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Litterfall and nutrient return along a disturbance gradient in a tropical montane forest

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ABSTRACT

Litterfall plays an important role in nutrient cycling and maintenance of soil fertility in terrestrial ecosystems. Annual and seasonal variation in litterfall have been investigated in various habitats, however, seasonality in nutrient supply is less well documented. We studied litterfall over two years and seasonal litter nutrient input over one year across a tropical disturbance gradient from mature forest to monoculture tea plantation. Total litter production in the mature forests and regenerating forests was not significantly different. However, tea plantations had significantly lower litter production. Total litterfall in forest habitats showed a clear seasonal pattern with a peak during the dry season (Mar.–May), as has been reported for other tropical seasonal forests. Contrary to expectations, there was no significant difference in litter nutrient concentrations across the disturbance gradient, although there was a substantial change in plant species composition. Litter nutrient concentrations also did not vary significantly across seasons, again contrary to our expectations. Thus, nutrient input was driven solely by the seasonal litterfall pattern. Our results suggest that at a landscape scale turnover in species composition linked to anthropogenic disturbance may not always lead to changes in litter quality, presumably because a similar spectra of leaf types may exist across communities. Seasonal litterfall patterns, which have been more commonly studied, may prove a reasonable proxy for nutrient input in forests.

1. Introduction

Litterfall and litter decomposition are the most important pathways for the transfer of nutrients from aboveground vegetation to soil (Berg and McClaugherty, 2014; Vitousek, 1982; Vitousek and Sanford, 1986) and are essential processes in maintaining the long-term forest nutrient status (Sayer and Tanner, 2010; Sayer et al., 2012; Tang et al., 2010; Vitousek and Sanford, 1986). For example, an experimental litterfall manipulation in a tropical forest drove rapid and substantial changes in the surface soil C pool (Leff et al., 2012), a doubling of litter input increased soil C by 31%, while removing surface litter decreased soil C by 26%. Litter turnover in terrestrial ecosystems is also a major carbon flux, and seasonal variation in litterfall and decomposition contributes to seasonal differences in the carbon cycle (De Weirdt et al., 2012). In addition, the leaf litter layer provides shelter to a wide range of organisms from microbes to small mammals.

Numerous studies have demonstrated that litterfall in forest ecosystems is dependent on seasonality, forest type or species composition, forest age, soil–water retention, and soil fertility (Facelli and Pickett, 1991; Vitousek and Sanford, 1986; Zhang et al., 2014). After reviewing a substantial number of articles, Zhang et al. (2014) reported that peaks of litterfall in tropical forests often occur during the dry season, suggesting that precipitation and radiation are controlling factors. In addition, litterfall seasonality in tropical forests also depends on plant composition, because plant phenological responses to environmental variation vary among species (Cuevas and Lugo, 1998; Duke, 1988; Harrison, 2008; Singh and Kushwaha, 2006; Zalamea and González, 2008). Inter-annual climatic variation is often substantial in the tropics and subtropics, and affects the phenology of the trees leading to irregular production of flowers and fruits, and ultimately drives inter-annual variation in total leaf litterfall (Liu et al., 2002; Sakai et al., 2006; Wright et al., 1999).

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Similarly, litter nutrient concentrations may be dependent on climate, plant species composition, and soil properties (Berg and McClaugherty, 2014; Dent et al., 2006; Liu et al., 2006). For example, across Puerto Rico litter nitrogen (N) concentration was found to be positively correlated with the basal area of N-fixing trees (Erickson et al., 2014). Leaf litter N concentration for different plant functional groups, as well as species overall, had a linear relationship with precipitation and temperature across the Eurasian continent (Liu et al., 2006). Litter chemistry is a critical factor in determining litter decomposition rates at global, regional, and landscape scales (Berg and McClaugherty, 2014; Cornwell et al., 2008; Gholz et al., 2000; Paudel et al., in press). While a number of studies in the tropics have demonstrated a clear pattern of litterfall seasonality, temporal variation in leaf litter nutrient concentrations and total nutrient supply is less well documented (Edwards and Grubb, 1982; Liu et al., 2002; Pande et al., 2002; Wood et al., 2005), although these may be critical for understanding variation in rates of litter decomposition and nutrient availability in forests (Vitousek and Sanford, 1986).

Tropical forests are the most diverse terrestrial systems on Earth. Anthropogenic activities are the main drivers of deforestation and forest degradation, resulting in high levels of biodiversity loss (Barlow et al., 2007a; Gibson et al., 2011; Morris, 2010; Wright, 2005). Forest disturbance generates local variation in the micro-environment, including soil surface temperature and soil moisture, among habitats (Zhang and Zak, 1995) and affects species composition (Estes et al., 2011). These changes in turn alter ecosystem processes, including nutrient cycling and productivity. A number of studies have investigated the effects of disturbance on litterfall, but these have mostly focused on the effects of catastrophic natural disturbances, such as typhoons (Barlow et al., 2007b; Cizungu et al., 2014; Dezzeo and Chacón, 2006; Gairola et al., 2009; Shure and Phillips, 1987; Vendrami et al., 2012). The effects of anthropogenic forest disturbance on litter nutrient quality and nutrient inputs is less well understood.

Our aim was to understand seasonal variation in litter nutrient concentrations and input, including carbon, nitrogen, phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg), across a disturbance gradient in a tropical seasonal rain forest in SW China. To this end, we examined the following hypotheses. (i) Annual leaf-litter flux decreases with increasing disturbance (mature forest > regenerating forest > open tea fields). (ii) Litter nutrient quality decreases with increasing disturbance (mature forest > regenerating forest > open tea fields). (iii) Litter quality varies seasonally, with lower nutrient concentrations in the dry season (wet season > dry season).

2. Methods

2.1. Description of study site

This research was conducted in Mengsong, Xishuangbanna, Yunnan, SW China (UTM/WGS84: 47 N 656355 E, 2377646 N, Fig. 1). Elevation ranges between 1500 and 1900 m asl. The climate is strongly seasonal with 80% of the precipitation occurring during the wet season (May–Oct., Fig. 2). Mean annual precipitation ranges from 1600 to 1800 mm (Xu et al., 2009). Forest in the area has been classified as seasonal tropical montane rain forest, which grades into seasonal evergreen broad-leaved forest on hill slopes and ridges (Zhu et al., 2005). The classification of the forest as a rain forest is based on floristic similarities and forest physiognomy, although the seasonality and total rainfall might suggest otherwise. In this region the colder season coincides with the dry season, creating fogs which reduce the water deficit that would be expected otherwise, enabling rain forest to persist. The forest contains many floristic elements in common with rain forests throughout SE Asia, although Dipterocarps are absent. The evergreen broadleaf forest is floristically similar to more seasonal forests to the north, with many species of Fagaceae and Lauraceae in the canopy.

The landscape has been occupied by Akha people for at least two centuries. Until the Chinese government logging ban in 1998, the Akha practiced slash-and-burn agriculture and depended to a large degree on forests for their livelihoods (Kai et al., 2014; Xu et al., 2009). Since 1998, Akha have increased production of perennial crops, in particular tea, in monocultures, but still depend on the forest for various items, including firewood and mushrooms. In some areas, rough grasslands are maintained for grazing cattle by regular burning. The entire landscape is thus a complex mosaic of mature forest, younger forest regenerating following cultivation or other disturbances, and open habitats including terraced tea fields and degraded, *Imperata* dominated grasslands.

In 2010 and 2011, 28 sampling plots were established throughout the landscape with the aim of obtaining a representative sample of biodiversity across the disturbance gradient (Beckschäfer et al., 2014, 2013; Paudel et al., in press). For biodiversity sampling, plots were divided into a 3×3 grid of nine subplots, with 50 m between subplot centers (Fig. 1).

To obtain an unbiased selection with sample plots of different degradation status distributed across the landscape, we derived plot locations by applying double sampling with stratification. A 500×500 m grid of points was placed over a remotely sensed image (SPOT 5 acquired in Oct. 2009) of the landscape and each point was classified by eye as mature forest, regenerating forest, or open-land. Approximately 10% of the points were ground-truthed to verify our classification and adjustments were made accordingly. Points were accepted as being mature forest if the site was dominated by large (>30 cm dbh) trees with no evidence of recent disturbance (stumps or visible char on trunks). Forests dominated by smaller trees or with signs of recent disturbance were classified as regenerating forest. Most of these were young successional seres re-growing from slash-and-burn, although some were older forests that were highly disturbed, for example, through cultivation of tea in the understory. Open-land points included grasslands and terraced tea fields, with few or no trees. Points landing on water bodies, within villages and within a small area of paddy field next to the largest village were removed from the selection. In addition, we removed points that fell on the boundary between land-cover categories, so that our sample plots could be unambiguously assigned to a single category. Next, we divided the landscape into 16 compact equal-area units from which 12 were randomly selected for sampling, and we selected points within these units using a random number generator. We selected a mature and regenerating forest point in each of the 12 units, although two of the units did not have any mature forest. Open-land points were selected from every second unit, because it was expected that these would be more self-similar and hence require a lower level of replication for our biodiversity studies. Thus, the process resulted in a final selection of ten mature forest points, twelve regenerating forest points and six open-land points.

Vegetation (trees, shrubs, lianas, and herbs) data were collected from all the 28 plots in 2010 and 2011. For each subplot, trees, lianas and bamboos with (dbh) > 10 cm were sampled with a 10 m radius circle and trees, lianas and bamboos with dbh 2–10 cm were sampled from 5 m radius circle. The coverage of herbs and woody plants <2 cm dbh were surveyed within a 1 m radius circle.

2.2. Monthly litterfall collections

For monitoring litterfall, we selected 12 out of the 28 plots based on accessibility. Five were located in mature forest, four in