. Annual leaf litter production of *Shorea* was twofold higher as compared to that of *Koompassia*. For the wood and residual litterfall, *Koompassia* recorded 653.94 and $1,567.19\text{ g m}^{-2}$ while *Shorea* recorded 523.91 and $1,353.31\text{ g m}^{-2}$, respectively. In this study, residual litter accounted for the highest fraction of total litterfall for both tree species with a value of 60.10 and 48.31 % for *Koompassia* and *Shorea*, respectively. For litter traps placed under *Koompassia*, the smallest litter fraction was leaf litter at 14.83 % while wood litter recorded a higher fraction at 25.08 %. The opposite was observed for litter traps placed under *Shorea* where wood litter accounted for only 18.71 % while species leaf litter recorded a value of 32.98 %. Total annual litterfall of the selected plant species could not be determined as the research was conducted in a tropical forest of high diversity resulting in a mixture of

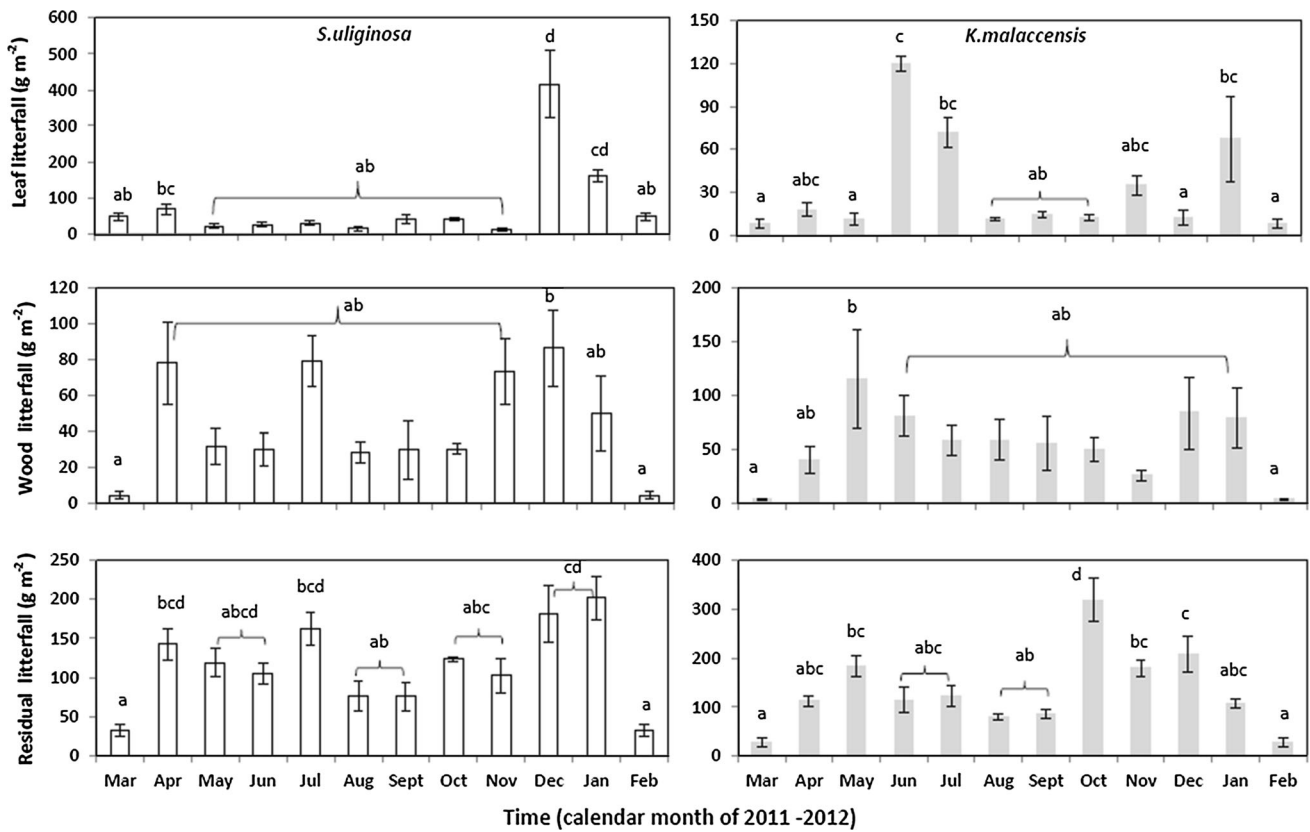


Fig. 1 Monthly leaf, wood and residual (reproductive organs and leaf litter of other unidentified plant species) litter of *Shorea* and *Koompassia*. Monthly values are expressed as $g\ m^{-2} \pm SD$

($n = 8$). Any two treatments sharing a lower case letter indicate amounts that are not significantly different

plant components from many different plant species, which could not be accurately separated in the litter trap.

Nutrient quality and physico-chemical traits of green leaves and litter of *Koompassia* and *Shorea*

Table 1 shows the nutrient concentrations of the leaf litter collected. Significant differences were observed between all samples for N ($F_{3,20} = 60.257, p < 0.01$), Ca ($F_{3,20} = 15.633, p < 0.01$), Mg ($F_{3,20} = 26.575, p < 0.01$), Na ($F_{3,20} = 24.340, p < 0.01$) and K ($F_{3,20} = 75.001,$

$p < 0.01$). *Koompassia* green leaves had the highest concentration for all nutrient elements studied except for P as there were no differences ($F_{3,20} = 5.058, p = 0.120$) observed for P concentrations among the four sample types collected. *Koompassia* litter had similar nutrient concentrations to *Shorea* litter except for N, which was significantly higher in *Koompassia* litter, and Na, which was significantly higher in the latter. However, the higher annual mass of *Shorea* litter will result in higher annual nutrient return per unit area to the forest when compared to *Koompassia*. When comparing green leaves to leaf litter,

Table 1 Nutrient concentration ($mg\ g^{-1}$ of dry mass $\pm SD$) of green leaves and leaf litter of K: *Koompassia* and S: *Shorea*

Sample	Nutrient concentration ($mg\ g^{-1}$ of dry mass)					
	N	P	Ca	Mg	Na	K
KG	22.43 \pm 0.89 ^a	0.22 \pm 0.10 ^a	1.67 \pm 0.19 ^a	0.49 \pm 0.02 ^a	3.80 \pm 0.54 ^a	0.29 \pm 0.06 ^a
KL	13.7 \pm 1.26 ^b	0.22 \pm 0.02 ^a	0.92 \pm 0.01 ^b	0.34 \pm 0.02 ^b	0.42 \pm 0.04 ^c	0.04 \pm 0.01 ^b
SG	7.45 \pm 0.31 ^d	0.21 \pm 0.02 ^a	0.63 \pm 0.07 ^b	0.23 \pm 0.01 ^c	2.16 \pm 0.54 ^b	0.05 \pm 0.04 ^b
SL	10.55 \pm 0.72 ^c	0.21 \pm 0.03 ^a	0.81 \pm 0.13 ^b	0.29 \pm 0.03 ^b	2.21 \pm 0.07 ^b	0.02 \pm 0.01 ^b

G green leaves, L leaf litter

Different letters indicate significant differences between the samples at $p < 0.05$ within a row

the data revealed consistently higher nutrient concentrations in *Koompassia* green leaves compared to its leaf litter. While *Shorea* leaf litter recorded higher N and Mg values compared to its green leaves, no differences were observed for the remaining nutrient elements.

Aside from nutrient concentration, it is also important to determine the leaf litter nutrient stoichiometry. Among all the nutrients listed in Table 1, N and P are the most common nutrients analysed as they are key nutrients required for plant growth. Therefore, only the leaf N:P ratios were reported. When leaf N:P ratio is <14, it indicates N limitation while values >16 indicate P limitation (Koerselma and Meuleman 1996). In this study, green leaf N:P ratios for *Koompassia* and *Shorea* are 102.0 and 35.5 which suggests P limitation for tree growth at the study site. Compared to green leaves, the leaf litter N:P ratios of both tree species are 62.27 and 50.23, respectively.

Table 2 shows the leaf litter physico-chemical traits of both tree species. These differed for leaf area ($F_{1,38} = 505.26$, $p < 0.01$), total phenols ($F_{1,38} = 23.49$, $p < 0.05$), total tannins ($F_{1,8} = 12.19$, $p = 0.013$), fibre concentration ($F_{1,8} = 20.33$, $p < 0.05$) and cellulose concentration ($F_{1,8} = 507.77$, $p < 0.01$). *Shorea* had higher leaf area and concentration of these litter chemicals compared to *Koompassia* except for phenol concentration where it was higher in the latter. No differences were observed for leaf toughness and lignin concentration between litters of the two species.

Annual changes in nutrient use efficiency and nutrient retranslocation efficiency of *Koompassia* and *Shorea*

Percentage nutrient retranslocation efficiency for *Koompassia* showed that it was capable of retranslocating its

Table 2 Leaf litter traits (mean \pm SD) of KL: *Koompassia* and SL: *Shorea*

Physico-chemical traits	KL	SL
Leaf toughness (kPa)	12,193.58 \pm 410.03	11,826.87 \pm 418.56
Leaf area* (cm ²)	13.68 \pm 3.70	135.15 \pm 23.88
Total phenols* (mg g ⁻¹)	50.15 \pm 7.47	30.67 \pm 2.97
Total tannins* (mg g ⁻¹)	21.11 \pm 6.86	38.92 \pm 7.56
Fibre concentration* (%)	59.17 \pm 3.25	68.01 \pm 2.20
Cellulose concentration* (%)	15.82 \pm 0.53	27.03 \pm 0.84
Lignin concentration (%)	43.46 \pm 2.61	41.10 \pm 2.74

* Significant differences between *Koompassia* and *Shorea* at $p < 0.05$

nutrients (except P) before leaf fall while negative values of % NRE for *Shorea* indicated that its nutrients (except for K) were retained in the senescing leaves (Table 3). However, this should be interpreted with care as only N and Mg concentrations differed between the green leaves and litter of *Shorea* (Table 2). This suggests that only N and Mg were retained in the senescing leaves of *Shorea* and the tree is not capable of retranslocating the rest of its nutrients except for K. Nutrient use efficiency depends on the ability of plants to reabsorb nutrients from the soil and also on their ability to store and use the nutrients (Biswas and Khan 2011). In this study, the NUE of *Koompassia* is low compared to the values reported by Biswas and Khan (2011) which ranged 103–5,428 but the % NRE was higher. This suggests that the nutrient retranslocation in *Koompassia* is high and it also suggests that the tree is suffering from nutrient limitation; thus it is minimizing the loss of nutrients to the environment. The NUE of the different nutrient elements in *Koompassia* was ranked as follows: Mg > Ca > N > K > Na > P.

Relationships among the leaf litter nutrient quality, physico-chemical traits and leaf litter types

Replicates of leaf litter samples from both tree species formed two separate clusters (Fig. 2) indicating that both tree species produced leaf litter with significantly different physicochemical properties. The data also indicate that *Koompassia* produces higher quality litter compared to

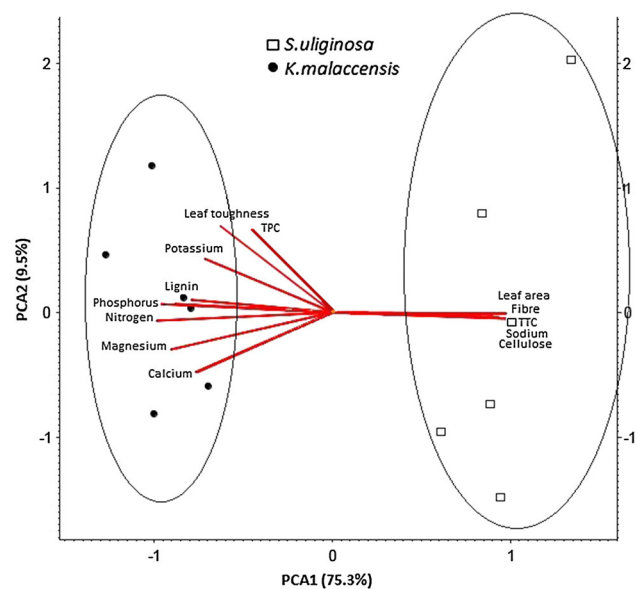


Fig. 2 Ordination of plant physico-chemical properties of *K. malaccensis* and *S. uliginosa* with respect to the first two principal components of the correlation matrix. Plots that cluster together have similar physico-chemical properties

Shorea. *Koompassia* litter exhibited higher nutrient content (total nitrogen, total phosphorus, calcium, magnesium and potassium) and also higher % lignin (Fig. 2). *Shorea* litter had low amounts of nutrients but higher total tannin content, % cellulose, % fibre and leaf area. PC1 was shown to explain 75.3 % of the variations observed between the two species and both PCs combined account for 84.8 % of the variations observed. This indicates that the variables measured are sufficient to explain the differences observed between the leaf litters of the two species.

Climatic measurements

During the study period, the total precipitation was 2,002 mm, which was in the range of annual rainfall in Peninsular Malaysia (2,000–3,000 mm). According to MMD, there are two main rainfall peaks in a year, which generally occur during October to November and April to May. Results obtained showed that the highest rainfall occurred in November followed by August and May. The study period showed a similar rainfall pattern to the general annual rainfall pattern in Peninsular Malaysia but a peak was also observed in August. Minimum rainfall generally occurs in January to February and June to July. However, during the study period minimum rainfall was observed in December and April. Mean maximum and minimum temperatures at the study site were stable throughout the study period with values of 31.6 ± 0.5 and 23.8 ± 0.2 °C, respectively (Fig. 3).

Relationship between litterfall and climatic variables

When the data between litterfall and climatic variables were analysed, significant correlation was only observed between monthly litterfall of *Shorea* and rainfall ($r = -0.644$, $p = 0.024$) (Table 4). The negative correlation obtained indicates higher leaf litterfall during the dry season, as shown by the highest recorded value of *Shorea* leaf

Table 3 % Nutrient retranslocation efficiency (NRE) and nutrient use efficiency (NUE) of *Koompassia* and *Shorea*

Nutrients	<i>Koompassia</i>		<i>Shorea</i>	
	%NRE	NUE	%NRE	NUE
N	47.35	13.81	−41.61	−
P	0	0	0	0
Ca	44.91	14.56	−28.57	−
Mg	30.61	21.36	−26.09	−
Na	88.95	7.35	−2.31	−
K	86.21	7.59	60.00	26.12

NUE for *Shorea* was not determined as negative values were obtained for its %NRE

Table 4 Correlation matrix indicating the correlation coefficient (r) of litterfall and environmental variables

Sample	Rainfall (mm)	Minimum temperature (°C)	Maximum temperature (°C)	Rainy days (days)
KL	−0.106	−0.382	−0.548	0.259
SL	−0.644*	−0.308	−0.189	−0.257

The correlation coefficients are marked * when $p < 0.05$

litterfall (Fig. 1) in the driest month (December 2012) of the study period (Fig. 3). No correlations were observed between monthly litterfall and temperature which is as expected because temperature showed little variation throughout the study period.

Discussion

Litterfall production of *Shorea* and *Koompassia*

In this study, the annual leaf litterfall mass of *Shorea* (918.14 g m^{-2}) and that of *Koompassia* (388.17 g m^{-2}) were comparable to data obtained from other tropical regions where annual species leaf litterfall ranged between 210 to 970 g m^{-2} (Cuevas and Lugo 1998; Hansen et al. 2009; Chave et al. 2010). Broadleaf forests generally have high litterfall, and among these, tropical moist broadleaf forests produce the highest litterfall, which can be attributed to the high productivity and high allocation of biomass to leaves in tropical regions (Liu et al. 2004).

When comparing litterfall mass between the two selected tree species, *Shorea* produced higher mass of leaf litter compared to *Koompassia*. Litterfall mass has been particularly noted to be associated with leaf lignin content. This point has been highlighted in a study conducted by Campanella and Bertiller (2008) in Patagonian Monte, a northeastern region of Chubut Province (Argentina), whereby high leaf litterfall masses of *Chuquiraga avelanadae*, *Chuquiraga hystrix* and *Atriplex lampa* were found to be associated with their high leaf lignin concentration. In this study, both leaf litter species had comparable lignin concentrations but the leaf size of *Shorea* was markedly greater than *Koompassia*, which could possibly be the main factor that explains the difference in litterfall masses between the two species. Nevertheless, it should be noted that the lignin concentration for a collection of other plants in published datasets is much lower (4–13 %) than the lignin concentration of *Koompassia* and *Shorea* (≈ 40 %). The high lignin concentrations could be an adaptation to reduce herbivory in the low nutrient environment of the peat swamp (Cornelissen and Thompson 1997). Trees growing in nutrient-poor ecosystems are also

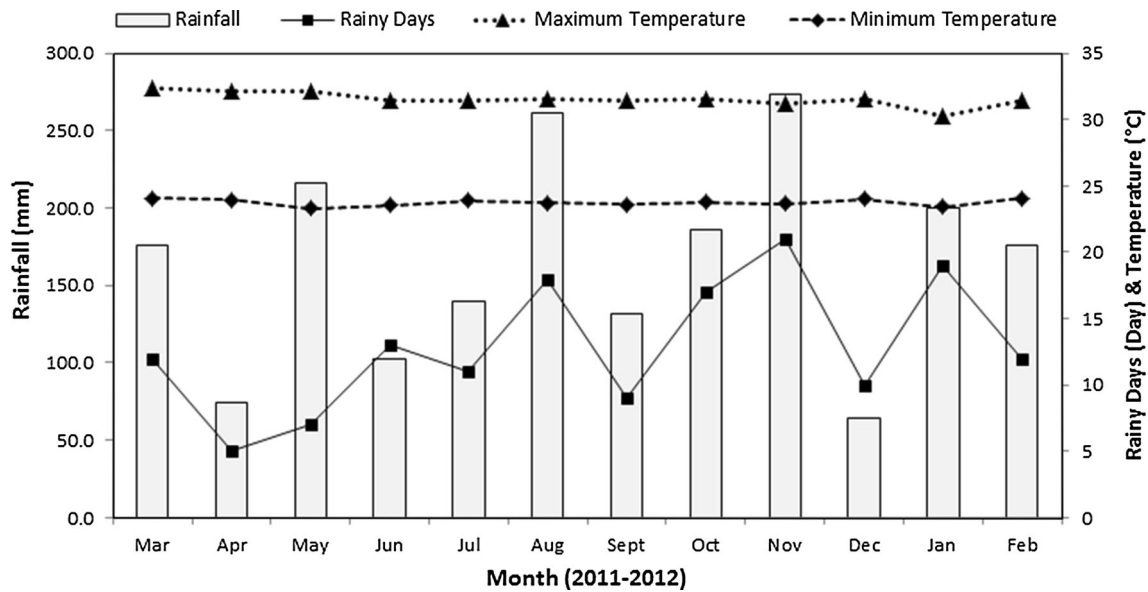


Fig. 3 Monthly records of total rainfall, minimum temperature and maximum temperature at Sungai Karang, North Selangor region, from March 2011 to February 2012. Temperature values are expressed as mean \pm SE

known to produce resistant litter to reduce the rate of litter decomposition and thus, nutrient mineralization in order to prevent surrounding fast-growing plants from outcompeting them.

Regulation of nutrients via litterfall and retranslocation within plant

The chemistry of the green leaves of the selected tree species was also compared to their leaf litter to detect any possible mechanism that could be used by the tree to conserve nutrients. The N and P concentration of green leaves and leaf litter of both tree species were comparable to other evergreen tropical plants but the concentrations of other nutrients were much lower (Cuevas and Lugo 1998, Campanella and Bertiller 2008). To examine possible mechanisms that may be involved in nutrient management, NUE and %NRE have been commonly used to describe the phenomenon. Results showed that the *Koompassia* had positive %NRE and NUE values while mostly negative values were obtained for *Shorea*. This suggests that *Koompassia* is capable of reabsorbing or retranslocating its nutrients from its leaves before leaf abscission while *Shorea* is not. It also suggests that *Koompassia* is capable of using the nutrient elements more efficiently, which enables it to survive in the extreme condition of the TPSF. Recovery of foliar nutrients from senescing leaves is a common phenomenon in plants growing on nutrient-poor soils (Milla et al. 2005) as this allows the plant to gain some independence from the soil nutrients. Aside from nutrient uptake, recovery of nutrients is also an important

component in nutrient conservation as it increases the residence time of nutrients within plants and reduces loss of nutrients to the surrounding environment. The results are in accordance with the study done by Milla et al. (2005) whereby plants with higher nutrient status are capable of recovering more nutrients from their senescing leaves as they have a higher amount of retranslocable nutrients as compared to low nutrient status plants. This explains the higher difference in nutrient content observed between *Koompassia* green leaves and its leaf litter as compared to *Shorea*, and this could be related to the fact that, as a legume, *Koompassia* is able to fix nitrogen. However, care should be taken in making conclusions using the results obtained as a solid conclusion can only be made about the selected tree species when a larger study involving the entire area of the forest for an extended period of time is conducted. Such studies should also include the study of the selected tree species in other TPSF.

The higher N and Mg content in *Shorea* litter as compared to its green leaves may be due to nutrient assimilation in the senescing leaves of *Shorea*. Similar results of negative %NRE have also been obtained in other studies involving *Phyllostachys pubescens* Mazel ex J. Houz (Lin et al. 2004) as well as mangrove trees such as *Kandelia candel* (L.) Druce, *Rhizophora stylosa* Griff., *Bruguiera gymnorhiza* (L.) Lamk (Lin and Wang 2001), *Rhizophora harrisonii* Leechm (Ricardo 1989) and *Arctostaphylos patula* Greene (Schlesinger et al. 1989). As *Shorea* did not display an ability to recover N from its leaves, this suggests that it is dependent on available N from the soil and subsequent uptake of N by its roots. For total P content, data

obtained differ from the remaining plant nutrients measured whereby no differences were observed between the green leaves and leaf litter of all samples. This can be an indication that both *Koompassia* and *Shorea* do not recover P from their senescing leaves but rely more on uptake of P by their roots. Another possible explanation for this is the acidic conditions of the forest itself (pH ≤ 4) and the interaction with peat microorganisms. According to Risswan (1989), acidic conditions facilitate the chelation of phosphate complexes which then enables plant extraction and uptake of P from peat.

Aside from foliar nutrient recuperation, trees are also known to use leaf chemicals and litterfall mass to regulate the nutrient return to the forest substrate via litterfall. The main nutrient cycling process that is affected by this is litter decomposition. Leaf chemical compounds such as phenols, tannins, fibre, cellulose and lignin have been reported to negatively affect decomposition by inhibiting processes such as N fixation and mineralization (Kraus et al. 2004; Wurzbürger and Hendrik 2007) as well as acting as toxins to neighbouring plants and microorganisms (Kuiters 1990; Hattenschwiler and Vitousek 2000; Fierer et al. 2001; Bais et al. 2003; Meier and Bowman 2008; Ushio et al. 2008). In this study, *Shorea* leaf litter had higher concentrations of plant defensive chemicals such as tannins, fibre and cellulose while *Koompassia* had higher concentration of phenols. Overall, *Koompassia* produces higher quality litter with higher nutrient content and lower concentrations of secondary compounds compared to *Shorea* (Fig. 2). Despite the lower mass of *Koompassia malaccensis* litter, its higher quality can provide an important pulse of nutrients to its surrounding environment, which will enable it to survive in the harsh nutrient-poor environment of the TPSF. *Shorea* may compensate for this by producing larger mass of litter. Therefore, *Koompassia* and *Shorea* both regulate the nutrient return via litterfall through different mechanisms whereby *Koompassia* may rely on high quality litter despite low litterfall mass while the opposite was observed for *Shorea*. These particular mechanisms have also been observed and described in other studies (Lugo et al. 1990). In order to better understand the mechanisms involved in litterfall and nutrient return of the selected tree species, a study that involves the identification and analysis of all the litter components (flowers, seeds, fruits, etc.) belonging to the selected tree species would be ideal. However, this proves to be a difficult process in a tropical forest due to the high diversity of plant species.

Litterfall pattern

Another important aspect of the litterfall is the annual litterfall pattern. Both tree species were observed to shed

their leaves once a year albeit at different times. *Koompassia* and *Shorea* are evergreen or semi-evergreen tropical moist forest tree species, which typically have long leaf life spans due to the low resource costs to support leaf life span and by producing leaves that have a longer duration of photosynthetic activity (Singh and Kushwaha 2005). The leaf life span of these types of tree is usually around 1 year (Singh and Kushwaha 2005), which supports the data obtained from this study. The chemistry of the leaf litter may also explain the single shedding event observed in this study. Leaves that have high amounts of secondary metabolites and have high tensile strength such as those of *Koompassia* and *Shorea* will usually have long leaf life spans as this reduces the amount of resources required for drought or herbivory tolerance. Long leaf life span is also a common characteristic for plants growing in water and N-stressed ecosystems such as the TPSF, which allows the plant to utilize N for an extended period of time (Campagnella and Bertiller 2008). Furthermore, the leaf nutrient profile of both tree species also showed that they are both late successional tree species, which typically have long leaf life spans.

Interaction between litterfall and climate

When litterfall was tested for interactions with climatic variables, no interactions were observed except for a weak negative correlation between *Shorea* litterfall and rainfall. Litterfall events during the drier part of the year have been frequently observed and described in many studies especially in tropical regions as water stress during the dry season promotes litterfall (Zhang et al. 2014). This has previously been reported as a survival strategy of *Shorea* trees that shed their old leaves of different ages during the dry season to prevent water loss via transpiration (Singh and Kushwaha 2005). However, given that the TPSF is permanently waterlogged, the trees would never actually experience water stress during dry periods; instead the lowering of the water table would decrease the size of pools and provide an increase in area of the forest floor that is above the water table. Further studies (Ong in prep.) showed that litter decomposition in Sungai Karang PSF is faster in leaves exposed on hummocks than those submerged in pools. Consequently, increased litterfall in the dry season could be an adaptation to promote more rapid litter decomposition and remineralization of nutrients.

Despite a weak negative correlation between *Shorea* litterfall and rainfall, this is an indication that *Shorea* may be more sensitive to weather or climate changes as compared to *Koompassia*. With the increasing rainfall variability along with longer periods of drought as projected by climate studies, *Shorea* may increase its annual leaf litterfall in response to that, as it has been documented to

shed its leaves during the dry period. However, more studies will be required to verify this. Aside from leaf litter, seed production may also be affected by climate change whereby germination and growth of certain seeds may be positively affected by dry periods or infrequent rainfall while others may not. In a study conducted by O'Brien et al. (2013), infrequent rainfall was found to positively affect germination of large seeds but negatively affect their growth while the opposite was observed for small seeds, which are also known to prefer growing in wetter areas. In general, large-seeded tree species tend to produce leaves with greater area and vice versa. In this study, *Shorea* produces larger leaves compared to *Koompassia*, which may suggest that its seeds have a greater mass as compared to the latter. Hence, higher seed production may be observed for *Shorea* during the dry season as compared to *Koompassia*. This can be another indication that *Shorea* is more affected by drought as compared to *Koompassia*, which is a good point to be considered for future studies on litterfall in TPSF.

Aside from dry periods, lower radiation paired with higher number of cloudy days during the rainy season also reduces tree photosynthetic rate and litterfall. In other tropical studies, mean minimum and maximum temperature as well as distribution of rainfall (number of rainy days) have been associated with litterfall (Williams-Linera and Tolome 1996; Liu et al. 2004; Chave et al. 2010) but similar interactions were not observed in this study due to the relatively aseasonal climate, with no seasonal changes in temperature.

The limited relationship observed between litterfall and climatic variables could also be due to the slightly unusual climatic pattern observed during the particular study period. The mean annual minimum and maximum rainfall events observed at the study site differed slightly from the mean annual pattern observed on the west coast of Peninsular Malaysia. *Shorea* litterfall occurred just before the normal dry period while *Koompassia* litterfall occurred during the typical, dry period. There is a possibility that the trees were adapted to the more typical annual rainfall pattern. Furthermore, recent studies span unusual or unstable climatic periods that resulted in drought in 2005 or extremely long rainy season such as the La Niña from 2008 to 2009 (Chave et al. 2010). Such data may not represent the long-term seasonality pattern and thus, this study may not be comparable to those datasets. Besides that, we should not disregard the fact that litterfall can also respond to variations in solar radiation (Wright and van Schaik 1994), rate of litter decomposition (Cuevas and Medina 1988), stand age, soil fertility (Vitousek 1984), heavy winds or rain (Cuevas and Lugo 1998) as well as interactions between plant species as well as other organisms such as pollinators and herbivores in an ecosystem.

Conclusion

Koompassia malaccensis and *Shorea uliginosa* in Sungai Karang TPSF showed marked differences with respect to litterfall mass produced despite the homogeneous TPSF environment. They exhibited differences in terms of internal and external nutrient regulation whereby the former was suggested to rely on nutrient retranslocation to living tissues from senescing leaves as well as a higher litter quality despite low litterfall mass while the latter used higher litterfall mass to compensate for low litter quality and, was also suggested to depend more on uptake of nutrients from the soil. Both tree species were shown to have a single shed annually and little or no relationship was observed between litterfall and climatic variables due to the relatively aseasonal climate. The data obtained contribute to the knowledge of litterfall process in the tropics where it is poorly understood especially in the unique TPSF of Southeast Asia. A better understanding of this process is vital as it aids in the appropriate management of the rapidly vanishing peat swamp forests and the conservation of the selected emergent tree species which are heavily logged in the region.

Author contribution The first author, Cheryl S. P. Ong, was involved in designing the research, acquiring research data, analysis as well as interpretation of data and drafting of the manuscript. Assoc. Prof. Yule CM and Assoc. Prof. Juan JC are the first author's main supervisor and co-supervisor, respectively, who were involved in the study conception and design as well as the revision of the manuscript.

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Conflict of interest The authors declare that they have no conflict of interest.

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