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REGULAR ARTICLE

Buttress trees elevate soil heterogeneity and regulate seedling diversity in a tropical rainforest

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Abstract Buttress trees are prominent in tropical rainforests, providing mechanical support for canopy trees. Other ecological functions of these structures remain unclear. Here we demonstrate that buttresses are physical structures that regulate soil moisture, soil nutrient status and seedling diversity near tree trunks. We monitored soil moisture over a year in plots on the uphill, downhill and lateral sides of buttresses on a tropical seasonal rainforest slope in Xishuangbanna, Southwest China. Soil nutrient status was examined in dry and rainy season and seedlings were identified and counted in the plots. Leaf litter accumulation was sampled at the end of the study. Higher levels of soil moisture were maintained uphill of the buttresses throughout the year and leaf litter accumulation was also much higher. Total soil carbon, total N, and hydrolysable N were much higher on the uphill side but other nutrient concentrations did not differ significantly. Seedling species composition varied significantly among different locations with the densest and most diverse seedling assemblages on the uphill side. This study illustrates an important function of buttress trees in providing soil heterogeneity and promoting seedling diversity in rainforests.

Keywords Buttress tree · Soil heterogeneity · Soil moisture · Soil nutrient · Xishuangbanna

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Introduction

Buttressed trees are prominent features of many tropical rainforests (Richards 1996). Buttresses are thought to function as supporting structures for large canopy trees, with their development being induced by unidirectional forces caused by prevailing winds or by asymmetric tree crowns (Smith 1972; Ennos 1993). Senn (1923) observed that a large proportion of poplars developed buttresses on their windward sides. Richter (1984) demonstrated both the windward occurrence and progressive growth of buttresses of *Quararibea asterolepis*. Furthermore, Warren et al. (1988) found that *Tachigalia versicolor* developed taller, longer and more voluminous buttresses on the windward than on the leeward side, although there was no relationship between the number of buttresses and the prevailing wind direction. Crown asymmetry

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is also common in tropical rainforest where treefall gaps may increase lateral growth on one side of the crown (Young and Hubbell 1991; Young and Perkocha 1994). A significant association between buttresses and asymmetrical tree crowns suggested that buttresses function as supporting structures (Young and Perkocha 1994). The mechanical support provided by buttresses may be particularly important on shallow, infertile and/or waterlogged soils, characteristic of many tropical rainforests where many trees lack well-developed tap roots (Smith 1972; Richards 1996).

Plants are known to interact with environment, contributing to environment heterogeneity and influencing species coexistence (Chazdon 1984; Grubb 1977). In addition to providing mechanical support for rainforest trees, buttresses may also function in other ways including retention of soil nutrients and water and reducing competition from other plants (Richards 1996). For example, buttresses may allow a much greater spread of the root systems that facilitate nutrient acquisition from nutrient-poor soils (Newbery et al. 2009). In addition, buttresses can also divert the nutrient-rich stem flow (rain water washed down tree trunk) into several smaller flows and act as barriers to ground flow and thus reduce soil erosion during heavy rains on hill slopes (Herwitz 1988; Johnson and Lehmann 2006). These functions together can increase the interception and retention of nutrients, leaf litter and water. Buttressed trees occupy more soil surface area than similar-sized trees lacking buttresses. Thus, buttressed trees may acquire a competitive advantage by more completely excluding the establishment of other plants, especially lianas that may be prevented from climbing by the enlarged buttresses (Black and Harper 1979). While plausible, there is no evidence that liana infestation is higher in non-buttressed than in buttressed trees (Black and Harper 1979), perhaps because the majority of lianas use a succession of small trees to reach the canopy rather than climbing directly up their final host trees (Putz 1984).

Despite the attention given to their function of providing mechanical support, surprisingly little attention has been paid to other ecological functions of rainforest tree buttresses. Since buttresses are such prominent structures in the rainforest, we would expect that by modification of microhabitats they may affect many ecological processes such as decomposition, seed dispersal, seed germination, seedling establishment and, consequently, the long-term maintenance of rainforest diversity. In this study, we measure effects of buttresses on soil water, leaf litter distribution and soil nutrient gradients in a rainforest on a hill slope, and demonstrate the function of buttress trees in increasing local habitat heterogeneity and promoting seedling diversity

Materials and methods

This study was conducted in a 1-ha permanent rainforest plot managed by the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, at Xishuangbanna, southwest China (21°51′ N, 101°12′ E). This area has a typical monsoon climate with an annual rainfall of 1,493 mm recorded at the climatological station of the Xishuangbanna Tropical Botanical Garden. There is a distinct rainy season between May and October, when the tropical Southwest Monsoon from the Indian Ocean brings 84% of the annual rainfall (Cao et al. 2006). The shortage of water during the dry season, with only 16% of the annual rainfall, is partially relieved by heavy fog (Cao et al. 2006). The plot is located in a wet valley between two hills extending west to east with a narrow stream (2 m wide) running through its center. The slopes of the two hillsides are 15 to 20 degrees. A complete description and survey of the plot is given in Cao et al. (1996). In the 1994 survey, 730 trees from 120 species (with DBH>5 cm) were recorded; *Pometia tomentosa* (Blume) Teijsm. & Binn, *Barringtonia macrostachya* Kurz and *Gironniera subaequalis* Planch. were the three most dominant species in terms of importance value. The plot has been resurveyed annually since 2001. As a long-term forest dynamics monitoring plot of the Chinese Ecosystem Research Network (CERN), this plot has also been used for monitoring hydrological, biological and other ecosystem processes.

There were 35 large trees (DBH>50 cm) in the 1 ha plot with large buttresses. In selecting trees for this study, we excluded trees growing on the flat stream bed, or within 10 m of the stream, to avoid the influence of running water. Twenty buttressed trees from ten species were selected for the study. The average diameter of the selected buttressed trees was 62.4 cm above the buttresses. Individual buttresses were mapped and the length and height of each buttress were recorded.

Three 1 m^2 seedling plots were established adjacent to the trunk (as close as possible) on uphill, downhill and one lateral sides of the 20 buttressed trees. All woody seedlings <1.5 m in height were identified and their height measured in these plots.

Soil moisture (top 10 cm) was measured twice monthly from September 2008 to August 2009, using a TDR Soil Moisture Meter (Mpkit-B, Huier instruments, Hangzhou, China). Due to the heterogeneity of soil moisture at a fine scale, five measurements of soil moisture, one at each of four corners and one in the center of seedling plots, were taken and those values averaged for each plot. Rainfall was recorded throughout the study period with a rainfall gauge on the top of a 70-m tall observation tower adjacent to the plot.

Soil samples were taken in September (rainy season) 2008 and March (dry season) 2009. Three soil cores were obtained from random locations in each seedling plot using a soil corer measuring10 cm in length and 5 cm in diameter. The three soil cores were then mixed thoroughly to give one composite sample and air dried. The soil samples were analyzed for total C, N, P, and K, hydrolysable N, available P and K at the Biogeochemisty Lab at the Xishuangbanna Tropical Botanical Garden. Total C and N were

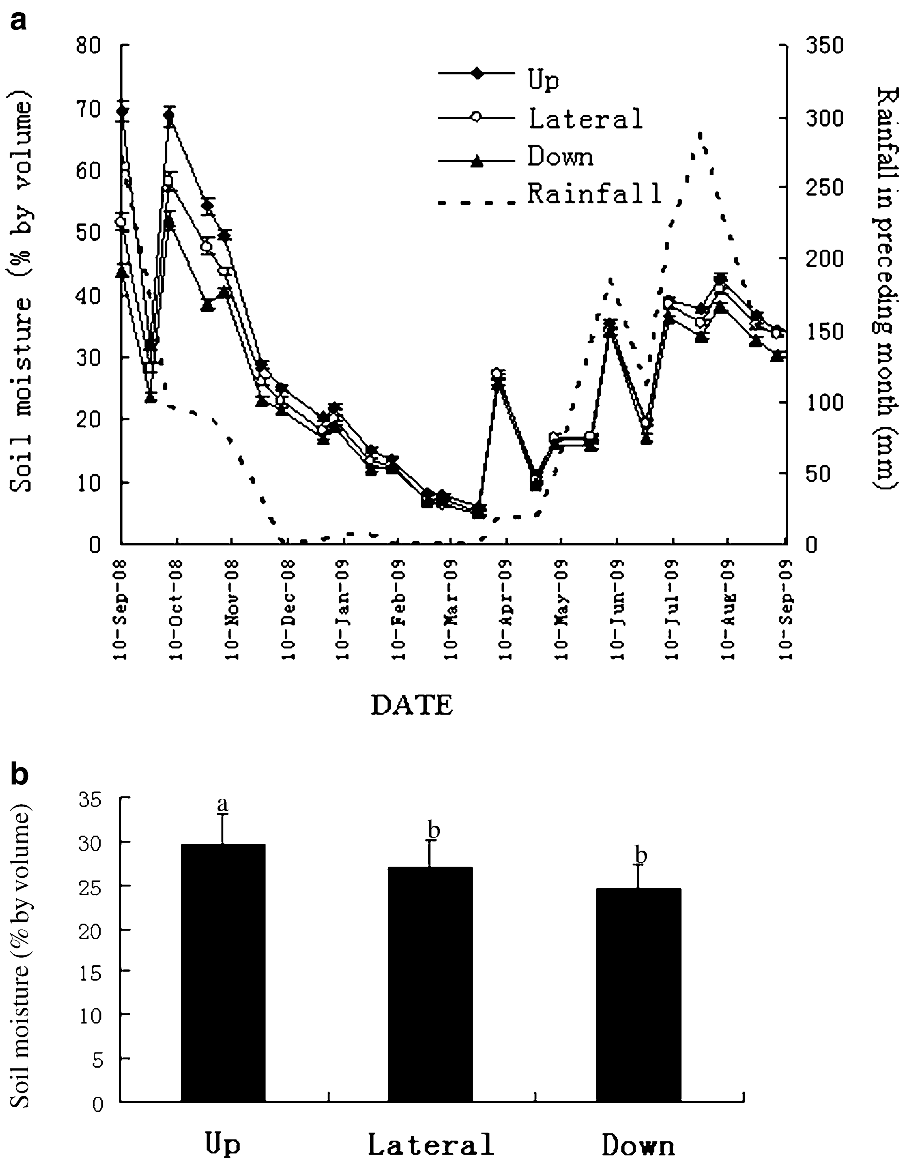

Fig. 1 Comparisons of soil moisture at different locations near buttresses in a tropical rainforest. *Error bars* represent stand errors of means for N=20. **a**, Changes in soil moisture over time; **b**, Average soil moistures over a year with different letters indicating significant differences detected by a post-hoc test after repeated-measure ANOVA

Table 1 Pearson correlations between the amount of rainfall in preceding month and week and the contrast in soil moisture among different locations near buttresses.

Comparison pairs	R^2	P
Rainfall in preceding month		
Up *minus* Down	0.407	0.044
Up *minus* Lateral	0.345	0.091
Lateral *minus* Down	0.445	0.026
Rainfall in preceding week		
Up *minus* Down	0.137	0.513
Up *minus* Lateral	0.055	0.793
Lateral *minus* Down	0.250	0.229

analyzed using a C-N analyzer (Vario MAX CN, Elementar Analysensysteme GmBH, Germany). Soil pH (1:2.5 v/v soil/water mixture) was measured using a digital pH meter (PHS-3C, Shanghai Leici Equipment Factory, China). Total P and K from hydrofluoric and perchloric acid digests, respectively, were determined by inductively coupled plasma–atomic emission spectrometry (IRIS Advantage-ER, Thermo Jarrell Ash Corporation, U.S.A). Hydrolysable N was converted to ammonium by reaction with iron (II) sulfate and sodium hydroxide by a diffusion procedure. Phosphorus was extracted with 0.03 mol/L NH_4F in 0.025 mol/L HCL and determined by molybdenum-antimony colorimetry.

Surface leaf litter was sampled in late August 2009 after other sampling was completed to avoid affecting soil moisture and nutrients. The leaf litter was sampled in all seedling plots using a 60-cm diameter steel ring. All visible leaf litter pieces (>5 mm in length) within the ring were collected by hand and fresh samples were sealed in plastic bags and weighed within 8 h. Litter samples were then oven dried at 80°C for 48 h to determine their dry weights.

Repeated Measures ANOVAs were performed to compare soil moisture and nutrients at different locations through time. The relationship between soil moisture and rainfall of the week and the month before each sampling time was analyzed by Pearson Correlations (Quinn and Keough 2002). One way ANOVAs were used to compare differences in surface leaf litter and seedling density and diversity among different locations. Seedling diversity among three locations was compared by Fisher's Alpha diversity index calculated using the software EstimateS (Colwell 2009). To compare the species composition of seedlings at different locations, an analysis of similarity (ANOSIM: Clarke and Green 1988) was used, with 999 permutations using the software package PRIMER5 (Clarke and Warwick 2001). To determine the species associations with the different locations with respect to buttresses, a Canonical Redundancy Analysis (RDA) was conducted using an R-package (rdaTest, Legendre and Legendre 1998). Locations to buttresses (uphill, lateral and downhill) were considered as independent variables and seedling abundance was set as the dependent variable.

Results

Soil moistures of the three locations decreased from the rainy to the dry season and were all significantly correlated with the rainfall of the preceding week and month (Pearson correlations, $P<0.01$, Fig. 1a). The difference in soil moisture between locations was higher during the rainy season (June to October) than during the dry season (November to May, Fig. 1). In addition, soil moisture was greater on the uphill side than other two locations of the buttress (Fig. 1b, Repeated measure ANOVA, $P<0.001$). Rainfall of the preceding month appeared to

Table 2 Comparison of surface leaf litter accumulation and seedling density, number of species and diversity (mean, S.E.) among different locations near the buttresses of trees in a tropical rainforest

	Leaf litter (g/m^2)	Number of seedlings	Number of species	Fisher's Alpha
Up	30.07(2.63)^{a}	7.65 (1.69)^{a}	4.85(0.51)^{a}	26.78
Lateral	22.80(2.01)^{b}	4.65 (0.49)^{ab}	3.15(0.25)^{b}	25.27
Down	20.92(2.32)^{b}	4.00 (0.50)^{b}	3.05(0.39)^{b}	19.76

For each variable, different superscript letters indicate a significant difference between locations as detected by one-way ANOVA followed by multiple comparisons (Tukey's HSD test, $P<0.05$)

be a better indicator of the contrast of soil moisture among locations than rainfall of the preceding week (Table 1). Differences in soil moisture between uphill and downhill locations from buttresses were maintained through the dry season, even though only 16.5 mm of rain fell from 16 November 2008 to 25 March 2009.

Surface leaf litter accumulation differed significantly among the three locations (ANOVA, $P=0.018$). Between-group comparisons showed that the uphill

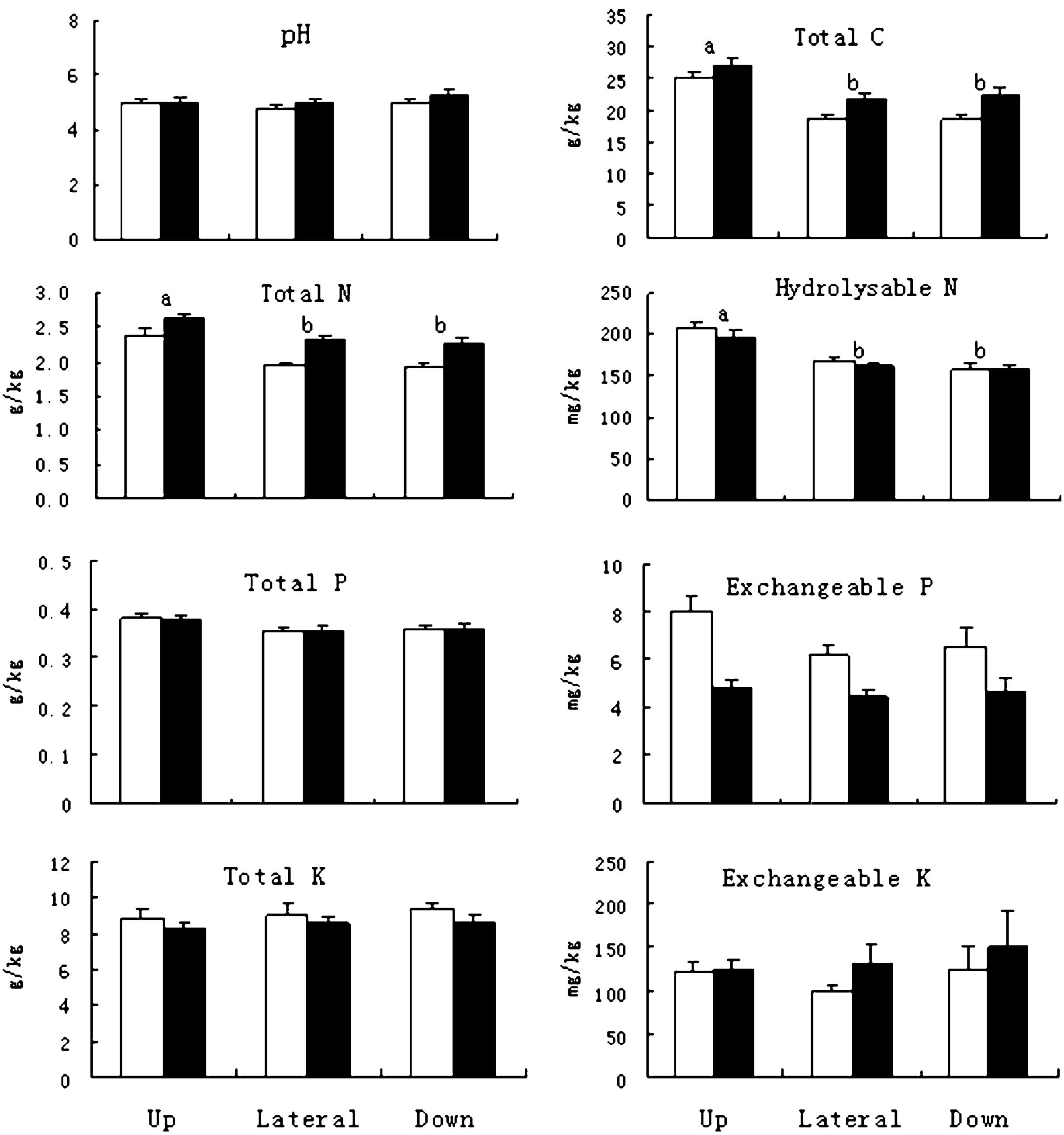

Fig. 2 Distribution of soil nutrients at different locations near the buttresses of trees during the rainy season (*white bars*) and dry season (*black bars*). *Different letters above the bars* indicate significant difference among locations as determined by post-hoc tests after repeated-measure ANOVA and *error bars* represent stand errors

side had higher litter accumulation than the other two locations, which did not differ from each other (Table 2).

Soil concentrations of total carbon, total N and hydrolysable N were higher at the uphill side of buttresses than at the other two locations (Fig. 2, Repeated Measures ANOVA, $P<0.01$). This pattern is consistent in both dry and rainy season as there were no significant interactions between the location and the season despite that the concentrations of all three elements exhibited significant seasonal changes (Fig. 2, Table 3). Mean concentrations of total P and exchangeable P were also higher on the uphill side of buttresses, but differences were not significant due to large variation in concentration among plots (up to an order of magnitude, Fig. 2).

The density and number of species of seedlings were significantly higher on the uphill than the downhill side of buttresses (one way ANOVA, $P=0.014$ and $P=0.003$, respectively, Table 2). Seedling species diversity was also higher on the uphill than on the other two locations (Table 2).

Multivariate analysis confirmed the difference in seedling species composition among the three locations (Table 4). Pair-wise comparisons showed that the only significant difference in seedling composition occurred between the uphill and downhill sides of buttresses; this difference is evident in the separation of sites from each location in ordination space (Fig. 3). Canonical Redundancy Analysis also detected a significant difference in seedling composition among different locations ($R^2=0.044$, $F=1.546$, $P=0.018$). Twelve species exhibited a significant association with the ordination coordinates (Fig. 3). Of these twelve species, *B. macrostachya* was associated with uphill side, *Randia yunnanensis* Hutch. was associated with downhill side, and *Ventilago calyculata* Tul and *Drypetes cumingii* (Baill.) Pax & K. Hoffm. were associated with the lateral side of buttressed trees. Other species showed associations with a combination of two of the three locations.

Table 3 Result of repeated measure of ANOVA on pH and soil nutrients measured in dry and rainy season at three different locations around buttress trees

Item	Location	Season	Location*season
pH	ns	ns	ns
Total C	***	***	ns
Total N	***	***	ns
Hydrolysable N	***	***	ns
Total P	ns	ns	ns
Exchangeable P	ns	***	*
Total K	ns	***	ns
Exchangeable K	ns	ns	ns

* $P<0.05$, ***$P<0.001$, ns not significant

Discussion

In addition to the recognition that buttresses provide mechanical support to rainforest trees, our study demonstrates that they function as barriers to downslope movement of nutrients and water, increasing habitat heterogeneity and promoting seedling diversity in this tropical rainforest. As the effects are likely to be largely physical and caused by the flatter trunks of buttress trees, we would expect non-buttressed tree to have some impact, depending on the size of the trees. We suggest that the phenomena observed here may be ubiquitous in tropical rainforests, at least for forests on slopes: thus buttress trees may play an important role in maintaining the high species diversity of tropical rainforests.

Habitat heterogeneity is important to provide regeneration niche of different species coexisting in forest (Grubb 1977). Buttresses showed a strong capacity to intercept water and thus to maintain higher uphill soil moisture levels, even during the dry season, when rainfall might not be expected to alter soil moisture levels. These pockets of higher soil moisture may play an important role in rainforest dynamics. Soil moisture is an important regulator of many ecological processes including litter decomposition (Swift et al. 1979), seed

Table 4 Comparison of seedling species composition at different locations of buttressed trees

	R statistic	P
(i) Overall Location	0.043	0.043
(ii) Pair wise contrasts		
Up vs Down	0.103	0.006
Up vs Lateral	0.027	0.150
Down vs Lateral	0.004	0.386

ANOSIM R, P calculated for (i) overall location; and (ii) pair-wise contrasts between locations

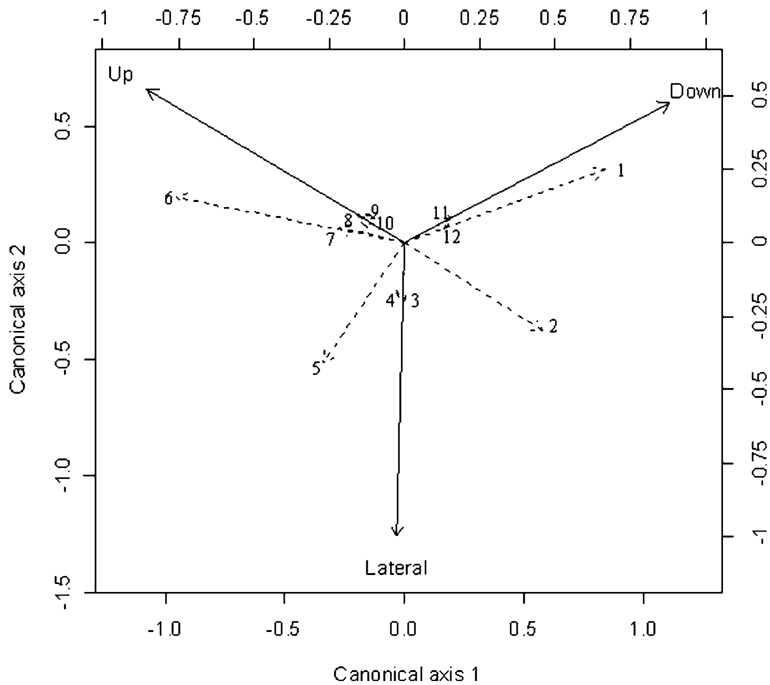

Fig. 3 Canonical Redundancy Analysis of the abundance of different species of seedlings at different locations around the buttressed trees. Biplot vectors (*dash line*) show the trends in increasing abundance for species in relation to the positions (*Solid line*) to buttressed trees in ordination space. 1. *Randia yunnanensis* Hutch.; 2. *Drypetes cumingii* (Baill.) Pax & K. Hoffm.; 3.*Ficus subincisa* J. E. Smith; 4. *Ventilago calyculata* Tul.; 5. *Pseuduvaria indochinensis* Merr.; 6. *Barringtonia macrostachya* (Jack) Kurz; 7. *Pavetta arenosa* Lour. 8. *Antidesma montanum* Bl. 9. *Morinda angustifolia* Roxb. 10. *Phoebe lanceolata* (Wall. Ex Nees) Nees; 11. *Canarium tonkinense* (Leenh.) Engl.; 12. *Dysoxylum densiflorum* (Blume) Miq

germination and subsequent seedling establishment and survival and tree growth (Whitmore 1998; Poorter and Hayashida-Oliver 2000; Yavitt and Wright 2008). Seedlings on the uphill side of buttresses may have higher survival rates than those in other locations as a consequence of the higher soil moisture levels. In particular, this may be the case in seasonal rainforests where dry-season soil moisture is a major factor affecting seedling establishment and survival (Poorter and Markesteijn 2008). The high seedling abundance and diversity may result from species partitioning soil resources (John et al. 2007). The high moisture maintained by buttress trees may also affect other ecosystem processes including the survival of seeds in the soil (Garwood 1989) and habitat availability for soil- and litter-dependent fauna (Voris 1977; Whitfield and Pierce 2005).

The higher total carbon, total N and hydrolysable N on the uphill side of buttresses probably results from long-term accumulation of leaf litter and other organic materials. The accumulation of organic matter may also increase the water-holding capacity of soils and could partly explain the higher soil moisture content at the uphill side of buttresses (Voris 1977). Consequently, the decomposition may be more rapid on the uphill side of the buttresses, contributing to the high N concentrations in soils (Swift et al. 1979). The interception of nutrient-enriched stem flow also may improve the nutrient status of the uphill locations (Herwitz 1988). Increased nutrient concentrations may increase seedling density on the uphill side of buttresses, since N availability is an important factor influencing seedling establishment (Bungard et al. 2000).

The difference in seedling species composition at different locations around buttressed trees is one of the most important findings of this study. As far as we know, this is the first report of buttresses affecting seedling composition. There are at least three factors may be involved: First, buttresses may intercept seeds, in particular large ones, during downhill transport. In our study, 15 out of 26 seedlings of *B. macrostachya*, which has seeds with a dry mass >30 g, were found on the uphill side, but only two seedlings of this species were recorded in downhill plots. Second, the moist nutrient-rich soil on the uphill side of buttresses may increase the germination and establishment of many species. A high proportion of rainforest plants produce recalcitrant seeds that are extremely sensitive to desiccation (Pammenter and Berjak 2000; Tweddle et al. 2003), and high soil moisture may be important in preventing them from losing viability, i.e. before germination (Vazquez-Yanes and Orozco-Segovia 1993). Moreover, seedling growth should be much faster at locations with high soil moisture and nutrients than in those with low soil moisture and nutrients (Yavitt and Wright 2008). However, the accumulation of leaf litter on the uphill side of the buttress may be unsuitable for the establishment of small-seeded species (Metcalfe et al. 1998). These mechanisms may work alone or together, promoting seedling diversity by creating habitat heterogeneity in tropical rainforest.

Habitat heterogeneity is considered to be one of the most important factors promoting the coexistence of species, and thus the maintenance of diversity in tropical rainforests (Wright 2002). As they are prominent structures in most rainforests, buttress trees may play an important role in increasing habitat heterogeneity, as demonstrated here. While this study focused only on trees growing on hill slopes, buttresses could also act as physical barriers regulating the flow of energy and materials in other locations, including flood plains and in forests subject to high winds. As a consequence of their effects on soil moisture and nutrients, buttresses may also influence other ecological processes, including the composition of the soil seed bank and assemblages of soil dwelling fauna, such as arthropods. Further investigations of the soil seed bank and soil-dwelling fauna would provide a more comprehensive understanding of the functions of buttress trees in the dynamics and evolution of tropical rainforests.

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