

Blowing litter across a landscape: effects on ecosystem nutrient flux and implications for landscape management

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Abstract Lateral flows in landscape mosaics represent a fundamentally important process in landscape ecology, but are still poorly understood in general. For example, windblown litter nutrient transfer across a landscape has rarely been studied from an ecosystem perspective. In this study we measured the litter nutrient transfer from an *Acacia mangium* plantation to a *Dimocarpus longan* orchard in an agroforestry landscape for 3 years from January 2002 to December 2004. About 11% of the total litterfall of the acacia plantation were transported to the longan orchard

annually, accounting for ca. 9–59% of the total litter nutrient input of the longan orchard. The windblown litter transfer showed high spatial variation mainly caused by wind speed and directions. Slope positions 5 m away from the source acacia plantation received significantly greater amount of allochthonous acacia litter than those 10 m away, and the northwest-facing slope of the longan orchard received 2 to 3-fold more litter than the southeast- and south-facing slopes because of the prevailing southeasterly wind in the region. To explore how different management practices may influence the litterfall, leaf production, and soil nutrient status of the two ecosystems, we developed a Meta-Ecosystem Litter Transfer (MELT) model to simulate the processes of litter-related transformation (production, deposition, and decomposition) and transfer (wind- and management-driven movement). Our simulation results suggest that less than 30% of acacia litter should be transferred to the longan orchard in order for the acacia plantation to sustain itself and maximize production of the longan. Connectivity of nutrient flow between adjacent ecosystems as shown here leads to a functional meta-ecosystem with higher landscape-scale production of ecosystem services. That is, managing this connectivity through landscape design or active litter transfers can lead to large changes in overall landscape functioning and service production.

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Introduction

Movements of inorganic nutrients, organic matter, pollutants, and living organisms are ubiquitous in natural and managed landscapes. Through these movements, outputs of materials, energy, and organisms from donor patches may become inputs for recipient patches, and can exert important influences on the structure, dynamics, and functioning of both patches and the landscape as a whole (Forman and Godron 1981; Risser 1990; Polis et al. 1997; Loreau et al. 2003; Gravel et al. 2010). Since the biogeochemical cycles of elements are key ecosystem processes, the transformation and vertical flows of elements in the plant-soil continuum have been the main foci of ecosystem ecology. Compared to the vertical ecosystem nutrient cycling, the lateral flows of elements across different patch ecosystems embedded in a landscape or a meta-ecosystem have been less studied (Loreau et al. 2003; Reiners and Driese 2004; Turner and Chapin 2005). Therefore, ecological flows including lateral nutrient fluxes across landscape mosaics have been recognized as one of the research frontiers in landscape ecology (Wu and Hobbs 2002; Turner 2005; Turner and Cardille 2007; Wu and Hobbs 2007).

Materials move between landscape components through mechanisms such as diffusion, gravity, and transport by surface and subsurface runoff, wind, or animals (Cadenasso et al. 2003). Among these driving forces, water-driven nutrient flows across heterogeneous landscapes have received much attention, mainly because excess nutrients (e.g., nitrogen (N) and phosphorus (P)) discharged from croplands and residential areas may cause the widespread problem of nonpoint source pollution in the receiving water bodies such as streams, lakes, and coastal oceans (Carpenter et al. 1998). For example, in an agroforestry landscape consisting of corn fields, riparian forest and stream, Peterjohn and Correll (1984) estimated that about 35 and 17% of the total N and P inputs (from wet deposition and fertilization) were transported from the corn fields into the down slope riparian forest via surface runoff and belowground water; contrastingly only 11 and 20% of the total N and P inputs (from wet deposition and cornfield runoff) were transported from the riparian forest to the stream. In another agroforestry watershed consisting of agricultural fields, forest shelterbelts and meadows, nitrate concentration in the groundwater

beneath the shelterbelts and meadows were found significantly (in some cases 26-fold) lower than those under the adjoining fields, and meadows could retain 90% of the P-PO_4^{-3} in the incoming ground water (Ryszkowski et al. 1999). These results suggest nutrient movements across landscape components are significant and biogeochemical barriers such as riparian forests and shelterbelts can play important role in regulating nutrient/pollutant fluxes (also see Haycock et al. 1997; Lowrance et al. 1997; Baker et al. 2006; Jones et al. 2006; Mayer et al. 2007).

Wind has also been widely recognized as an important driver in transporting materials across landscape components. Most previous studies have focused on wind-eroded dust or soil particles (Breshears et al. 2003; Reiners and Driese 2004; Li et al. 2008). Relative to hydrological and windblown nutrient movements associated with soil solutions or soil particles, windblown litter nutrient transfer and its ecological significance have been less studied. This is despite the fact that litter plays a key role in ecosystem nutrient cycling (Hattenschwiler et al. 2005; Berg and Laskowski 2006). A few studies have shown that wind can play an important role in litter fall and litter transfer processes. In Arctic landscapes, wind often redistributes litter and snow from hill and ridge tops to leeward locations during winter time, subsequently forming patches of litter accrual after the snow melts in spring, which can further reduce photosynthetically active radiation and soil temperature, increase C and N accumulation, and stimulate soil CO_2 efflux at the litter deposition sites throughout the growing season (Fahnestock et al. 2000). In arid and semi-arid landscapes, windblown fine soil particles and plant detritus from inter-shrub spaces help form islands of fertility after deposition on the shrub-occupied patches, therefore altering the spatial distribution patterns of soil properties and posing a sign of desertification (Schlesinger et al. 1996). Nutrients bound in soil particles and plant residues may also be transported from nearby croplands to remnant native woodlands and have negative impacts on the regeneration of native vegetation in semiarid agricultural regions of Australia (Duncan et al. 2008). In riverscapes, most of carbon used by stream organisms originates from litterfall and other materials produced by riparian forests (Fisher and Likens 1973; Johnson and Covich 1997). Thus, windblown litter transfer is a common phenomenon with important ecological impacts in various landscape types and deserves more study.

Under the pressure of human population growth and economic development, it is of paramount importance to use shrinking land resources efficiently in order to harmonize human demand and environment protection such that the production of ecosystem services are sustainably maintained. Agroforestry, being widely practiced in both the developed world such as Europe (Rigueiro-Rodriguez et al. 2009) and North America (Blanco-Canqui and Lal 2008), and the developing countries such as China (Zou and Sanford 1990; Fu et al. 2004), India (Puri and Nair 2004) and Africa (Kwesiga et al. 2003), has been recognized as one of the best land management practices in conserving soil and water, improving farm economy, advancing food security, and mitigating atmospheric and water pollution (Blanco-Canqui and Lal 2008). Agroforestry systems often combine trees/shrubs with crops and/or livestock on the same unit of land, thus forming a spatially heterogeneous landscape or meta-ecosystem comprised of tree plantations, croplands, and/or pastures. With such diverse spatial composition and configuration, agroforestry systems are useful for studying the reciprocal relationships between landscape pattern and ecological processes in the production of ecosystem services. Practically, understanding nutrient transfer across the components of agroforestry landscapes can also provide management guidance to land practitioners and policy makers.

In this study, we chose a typical agroforestry system in southern China to investigate dynamics of wind-blown nutrient transfer between two contrasting patches. This agroforestry landscape occupies a small catchment and is composed of a legume tree (*Acacia mangium*) plantation on the upper slopes (1.3 ha), a longan fruit-tree (*Dimocarpus longan*) garden on the middle (0.87 ha), a fish pond at the bottom (0.29 ha), and a napiergrass (*Pennisetum purpureum*) strip (0.3 ha) along the fish pond banks (Fig. 1). The aim of this design was to create a self-sustaining system that can efficiently control soil erosion and water loss while simultaneously increasing the economic gain of local farmers. In this agroforestry watershed, the acacia plantation can serve to regulate the local climate and control soil erosion from steeper upper slopes; the napiergrass can be used to feed fishes and buffer longan garden originated nutrients; the litter from the acacia plantation and sediments from the fish pond can be moved to the longan garden as organic fertilizers; fish (mainly grass carp and tilapia) and

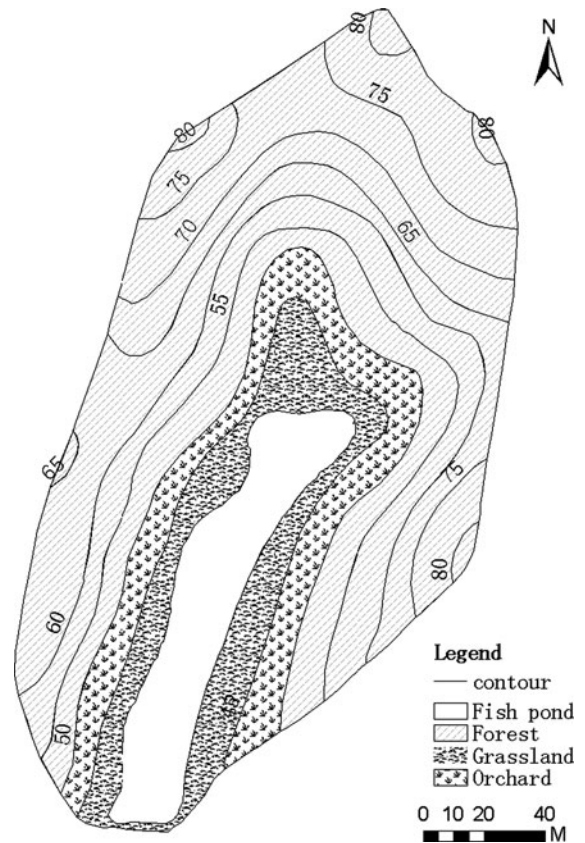


Fig. 1 The spatial composition and configuration of the studied agroforestry landscape

longan fruits are the products to be sold for monetary income. Thus, these systems provide multiple ecosystem services with several direct and indirect consequences for human well-being. Our previous studies on nutrient movements in this agroforestry landscape had been mainly focused on nutrient fluxes associated with hydrological flows and found that groundwater could transport a substantial amount of nutrients (e.g., 1.3–3.7 g N m⁻²) from the acacia plantation to the down-slope patches (Ding et al. 1995; Shen et al. 2007). This study emphasizes windblown- and management-litter nutrient transfer processes that mainly occur between the acacia plantation and the longan orchard.

Specifically, we aimed to quantify the amount of windblown nutrient flow between the two patch ecosystems, analyze how it varied spatially with slope aspects and distance to the source patch, and derive the relationships between windblown litter nutrient transfer and wind conditions. Based on the observed data,

we also aimed to develop a model to simulate the litter-related transformation and transfer processes by viewing the two patch ecosystems as a meta-ecosystem. The model was further used to analyze how different management litter transfer scenarios could influence the litter and nutrient pool sizes of the meta-ecosystem and from these results derive practical guidance on managing the landscape for sustainable production of ecosystem services.

Methods

Study site description

The study site is located at the Heshan National Field Research Station (Heshan-NFRS) of Forest Ecosystems (112°54'E, 22°41'N), Heshan City, Guangdong province, southeastern China. This site is characterized by a typical subtropical monsoon climate. The mean annual temperature is 21.7°C, with the maximum mean monthly air temperature of 29.2°C in July and the minimum of 12.6°C in January. The mean annual precipitation is 1700 mm, nearly 80% of which falls in the wet season from April through September. The soil is an oxisol developed from sandstone, with a pH of about 4.2. The study area is typical of the region with low hills (peak elevation of 98 m) and small watersheds (area of about 3–100 ha). This region was historically covered by evergreen broadleaved forests but its land cover had been transforming into agricultural lands and abandoned hilly slopes since 1960s. Starting from the early 1980s, most of the abandoned hilly slopes were replanted with fast-growing tree species such as *Pinus massoniana*, *A. mangium*, and *Euclyptus citriodora*, and those vicinal to villages were turned into agroforestry systems that are often managed by a group of households.

Litter collection and chemical analysis

Ten litter traps were placed randomly on the acacia plantation floor and 12 were placed systematically on the longan orchard floor. Each of the three aspects of the orchard slope had four litter traps, with two of them 5 m away and the other two 10 m away to the lower edge of the acacia plantation. The litter traps were made from fine nylon mesh cloth (1 mm mesh size) with a size of 1 × 1 m and a depth of 40 cm. The

bottom of the trap was 15 cm above the ground and the top of the trap was supported horizontally. All accumulated materials in the traps were collected every month from January 2002 to December 2004. The materials from each trap were weighted and sorted into leaves, branches, and other with respect to litter species (i.e., acacia and longan). Five subsamples from the pooled litter of each ecosystem were oven-dried at 65°C to constant weight and the water content was calculated based on the fresh weight and dry weight.

Nutrient contents of acacia and longan litter were analyzed twice with litter samples from March 2002 and July 2003. The dry litter samples were first pooled in proportion to quantity and then milled to pass a 1 mm sieve for nutrient analysis. Total organic C and N concentrations were determined by coupled combustion/reduction and gas chromatography (CHN Analyzer, Perkin Elmer II 2400). Dry litter powder was wet digested in a mixture of HNO₃ + H₂O₂. The concentrations of Ca, K, Na, Mg, P and S in the solution were measured by inductively coupled plasma atomic emission spectrometry (ICP AES, Perkin Elmer Optima 3100XL). The size of the subsample for CHN analysis was 0.1–0.3 g and wet digestion 0.5 g.

Observed data analysis

The relationships between litterfall and wind speed (including monthly mean wind speed and peak wind speed) were analyzed using correlation analysis. The difference of acacia litter transfer among the three slope aspects (i.e., southeast-, northwest-, and south-facing slopes, see Fig. 1) and between the two distances (5 and 10 m to the lower edge of the acacia plantation) were analyzed using repeated-measures ANOVA. All the statistical analyses were performed in SPSS 13.0 and SigmaPlot 7.0. The significance level was 0.05.

Model development

Based on the meta-ecosystem concept (Loreau et al. 2003; Gravel et al. 2010) and the approach used to model carbon transfer following soil erosion and deposition (Jenerette and Lal 2007), we built a simple Meta-Ecosystem Litter Transfer (MELT) model to simulate the wind- and management-driven litter transfer processes from the source acacia plantation to the sink longan orchard without considering their spatial variation. Figure 2 is a conceptual diagram of

the MELT model, which consists of two types of pools (leaf biomass and litter pools) and the input, output, and transfer processes determining the dynamics of these pools. Table 1 provides the description and parameterization on the variables used in Fig. 2 and equations below.

The dynamics of leaf biomass pool (B , $g\ C\ m^{-2}$) were determined by the rates of leaf production (P , $g\ C\ m^{-2}\ month^{-1}$) and litter fall (F , $g\ C\ m^{-2}\ month^{-1}$), and the dynamics of the litter pool (L , $g\ C\ m^{-2}$) were determined by the rates of litter fall, litter decomposition (D , $g\ C\ m^{-2}\ month^{-1}$), and litter transfer driven by wind (W , $g\ C\ m^{-2}\ month^{-1}$) and management (M , $g\ C\ m^{-2}\ month^{-1}$), i.e.,

$$\frac{dB}{dt} = P - F \tag{1}$$

$$\frac{dL}{dt} = F - D - W - M \tag{2}$$

To simplify the model for this study and emphasize the effects of litter fall and litter transfer processes, the production rate (P) was calculated as the product of a fixed growth coefficient (μ , $month^{-1}$) and a N modifier $f(N)$ (i.e., $P = \mu \cdot f(N)$), where μ for acacia and longan were derived from literature (Shen

et al. 2003; Fu et al. 2010) and the calculation of $f(N)$ shall be described later in Eq. 7. Litterfall rate (F) was modeled by subtracting a fixed proportion (λ) of leaf biomass (B) in each month (i.e., $F = \lambda \cdot B$). The proportion (λ) was the ratio of the observed monthly litterfall to the total annual litterfall. The litter decomposition rate (D) was a product of the decomposition coefficient (k), litter mass (L), and temperature scalar ($f(T_s)$):

$$D = k \cdot L \cdot f(T_s) \tag{3}$$

where k ($month^{-1}$) was derived from literature (Li et al. 2001) and had a lower value for acacia than that for longan (see Table 1). The k value for the mixed acacia and longan litter was a weighted average based on the proportion of the two litter species. The temperature scalar $f(T_s)$ incorporated temperature (T_s) influences on litter decomposition:

$$f(T_s) = 0.0326 + 0.00351 \cdot (T_s)^{1.652} - \left(\frac{T_s}{41.748}\right)^{7.19} \tag{4}$$

although this function was not specifically derived from the acacia and longan ecosystems, it had been used as a general modifier for a variety of ecosystem

Fig. 2 A conceptual schematic diagram of the MELT (Meta-Ecosystem Litter Transfer) model. Boxes represent pools; pipe lines with arrows represent processes that link the pools; circles represent the auxiliary variables used to calculate the rates of processes; and thin lines with arrow show the connections among pool, process, and auxiliary variables. Descriptions and initial/fixed values of all the variables are given in the Table 1

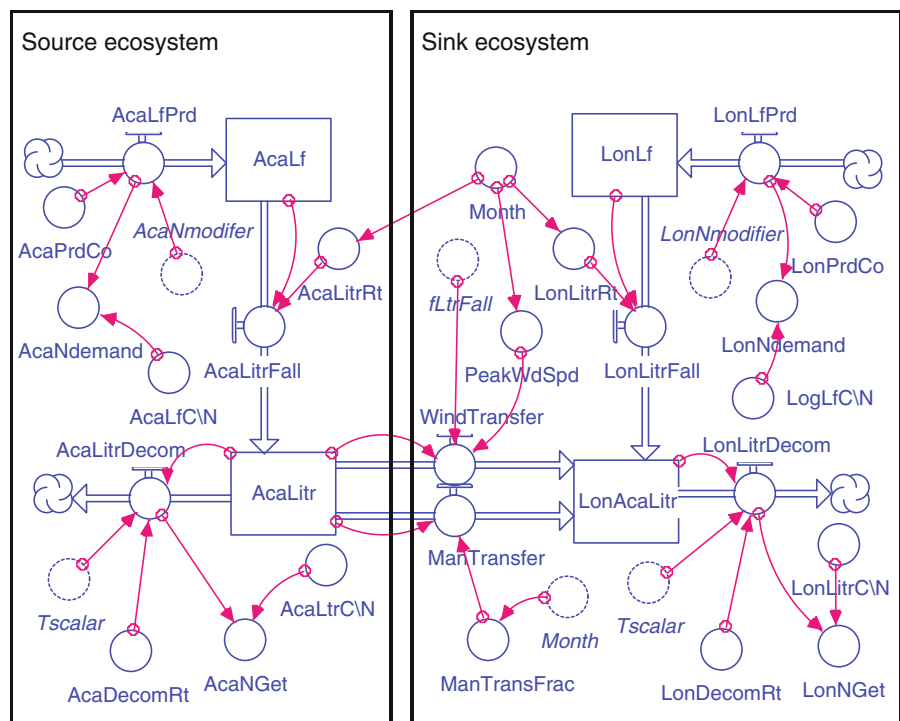


Table 1 Variable description and parameterization of the MELT model

Symbol in equations	Abbreviation in Fig. 2	Description	Value	Unit	Source/notes
P	AcaLfPrd LonLfPrd	Leaf production rate	Eq. 1	$\text{g C m}^{-2} \text{ month}^{-1}$	Fixed
μ	AcaPrdCo LonPrdCo	Leaf production coefficient	50.5 21.0	$\text{g C m}^{-2} \text{ month}^{-1}$	Shen et al. (2003), Fu et al. (2010)
B	AcaLf LonLf	Leaf biomass (initial values)	558 225.5	g C m^{-2}	Shen et al. (2003), Fu et al. (2010)
L	AcaLitr LonAcaLitr	Litter pool size (initial values)	1617 567	g C m^{-2}	Zou et al. (2006), Fu et al. (2010)
F	AcalitrFall LonLitrFall	Litterfall rate	Eq. 2	$\text{g C m}^{-2} \text{ month}^{-1}$	Varies monthly
λ	AcalitrRt LonLitrRt	Litterfall coefficient	4.7–21.2%	month^{-1}	Derived from the 3-year observation
C/N_{lf}	AcaLfCN LonLfCN	Leaf C/N ratio	20.45 30.76	Unitless	Shen et al. (2003)
C/N_{lt}	AcaLtrCN LonLtrCN	Litter C/N ratio	29.2 44.3	Unitless	Measurements of this study
D	AcaLitrDecom LonLitrDecom	Litter decomposition rate	Eq. 3	$\text{g C m}^{-2} \text{ month}^{-1}$	Shen et al. (2008)
k	AcaDecomRt LonDecomRt	Litter decomposition coefficient	0.051 0.063	month^{-1}	Li et al. (2001)
$f(T_s)$	Tscalar	Soil temperature modifier	0–1, Eq. 4	Unitless	Shen et al. (2008), Eliasson et al. (2005)
δ_w	PeakWdSpd	Peak wind speed		m s^{-1}	Measurements of this study
W	WindTransfer	Windblown litter transfer rate	Eq. 5	$\text{g C m}^{-2} \text{ month}^{-1}$	Derived from the 3-year observation
M	ManTransfer	Management-driven litter transfer	10–100%	$\text{g C m}^{-2} \text{ month}^{-1}$	Designed scenarios
N_{dmd}	AcaNdemand LonNdemand	Nitrogen used in leaf production	Eq. 6	$\text{g N m}^{-2} \text{ month}^{-1}$	
N_{get}	AcaNGet LonNGet	Nitrogen from litter decomposition	Eq. 6	$\text{g N m}^{-2} \text{ month}^{-1}$	
$f(N)$	AcaNmodifier LonNmodifier	N modifier to leaf production	Eq. 7	Unitless	Steady state value = 1
N_{mint}	AcaNmin LonNMin	N mineralization rate	0.7407 0.2080	$\text{g N m}^{-2} \text{ month}^{-1}$	Initialization steady state model run
N_{soil}^{std}	AcaNsoilStd LonNsoilStd	Steady-state soil N content	55.7 12.7	g N m^{-2}	Initialization steady state model run

types such as grassland (Parton et al. 1993), shrubland (Shen et al. 2008), and forest (Eliasson et al. 2005). Monthly mean T_s ($^{\circ}\text{C}$) was generated by a normal distribution function with the means and standard deviations obtained from the meteorological station at

Heshan-NFRS. Similarly, monthly peak wind speed (δ_w , m s^{-1}) was generated by a lognormal distribution function with the means and standard deviations derived from our 3-year observation. The windblown litter transfer rate (W, $\text{g C m}^{-2} \text{ month}^{-1}$) was

simulated by a regression equation derived from our 3-year observation data:

$$W = 2.6283\delta_w - 7.0907 \quad (5)$$

Besides simulating the carbon (defined as dry matter times litter C content) flow associated with litter production, transfer and decomposition processes, the MELT model also computed the amount of nutrients (represented by N) required to produce leaf biomass (N_{dmd} , g N m⁻² month⁻¹) and N gained from litter decomposition (N_{get} , g N m⁻² month⁻¹):

$$N_{dmd} = \frac{P}{C/N_{lf}} \text{ and } N_{get} = \frac{D}{C/N_{lt}} \quad (6)$$

where P was the rate of leaf production and D the rate of litter decomposition; C/N_{lf} and C/N_{lt} were the C to N ratios for leaf and litter, respectively (see Table 1). At steady state, we assumed that N_{dmd} was balanced by N gained from litter decomposition (i.e., N_{get}) and from mineral soil organic matter mineralization (denoted as N_{min}), which were also constants derived from the initialization steady-state model run (see Table 1 for their values). We then used the relative change of soil N pool size (N_{soil} , g N m⁻²) to the steady-state soil N pool size (see Table 1 for their values) as the N modifier to provide the N limitation/stimulation feedbacks to acacia/longan leaf production.

$$f(N) = \begin{cases} 1 - \left| \frac{N_{soil} - N_{std}}{N_{std}} \right|, & N_{soil} < N_{std} \\ 1 + \left| \frac{N_{soil} - N_{std}}{N_{std}} \right|, & N_{soil} \geq N_{std} \end{cases} \quad (7)$$

Management transfer scenarios and model execution

The main goal of litter transfer management is to increase litter nutrient input for the longan orchard but not seriously influence the nutrient status of the acacia plantation. Therefore, we adopted five management transfer scenarios, i.e., moving 10, 30, 50, 70, and 100% of the acacia litter into the longan orchard, to infer the appropriate amount of acacia litter that should be transferred. Managed litter transfers occur once a year in October, mainly because it would be easier for working with comparatively dry litter in the field during this time of the year. Besides the management transfer scenarios, we also ran a baseline scenario that had no management

transfer and no wind transfer, and a scenario with wind transfer only. For each scenario, we ran the model 50 times with a monthly time step and a simulation length of 360 months. This simulation design resulted in 301 model runs in total (6 transfer scenarios × 50 replicate runs + 1 baseline run). All the wind and management transfer actions were set to take place in the 120th month when the model was initialized to a steady state.

Results

Meteorological variables

Since meteorological variables (e.g., wind speed and temperature) were used to drive the MELT model and derive the quantitative relationships in the model, we briefly summarize the major variables here. During the three years of observation at the Heshan-NFRS, annual precipitation was 1004 and 970 mm for 2003 and 2004, respectively, but about 60% greater in 2002 (1618 mm), which was mainly due to the large rainfalls in July through September (Fig. 3a). The prevailing wind direction was north to northwest (300–360°) from October through March and south to southeast (90–180°) from April through September (Fig. 3b). Monthly mean wind velocity showed large variation (1.2–2.2 m s⁻¹) but was generally higher in March through October than in other months (Fig. 3c). Monthly peak wind speeds were mostly in the range of 4.5–7.5 m s⁻¹ and could reach as high as 11 m s⁻¹ (Fig. 3d). Monthly mean air temperature varied from 14.1°C in the coolest January to 29.8°C in the warmest July (data not shown in Fig. 3), with small difference (<1.5°C) among the 3 years.

Litter fall and litter nutrient input into the two patch ecosystems

Litterfall of the acacia plantation peaked in July through September (Fig. 4a) whereas it peaked in March for the longan orchard (Fig. 4b). Although such seasonal patterns of litter fall were clear, monthly litterfall varied markedly among the 3 years. The acacia litterfall was significantly correlated with the mean and peak wind speeds (Fig. 4c) whereas the longan litterfall was not (Fig. 4d, f). On average, annual litterfall collected in the acacia plantation was

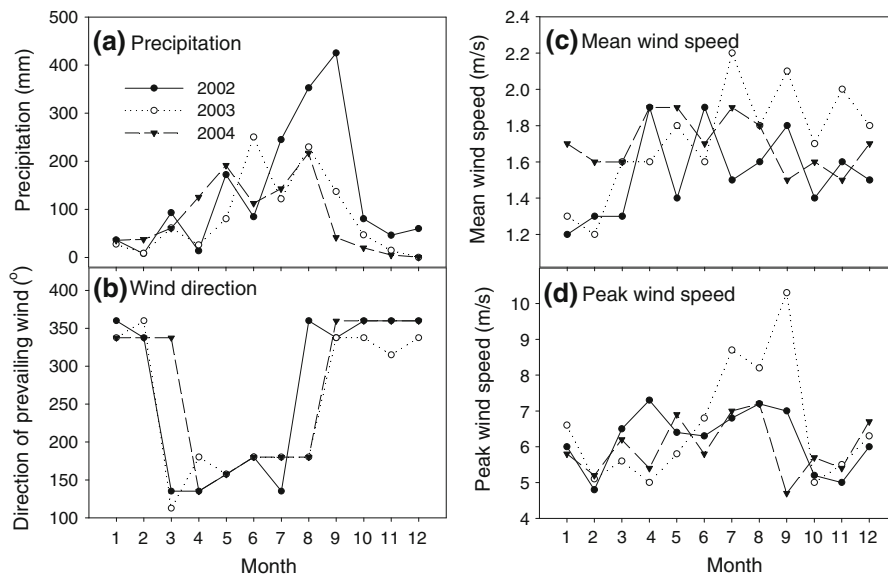


Fig. 3 Monthly precipitation (a) and wind conditions (b–d) in 2002–2004 at the study site. All the graphs share the same legend as shown in (a)

1026.3 g DM m⁻², nearly twice as much as that of the longan orchard (599.6 g DM m⁻²). Wind blew about 130 g DM m⁻² of acacia litter into the longan orchard, accounting for 11% of the total annual litterfall in the acacia plantation and 21.6% in the longan orchard (Table 2). The wind-transferred acacia litter was also correlated with the mean and peak wind speeds (Fig. 4e).

Our chemical analysis showed that the litter nutrient contents of the two species were different. Acacia litter had higher N and Na contents whereas longan litter had higher Ca, K and P contents (Fig. 5). S, Mg and organic C concentrations were similar for the two species. The amount of nutrients (litter dry matter times nutrient concentration) returned to the acacia plantation floor was about 1.5–2.4 times larger than those to the longan orchard floor, particularly for C, N, S, K, and Mg (Table 2). In the longan orchard, nutrient inputs contributed by the allochthonous acacia litter could account for 9–59% of the total nutrient inputs of the longan orchard, depending on the nutrient species of interest (Table 2).

Spatial variation of windblown litter transfer

The amount of acacia litter deposited onto the longan orchard varied with the distance to its source (i.e., the acacia plantation; Fig. 6). The acacia litter collected at

the upper slopes of the longan orchard (5 m to the lower edge of the acacia plantation) were significantly greater than those collected at the lower slopes (10 m away from the lower edge of the acacia plantation; $F = 5.32$, $P = 0.04$; Fig. 6a). Averaged over the 3 years, the acacia litter transferred by wind to the upper slopes of the longan orchard (232.9 g DM m⁻² year⁻¹) was nearly 8 times the rate to the lower slopes (30.1 g DM m⁻² year⁻¹; Table 3). On the upper slope of the longan orchard, the percentage of allochthonous acacia litter to the total litterfall was 20–65% whereas this ratio was generally less than 20% for the lower slope of the longan orchard (Fig. 6c). Larger litter deposition on the upper slope also means more nutrient input. Taking N as an example, the upper slope of the longan orchard received the allochthonous N of 3.9 g m⁻² year⁻¹ compared to 0.5 g N m⁻² year⁻¹ at the lower slope (Table 3). In contrast, the longan litter collected at the upper slope (384.7 g DM m⁻² year⁻¹) was significantly less than that at the lower slope (582.1 g DM m⁻² year⁻¹; $F = 15.4$, $P = 0.003$; Fig. 6b).

The windblown acacia litter deposition also varied with slope aspects. The northwest-facing slope of the longan orchard received significantly greater amounts of acacia litter than the south- and southeast-facing slopes (Fig. 7a; $F = 23.44$, $P = 0.001$). Based on annual averages, acacia litter deposition on the

Fig. 4 Monthly litterfall of the acacia plantation and the longan orchard (a, b) and their correlations with mean and peak wind speeds (c–f). Plots (a) and (b) share the same legend as shown in (b). Plots (c)–(f) share the same legend as shown in (d). Bars in plots (a) and (b) are standard deviations representing the variability of the 10 and 12 litter traps in the acacia and longan ecosystems, respectively

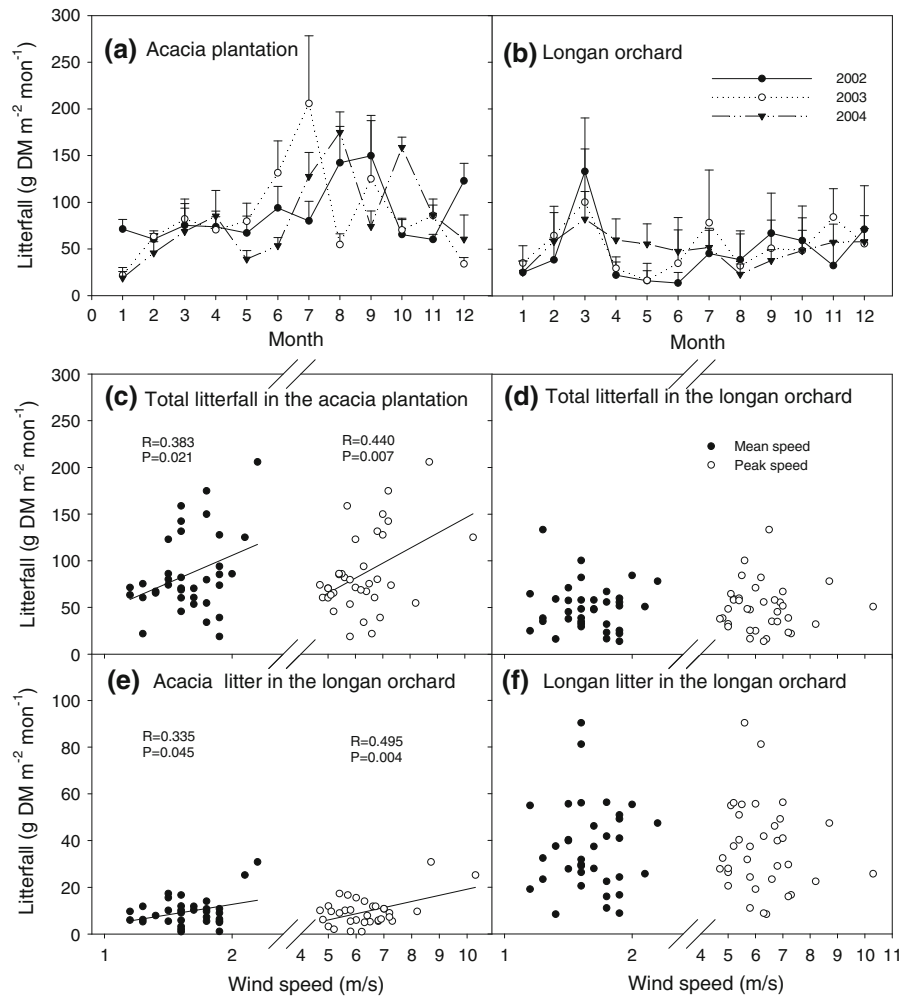


Table 2 Annual litter nutrient input (3-year average \pm SD; in g m^{-2}) onto the acacia plantation and longan orchard floors

Nutrient species	Acacia plantation	Longan orchard			
		Acacia litter	Longan litter	Total	% Acacia to total ^a
TN	17.3 \pm 0.59	2.18 \pm 0.67	4.96 \pm 0.29	7.14	30.6
TP	0.26 \pm 0.01	0.03 \pm 0.01	0.30 \pm 0.02	0.33	9.1
TS	1.41 \pm 0.05	0.18 \pm 0.05	0.66 \pm 0.04	0.84	21.4
K	5.01 \pm 0.17	0.63 \pm 0.19	2.72 \pm 0.16	3.35	18.8
Na	2.42 \pm 0.08	0.31 \pm 0.09	0.22 \pm 0.01	0.53	58.5
Ca	6.31 \pm 0.22	0.80 \pm 0.24	8.27 \pm 0.48	9.07	8.82
Mg	0.86 \pm 0.03	0.11 \pm 0.03	0.35 \pm 0.02	0.46	23.9
OC	505.3 \pm 17	63.7 \pm 19.5	219.6 \pm 12.9	283.3	22.5
DM	1026.3 \pm 34	129.4 \pm 38	470.2 \pm 48	599.6	21.6

TN total nitrogen, TP total phosphorus, TS total sulfur, OC organic carbon, DM dry matter

^a Percentage of acacia litter nutrient to the total litter nutrient received in the longan orchard

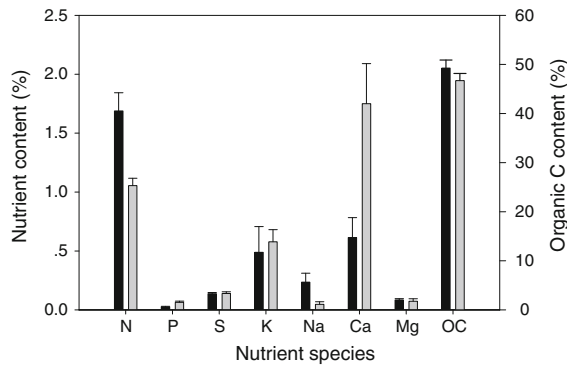


Fig. 5 Nutrient concentrations of the acacia and longan litter. Bars are standard deviations representing the variability of the two-time measurements in March 2002 and July 2003

northwest-facing slope of the longan orchard was $228.4 \text{ g DM m}^{-2} \text{ year}^{-1}$, compared to $63.4 \text{ g DM m}^{-2} \text{ year}^{-1}$ for the south-facing slope and $102.6 \text{ g DM m}^{-2} \text{ year}^{-1}$ for the southeast-facing slope (Table 3). Corresponding to nutrient contents, litter nutrients received at the northwest-facing slope were 1.1–3.5 times those of the south- and southeast-facing slopes, especially at the upper slope positions (Table 3). In contrast, the longan litterfall at different aspects of slopes were not statistically different (Fig. 7b). As a result, the northwest slope received more litter in total, of which the allochthonous acacia litter accounted for 29.3% on average, much higher than the percentages for the southeast-facing (20.2%) and south-facing (11.%) slopes (Fig. 7c).

Modeled response of the meta-ecosystem to management litter transfer

Compared with the observed values (see Table 2), the MELT model overestimated the wind-transferred acacia litter by 2.5% and the annual litterfall of the two systems by ca. 10% (Fig. 8, insets). These simulated results are reasonably good, indicating that the model is a useful representation of the observed data. It also indicates that the logic and quantitative relationships built into the model are suitable for describing litter-related processes in a meta-ecosystem. As 10–100% of acacia litter was moved into the longan litter pool, both the acacia litterfall and wind-transferred acacia litter declined, whereas longan litterfall increased (Fig. 8). This is a result of the suppressed/amplified leaf and litter production

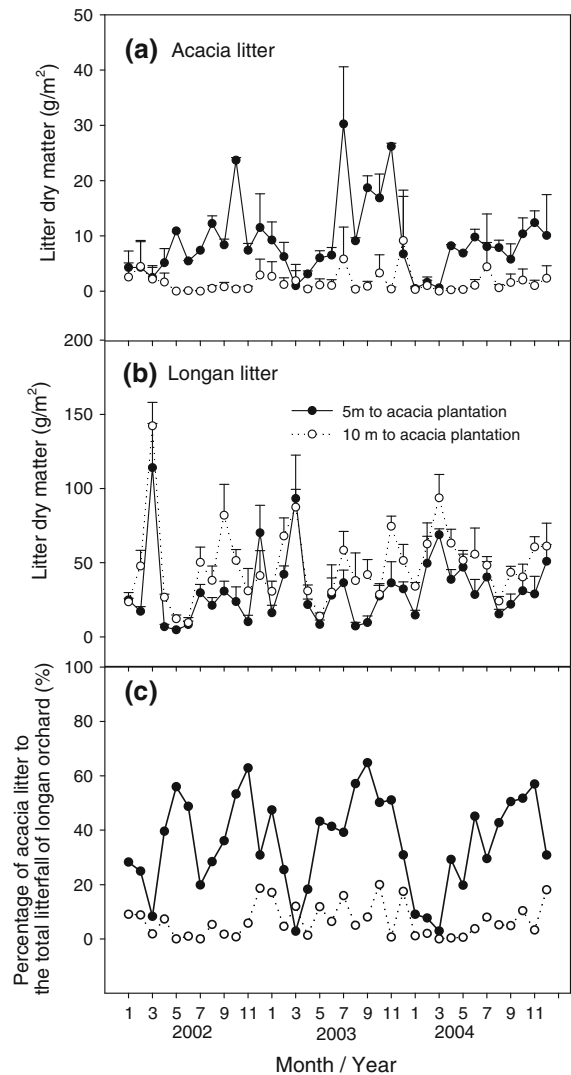


Fig. 6 Acacia (a) and longan (b) litter collected in the longan orchard at the distance of 5 and 10 m to the source acacia plantation. Bars are standard deviations representing the variability among six litter traps at each of the two distances

(Fig. 9) due to the litter-related nutrient reduction/addition in the two systems. For the five management litter transfer levels, our modeling results showed that leaf/litter production and litter pool size responded nonlinearly to the linear increase of litter transfer amount. After the transfer level exceeded 30%, the acacia system quickly declined to a low-level steady state in terms of litter pool size and leaf production, and the longan system was less responsive than below 30% transfer levels (Fig. 9)—the difference of relative longan leaf production increase was 41% between the

Table 3 Spatial variation of the annual litter nutrient input (3-year average \pm SD; in g m^{-2}) from the acacia plantation into the longan orchard

Position	Slope aspects	Nutrient species										
		TN	TP	TS	K	Na	Ca	Mg	OC	DM		
5 m to the acacia plantation	SE	2.74 \pm 1.49	0.04 \pm 0.02	0.22 \pm 0.12	0.79 \pm 0.43	0.38 \pm 0.21	1.00 \pm 0.54	0.14 \pm 0.07	79.88 \pm 43.5	162.22 \pm 88.4		
	S	2.05 \pm 0.65	0.03 \pm 0.01	0.17 \pm 0.05	0.59 \pm 0.19	0.29 \pm 0.09	0.75 \pm 0.24	0.10 \pm 0.03	59.73 \pm 18.9	121.31 \pm 38.3		
	NW	7.01 \pm 0.91	0.10 \pm 0.01	0.57 \pm 0.07	2.03 \pm 0.26	0.98 \pm 0.13	2.55 \pm 0.33	0.35 \pm 0.05	204.39 \pm 26.6	415.09 \pm 54.1		
10 m to the acacia plantation	SE	0.73 \pm 0.37	0.01 \pm 0.01	0.06 \pm 0.03	0.21 \pm 0.11	0.10 \pm 0.05	0.26 \pm 0.13	0.04 \pm 0.02	21.20 \pm 10.7	43.06 \pm 21.7		
	S	0.09 \pm 0.05	0.001 \pm 0.001	0.01 \pm 0.00	0.03 \pm 0.01	0.01 \pm 0.01	0.03 \pm 0.02	0.001 \pm 0.001	2.68 \pm 1.5	5.45 \pm 3.0		
	NW	0.71 \pm 0.17	0.01 \pm 0.001	0.06 \pm 0.01	0.20 \pm 0.05	0.10 \pm 0.02	0.26 \pm 0.06	0.04 \pm 0.01	20.57 \pm 5.1	41.78 \pm 10.3		

SE southeast facing slope, S south facing slope, NW northwest facing slope, TV total nitrogen, TP total phosphorus, TS total sulfur, OC organic carbon, DM dry matter

10 and 30% transfer levels, compared to 14.6% between the 30 and 50% transfer levels.

Discussion

Spatial variation of litter transfer

Although the studied landscape is small in area (ca. 3 ha), litter transfer between patches showed high spatial variation. The windblown acacia litter could reach as far as more than 50% of the width of the orchard. The closer the position to the source ecosystem (i.e., the acacia plantation), the more the litter deposited to the sink ecosystem (i.e., the longan orchard; Fig. 6a). Based on our correlation analysis, acacia litterfall was significantly related to wind speed, particularly peak wind speed, which also determined the distance of acacia litter transfer into the longan orchard. Litter transfer did not only happen from the acacia plantation to the longan orchard, longan litter also drifted from the upper slope to the lower slope positions within the longan orchard, causing greater longan litterfall on the lower slopes than on the upper slopes (see Fig. 6b). But the amount of acacia litter transferred from the acacia plantation to the longan orchard was much greater than the amount of longan litter transferred from the upper to the lower slopes of the orchard. We argue this was mainly because the upper slope acacia plantation with the height of about 20 m acted as a wind barrier to reduce the wind speed in the down slope longan orchard. Moreover, the lag periods between peak wind (in July–September) and longan litterfall (in March) might also be responsible for the weak correlation between the two (see Fig. 4).

While wind speed determines the distance of acacia litter transfer into the longan orchard and therefore in part causes the variation of litter deposition with slope positions, wind direction is responsible for the variation of litter deposition with slope aspects. Based on our observation (Fig. 4a) and other studies on the litterfall of *A. mangium* plantation (Tsai 1988; Saharjo and Watanabe 2000), April through October was the period with greater litterfall compared to other months. During this period at our study site, the prevailing wind direction was southeast (Fig. 3b), which therefore likely caused the 2–3 fold more acacia litter deposition on the northwest-facing slope than on the southeast- and south-facing slopes of the longan orchard. Such a

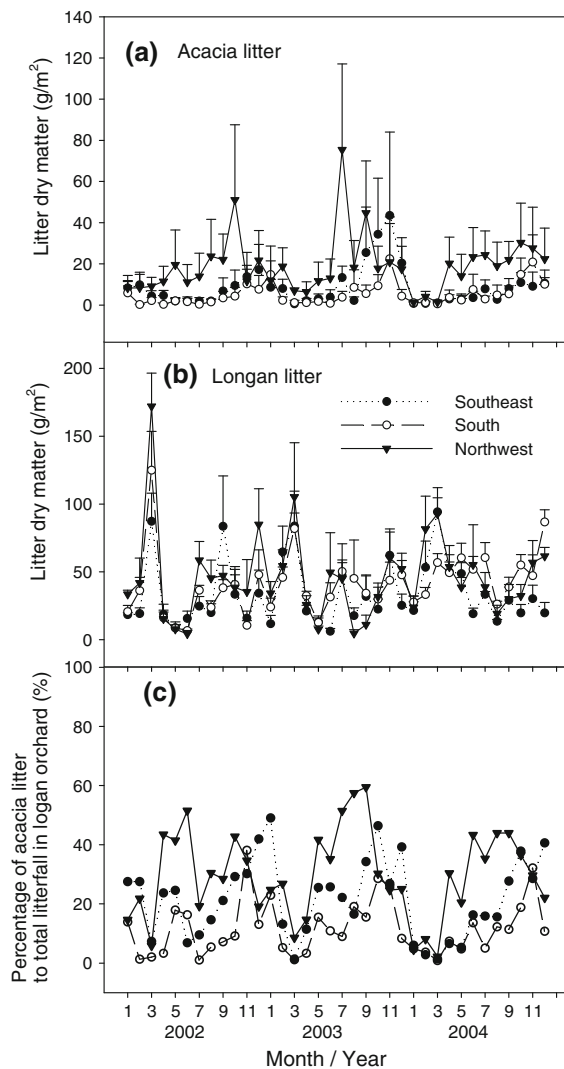


Fig. 7 Acacia (a) and longan (b) litter collected in the longan orchard at the slope aspects of southeast, south, and northwest. Bars are standard deviations representing the variability among four litter traps on each of the three aspects

pattern was particularly obvious from July to September (see Fig. 7), the typhoon season with strong southeast wind and large rainfall (Fig. 3a). During the period from November to March, the prevailing wind direction was northwest (Fig. 3b). Therefore, the southeast-facing slope generally received more allochthonous acacia litter than the other two slopes (Fig. 7). Some other factors such as the growth conditions and the slope steepness of the acacia plantation might also contribute to the spatial variation of litter transfer—larger canopy biomass may result in greater litter production and litter transfer and less steep slopes may result in shorter

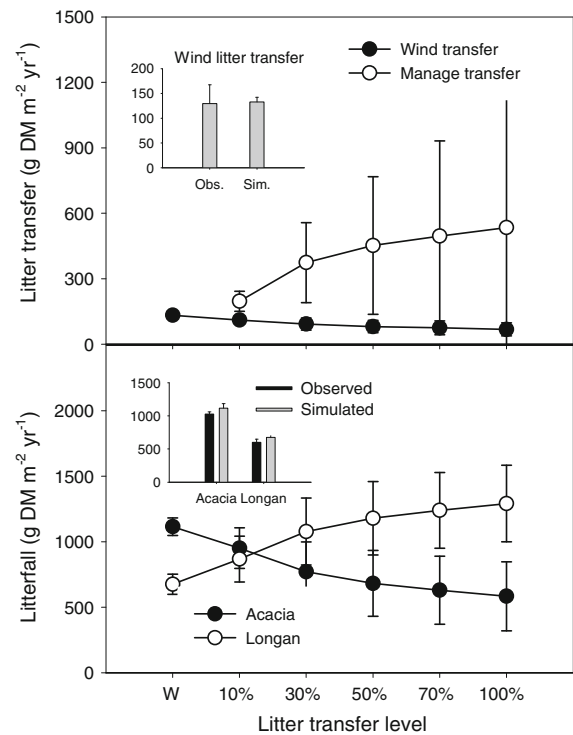
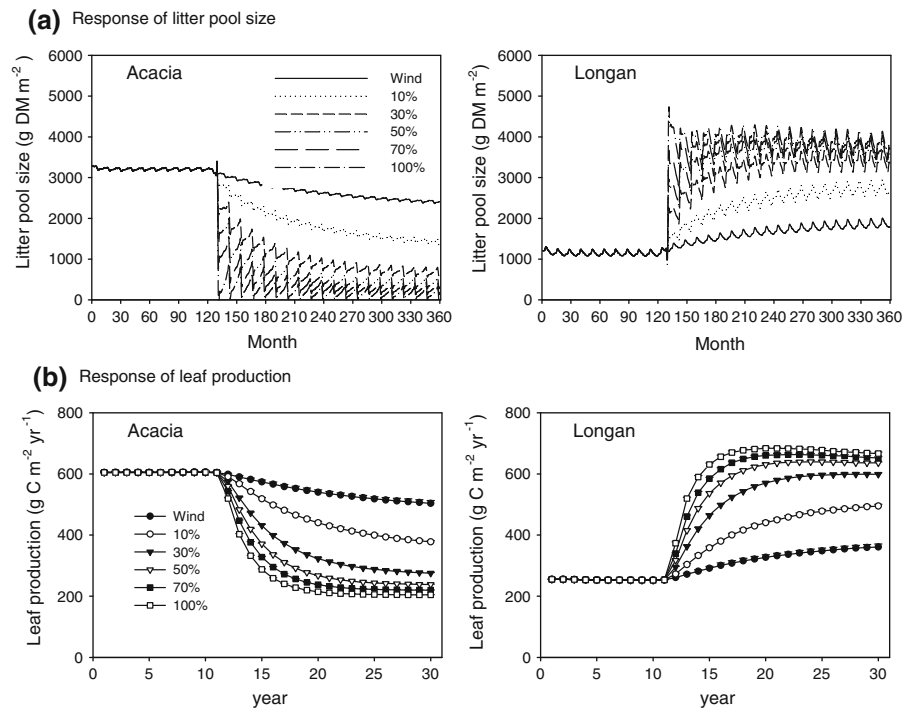


Fig. 8 MELT-simulated litterfall (upper panel) and litter transfer amount (lower panel) under different transfer scenarios. W on the X-axis stands for the scenario with wind transfer only. Inlets show the comparison between observed and simulated litterfall and litter transfer. Bars are standard deviations reflecting the inter-annual variability among the 3 years of observation or 20 years of simulation

distance of litter transfer. The contribution of these factors to the spatial variation of acacia litter transfer needs further investigation.

Unlike the windblown surface litter transport in arctic (Fahnestock et al. 2000) and desert landscapes (Duncan et al. 2008), the litter transfer in our agroforestry landscape was mainly from canopy to ground. Therefore, both wind and gravity were important for litter transfer and deposition. Due to the restriction imposed by gravity and rough boundary layer surface, the distance of litter transfer was limited—very sparse acacia and longan litter were observed in the grass slope and fish pond at the lower positions of the landscape (see Fig. 1). However, the importance of such short-distance litter transfer between patches may be a common feature of patch edges. The edges lead to increase of total litter production resulting from greater wind exposure and increased plant desiccation stress (Sizer et al. 2000;

Fig. 9 Changes in litter pool size (a) and leaf production (b) of the acacia plantation (left) and longan orchard (right) under different litter transfer levels. Bars barely seen are standard deviations among the 50 replicated simulation runs. The nearly flat lines in the first 10 years (or 120 months) show the steady state in model initialization



Vasconcelos and Luizao 2004), Edges also lead to accumulation of material from lower lying vegetation to higher statured vegetation (Feeley 2004). Furthermore, litter accumulation within a patch gradient can be found corresponding to wind direction as fine litter materials are carried over from the windward sides to the leeward sides (Feeley 2004). Greater litter production and accumulation on forest edges may exert a series of edge effects such as affecting the litter dwelling faunal and microbial communities, increasing seed and seedling mortality, and causing forest fragments to be more vulnerable to destructive surface fires (Vasconcelos and Luizao 2004). Here we suggest these cascades of effects can also lead to overall changes in productivity in both the source and sink patches. Therefore, windblown litter transfer is an important landscape process that causes a redistribution of organic matter within and between patches and creates spatial heterogeneity for a variety of ecological properties.

Litter transfer for management of ecosystem services

The main challenge of managing the agroforestry landscape is to maximize its ecosystem services such

as reducing nutrient loss and increasing fruit production of the longan orchard. These ecosystem services lead to direct economic benefit for the local residents. To maximize fruit production, management activities commonly adopt heavy fertilization practices. The use of fertilizer however has an economic, greenhouse gas, and pollution cost associated with its production. Our data showed that the acacia plantation placed on the upper slope of the agroforestry landscape provides a source of nutrients to the orchard through the wind-blown litter transfer. About 2.2 g m⁻² of acacia litter N was blown into the longan orchard annually (Table 2), and a previous study had shown that the contents of organic carbon, total N and P in the upper slope soils of the longan orchard (with greater acacia litter deposition) were about 20–30% larger than those in the soils of the lower slope positions with less acacia litter deposition (Li et al. 2004). These litter nutrient exchanges between patches are ecosystem services that have cascading effects on both immediate economic resources and sustainability. These effects occur by altering the spatial patterns of ecosystem stoichiometry, with relative increases in nitrogen in the sink patch and decreases in the source patch (Ptacnik et al. 2005). These landscape characteristics of the production of ecosystem services from agricultural

regions can have substantial effects on their sustainability (Kremen 2005; Tschamtket et al. 2005). The *A. mangium* plantation with large annual litterfall is particularly suitable for this purpose. By the age of 4–9 years old, the litterfall of *A. mangium* plantations can reach as high as $1100 \text{ g DM m}^{-2} \text{ year}^{-1}$ (Tsai 1988; Kunhamu et al. 2009), very close to the 18-year old acacia plantation in our study ($1155.7 \text{ g DM m}^{-2}$; Table 2) and much higher than those of the subtropical evergreen broadleaved forests in the region ($560\text{--}850 \text{ g DM m}^{-2} \text{ year}^{-1}$; Liu et al. 2004; Zhou et al. 2007). In addition to the benefits associated with nutrients the acacia litter may also reduce the risk of surface soil erosion, as many studies have found litter cover can markedly ameliorate soil erosion (Sayer 2006; Verbist et al. 2010) and buffer the generally low soil pH and severe acid rain (Pocknee and Sumner 1997; Li et al. 2003).

Because of its large annual litterfall and relatively slow decomposition rate (Li et al. 2001), the acacia plantation had accumulated a large amount of litter ($>3000 \text{ g DM m}^{-2}$) on its floor (Zou et al. 2006). Based on our MELT model simulation analyses, we suggest less than 30% of the accumulated litter should be moved into the longan orchard as organic fertilizers and maintain high production in the acacia forest. This suggestion is based on two response patterns of the model to different scenarios of management litter transfer (Fig. 9): (i) the acacia plantation (measured by litter pool size, leaf production, and soil N content) could only sustain itself for a few years if over 30% of its litter were removed; and (ii) the litter addition stimulation effect on the longan orchard quickly declined when the litter transfer intensity surpassed 30%. The declined response of longan leaf production to acacia litter addition might be ascribed to the reduction of litter decomposition rate as the proportion of acacia litter increased in the longan orchard litter pool, thus retarded the release of nutrients into the longan orchard soil and slowed the response of longan leaf production as shown in Fig. 9b. It is noted here that this management guidance is on the basis of our model assumptions. For example, we assumed that the nutrients derived from acacia litter were entirely released into the soil nutrient pool and readily taken up by longan trees, but in reality some litter-derived nutrients might be leached away by runoff or had little influence on longan production. Furthermore, some important variables such as the rates of leaf production

and soil N mineralization were assumed to be constants in the MELT model, this could also potentially influence the long-term response behaviors of longan production to acacia litter addition. Therefore, our future study may consider conducting a series of litter manipulation field experiments to see how the longan orchard system would respond to acacia litter addition in reality. The relationships between litter addition and a series of ecological variables, such as soil pH, nutrient availability, temperature, moisture, erosion intensity, and the growth and fruit yield of longan tree, may be established after such experiments and readily incorporated into the MELT model.

In conclusion, our study found that windblown litter nutrient movement was substantial across the landscape. As litter transferred by wind was also influenced by gravity and topographical conditions, the windblown litter deposition varied significantly with the distance to its source and the slope aspects, which could further exert a series of cascading effects on their nutrient status, production, as well as soil physical and chemical properties of the source and sink ecosystems. Such effects may be positive by increasing soil nutrient availability and reducing soil erosion as in our agroforestry landscape, or negative by increasing seed and seedling mortality and fire occurrence probability as in fragmented forest remnants. Through optimized landscape design and active management strategies, litter nutrients may be more efficiently used to promote the services provided by the landscape to human society. Our MELT model provides a quantitative modeling framework to describe the litter transfer-related processes across landscape components. It can be used to identify key empirical research needs, derive specific management strategies for individual patches, and be extended into spatially interactive landscape models to understanding the reciprocal relationships between landscape pattern, nutrient cycling, and the production of ecosystem services.

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