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Seasonal variation in the litter chemical quality of a wet evergreen forest in the Western Ghats

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Seasonal pattern in the resource quality of freshly fallen leaves in a wet evergreen forest floor of Western Ghats was assessed. High resource quality litter was shed during monsoon seasons and low quality litter during the summer season. We propose that the observed variations are related to nutrient source–sink interactions during summer periods and pulse of increased soil nutrient availability and uptake during rainy season, resulting from wind-mediated green leaf fall. Significant seasonal variations in the nutrient content of fresh litter suggest complex decomposition patterns during different seasons of a year.

Keywords: Evergreen rain forest, litterfall, nutrient levels, seasonal variation, Western Ghats.

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THE view that tropical evergreen rainforests are static communities which function under consistently optimal moist and warm climatic conditions[1], has changed with the recent recognition of a strong seasonality of leaf litterfall, with a peak at the end of the dry season followed by a surge in nutrient availability in the forest floor[2]. The following potential mechanisms lead to seasonal variation in leaf litter quality in tropical wet forests. (i) Rainfall-mediated leaching of nutrients from live and senescent leaves and decomposing litter in forests[3], known as low nutrient and high rainfall hypothesis. (ii) Stronger winds during high precipitation and consequent rise in nutrient-rich green litterfall[4]. (iii) Persistent cloud cover and reduced insolation reaching the canopy during rainy seasons leading to lower photosynthetic rates and lower litter nutrient levels in wet tropical forests[5]. (iv) Fall in litter nutrient concentration arising from mobile nutrients from old tissue (source) to new tissue (sink) during flushing of new leaves and fruit production[6,7] in summer. (v) Premature senescence of leaves due to water stress during non-rainy periods[8].

Despite these evidences indicating the influence of seasonality on patterns of nutrient cycling in wet evergreen tropical rainforests, litterfall nutrient measurements beyond a single season are never considered in the tropical moist evergreen forests of the Western Ghats. In the present study, we report the seasonal variation in leaf litter nutrient levels of freshly fallen litter present in a wet evergreen forest in the western windward region of the Western Ghats.

The study was conducted in a wet evergreen forest at Chanthanathode, North Wayanad, the Western Ghats eco-region (11°50′N lat. and 75°49′E long.), 800 m asl and having an area of 85.12 sq. km. An annual precipitation of 3752 mm was received during the study period (2002–03), of which 81% was received during the southwest monsoon (June–August), 10% during the northeast monsoon (September–November), 8% during summer season (March–May) and 1% during presummer season (December–February; KSEB Rain Gauge Station, Periya).

Two samples of freshly fallen litter were collected using 20 × 20 cm wooden frame from randomly located plots of 20 m × 80 m, three times during a season and covering all ffour seasons in 2002–03. Samples were dried at 30°C to constant weight, ground and passed through a 1 mm mesh screen. Thereafter, required amount of sub-samples of litter were taken for nutrient analysis. Total phenols were quantified by Folin Ciocalteu method[9], carbon by Walkley and Black method[10], nitrogen levels by micro-Kjeldahl digestion[11] followed by distillation and titration; Na, Ca and K levels by acid digestion and flame photometery[12] and lignin by acetyl-bromide extraction procedure[13]. All analyses were carried out in triplicate and mean values were taken. Significance levels of the seasonal variation in chemical variables were analysed using non-parametric statistics (Mann–Whitney U test) after multivariate com-

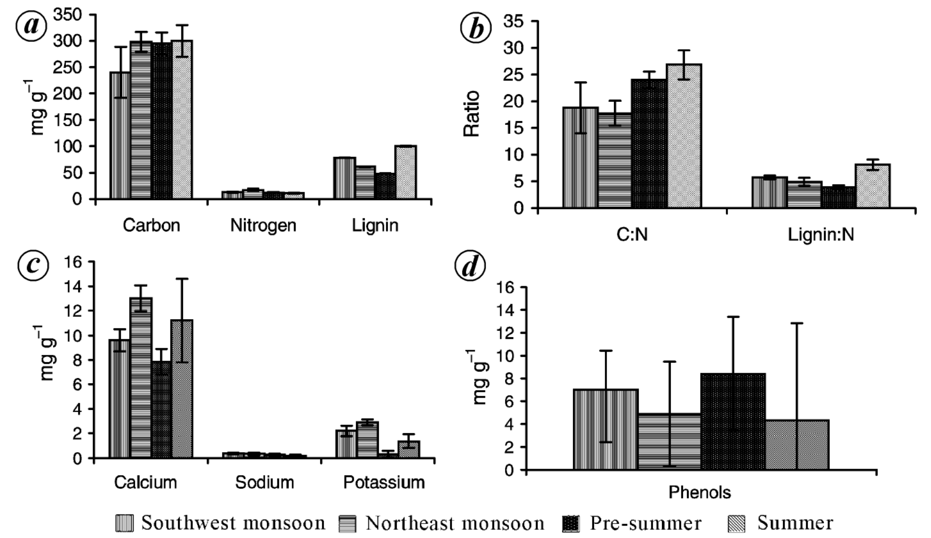

Figure 1. Seasonal variation in the levels of (*a*) carbon, nitrogen and lignin, (*b*) C : N and lignin : N, (*c*) calcium, sodium and potassium, and (*d*) total phenols (mg g^{-1}) in freshly fallen litter in a wet evergreen forest in Wayanad region of the Western Ghats.

parison through Kruskal–Wallis H test. Statistical analysis was done with GRETL software, version 0.93.

Significant seasonal variation ($P < 0.05$) in the levels of litter chemical variables was evident with a peak during rainy season and low values in dry periods (Figure 1; Table 1). The C : N values were <25, except during summer season. High levels of total phenols and low levels of L : N and lignin were recorded during presummer season. N levels peaked during the northeast monsoon and carbon, lignin, L : N and C : N during summer season. Sodium levels were high during the southwest monsoon, while calcium and potassium levels peaked during the northeast monsoon season.

According to the litter quality indices, viz. C : N and cation levels, litter of high resource quality is shed during the monsoon seasons and of low quality during summer and presummer seasons. High resource quality of litter during monsoon must be related to the pulse of increased soil nutrient availability at the beginning of the rainy season[8] and to the wind-mediated green leaf fall deposition by branch-breaking and by the thrashing action of branches on leaves during monsoon seasons in evergreen forests[14]. Though significant seasonal differences in litter quality were evident, on the basis of a threshold value of 25 (for mineralization) for C : N, it can be stated that the litter of the study habitat was not N-limited, except during summer season[15]. Plant litter[15] is considered as high quality when C : N < 25 and of low quality when C : N > 25.

Significantly high values of C : N during presummer and summer result primarily due to low nitrogen concentration, as C levels do not vary much during the period. We associate this to the source–sink interactions related to peak fruit production and leaf flushing in tropical rainforests[2] and also to the initiation of flowering and fruit production in the region. According to the source–sink interactions, when new plant tissue (fruits and leaves) is produced, greater translocation of mobile nutrients from old tissue (senescent leaf/source) to new tissue (sink) occurs[7]. On an average, plants withdraw about 50% of leaf N prior to leaf abscission[16], with most retranslocated to well-lit, newly developing leaves. Therefore, if senescing leaves are a good source of mobile nutrients, lower leaf litter nutrient concentrations during presummer period could be related to initiation of reallocation of nutrients from senescent leaves, and in summer to the intensive foliar reallocation of nutrients during the peak of leaf flushing and fruit production in the region. Sharp decline in C : N values during the southwest monsoon season is due to the increased soil nutrient availability and green leaf fall during rainy season, leading to a steep rise in N levels. Green leaves have significantly higher nitrogen concentration and lower lignin to nitrogen ratio compared to senescent leaves[14]. Prior to the fall of senescent mature leaves, plants reallocate mobile nutrients, especially N[3]. However, when leaves are lost due to unexpected hazards like wind-mediated fall, where the plant does not have the opportunity to withdraw nutrients, foliar nutrient withdrawal is more or less zero, leading to a seasonal rise in litter nutrient pool[17], as observed in the region during the southwest monsoon.

High levels of all major cations, viz. Ca, Na and K during the rainy season are probably related to wind-mediated green-leaf deposition and high nutrient reabsorption from the soil. Low Ca, K and Na levels during presummer and summer indicate nutrient sink absorption associated with the fruiting–flushing events as well as retrieval by plants prior to leaf fall. However, what leads to high levels of Ca during the summer season is not understood.

Increase in phenol levels during the southwest monsoon might be due to the addition of green leaf fall. Presummer rise in phenol levels could be related to the rise

Table 1. Results of Kruskal–Wallis and Mann–Whitney tests on seasonal variation of biochemical parameters

Biochemical parameters	*P*	*H*	Differences found (Mann–Whitney at 5%)
Carbon	< 0.05	8.65	s.w < p.s.; s > s.w. < n.e.
Nitrogen	< 0.05	14.15	p.s. < n.e. > s.w. > s; n.e. > s
C : N	< 0.05	15.61	n.e. < p.s. > s.w. > s > n.e.
Lignin	< 0.05	21.63	p.s. < s.w. < s > p.s. < n.e. < s
Lignin : N	< 0.05	19.73	s.w. > p.s. < s > s.w. > n.e.; p.s. < n.e.
Sodium	< 0.05	14.00	p.s. < s.w.; s.w. > s < n.e.
Calcium	< 0.05	15.86	s.w. < n.e. > p.s. < s
Potassium	< 0.05	19.78	n.e. > p.s. < s.w. > s
Total phenols	< 0.05	19.50	n.e. < p.s. > s.w.; p.s. > s < s.w. > n.e.

s.w., South-west monsoon; n.e., North-east monsoon; p.s., Pre-summer, and s, Summer.

in herbivore and pathogen pressure in humid forests, succeeding the long wet monsoon periods[18]. Sudden changes in photosynthetic productivity of canopy trees linked to the solar insolation availability after cloud covered monsoon periods lead to variation in foliar nutrient levels[5]. However, we are unaware of how much the differences in average daily light availability during the rainy season contributed to the observed patterns of litter nutrient variability and abundance of herbivore in the study region.

We observed higher lignin : nitrogen ratios during summer and southwest monsoon seasons. High availability of rainfall and low water stress increase allocation to carbon-rich compounds such as lignin[19] and possibly other phenolic and primary metabolites in mature leaves. So the high lignin levels which are negatively correlated with herbivory as indigestible to most insects[20] during the summer and southwest monsoon seasons might be a structural defence mechanism against herbivory during leaf expansion facilitated by low water stress in the region. However, such antiherbivore defences may function against decomposers during decomposition[21]. Hence, it is reasonable to expect that litter with high initial lignin shed during summer and southwest monsoon seasons would remain in the humus pool of the region as accumulated recalcitrant materials for prolonged period[22], than litter fallen during other seasons.

Seasonal variation in L : N and C : N values of fresh litter indicates that litter of variable quality is produced. Hence the limit value[15] of the litter shed during each season might be varying, unless climate and fauna strongly influence litter decomposition. These observations highlight the need to conduct litter decomposition studies in evergreen forests, employing litter shed during different seasons as against the general practice of employing single-season litter, as it would potentially miss the influence of seasonal variations of litter quality on these processes. High levels of litter nutrients during the rainy season indicate increased nutrient reabsorption from soil. This necessitates further research on seasonal changes in forest floor soil nutrient availability in the moist evergreen forests of the Western Ghats, which will broaden our understanding of how seasonal variation in soil nutrient availability affects canopy leaf traits as well.

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Fundamental mass ratio relationships of whole-rock chondritic major elements: Implications on ordinary chondrite formation and on planet Mercury's composition

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The high occurrence on earth of ordinary chondritic meteorites and the making of models based upon assumptions has led to some confusion about the origin of ordinary chondrites and their role in planet formation. Major element fractionation among chondrites has been discussed for decades as ratios relative to Si or Mg. Expressing ratios relative to Fe leads to a new relationship admitting the possibility that ordinary chondrite meteorites are derived from two components: one is a relatively undifferentiated, primitive component, oxidized like the CI or C1 chondrites; the other is a somewhat differentiated, planetary component, with oxidation state like the reduced enstatite chondrites. Such a picture would seem to explain for the ordinary chondrites, their major element compositions, their intermediate states of oxidation, and their ubiquitous deficiencies of refractory siderophile elements. I suggest that the planetary component of ordinary chondrite formation consists of planet Mercury's missing complement of elements, presumably separated from protoplanetary Mercury during its formation.

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Keywords: Asteroid, element fractionation, mercury, meteorite formation, ordinary chondrite.

DIFFERENCES in mean densities of the terrestrial planets have long been interpreted as implying differences in the major element compositions of the inner planets. As first noted by Urey[1], the planet Mercury consists mainly of iron; at some point during the formation of Mercury, a significant portion of the silicate-forming elements, originally associated with that mass of iron was lost[2,3]. Although various mechanisms have been proposed to account for the high density of Mercury[4], the ultimate fate of its complement of lost elements, what became of them, has not, to my knowledge, been addressed.

The constancy in isotopic compositions of most of the elements of the earth, the moon, and the meteorites indicates formation from primordial matter of common origin. Primordial elemental composition is yet manifest and determinable to a great extent in the outermost regions of the sun. The less volatile rock-forming elements, present in the outer regions of the sun, occur in nearly the same relative proportions as in chondritic meteorites. For more than a century, chondrite compositions have been considered relevant to the bulk compositions of the terrestrial planets[5–8]. But chondrites differ from one another in their respective proportions of major elements[9,10], in their states of oxidation[11,12], mineral assemblages[13], and oxygen isotopic compositions[14] and, accordingly, are grouped into three distinct classes: enstatite, carbonaceous and ordinary. Understanding how these three distinct classes originated and how they are related to the compositions of planets are among the most fundamental problems in solar system science.

The ordinary chondrites comprise 80% of the meteorites that are observed falling to the earth. Last century, during the 1970s, the widely cited 'equilibrium condensation model' was predicated on the assumption that minerals characteristic of ordinary chondrites formed as condensate from a gas of solar composition[15]. However, Herndon and Suess[16] demonstrated from thermodynamic considerations that the oxidized iron content of the silicates of ordinary chondrites was consistent instead, with their formation from a gas phase depleted in hydrogen by a factor of about 1000 relative to solar composition. Subsequently, the present author[17] showed that if the mineral assemblage characteristic of ordinary chondrites