

Buttress formation and directional stress experienced during critical phases of tree development

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ABSTRACT. Patterns of buttress formation in tropical trees vary greatly within and among species. In Kibale National Park, Uganda, some form of a buttress was found on 23% of the 78 species (1785 trees) sampled from a variety of distantly related families. Large differences in buttress formation were documented within a single family and even within the same genus. Previous studies have suggested that buttresses are mechanical adaptations to counter asymmetric loads experienced during brief critical phases in a tree's development and these persist after the need for a mechanical support has disappeared. As a tree grows from the understorey, up to the canopy, or emerges from the canopy, the potential number of occasions that a tree will experience directional stress increases. Many canopy level trees will probably have been in the vicinity of a treefall gap during their development, while emergent trees may experience gap exposure in addition to wind stresses associated with canopy emergence. Therefore, it is predicted that understorey trees should have fewer and less developed buttresses (after correcting for overall tree size) than canopy trees, which should have fewer and less developed buttresses than emergent trees. Detailed measurements of buttresses from 194 trees of eight species support this prediction. There was no evidence that trees thought to have experienced directional stress associated with selective logging almost 30 y ago had increased the number or size of existing buttresses. The pattern of buttressing in Kibale generally supports the idea that buttresses are mechanical adaptations to counter episodic asymmetric loads, and that buttresses persist after the need for a mechanical support has disappeared.

KEY WORDS: Buttress, life history, phenotypic plasticity, Kibale National Park, Uganda

INTRODUCTION

Patterns of buttressing in tropical trees vary greatly within and among species. This variability has engendered much debate and speculation as to the functional significance of these structures. Buttresses have been viewed as a

response to physiological stresses that could force aerial proliferation of shallow root systems (Davis & Richards 1934, Hallé *et al.* 1978, Petch 1930) or as mechanical adaptations to support trees against asymmetrical loads (Baker 1973, Chalk & Akpula 1963, Fisher 1982, Henwood 1973, Jenik 1978, Richter 1984, Smith 1972, Wilson & Archer 1979). Recent analyses present convincing evidence that trees lay down wood faster in areas which are subjected to mechanical stress (Ennos 1993, Mattheck & Kubler 1995). Forces that act to push a tree over create tension that is concentrated at the top of the junction between a lateral sinker root and the trunk. This results in growth of the most heavily stressed area near the trunk and results in the formation of a buttress (Ennos 1993, Mattheck 1991, Mattheck *et al.* 1997). Such modeling has gone a long way to explain variation in buttress formation (e.g., longer buttresses are found on the side of the trunk pointing towards the prevailing wind – Baker 1973, Richter 1984). However, such functional explanations, while outlining general principles, often seem inadequate in accounting for all of the variability in buttress formation seen in nature. For example, neighbouring trees of different species or of the same species often exhibit remarkably different buttress formation in terms of their length or orientation, despite the likelihood that they share similar soil and prevailing winds.

It has been postulated that if directional stresses are experienced at an early critical stage in tree development, the resulting buttresses may persist long after the stress has disappeared (Kaufman 1988). Thus, the length and distribution of buttresses in a mature tree could represent a record of the imbalances experienced by the tree throughout its development. If buttresses do represent this and not just the stresses that the tree is currently experiencing, this may account for much of the variation which remains when functional explanations that only consider current stresses are evaluated. It follows that trees with life history strategies characterized by a high probability of experiencing episodic directional stress should exhibit more extreme buttress formation.

In this paper we first describe patterns of buttress formation in the tree community of Kibale National Park, Uganda. Subsequently, we examine two situations in which trees are likely to have experienced directional stress at some critical phase of their development, and relate this to buttress development. We make two specific predictions: (1) Understorey trees are predicted to have less developed buttresses (after correction for overall size) than canopy trees, which in turn are predicted to have less developed buttresses than emergent trees. As a tree grows from the understorey into the canopy or emerges above the canopy there is an increase in the potential number of crises that an individual experiences. It is likely that most canopy-level trees will have been in the vicinity of a light gap during their development. Emergent trees are expected to have experienced all the crises of a canopy tree, plus exposure to stresses associated with winds after emerging above the canopy (see

Young & Hubbell 1991 for an analysis of crown asymmetry of emergent trees and directional stress). (2) Trees that are presently along roadsides or in logging clearings are predicted to have experienced a change in the directional stress at the time of human disturbance associated with the opening of the canopy on one side and should show evidence of redistribution of the support.

METHODS

Study site

Kibale National Park (760 km²), in western Uganda near the base of the Ruwenzori Mountains (0°13′–0°41′N and 30°19′–30°32′E), is a moist, evergreen forest, transitional between lowland rain forest and montane forest (Butynski 1990, Chapman *et al.* 1997, Wing & Buss 1970). The main study site, Kanyawara, is situated at an elevation of 1500 m has an annual rainfall averaging 167 cm, and has a daily maximum temperature averaging 23.3 ± 0.6 °C (SE) (1977–1995). Kibale forest received the protected status of a National Park in 1993. Prior to this date, it was a Forest Reserve, gazetted in 1932, with the stated goal of providing a sustained production of hardwood timber (Osmaston 1959). A polycyclic felling cycle of 70 y was initiated, and it was recommended that logging should open the canopy by *c.* 50% by the harvest of trees over 1.52 m in girth (Kingston 1967).

We contrasted buttress formation between a logged area (Forestry Compartment K-15) and an unlogged area (K-30) for eight species. K-15 is a 360-ha section of forest that experienced heavy selective felling in 1968 and 1969. Total harvest averaged 21 m³ ha⁻¹ or *c.* 7.4 stems ha⁻¹ (Skorupa 1988); however incidental damage was much higher. A total of 18 tree species were harvested, with nine species contributing >95% of the harvest volume (Kasenene 1987, Skorupa 1988). K-30 is a 300-ha area that has not been commercially harvested; however, prior to 1970, a few large stems (0.03–0.04 trees ha⁻¹) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa 1988, Struhsaker 1997).

Survey of buttress formation

To provide a community level description of buttress formation we established, at random, 24 vegetation transects that were each 200 m × 10 m (Chapman & Chapman 1997). The number, length, and height of the longest buttress on each tree >10 cm DBH (Diameter at Breast Height) were measured. Buttress length was measured from its intersection with the bole of the tree to where the uppermost surface of the buttress first entered the ground. Buttress height was measured from the ground to where the buttress becomes even with the trunk of the tree. Trees were categorized as below, equal to, or emergent from the canopy, and the slope of the ground was measured with a clinometer.

Test of predictions

We quantified the number of buttresses, length of all buttresses, length of secondary projections coming off main buttresses, height of all buttresses, DBH, and tree height for eight species in logged and unlogged areas (*Balanites wilsoniana* (Balanitaceae, $n = 10$), *Celtis africana* (Ulmaceae, $n = 32$), *Celtis durandii* (Ulmaceae, $n = 40$), *Chrysophyllum gorganusanum* (Sapotaceae, $n = 12$), *Ficus exasperata* (Moraceae, a free standing fig; $n = 30$), *Mimusops bagshawei* (Sapotaceae, $n = 4$), *Olea welwitschii* (Oleaceae, $n = 34$), and *Parinari excelsa* (Rosaceae, $n = 32$, for a total of 194 trees). From this information, the following indices were calculated: mean buttress length, total buttress length, total buttress length plus the length of the secondaries, buttress number, and maximum buttress height. Each tree was categorized as emergent, canopy level, or understorey, and the slope of the ground was measured.

Buttress size increases with tree age and size (Richter 1984, Warren *et al.* 1988, Young & Perkocha 1994). To control for the effect of tree size, a regression was established between each index describing buttress formation (e.g., total buttress length) and tree size (DBH). All measures describing buttress size were strongly correlated with tree size ($P < 0.0001$). To control for tree size we used the residuals from the regression in comparisons between canopy categories (understorey, canopy level and emergent) and disturbance history (logged and unlogged). The effects of canopy category, disturbance history, and the interaction of canopy category and disturbance on different indices of buttress formation were examined using analysis of variance.

RESULTS

Survey of buttress formation

To provide a forest-wide description of buttress formation, buttresses on 1785 trees (> 10 cm DBH) from 78 species were measured on the 24 vegetation transects (Table 1). Buttresses were found to occur in 18 (23.1%) of the 78 tree species. The percentage of tree species with buttresses varied among size classes, with smaller size classes having a lower proportion of trees with buttresses than the larger size classes (10–30 cm DBH = 19%, $n = 1381$; 30–50 cm DBH = 17%, $n = 268$; 50–70 cm DBH = 31%, $n = 63$; > 70 cm DBH = 69%, $n = 73$).

Buttress formation was analyzed only for the 29 species for which more than 12 individuals (total number = 1586) were measured. Nine of these species (31%) had some form of buttress (Figure 1). However, only two of these nine species (7%; *Olea welwitschii*, *Celtis durandii*) typically had buttresses (Figure 1).

For those trees that had buttresses, there was no relationship between either the length (corrected for tree size by dividing by DBH, $r = -0.072$, $n = 221$, $P = 0.286$) or height ($r = 0.022$, $n = 220$, $P = 0.746$) of the longest buttress and the slope of the ground on which the tree was growing. Not correcting for tree size

Table 1. Description of the number and size of buttresses found on trees from three size classes in Kibale National Park, Uganda. Buttress length was measured from the bole of the tree to where the uppermost surface of the buttress first entered the ground. Buttress height was measured from the ground to where the buttress became even with the trunk of the tree. DBH is the Diameter at Breast Height, measured in cm. NT is the number of trees found on the transect NWB is the number of trees on the transect that had buttresses, Mean NB is the number of buttresses on those trees that had buttresses. Buttress length and height (cm) are reported for those trees that had buttresses.

Species	Family	DBH Size Class	NT/NWB	Mean NB (SE)	Length (SE)	Height (SE)
<i>Albizia grandbracteata</i>	Leguminosae	10–40	12/2	3(1.0)	270(30)	455(345)
		>70	1/1	6	270	305
<i>Balanites wilsoniana</i>	Balanitaceae	10–40	3/1	2	145	350
<i>Blighia unijugata</i>	Sapindaceae	>70	1/1	8	550	80
<i>Bosqueia phoberos</i>	Moraceae	10–40	109/3	1.67(0.7)	436(183)	310(169)
<i>Celtis africana</i>	Ulmaceae	10–40	34/3	3(1.2)	468(206)	299(76)
		40.1–70	5/2	7.5(2.5)	160(40)	575(326)
		>70	3/0	6	700	134
<i>Celtis durandii</i>	Ulmaceae	10–40	127/104	4.9(0.1)	334(26)	343(29)
		40.1–70	41/39	5.6(0.3)	243(25)	227(21)
		>70	4/3	6.3(0.9)	310(42)	313(52)
<i>Chrysophyllum sp.</i>	Sapotaceae	10–40	1/1	5	158	235
		40.1–70	1/1	8	125	335
		>70	1/1	8	125	335
<i>Diospyros abyssinica</i>	Ebenaceae	10–40	195/2	3.5(0.5)	130(90)	75(3)
<i>Fagaropsis angolensis</i>	Rutaceae	10–40	28/1	3	400	800
		10–40	13/1	6	360	120
		>70	1/1	4	240	140
<i>Ficus exasperata</i>	Moraceae	10–40	12/7	7(1.9)	376(80)	252(83)
		40.1–70	1/1	9	185	300
		>70	1/1	7	180	340
<i>Markhamia platycalyx</i>	Bignoniaceae	10–40	161/1	7	100	105
		40.1–70	30/2	3.5(0.5)	80(10)	147(8)
		>70	1/1	7	100	105
<i>Mimusops bagshawei</i>	Sapotaceae	10–40	3/1	8	190	180
		40.1–70	4/2	7(1.0)	298(202)	155(35)
		40.1–70	2/1	5	260	760
<i>Newtonia buchananii</i>	Leguminosae	10–40	5/2	4.5(0.5)	225(125)	300(100)
<i>Olea welwitschii</i>	Oleaceae	10–40	9/6	4.7(0.7)	222(80)	179(47)
		40.1–70	3/3	5.7(1.2)	670(182)	135(22)
		>70	1/1	7	340	285
<i>Parinari excelsa</i>	Rosaceae	10–40	5/3	7.3(0.9)	141(46)	217(124)
<i>Premna angolensis</i>	Verbenaceae	10–40	9/1	4	115	70
		>70	3/1	8	80	220
		>70	3/1	8	80	220
<i>Pseudospondias microcarpa</i>	Anacardiaceae	10–40	2/2	6.5(15)	145(35)	403(47)
		>70	2/2	6(1)	360(140)	575(225)
		>70	2/2	6(1)	360(140)	575(225)
<i>Spathodea campanulata</i>	Bignoniaceae	10–40	1/1	3	40	200
		>70	1/1	8	140	625
		>70	1/1	8	140	625
<i>Strombosia scheffleri</i>	Olacaceae	10–40	21/3	5.7(0.9)	171(16)	228(86)
		40.1–70	10/6	4.8(0.9)	385(143)	238(47)
		>70	5/3	5.3(0.3)	347(178)	370(273)
<i>Strychnos mitis</i>	Loganiaceae	10–40	11/1	3	220	100

For those trees on the transects that did not have buttresses, we report the number of trees examined for each DBH size class. *Albizia gummifera* (Leguminosae) 10–40 3, *Aningeria altissima* (Sapotaceae) 10–40 7, *Antiaris toxicaria* (Moraceae) 10–40 3, *Aphania senegalensis* (Sapindaceae) 10–40 9, *Adodytes dimidiata* (Icacinaceae) 10–40 2, *Belschniedia ugandensis* (Lauraceae) 10–40 1, *Bersania abyssinica* (Melinathaceae) 10–40 3, *Blighia unijugata* (Sapindaceae) 10–40 5, *Bosqueia phoberos* (Moreaceae) 40.1–70 1, *Carterispermum laurinum* (Rubiaceae) 10–40 4, *Casearia battiscombei* (Flacourtiaceae) 10–40 4, *Cassine buchananii* (Celastraceae) 10–40 1, *Cassipourea ruwensorens* (Sapotaceae) 10–40 30, *Chaetacme aristata* (Ulmaceae) 10–40 52, *Coffea eugenioides* (Rubiaceae) 10–40 2, *Cordia abyssinica* (Boraginaceae) 10–40 11, 40.1–70.1, *Cordia millenii* (Boraginaceae) 10–40 2, *Craterispermum laurinum* (Rubiaceae) 10–40 1, *Croton macrostachyus* (Euphorbiaceae) 10–40 4, *Croton sylvaticus* (Euphorbiaceae) 10–40 2, *Dasylepis eggelingii* (Flacourtiaceae) 10–40 4, *Dictyandra arborecens* (Rubiaceae) 10–40 1, *Dombeya mokule* (Sterculiaceae) 10–40 27, 40.1–70 3, *Ehretia cymosa* (Boraginaceae) 10–40 5, *Erythrina abyssinica* (Leguminosae) 10–40 4, *Eudenia* sp. (Capparidaceae) 10–40 3, *Fagara angolensis* (Rutaceae) 10–40 3, *Funtumia latifolia* (Apocynaceae) 10–40 122, 40.1–70 8, >70 1, *Kigela moosa* (Bignoniaceae) 10–40 12, *Leptonychia mildbraedii* (Sterculiaceae) 10–40 59, *Linociera johnsonii* (Oleaceae) 10–40 12, 40.1–70 1, *Lovoa swynnertonii* (Meiliaceae) 10–40 1, *Macaranga* spp. (Euphorbiaceae) 10–40 1, *Maerua duchesnei* (Capparidaceae) 10–40 14, *Margaritaria discoidea* (Euphorbiaceae) 10–40 1, *Markhamia platycalyx* (Bignoniaceae) >70 2, *Milletia dura* (Leguminosae) 10–40 28, 40.1–70 4, *Mimusops bagshawei* (Sapotaceae) >70 2, *Mitragyna rubrostipulata* (Rubiaceae) 10–40 2, *Monodora myristica* (Anonaceae) 40.1–70 1, *Myrianthus* sp. (Moraceae) 10–40 23, *Oxyanthus speciosus* (Rubiaceae) 10–40, 8, *Pancovia turbinata* (Sapinaceae) 10–40 18, *Parinari excelsa* (Rosaceae) 40.1–70 2, *Premna angolensis* (Verbenaceae) 40.1–70 6, *Prunus africana* (Rosaceae) 10–40 2, *Rauwolfia oxyphylla* (Apocynaceae) 10–40 3, *Rothmannia urcelliformis* (Rubiaceae) 10–40 6, *Sapium ellipticum* (Euphorbiaceae) 10–40 1, *Strychnos mitis* (Loganiaceae) 40.1–70 5, *Symphonia globulifera* (Guttieraceae) 10–40 1, *Tabernaemontona* sp. (Apocynaceae) 10–40 18, *Tarena pavetoides* (Rubiaceae) 10–40 1, *Teclea nobilis* (Rutaceae) 10–40 57, *Trema orientalis* (Ulmaceae) 10–40 19, *Uvariopsis congensis* (Anonaceae) 10–40 162, *Vangueria apiculata* (Rubiaceae) 10–40 1, *Xymalos monospora* (Monimiaceae) 10–40 18.

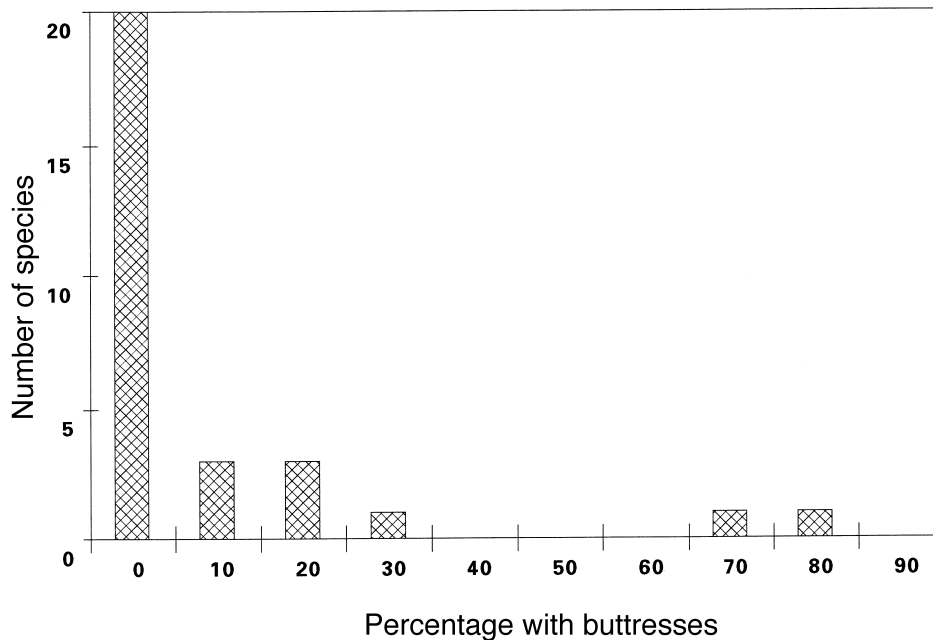


Figure 1. A frequency distribution illustrating for each species the percentage of the individuals with buttresses. Based on a survey of 1785 individuals and 78 species in Kibale National Park, Uganda.

produces similar nonsignificant probabilities. However, over 87% of the trees occurred on shallow slopes of <20 degrees (average slope 12.5° , range 0–46).

Tests of predictions

We predicted that understorey trees should have less developed buttresses (after correction for overall size) than main canopy trees, which should have less developed buttresses than emergent trees, and that buttress size and/or number should be affected by previous exposure to canopy opening associated with selective logging. Buttress number and four different measures of buttress size were examined (total buttress length, mean buttress size, total buttress and secondary length and buttress height). Canopy category had a significant effect on all measures of buttress size and on buttress number (Table 2). Measures for buttress size from understorey trees were less than those for main canopy trees, which were less than those for emergent trees (post-hoc comparisons $P < 0.05$). Disturbance history associated with logging showed no effect on any indices of buttress size or on the number of buttresses (Table 2).

DISCUSSION

From the survey conducted in Kibale it is clear that buttresses develop on trees in a variety of distantly related families (Richards 1996). There were not enough commonly occurring species per family to permit a quantitative analysis of the nature of buttress formation across tree families. However, it is

Table 2. Effect of canopy category, disturbance history, and canopy category x disturbance history (interaction) on standardized residuals of measures of buttress size or number versus tree size (DBH). F-values are presented in the body of table.

Variable	Canopy	Disturbance history	Interaction	Overall model
	df: 2	1	2	5
Total buttress length	5.04**	0.09	1.60	4.93**
Mean buttress length	6.07**	0.01	2.26	6.21**
Total + secondaries length	5.34**	0.31	2.46	6.06**
Buttress height	3.05*	1.09	2.32	4.44**
Buttress number	4.80**	2.27	1.39	5.10**

* $P \leq 0.05$, ** $P \leq 0.01$, error df in all cases 188.

noteworthy that sharp differences in buttressing can occur even within a single genus. For example, 83% of *Celtis durandii* trees along transects had buttresses, while only 17% of the *Celtis africana* trees had buttresses (Table 1). This difference may relate to interspecific differences in seedling and sapling growth forms. *C. africana* can remain very thin in its initial growth phase, while *C. durandii* seedlings and saplings take on a much more typical seedling structure. This suggests that *C. africana* could grow to the canopy without having been exposed to gap conditions, while *C. durandii* probably requires gap formation to reach the canopy. Baker (1965) documented a similar example of variable buttress formation in situations with and without directional stress. When *Ceiba pentandra* grows in a forest environment it is always buttressed, but when it grows in the savanna it is unbuttressed (Baker 1965)

There are a number of species (e.g., *Mimusops bagshawei* and *Uvariopsis congensis*) for which there was little or no evidence that buttresses were used for support. Following the logic presented here, such species should have life history strategies that make them relatively immune to the ontogenetic crises typically experienced by rainforest trees or they must employ some other means of obtaining support. There is evidence to support the first alternative. The growth and survival of seedlings of six tree species has been contrasted among understorey, small gap (treefalls) and large gap conditions for 36 mo in Kibale (C. A. Chapman *et al.*, unpubl. data). The growth rate of *U. congensis* and *M. bagshawei* did not differ between the small gaps and understorey. Both species had 100% mortality in large gaps. These data suggest that these species can regenerate in the absence of treefall gaps, and thus may not experience periods of changing directional stress associated with gap formation. In contrast, growth experiments of *Pseudospondias microcarpa* demonstrate that this species grows more quickly in small gaps relative to the understorey. Correspondingly, all *P. microcarpa* individuals examined had large well-formed buttresses.

Contrasting buttresses of understorey, canopy level and emergent trees suggests that trees potentially exposed to more episodes of directional stress, have a greater number and more developed buttresses than trees less likely to have asymmetric load crises. This suggests that buttresses are adaptations to counter asymmetric loads that persist after the need for mechanical support has

disappeared. However, there was no evidence that trees in the logged area had increased buttress size or number in response to logging activities. It is possible that the stress caused by canopy opening associated with logging may not be as directional as stresses caused by proximity to a single gap. If the canopy surrounding a tree left after logging was open on all sides, there would be no directional stress caused by the tree growing towards light coming predominantly in one direction, thus no buttress would form. Since tree mortality in logged areas is high even 25 y after logging (74% higher than unlogged areas, Chapman & Chapman 1997), it is difficult to reconstruct the neighbourhood of trees in such an area. As a result it is not possible to estimate the recent history of directional stresses experienced by a tree.

Our current observations of relationships between life history and buttress formation suggest that buttresses could be used as a record of gap dynamics in a given forest. The proportion of a forest that is composed of species that typically produce large buttresses may be an indicator of the frequency with which small gaps form. We still know little about the life histories of most rainforest tree species, and life history crises may not be the only determinant of buttressing behaviour. However, these results warrant a cautious examination of the potential for using buttress morphometrics as an indicator of disturbance regimes in tropical forests.

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