

Buttress trees in a 20-hectare tropical dipterocarp rainforest in Xishuangbanna, SW China

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Abstract

Aims

Buttresses are prevalent and are important to many ecological processes in tropical rainforests but are overlooked in many rainforest studies. Based on a buttress survey in a 20-hectare plot, this study aims to answer the following questions: (i) Is buttress forming a fixed species characteristic? (ii) Is there any phylogenetic signal for buttress forming across a broad taxonomic scale? (iii) Is buttress forming an inherent feature or simply induced by environmental factors, and how is this relevant to the size of the tree?

Methods

We surveyed buttresses for all 95 940 trees with diameter at breast height (DBH) ≥ 10 mm in a 20-ha tropical dipterocarp rainforest in Xishuangbanna, SW China. The occurrence of buttresses was compared across different taxa and across different tree-size classes. A phylogenetic analysis was conducted among buttressed

and non-buttressed species in order to understand the evolutionary background of buttress formation.

Important Findings

This preliminary study showed that buttress trees are very abundant (making up 32% of trees with ≥ 100 mm DBH) in this 20-ha tropical rainforest situated at the northern edge of the tropics. Fifty-one percent of the 468 tree species in the plot had stems that produced buttresses. Large trees were more likely to develop buttresses than smaller ones. We found that although buttress formation is not a fixed species characteristic, there is a strong phylogenetic signal for buttress formation in larger species.

Keywords: buttress • phylogenetic signal • tropical rainforest • species size • Xishuangbanna

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INTRODUCTION

Buttresses are prevalent in many tropical forests, in particular in lowland tropical rainforests (Richards 1996 CIT0030CIT0030), but trees may also develop significant buttresses in sub-tropical and wet temperate forests (Francis 1924; Nicoll and Ray 1996). The size and frequency of buttresses appear to decrease with increasing latitude, and from low to high altitudes (Smith 1972).

Buttresses are generally considered mechanical structures that support tree boles and balance the trees against unidirectional stresses received from prevailing winds, asymmetric canopy, leaning stem and gravity caused by growing on slopes (Navez 1930; Richter 1984; ter Steege *et al.* 1997; Warren *et al.* 1988; Young and Perkocho 1994). In swamp

rainforests of Guyana, buttresses developed mainly on the opposite side of the leaning direction of *Caryocar nuciferum* L. (ter Steege *et al.* 1997). In Barro Colorado Island (BCI) and Costa Rica, the largest buttresses occur mainly on the sides of trees away from the direction of asymmetrical crowns (Young and Perkocho 1994). However, in another study in BCI, the size of buttresses was not correlated with crown asymmetric stress but with the prevailing wind load (Richter 1984). Furthermore, Lewis (1988) found that the arrangements of buttresses in *Pterocarpus officinalis* Jacq. showed no association with either prevailing wind direction or asymmetrical tree crowns. Subsequently, mechanical models were developed to test supporting hypotheses using engineering and anatomical structure analysis (Clair *et al.* 2003; Crook *et al.* 1997; Ennos 1995; Fisher 1982; Henwood 1973; Young and Perkocho

1994). Most of these studies have shown that buttresses are supporting organs of trees, especially of large trees.

Apart from serving as supporting structures for trees, buttresses also have other important ecological functions (Tang *et al.* 2011). Buttresses may increase the contact area between the tree and the ground and become barriers to matter flow, leading to a high accumulation of litter and high soil moisture and nutrients (Pandey *et al.* 2011; Tang *et al.* 2011). Buttresses may limit soil erosion and nutrient loss following overland flow around trees by promoting infiltration of stem flow during heavy rainfall events on hill slopes (Herwitz 1988). Buttresses are also proposed to be an important organ in nutrient acquisition, and trees with buttresses are more competitive than trees without them, providing an explanation for the dominance of buttressed trees in rainforests (Newbery *et al.* 2009). Buttresses also provide important microhabitats for many life forms. For example, three species of lizards in Sumatra and a whip spider in Central Amazon are particularly found near buttresses (Dias and Machado 2006; Voris 1977) and species diversity of herpetofauna is higher around buttresses than in other rainforest habitats (Whitfield and Pierce 2005). The abundance of mycelial mat is also found to be higher near buttresses than in conjoint habitats (Guevara and Romero 2007). The microhabitats formed by buttresses may also affect seedling germination and establishment and result in different seedling assemblages at the upslope and downslope sides of buttress trees, and, consequently, in the long run, contribute to the maintenance of rainforest diversity (Tang *et al.* 2011).

Buttresses occur in many distantly related families and species from some families are more likely to develop buttresses than others (Chalk and Akpalu 1963; Chapman *et al.* 1998; Fisher 1982; Francis 1924; Richards 1996). For example, species in the families Dipterocarpaceae, Leguminosae, Sterculiaceae and Burseraceae are more frequently found to have large buttresses, while species from Annonaceae and Fagaceae rarely have buttressed trees (Porter 1971; Richards 1996). The same species may have both buttressed and non-buttressed individuals and the proportion of buttressed stems appears to increase with tree size (Chapman *et al.* 1998; Kaufman 1988). Emergent trees >30 m high always develop large buttresses (Richards 1996) and buttress size was correlated with potential height of tree species in a tropical montane rainforest on Hainan Island, China (Deng *et al.* 2008). However, there are also exceptions; e.g. some dominant species with large spreading crowns are generally un-buttressed in rainforests in Southern Queensland, Australia (Francis 1924). A possible reason why those big trees do not develop buttresses from their well-developed tap roots may be because it was suggested that buttress trees usually have superficial root systems (Richards 1996). Due to limited information, the prevalence of buttresses across taxa and whether they are associated with tree size is still not clear.

Although buttresses are very distinctive and may play important roles in many ecological processes in rainforests, they have largely been neglected in many rainforest studies and there is still no clear answer on many aspects of the origin and functions of buttresses. We compare the occurrence of buttresses across species and among families in a 20-ha tropical dipterocarp rainforest in SW China and test for the presence of an evolutionary signal in buttress formation using phylogenetic analyses to determine whether (i) buttress forming is a fixed species characteristic, (ii) there is a phylogenetic signal for buttress formation across broad taxa, (iii) buttress formation is an inherent feature or is simply induced by environmental factors and how this is relevant to the size of a tree.

MATERIALS AND METHODS

Study site

This study was conducted in a 20-ha tropical seasonal dipterocarp rainforest dynamic plot (101°34'E, 31°36'N) in the Mengla National Nature Reserve in Xishuangbanna, SW China. The Xishuangbanna region is dominated by a typical monsoon climate, with alternation between a dry season from November to April and a rainy season from May to October. As recorded by the Mengla weather station 14 km from the study site, the mean annual temperature of the area is 21.0°C, and the mean annual precipitation is 1532 mm, of which ~80% occurs during the wet season (Lan *et al.* 2011). The 20-ha dynamic plot was established in 2007 following the protocol for large forest dynamics plot of Center for Tropical Forest Science (CTFS; Condit 1998). The plot is 400 by 500 m, with elevation ranging from 709.27 to 869.14 m above sea level. The slopes in the plot range from 7° to 47°. Three perennial creeks wind through the plot and join together at the south-eastern corner of the plot. The forest is developed mainly on laterite and lateritic red soils with pH values of ~4.5–5.5 (Cao *et al.* 2006) and is dominated by *Parashorea chinensis* (Dipterocarpaceae; Lan *et al.* 2011). All free-standing stems with DBH ≥ 10 mm were tagged, mapped and identified and their DBH was measured. The initial survey recorded 95 940 trees from 468 species.

Buttress survey

All living standing trees (DBH ≥ 10 mm) in the 20-ha plot were carefully checked for buttresses around their base from January to March in 2011. The more or less flat triangular wood structure connecting the tree trunk with lateral roots running at or a little below the surface of the soil was regarded as a buttress (Richards 1996). Buttress trees were classified into five categories according to the size of the buttress. For buttressed trees in Class 3 and above, the height, length and thickness of each buttress was measured and their orientations were recorded. Buttress length was measured from its intersection with the trunk of the tree to the point where the ridge of the buttress first entered the ground (Chapman *et al.*

1998). Buttress height was measured as the vertical distance from where the buttress becomes even with the trunk of the tree to the ground. Buttress thickness was measured at a regular point in the middle of the buttress. Buttress orientation was recorded as degrees to the north with a compass (Lewis 1988). The identification, location and measurements of each tree were obtained from the database of the first survey of the 20-ha plot conducted in 2007 (Lan et al. 2009).

Data analysis

Species with at least one individual developed buttress was considered to have the potential of producing buttresses and was defined as a buttress species. The percentage of buttress species was calculated for the 20 most dominant families in the plot. Importance values of the families were calculated by the sum of the relative diversity, relative density and relative dominance of each family, according to the work by Mori et al. (1983).

Among the 468 tree species in the plot, we identified 241 buttress species and 86 non-buttress species (Supplementary Table S1), the latter had no buttress in at least 10 individuals. To compare similarity in buttress formation with phylogenetic similarity, a phylogenetic tree including the 327 buttress and non-buttress species was constructed based on the APGIII system (The Angiosperm Phylogeny Group III 2009) in Phylomatic and then a test of phylogenetic signal of buttressing characteristic was conducted using the K statistic (Blomberg et al. 2003). All phylogenetic analyses were performed using the phylo signal function in the “picante” package of the R statistical environment (Kembel et al. 2010).

Tree size (DBH) was arbitrarily classified into five classes using 200-mm intervals, following Slik and Eichhorn (2003): 10 to 200 mm (small trees), 200 to 400 mm (lower canopy trees), 400 to 600 mm (middle canopy trees), 600 to 1000 mm (upper canopy trees) and 1000 mm (emergent trees). The percentage of buttressed trees that occurred in each tree-size class was calculated. The relationship between tree size (DBH) and the occurrence of buttress trees was examined using a binomial GLM model. We calculated the Pearson’s correlation of the observed buttressing percentage in each DBH size class ($n = 138$, range: 1–255 cm) and the corresponding fitted values. To understand whether the size of a species could be related to the potential for buttress formation, we defined the DBH size of the largest individual within a species in the plot as the size of this species, represented as DBHmax, and classified the species into four classes according to the DBHmax (Aiba and Kohyama 1996). We used a Pearson’s correlation test between species size (DBHmax classes) and the percentage of buttress species in each DBHmax class to test whether there is an association of buttress formation with the size of species.

RESULTS

Of the 95 940 trees with DBH > 10 mm in the 20-ha plot, we identified buttresses on 4669 trees (5%), which were from

241 out of the 468 species (51%), 132 out of the 213 genera (62%) and 56 out of the 70 families (80%) in the plot. Of the trees with DBH > 100 mm, 3930 (32%) of 12 344 individuals and 230 (68%) of 339 species were buttressed. Of the 13 most abundant species (with >1000 individuals), only one species, *Leea compactiflora* Kurz, was not buttressed. Among the other 12 species, the percentage of buttressing varied from 0.07% in *Saprosma ternatum* Hook. f. to 21.27% in *Ficus langkokenensis* Drake. Buttresses were found in all the dominant emergent and canopy species (e.g. *Parashorea chinensis* Wang Hsie, *Sloanea tomentosa* (Benth.) Rehd. et Wils., *Pometia tomentosa* (Blume) Teijsm. and Binn., *Semecarpus reticulata* Lecte.) and 103 species had large buttresses of category \geq size Class 3 in the 20-ha plot.

Among 15 of the top 20 most dominant families, >50% of the species and genera produced buttresses (Table 1). Fourteen of the 17 species in Elaeocarpaceae were buttressed and three other species without buttressed individuals had <10 individuals. Similarly in Fagaceae, only 4 of the 14 species were not buttressed and each was represented by only a single individual. However, the families Rubiaceae, Leguminosae and Rutaceae have a low possibility of buttressing both at the species and the genus levels.

The buttressed species showed aggregated distributions on the phylogenetic tree. The observed ‘Phylogenetic

Table 1: a comparison of buttress formation in the 20 most important families (of 468 species and 213 genera) in the 20-ha plot

Family	Number of genera	Number of species	Number of buttressed genera	Number of buttressed species
Icacinaceae	4	6	3 (75%)	4 (66.7%)
Lauraceae	11	52	10 (90.9%)	28 (53.8%)
Euphorbiaceae	19	38	15 (78.9%)	20 (52.6%)
Dipterocarpaceae	1	1	1 (100%)	1 (100%)
Fagaceae	2	14	2 (100%)	10 (71.4%)
Moraceae	5	30	3 (60%)	22 (73.3%)
Rubiaceae	19	28	8 (42.1%)	8 (28.6%)
Annonaceae	7	15	4 (57.1%)	5 (33.3%)
Meliaceae	11	25	8 (72.7%)	17 (68%)
Elaeocarpaceae	2	17	2 (100%)	14 (82.4%)
Guttiferae	3	7	1 (33.3%)	4 (57.1%)
Sapindaceae	8	8	5 (62.5%)	5 (62.5%)
Myristicaceae	3	8	3 (100%)	4 (50%)
Myrtaceae	2	14	2 (100%)	10 (71.4%)
Leguminosae	9	19	4 (44.4%)	4 (21.1%)
Ebenaceae	1	4	1 (100%)	3 (75%)
Burseraceae	2	5	2 (100%)	4 (80%)
Anacardiaceae	6	7	4 (66.7%)	4 (57.1%)
Araliaceae	6	10	3 (50%)	5 (50%)
Rutaceae	5	12	2 (40%)	2 (16.7%)
Total	126	320	83 (65.9%)	174 (54.4%)

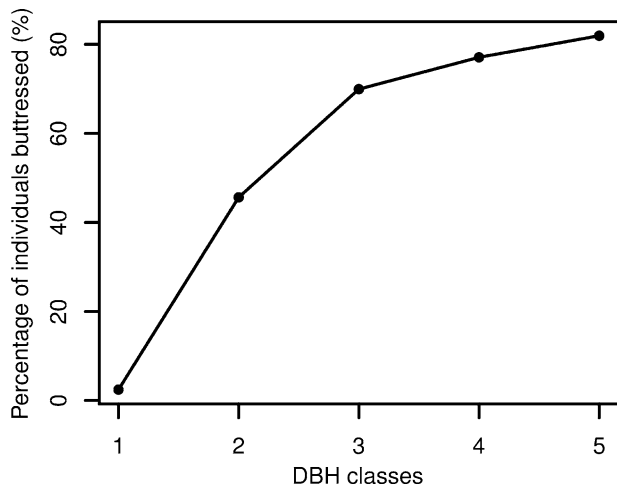


Figure 1: the percentages of buttressed trees in different DBH size classes. DBH Classes 1 to 5 represent trees with DBH ranges of 10–200, 200–400, 400–600, 600–1000 and ≥ 1000 mm.

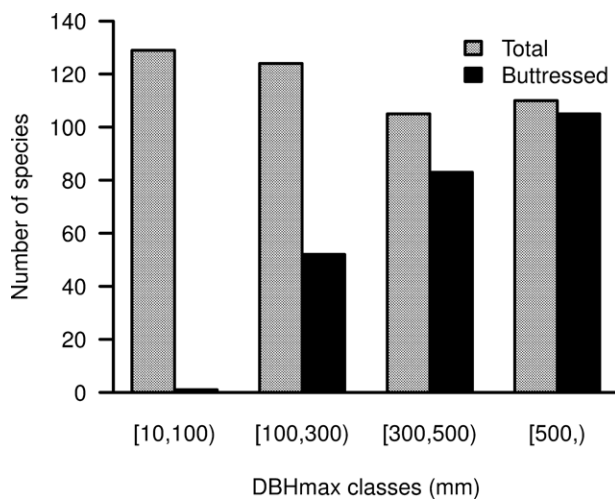


Figure 2: number of buttressed species in different DBHmax classes.

Independent Contrasts (PIC)' is significantly higher than the random values of PIC ($K = 10.2456409$, $P < 0.001$, repetitions (reps) = 999), indicating a strong phylogenetic signal for buttress formation among species.

The percentage of buttressed trees increased with tree size ($t = 9.6969$, $df = 136$, P value < 0.001 ; Figure 1). For trees with DBH > 100 mm, 31.87% of individuals from 230 species (67.8%) were buttressed. The percentage of buttressed species also increased with DBHmax of the species ($t = 7.8739$, $df = 2$, P value = 0.01575; Figure 2). The larger the DBHmax of a species, the more likely that some of the individuals will produce buttresses. Of the 111 species with DBHmax > 500 mm, 106 (95%) had buttressed stems. However, only 1 (0.78%) of the 129 species with DBHmax < 100 mm had buttressed stems.

DISCUSSION

The results from this study provide evidence that buttress formation is not a fixed species characteristic, as predicted by previous studies in smaller areas (Chapman *et al.* 1998; Kaufman 1988). Both buttressed and non-buttressed stems are found in many species across a broad spectrum of taxa. Although our study is one of the largest buttress surveys thus far, we are still not confident about the probability of buttress formation in species that are under-represented (i.e. with only few stems or small young individuals) in the plot. Unexpectedly, the percentage of buttress-forming species is much higher in this study than in previous studies in different forests around the world despite the fact that the plot is close to the Tropic of Cancer (Table 2). The most likely explanation is that we surveyed a much larger area than other studies that may have underestimated the number of buttress-forming species due mainly to the limited sizes of the study areas. Also, different criteria may have been used in different studies as there is still no standard protocol for buttress surveying. Buttresses are normally considered to be absent in Annonaceae and Fagaceae (Richards 1996), but 5 of the 15 Annonaceae species and 10 of the 14 Fagaceae species had buttresses in the rainforest we surveyed. A standardized survey in reasonably large areas is needed for comparison of buttress compositions at different locations.

The close association of the likelihood of buttress formation with the size of trees and the maximum diameter of a species supports the hypothesis that buttresses act as supporting structures. Other studies also found that buttresses are more common among trees in large size classes (Kaufman 1988; Chapman *et al.* 1998), especially rainforest emergent trees (Richards 1996 CIT0030CIT0030). It has been suggested that trees with buttresses may have a higher survival rate than trees without them, in the view that buttresses provide better support structures (Crook *et al.* 1997; Mattheck and Bethge 1990) and stronger nutrient acquisition ability (Newbery *et al.* 2009; Tang

Table 2: comparison of percentage of buttressing in different study sites (trees with ≥ 10 cm DBH)

Study sites	Percentage of species with buttress (%)	Percentage of trees with buttress (%)	Reference
Kibale National Park, Uganda (twenty-four 0.2-ha plots)	23%	21%	(Chapman <i>et al.</i> 1998)
Central Amazonian (1-ha plot)	42%	28%	(Milliken 1998)
Southern Bahia	—	17%	(Mori <i>et al.</i> 1983)
Northern Brazil (three 0.25-ha plots)	—	12%	(Thompson <i>et al.</i> 1992)
Xishuangbanna, China (20-ha plot)	68%	32%	This study

et al. 2011). The advantages buttressed trees receive allow them to gradually become dominant in frequently disturbed and generally nutrient-poor rainforests. However, the increase in the percentage of buttressed stems with the tree size may also be a response to environmental conditions. The longer a tree stands in the forest, the more likely it will form a buttress induced by unidirectional force caused by wind and asymmetrical crown and gravity when growing on slopes (Navez 1930; Richter 1984; ter Steege *et al.* 1997; Warren *et al.* 1988; Young and Perkoča 1994). In addition, the higher proportion of buttress-forming species in taxa with larger maximum DBH suggests there may be also an evolutionary force on buttress formation towards large-sized trees. Answers to these questions may need long-term monitoring of the dynamics of buttress trees.

Buttressed trees have been recorded from many distantly related families and many families have both buttress and non-buttress species (Chapman *et al.* 1998; Richards 1996). However, some families such as Dipterocarpaceae, Leguminosae, Sterculiaceae and Burseraceae tend to have more species forming large buttresses in many tropical rainforests (Porter 1971; Richards 1996). In the dipterocarp rainforest we studied, Elaeocarpaceae and Fagaceae are the two families that had the highest percentage of buttress-forming species. The clustered distribution of buttressed and non-buttressed species on the phylogenetic tree suggests that there is a strong evolutionary background of buttress formation. Non-buttressed species from families such as Rubiaceae, Rutaceae and Ardisiaceae, however, are small trees that grow in the understory or sub-canopy of the forest. This further emphasizes the effect of species size on buttress formation and provides support for the supporting hypothesis, i.e. that buttresses function as structural supports of large trees. By comparing the heights of 5784 species from 222 locations ranging from 74°29'N to 54°30'S, Moles *et al.* (2009) found that plants are significantly taller in the tropics than in other regions. Her study, together with the supporting hypothesis, may partly explain why there are more buttress trees in tropical areas.

In conclusion, this preliminary study showed that buttresses are very abundant in the 20-ha tropical rainforest plot studied here, which is situated at the northern edge of the tropics. As the largest buttress survey so far, we suggest that buttress formation is a plastic species characteristic and has a strong phylogenetic signal towards large-sized species.

SUPPLEMENTARY DATA

Supplementary material is available at *Journal of Plant Ecology* online.

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