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Buttress form of the central African rain forest tree *Microberlinia bisulcata*, and its possible role in nutrient acquisition

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Abstract Buttressing is a trait special to tropical trees but explanations for its occurrence remain inconclusive. The two main hypotheses are that they provide structural support and/or promote nutrient acquisition. Studies of the first are common but the second has received much less attention. Architectural measurements were made on adult and juvenile trees of the ectomycorrhizal species *Microberlinia bisulcata*, in Korup (Cameroon). Buttressing on this species is highly distinctive with strong lateral extension of surface roots of the juveniles leading to a mature buttress system of a shallow spreading form on adults. This contrasts with more vertical buttresses, closer to the stem, found on many other tropical tree species. No clear relationship between main buttress and large branch distribution was found. Whilst this does not argue against the essential structural role of buttresses for these very large tropical trees, the form on *M. bisulcata* does suggest a likely second role, that of aiding nutrient acquisition. At the Korup site, with its deep sandy soils of very low phosphorus status, and where most nutrient cycling takes place in a thin surface layer of fine roots and mycorrhizas, it appears that buttress form could develop from soil-surface root exploration for nutrients by juvenile trees. It may accordingly allow *M. bisulcata* to attain the higher greater competitive ability, faster growth rate, and maximum tree size that it does compared with other co-occurring tree species. For sites across the tropics in general, the degree of shallowness and spatial extension of buttresses of the dominant species is hypothesized to increase with decreasing nutrient availability.

Keywords Buttresses · Nutrient exploration · Rain forest · Structural support · Surface rooting

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Introduction

Tropical tree ecologists have long been fascinated by buttresses. These external woody lateral–vertical structures of stems are the result of secondary epinastic growth of surface roots (Richards 1996). They are found on a wide range of trees and are nearly always associated with species whose adults grow into the canopy and emergent layers (Kaufman 1988). Buttresses are a distinctive feature of the tropical rain forest and are very rarely found outside this biome (Richards 1996). Two main hypotheses have been advanced to explain their occurrence: (1) structural, that larger (older) trees require them for stem and crown support, and for stabilization when loads are asymmetrical or winds are a major force (Smith 1972; Ennos 1993), and (2) nutritional, that smaller (younger) trees develop them as a consequence of their surface roots spreading out laterally to acquire soil resources (Petch 1928; Richards 1996). The two hypotheses are not mutually exclusive though, and the relative importance of each will vary from site to site (Henwood 1973).

In recent years, the structural hypothesis has received more attention than the nutritional one, although the latter

was proposed earlier. This might have happened because of the relative ease with which physics could be applied to testing the structural hypothesis (Mattheck 1991, 1993), combined with a lack of detailed studies on strategies of nutrient acquisition by tropical trees. Clearly a more integrated and general hypothesis is called for which recognizes that natural selection of a tree feature can solve more than one problem over the life-time of the individual (Kaufman 1988). Different habitats would be expected to influence the size and shape of buttresses, and these characteristics should be explainable in physiological and ecological terms.

Buttresses are stress-and-strain bearing components of a tree and not buttresses per se. They are formed from tension- or compression-reaction wood (Fisher 1982; Mattheck 1993; Crook et al. 1997). The word 'buttress' is unfortunately something of a misnomer and it probably arose originally from architecture where stone buttresses are used to support walls (Navez 1930). Whitford (1906) observing buttresses in rain forests in the Philippines, first suggested that they counteracted unequal loads caused by crown asymmetry, and he imagined that the point where the roots below the heaviest branches joined the stem was most under pressure. By contrast, Navez (1930) studying the direction of buttress formation on *Ceiba pentandra* (L.) Gaertn. (Bombacaceae) in Cuba and Brazil found that they corresponded well to the predominant wind direction, and especially in the soft flooded soils of the Amazonian *varzea*, but were growing on the side of the tree towards the wind. Young and Perkocha (1994), among others, also found that the largest buttresses generally occurred on the side of the tree opposite to the largest part of the crown. The interpretation was that buttresses act vectorially like 'tension cables' to achieve load compensation, and thereby prevent torque and buckling or snapping of the stem (at least at its base), or uprooting. The structural hypothesis has been well explained on mechanical engineering principles by Mattheck (1991, 1993), who showed how secondary sinker roots below the buttresses can anchor the whole structure by spreading and absorbing the stress optimally over a large surface area, counteracting compression forces on the opposite side of the tree. Ennos (1993) has argued that wind is the most important factor determining buttress formation.

In a strongly buttressed tree the stem proper tapers downwards so that at ground level its diameter is about one-third of that above the buttress (Francis 1924; Richards 1996). Smith (1972) proposed that if the gravitational force of a tree's mass were to be spread out over the soil surface in an area larger than that of its stem bole (with buttresses and tapered stem forming a frustum), this would prevent the tree from 'piling', i.e., working itself downwards into the ground. This would be especially

important in silty/clayey rather than sandy soils, because silt and clay (when wet) offer less resistance to movement than sand. A tree would also be more prone to movement under lateral forces in silty/clayey soil. Smith (1972) accordingly predicted that buttresses would be unlikely to occur on sandy soils.

Buttressed large trees have been reported to have no, or poorly developed, taproots, and several authors have implied a trade-off, or design alternative, between having a well developed taproot and a set of buttresses in tropical trees (Richards 1996). An important example is *Gilbertiodendron dewevrei* (De Wild.) J. Léonard (Caesalpiniaceae, Leguminosae) which forms large monodominant stands in the Congo Basin, has relatively big seeds for a caesalp, shade-tolerant seedlings and slow growth. Although it can reach 45 m in height, it has no buttresses but a very large and deep tap-root which enables both support in sandy–clay soils and access to ground water in the dry months (Louis and Fouarge 1949). Crook et al. (1997) reported on two species in a Bornean rain forest (*Aglaia affinis* Meur., Meliaceae, and *Nephelium ramboutan-ake* Labill., Sapindaceae) which had both buttresses and taproots: the observations were made, however, on very small trees of only 11–13 cm stem diameter. It is possible that most trees start with a taproot but as they mature to become large canopy individuals the taproot plays a reduced role in support as buttresses develop.

The structural hypothesis has received only moderate support, however, which suggests that it alone is not a full explanation for buttressing. Lewis (1988), found no differences in distribution and sizes of buttress of failed and alive trees of *Pterocarpus officinalis* Jacq. (Leguminosae) subject to strong winds. Where soils are thin they give little possibility of tap-root anchorage and therefore buttressing would be a suitable alternative. Warren et al. (1988) found that number and direction of the spreading buttresses of *Tachigalia versicolor* Standl. & L. O. Williams (also Leguminosae) were not related to orientation of the wind nor were they consistently on the uphill side of leaning trees, although the largest buttresses were often on the windward side. Richter (1984) working on *Quararibea asterolepis* Pittier (Bombacaceae) found correlations between buttress direction, size and branches to be weak although the longest buttress (up to 2 m) tended to grow away from the point of largest crown load. Most authors have noted that buttresses grew allometrically at faster rates than stems, suggesting that buttress wood can react effectively when needed.

A buttressed tree can probably attain more rapid growth into the canopy, and a more flexible growth strategy, than an unbuttressed one. This is because, as the tree crown grows laterally into above-ground gaps in the canopy (over some years), the increasing asymmetry in load is better supported (Kaufman 1988). More sudden would be the

instability caused by the loss of a large branch for which the tree must presumably compensate by further buttress growth over some further years. In exploring the above-ground environment the buttresses of large tropical trees might be interpreted as a record of past growth episodes (Chapman et al. 1998). Current buttress structures cannot therefore be expected to correspond exactly to current branch and canopy shape.

Francis (1924) noticed that buttresses of rain forest trees in Queensland started early in the understorey where there was no wind stress or appreciable crown asymmetry. Buttresses were found at high rainfall sites, associated with heavily shaded forest floors, where trees had a tendency to form many roots at or near the soil surface. This was one of the first realizations that buttresses might have evolved, in part, as a consequence of root exploration in the surface soil layers. The impression gained from many of the illustrations in Francis (1929), however, is that most species had their buttresses steeply close-to-perpendicular to the stem and not spreading far out.

Petch (1928) working on *Poinciana regia* Boj. ex Hook (Leguminosae) in Ceylon also recorded how buttresses developed on small trees well before any possible need for support, although clearly juveniles would need to have developed them to some degree if they were to be of increasing service as the tree became larger. In common with later findings, Petch (1928) found that the buttresses appeared to form at random orientations on young trees. In *Canarium commune* L. (Burseraceae) the buttresses ran out straight from the stem, held down by vertical sinker roots; the taproot had either died back or not formed at all. Petch's hypothesis was that presence of buttresses is due to (1) lack of a taproot, and (2) the need for lateral exploration for resources by roots.

Mora excelsa Benth. (Leguminosae) in Guyana has large spreading buttresses (Davis and Richards 1934). Since wind is not a significant factor, their role was considered coincidental and secondary to another factor. Davis and Richards (1934) proposed that buttresses on this species originated in exploration for water and nutrients. Interestingly, buttressed trees were found mostly in sheltered creeks and not on ridges and plateaus. Richards (1996) contention was that the laterals were forced to grow near the surface because poorly drained creek soils became anaerobic, the trees often lacking or having very reduced taproots. Henwood (1973) considered the trade-off between a tap-root system and a buttress/surface system of rooting, and suggested that the surface roots would be a strong advantage in poor soils where nutrients were mostly near the surface. In other words, where root growth was allocated more laterally at the cost of a large taproot that might otherwise have afforded tree support, buttresses had to fulfill this structural role instead. Buttresses also allow a

tree to exploit a large soil surface area and thus be more competitive for nutrients (Black and Harper 1979), not only because buttress area can be up to ca. fourfold that of a simple stem, but additionally a buttress system allows a much greater spread of the root system.

In this paper the buttress architecture of a large rain forest tree, *Microberlinia bisulcata* A. Chev. (Caesalpiniaceae, Leguminosae), on low-nutrient sandy soils and under a strongly seasonal climate, at Korup, Cameroon, is investigated. The aim was to explore which of the structural or nutritional hypotheses had more support, and to ask how buttresses might explain other aspects of this species' ecology. The lack of buttresses on codominant caesalpiniaceous species *Tetraberlinia bifoliolata* (Harms) Hauman and *T. korupensis* Wieringa (previously named *T. moreliana* Aubr. in Korup) will be discussed in this context. Relevant details of the Korup site and background ecology of species mentioned can be found in Gartlan et al. (1986) and Newbery et al. (1988, 1997, 1998, 2004).

Methods

Sampling of adult trees

In 1991 an 82.5-ha plot was established along the central part of transect P (see Gartlan et al. 1986). The plot (1,650 m long and 500 m wide) was subdivided into 330 subplots of 50 m × 50 m. All trees ≥50 cm stem diameter above buttresses (≥157.1 cm girth), were mapped, measured and identified. Of a total of 1,656 individuals, 293 were of *M. bisulcata* (Newbery et al. 1998). Three size classes were defined for the present study: 1, 157.1–249.9; 2, 250–349.9; and 3, ≥350 cm girth. Seven trees were randomly selected from each class. One was omitted because it was next to a gap and débris covered the buttresses, to give a sample of 20 trees for the measurement of buttress architecture. Two leaning trees, one tree with visibly broken branches, and another tree whose branches were above a very dense understorey which made measurements difficult, were further disregarded to give a sample of 16 suitable trees.

Tree architecture measurements

Three to five measuring points were chosen in order to have full view of the buttress system. One point was taken as the origin and the x-, y- and z-coordinates of the other measuring points were estimated in relation to it. Measurements were made with a laser survey instrument (LSI; Model Criterion-400, Positioning Resources Ltd, USA) with specially programmed tree functions.

Buttresses were mapped in three dimensions from the points where they emerged from the stem to the points where they disappeared into the ground. The continuous shape of a buttress in the vertical plane was approximated by a set of contiguous segments each with a close-to-straight upper edge. Each segment approximated a trapezium, and total area of each buttress was given by the sum of the connected trapezia. The buttress angle was found for the first two segments lying away from the stem. The stem diameter was measured above the buttresses.

Each buttress was individually identified. Its *main* part was that which ran continuously across dividing points whilst maintaining maximum height until disappearing below ground. Side buttress was usually found to each main buttress. The main buttresses were the longest buttress part and practically always that which entered the soil furthest from the center of the stem.

Branch directions were found with a compass, heights above the ground with a clinometer, and lengths from the stem to first fork by vertical projection to the ground. Branch diameters could not be measured with the LSI because angles between stem-base and where the branch joined the stem were often >60°. A simple optical relascope was constructed from a 50-cm length of plastic tubing and a pair of calipers to measure branch diameters, this being at ca. 1 m out from the stem. From these measurements branch volumes (stem-face to fork) could be estimated, assuming that branch diameter found applied along the branch's entire length. Buttress work was conducted between December 2002 and March 2003 (Schwan 2003). In May 2007 the 16 trees were re-measured for maximum buttress height using a clinometer.

Tree and above-buttress heights

The average maximum tree height of *M. bisulcata* was found later from clinometer readings of 15 strongly buttressed individuals (including the largest) in the plot (5 in September 2004 and 10 in May 2007). They were located haphazardly within the plot as sighting of the crowns permitted.

As part of a main plot re-enumeration in 2005 all *M. bisulcata* trees with buttresses (n = 243; unpublished data) were measured for stem diameter (at ca. 0.5 m above buttresses) using the LSI, and in doing so height of measurement on the stem was recorded. Seventeen of the trees of the present study were included. In May 2007 a subset of these trees with unusually high height-on-stem records were measured for maximum buttress height using the clinometer. Since the height (point-of-) measurement necessarily moves up the stem with time onto the flattest part

over the buttresses, it results in the least biased estimate of stem diameter increment.

Forest juvenile and nursery trees

In 2004 all juvenile *M. bisulcata* trees were mapped and measured in the plot (unpublished data). The 27 undamaged and free-standing survivors out of 31 with stem diameters of 10 to <30 cm were selected for surface root and buttress architecture measurement. These were spread evenly across the plot. In December 2006 a scaled diagram of each trees' buttress (surface root) was made, and diameter at breast height (dbh) recorded. The heights of each buttress at the stem, and of those points where the immediately sharp down-taper changed to a flatter outward spread of the buttress/root were recorded.

In May 2006 early-developing surface roots of seven plantation *M. bisulcata* trees, at Mana Bridge near Korup (2-year old seedlings out-planted in 1999), were measured for root length, direction and diameter.

Calculations

Buttress systems were drawn in three dimensions using the graphics program Sigma-Plot (SPSS 2002) and the branch systems overlain in vertical projection for each tree. The common center of the stem, buttresses and branches was estimated from the drawings. A circle around a stem's center was divided into eight segments (1: 0 to <45°; 2: 45 to <90°; ….; 8: 315 to <360°), and total buttress area and branch volume found for each one. The mean angles of buttresses and of branches for each tree were calculated following Fisher (1993) and using the circular statistics functions of GenStat 7.2 (Payne 2000). Tests of angular correlation and difference followed Zar (1996).

The areas of the polygons (convex hulls) enclosing first the buttress system, and then separately the vertical projection of the branch system, of each tree were found by tracing onto paper, weighing and direct area conversion.

Allometric analysis was achieved by major axis (model II) regressions (Clarke 1980; McArdle 1988; Legendre and Legendre 1998) of logarithmically transformed mean height, length and area of main (longest) buttress per tree against logarithm of tree stem diameter. The regression slopes were tested against hypothetical equal rates of growth where the coefficients would be 1.0, 1.0, and 2.0, respectively (Niklas 1994).

From the diagrams of the juvenile trees, angles (referenced on stem centers) at which each buttress-root departed from its stem and where it entered the soil were determined.

Results

Development from the lateral surface-soil root system into large set of buttresses on *M. bisulcata*, with the very large branches and canopy they support, is illustrated in Fig. 1.

Buttress systems of adult trees

Two-dimensional ground plans of the 20 buttress systems are shown in Fig. 2. The impression is one of considerable variability in radial distribution and length between individual trees. Biometrical characteristics of the trees studied

Fig. 1 Surface roots and buttresses of *Microberlinia bisulcata* in various stages of development, and the branches of adult trees, in Korup National Park, Cameroon
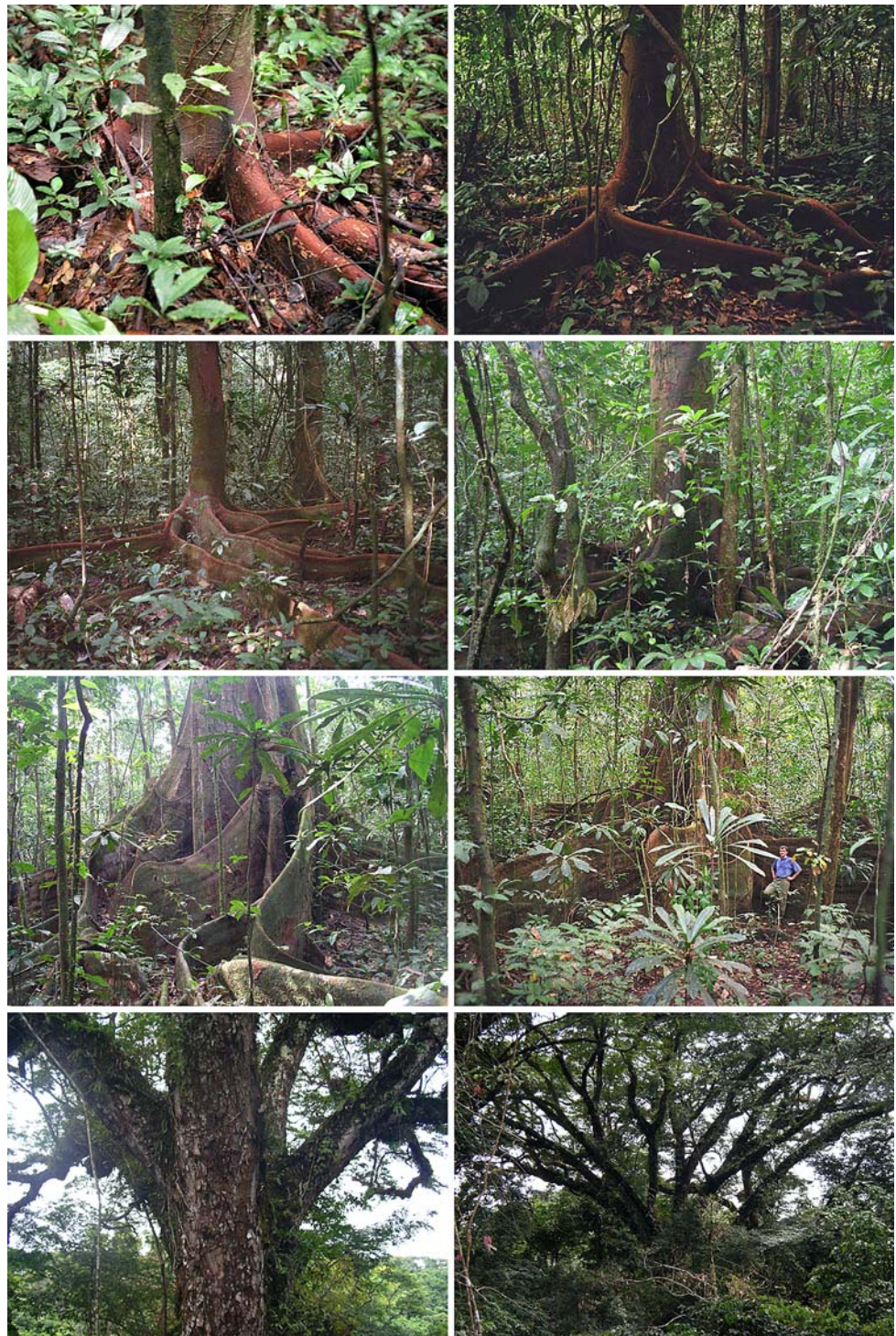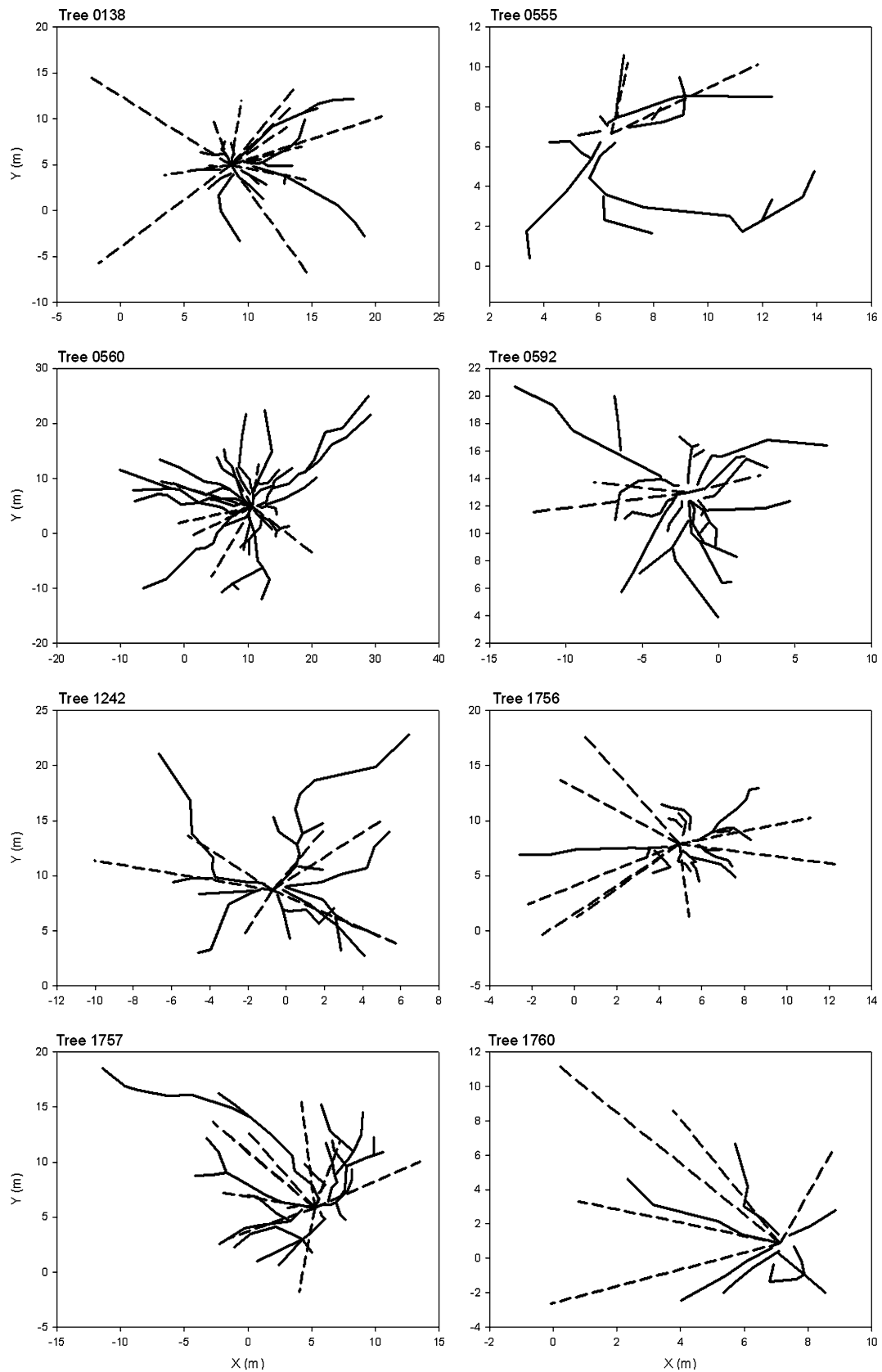
Fig. 2 Vertical projections of the buttresses (*solid lines*) and branches (*dashed lines*) of 16 *Microberlinia bisulcata* trees
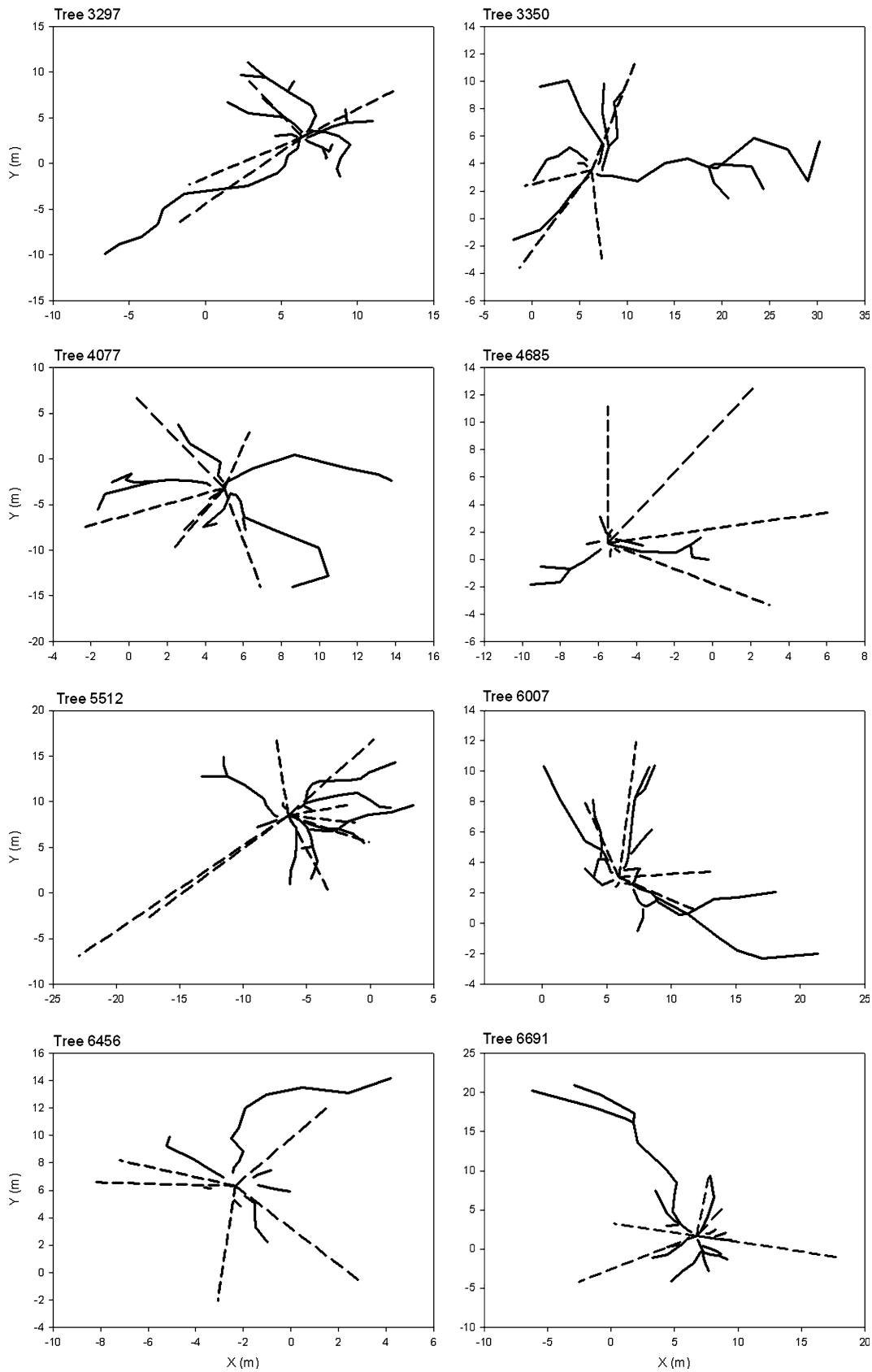
Fig. 2 continued

Table 1 Architectural characteristics per tree of a sample of trees of adult *Microberlinia bisulcata* in Korup National Park ($n = 20$ for stems and buttresses; $n = 16$ trees for branches)

	Averages			Sums		
	Mean ± SE	Median	Range	Mean ± SE	Median	Range
Stem						
Diameter (cm)	119.9 ± 6.6	125.1	68.1–175.4			
Buttress						
Number						
Main	5.6 ± 0.3	5.5	4–10			
Side	4.5 ± 0.9	3.0	0–16			
Height (m)						
Main	3.1 ± 0.2	3.2	1.3–5.5	17.1 ± 1.8	15.6	8.5–41.1
Length (m)						
Main	7.4 ± 0.9	6.7	2.18–15.8	38.7 ± 4.0	38.9	15.3–79.1
All	15.0 ± 3.3	10.0	2.6–56.9	75.8 ± 14.7	60.9	16.6–284.5
Area (m^2)						
Main	4.2 ± 0.6	3.6	0.9–12.0	22.3 ± 3.1	18.8	6.1–49.6
All	6.7 ± 1.5	4.9	0.9–26.1	34.6 ± 7.0	23.4	6.1–130.6
Branch						
Number	5.8 ± 0.6	5.0	2–12			
Height to branch (m)	10.5 ± 0.4	10.5	7.6–12.7			
Basal diameter (m)	0.47 ± 0.02	0.46	0.28–0.65			
Length to fork (m)	9.53 ± 0.43	9.30	6.00–12.36	57.1 ± 7.9	47.8	12.0–138.9
Volume (m^3)	1.90 ± 0.21	1.66	0.62–3.28	11.05 ± 1.70	8.83	2.6–25.0

are summarized in Table 1. Mean lengths, sums of lengths and areas of all and main (longest) buttresses were all positively significantly correlated with stem diameter ($r_{18} = 0.463$–0.691, $P < 0.001$–0.040). Mean numbers of buttresses and branches were very similar (on average 5.7/tree), and branch diameters were 39% those of stems. The main buttresses contributed 40% of the total length, and 61% of the total area, of the buttresses. Length of main branches to the forks was relatively constant and close to the mean height to branching. The buttress variables in Table 1 were often moderately positively skewed and logarithmic transformation normalized their frequency distributions. Accordingly, medians are also shown in Table 1 and the Appendix Table 4 gives the corresponding back-transformed means and confidence limits.

Mean ± SE tree height was 44.29 ± 1.44 m ($n = 15$; range 35.0–53.2 m) for trees of mean ± SE stem diameter 137.4 ± 9.4 cm (range 102.2–252.1 cm). Buttresses reached up to 30% of the stem bole to the main branches (Table 1—height to branches having low variability between trees) and to 7% of total tree height.

Buttress height with distance from tree

Buttresses decreased rapidly in height close to the tree, and then spread out, reaching a height often of only a few centimeters at considerable distances away (up to 20 m)

before entering the ground (Fig. 1). Heights of main buttresses along their lengths (i.e., at the points where the segments joined) were pooled across all trees ($n = 188$) since there were few heights (ca. 10) per tree. Decline in height (ht, m) with distance (dist, m) followed a rectangular hyperbola (Fig. 3) of the form, $\text{ht} = -0.0230 + (3.110/(1 + 1.840\ \text{dist}))$ ($F_{2,185} = 272.1$, $P < 0.001$). At the stem (dist $= 0$), the inferred ht was 3.11 m. An improved fit was obtained by expressing buttress height for each tree as a percentage of the (maximum) height (%ht) at the stem: $\%\text{ht} = -0.077 + (99.4/(1 + 2.134\ \text{dist}))$ ($F_{2,176} = 1684$, $P \ll 0.001$; discounting 19 *df* for the multiple points at $\%\text{ht} = 100$). Most of the scatter in height was between 4 and 12 m from the stem (Fig. 3).

Whilst there was some additional heterogeneity in mean buttress height across trees for %ht ($F_{19,166} = 4.19$, $P < 0.001$), the interaction tree × distance was not significant ($F_{19,147} = 0.87$, $P = 0.62$). An REML mixed-model analysis in which trees were a random factor and ht or %ht were fitted to $1/(\text{dist} + 1)$ in a linear model resulted in very high significance ($F_{1,178} = 770$ and 2483, $P \ll 0.001$).

Buttress directions and relationship to branches

The correlation between buttress and branch distributions (Fig. 4) was only significant ($P \leq 0.05$) for one of the 16 trees. Segment number having the largest buttress area was

Fig. 3 Decline in buttress height as a percentage of height at the stem, pooled for 16 *Microberlinia bisulcata* trees. The *open symbol* at 100% is thus the superposition of 16 points. The *dotted curve* is the best fit rectangular hyperbola: see text for equation and statistics
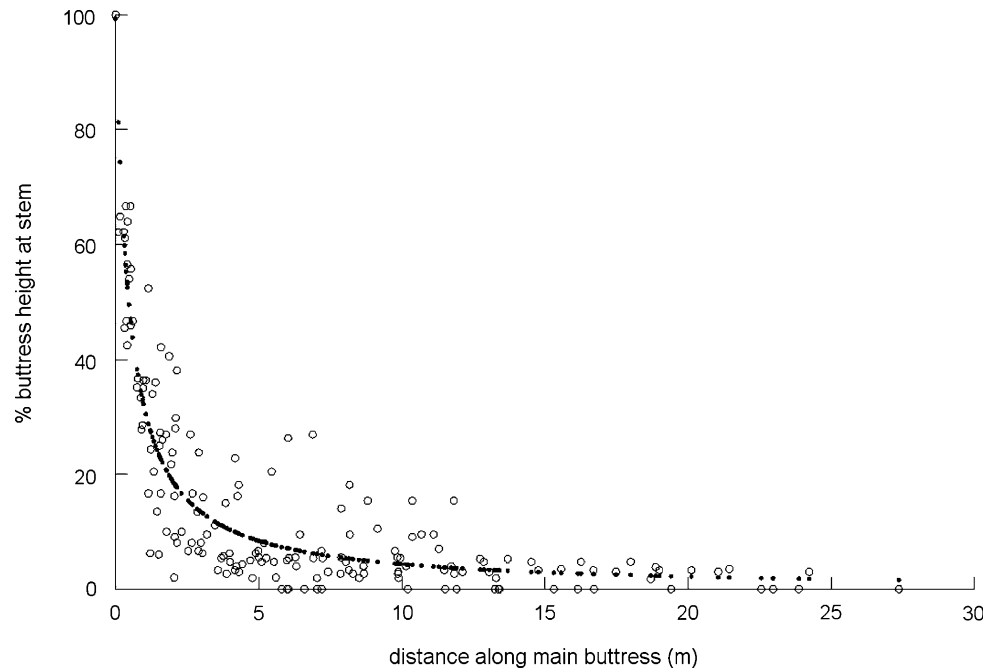
not significantly correlated with that having the highest branch volume across trees either ($r_{aa} = -0.043$; $P > 0.1$).

Von Mises' test of randomness could only be applied to four trees for buttresses but 14 trees for branches: sample sizes were otherwise too small. In no case was the null hypothesis of random directions rejected: probabilities of χ^2_{15} (i.e., using 18 segments; Genstat 7.2) ranged from 0.749–0.913 and 0.775–0.944 for buttresses and branches, respectively. There was, furthermore, no tree for which Rayleigh's test of uniformity of buttresses could be rejected ($P = 0.175$–0.924), although four trees had significantly

non-uniform branch arrangements ($P = 0.001$–0.018; for the other 12, $P = 0.113$–0.667). In the significant cases branches were more to one side of the tree than the other (Fig. 4).

The SDs of mean angle per tree were high: for buttresses this was 108° (range 76–131°, $n = 16$) and for branches 77° (range 24–105°, $n = 16$) on average. The mean buttress angle (i.e., mean of the 16 trees' mean angles) was 92° ($n = 16$, SD = 83°) and the corresponding mean for branches 312° ($n = 16$, SD = 84°). Moore's paired non-parametric test showed also no significance between
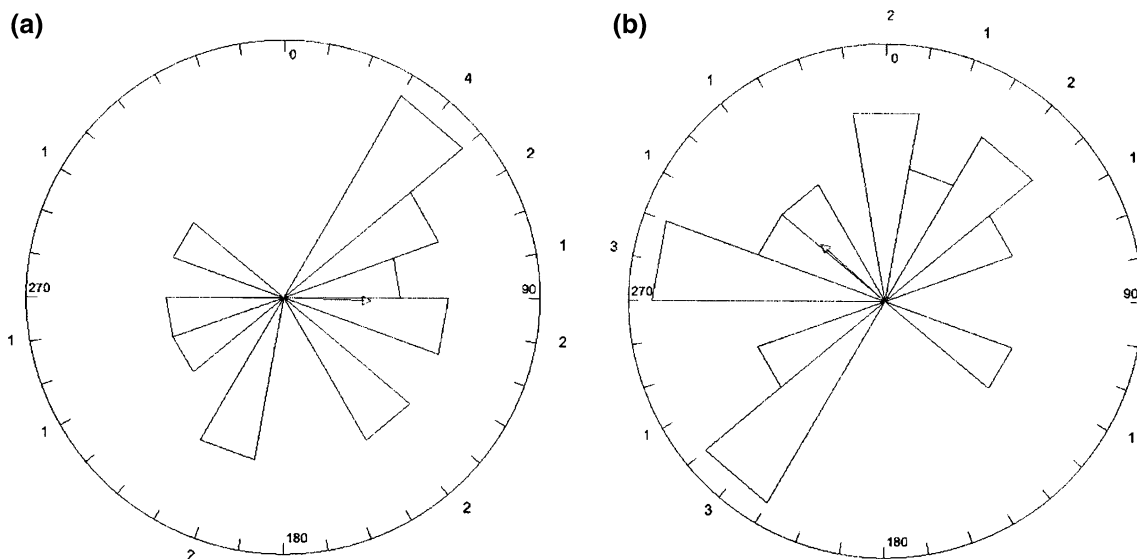

Fig. 4 Circular plots of **a** buttress and **b** branch angles grouped in 20°-segments. Segment areas are proportional to number of observations (shown) in that sector; *arrows* indicate the mean angles

Table 2 Architectural characteristics per tree of a sample of trees of juvenile *Microberlinia bisulcata* in Korup National Park, and of plantation saplings of the same species in the Mana Nursery, outside of the Park

	Mean ± SE	Median	Range
Juveniles (n = 25)			
Stem			
Diameter (cm)	22.4 ± 1.2	23.0	11.3–33.4
Buttress			
Number			
Main	4.20 ± 0.46	4.0	1–11
Height (cm)			
At stem	27.9 ± 2.0	27.0	11.0–42.1
Change point	11.1 ± 1.3	10.3	0.0–28.0
Length (m)			
Sum	6.10 ± 1.22	3.51	0.36–27.57
Mean	1.25 ± 0.13	0.97	0.36–2.51
Maximum	2.04 ± 0.23	1.67	0.36–4.20
Plantation saplings (n = 7)			
Stem			
Diameter (cm)	6.63 ± 0.55	6.27	5.25–8.98
Surface roots			
Number	2.86 ± 0.74	2.0	1–7
Length (m)			
Sum	3.51 ± 1.36	2.65	1.49–11.49
Mean	1.15 ± 0.15	1.14	0.50–1.64
Maximum	1.58 ± 0.28	1.37	0.67–2.73
Diameter[a] (cm)	6.14 ± 0.41	6.25	4.75–8.00

[a] 10 cm from stem

Table 3 Polygon areas of vertically projected buttress and branch systems of trees of *Microberlinia bisulcata* in Korup National Park (n = 16), with the ratios of areas and of logarithms of areas

|	Mean ± SE	Median	Range
Polygon areas (m^2)			
Buttresses	177 ± 53	156	14–918
Branches	140 ± 26	118	8–397
Buttress/branch	2.55 ± 0.93	1.32	0.06–13.9
ln(buttress)/ln(branch)	1.10 ± 0.10	1.06	0.48–2.04

Tree allometry

Allometric analysis indicated that height, length and area of main buttresses were growing relatively faster than stem diameter ($b_{MA} = 2.39$, 4.52, 4.64, respectively; significantly different from b_{HYP} at $P < 0.00005$ in all cases), with buttress lateral extension almost twice as fast as height. Major axis regression using mean total buttress length and area per tree showed very similar results ($b_{MA} = 5.70$, 5.88; $P < 0.00001$). The corresponding coefficients for length and area of main buttress versus height were also significantly different from null-hypothesized values ($b_{MA} = 2.01$ and 3.04, respectively, $P = 0.0003$ and <0.0001).

Estimated maximum buttress heights and buttress 'creep'

The relationship between maximum buttress height (mxbht) and height of diameter measurement on the stem (hms), both in m, was found as: mxbht = $-2.577 + 2.150$ hms $- 0.1310$ hms^2 ($F_{2,15} = 7.13$, $P = 0.008$, $r^2 = 0.45$); and the mean difference between hms and mxbht was 0.46 m. This regression was applied to all relascope-measured trees to obtain their estimated heights, emxbht, and these were then plotted against the stem diameters of 2005 (Fig. 5). Apart from two exceptionally large-diameter trees (the largest having, remarkably, a branch of 41 m length), a collection of 11 points lying above the main cluster was obvious. These, on inspection in May 2007, were found to consist of six trees that were leaning, four that had twisted stems and one with very weak lateral extension, which explained the very tall and slim buttressing and necessity of measuring diameter before at a much higher-than-normal hms. In the relascope survey leaning was noted for just two other trees in the plot (hms = 7.1, 7.8 m). Mean ± SE hms of these taller buttresses was 8.22 ± 0.61 m (n = 11), and the matching values for the next-lowest, and obviously more typically lateral, buttresses were 5.15 ± 0.47 m (n = 11).

Excluding the 13 outliers mentioned, the relationship (Fig. 5) between emxbht and stem diameter (diam), both in

buttress and branch angles (n = 16, P > 0.05). Non-parametric correlation (Mardia's method) between the mean angles of buttresses and branches per tree (Fig. 4) was not significant ($r_{aa,14} = -0.080$, $P > 0.20$), nor was the angle of the highest or largest-area buttress with the angle of the branch containing the highest volume correlated ($r_{aa,14} = -0.085$ and -0.060, $P > 0.05$).

Buttress and branch polygon projections

Polygon projection areas for both buttresses and branches varied considerably (Table 3). Both had positively skewed frequency distributions, particularly for buttresses with one very high outlying value of 918 m^2 (tree #560). Logarithms of polygon buttress and branch areas were weakly and insignificantly correlated ($r_{14} = 0.054$, $P = 0.84$), and the ratio of these transformed values per tree had a mean close to 1.0 yet a range of two orders of magnitude (ca. 0.1–10; Table 3). Whilst branch polygon area was strongly correlated with stem diameter ($r_{14} = 0.725$, $P < 0.001$), for buttress area the correlation was only marginally significant ($r_{14} = 0.516$, $P = 0.041$).

Fig. 5 Relationship between estimated maximum buttress height and stem diameter above buttresses for 246 trees of *Microberlinia bisulcata* measured with a relascope (for diameter): *inverted triangles* trees with extremely large stems and buttresses; *squares* trees with leaning or twisted stems (an outlier group); *open circles* those trees forming the architecture study; and *diamonds* small trees without buttresses
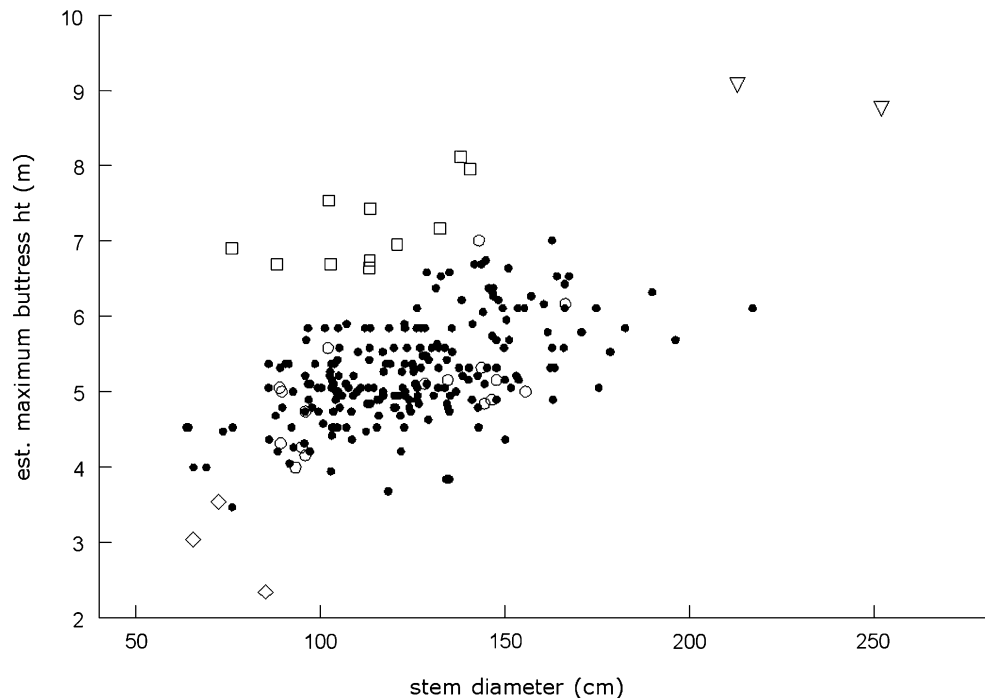
m, was: emxbht = 3.5 + 1.40 diam ($F_{1,228} = 99.3$, $P < 0.001$, $r^2 = 0.30$: a quadratic fit improved r^2 by only 0.2%). The positions of the 20 trees from the architecture study are also shown in Fig. 5: the mean and range in diameter (Table 1) of 17 trees that were relascoped sit well within the spread of the larger sample (1.24 ± 0.02, 0.64–2.17). For the others with low buttresses that were measured with a tape, their heights were inserted as POM −0.46 m. Overall mean ± SE emxbht was 5.24 ± 0.04 m ($n = 230$).

The re-measured mxbht of the architecture study trees showed a close relationship the values in 2003: mxbht$_{2007}$ = 1.03 mxbht$_{2003}$ ($F_{1,15} = 322.8$, $P < 0.001$; constrained through origin, $n = 16$).

Between 1991 and 2005 mean stem diameter of the relascoped (buttressed) *M. bisulcata* trees changed from 110.07 ± 1.70 to 124.47 ± 1.75 cm (1.0286 cm year^{-1}). Using the equation above, the corresponding mean *emxbht* would have been 504.1 and 524.3 cm (1.4429 cm year^{-1}), i.e., a relative rate of buttress height to stem diameter increase of 140%.

Surface roots of nursery trees

Of the 24 trees established in the plantation, the seven largest had well exposed surface roots by 2006 (Table 2), numbering almost 3/tree on average and reaching over 10 m total extent per tree. As for the forest juveniles there was considerable variation between individuals.

Buttresses of juvenile trees

Two of the 27 juvenile trees (7.4%) had no surface roots or buttress: they had typical stem diameters of 12.9 and 16.9 cm in 2005. Surface roots and young buttresses were spread in all directions in a seemingly random-to-even manner. Sample sizes were generally too low to test for circularity, however. Only three out of the 105 buttresses recorded had side roots/buttresses (2.9%) and these were very short. Number of buttresses varied considerably with median of 4 per juvenile tree: and height on stem was just less than 30 cm on average (Table 2). Unlike heights, buttress lengths were more positively skewed and with large ranges in both mean and maximal values. Juveniles could on average reach 2.5 m away from the stem, and some buttresses individually over 4 m (Table 2). Mean length and heights per tree were significantly positively correlated with stem diameter in 2006 ($r_{23} = 0.401$–0.423, $P = 0.035$–0.045), and slightly better correlated with maximum length and height per tree ($r_{23} = 0.450$–0.452, $P = 0.023$–0.024). The numbers of buttresses per tree were again too few to apply tests of circular statistics.

Discussion

Buttress form

In contrast to *M. bisulcata*, neither *Tetraberlinia bifoliolata* nor *T. korupensis* trees form buttresses. This statement is

based on several years of enumeration and tree identification work in the main plot and surrounding forest in Korup. *Tetraberlinia* trees do not reach the largest sizes of *M. bisulcata* (upper quartile and maximum stem diameters (cm): *Mb*, 136, 252; *Tb*, 99,150; *Tk*, 89, 142—from the 2005 unpublished main plot data), and this may be a consequence in part of their failure to form buttresses. That *M. bisulcata* is so obviously dominant in forming groves where it is strongly associated with the two *Tetraberlinia* codominants, points to buttressing helping it to achieve this position. This size aspect accords with other studies where the largest proportions of buttresses were found among trees of the largest stem diameter classes (Kaufman 1988; Chapman et al. 1998) or among emergent trees over ca. 30 m high (Richards 1996).

No comparative below-ground study of root architecture of the three species in Korup has been possible so far, for the obvious practical reasons. However, observations of root systems upturned when trees died did not lend support to the idea of a trade-off in traits between *M. bisulcata* having only buttresses and lateral roots but no taproot and the *Tetraberlinia* spp. the opposite. This trade-off idea was originally considered by Petch (1928) and taken up later by Henwood (1973) and Richards (1996) among others. Four of nine trees of *M. bisulcata* which had died since 1991, and were remeasured in 2005, had upturned roots; and three of these had taproots. (The one without was at a location with a very high water table.) The tap-roots had diameters of ca. 40, 40 and 50 cm diameter at depths of 1.0, 1.0, and 1.5 m, respectively. Whilst *Tetraberlinia* spp. probably do mostly have taproots, there is to hand only one observation of a *T. korupensis* with an upturned root system: otherwise trees mostly died from snapped boles.

Microberlinia bisulcata seems to combine lateral roots (leading to buttresses) with a substantial combined taproot, an example contrary to the general rule suggested by Henwood (1973). For all these species, as indeed all other species with large trees, a deep tap-root is probably essential for accessing the water table in the dry season, particularly when that season is prolonged (Newbery et al. 1998). And *M. bisulcata* even flushes its new leaves annually at the start of the dry season which necessitates a ground water supply to support onward leaf growth (Newbery et al. 2006). Early work in Zaïre showed *Julbernardia seretii* (Caesalpiniaceae, Leguminosae) to be strongly buttressed with shallow near-surface roots and no taproot, whilst *Gilbertiodendron dewevrei* displayed the opposite traits (Gérard 1960; Louis and Fouarge 1949). Soils in the central Congo basin are, however, generally nutrient-richer than those in southern Korup (Lebrun and Gilbert 1954; Germain and Evrard 1956; Gérard 1960).

The most prevalent feature of the *Microberlinia* architecture is the high lateral extension of the buttresses, these decreasing in height relatively rapidly away from the stem and not immediately entering the ground. Instead they spread out on the upper soil layer for considerable distances, in some cases even beyond the crown radius, before the roots disappear into the ground. There must be a reason for the association with the upper soil layer, and even the litter layer, besides supporting the stem above ground. Earlier authors also noticed that buttress-like wings were sometimes developed on horizontal roots at some distance from the stem where they could be of no value as supports and could not play a role in countering tensile stress (Henwood 1973; Lewis 1988). When *M. bisulcata* trees were leaning or twisted their buttresses were very tall and narrow showing that they could respond strongly to pronounced decentralization of the canopy mass.

The allometric analysis indicated that height and lateral spread of buttress was faster than stem diameter. If buttresses functionally support the tree in ways related to its three-dimensional biomass or volume, rather than the two-dimensional stem diameter, then the result is not unexpected. The functional basis could be mass loading/support or nutrient acquisition or both. More essential, however, was the finding that lateral spread and area of buttresses was faster than buttress height, highlighting that lateral spread was the more important variable. No correlation was found between diameter of the stem and number of buttresses. *M. bisulcata* trees of larger stem diameter classes did not possess a higher number of buttresses, as found for other tree species (Young and Perkocha 1994).

Judging from field observations (see Fig. 1) the buttressed lateral roots probably extend outwards so long as the tree is actively growing under and up into the main canopy, but once the tree becomes mature and emerges out of the canopy, resources would be switched to growth in buttress height. Buttress creep, or the rate of buttress growth in height, nevertheless was surprisingly high at 40% faster than the rate of stem diameter growth. This is, nevertheless, an average value for average-sized trees, and the relationship between creep and size would be expected to be higher, or lower, for respectively smaller or large trees.

The measurements on the nursery-raised small trees, and on the forest juveniles, of *M. bisulcata*, confirmed the variable and random-to-even establishment of the surface roots in early growth which matches number and placement of those of the adults. Where several small laterals grew close to one another it appears that one eventually superimposed itself upon the others to locally form a buttress.

Mechanical considerations

Smith's (1972) hypothesis that buttresses serve to prevent piling of heavy trees into unstable silty substrates, and therefore would not be found on more stable sandy ones, is clearly refuted here in the case of *M. bisulcata*. Korup with its deep sandy and partly rocky profile potentially affords deep anchorage for any large tree's roots, and soils are not, as assumed by Warren et al. (1988) and Ennos (1993), so generally thin. Based on observations in Guyana, Richards (1996) also thought that buttressed tree species mainly occurred on loamy-clay soils at sites with high rainfall, the poor drainage leading to anaerobic conditions below the surface layer.

Further evidence to support the view that mechanical support is not the only selective cause for buttresses in *M. bisulcata* comes from the buttress and branch size and direction data. There is no doubt that buttresses do support the crown in an overall way, but care is needed in interpreting static data. Whilst branches can fall from a tree, buttresses cannot. A buttress system recorded contemporaneously is the accumulated outcome of a tree's history (Chapman et al. 1998). The lack of a match between large branches and buttresses is quite likely because buttresses were largely formed from mid-tree size onwards to balance the developing crown but then (1) the crown may have altered due to competition with neighboring trees (Young and Perkocha 1994; Chapman et al. 1998), and (2) large branches were shed (Kaufman 1988), a process not uncommon in older *M. bisulcata* (personal observation).

That trees did not have common direction to their buttresses rules argues against a unilaterally applied external force such as wind being significant (cf. Navez 1930; Richter 1984; Lewis 1988; Ennos 1993). Strong gusts of wind ahead of thunderstorms over Korup are known but not with a consistent wind direction. If buttresses grew up where the lateral roots first spread out, and their sizes and shapes adjusted to deal with the tree asymmetry in patterns different and special to each tree, this provides the best strategy against rare wind events (Kaufman 1988; Lewis 1988), and it would allow most resistance to torque forces (Mattheck 1991; Young and Perkocha 1994). A large gap south of the main P-plot, caused in 2000 by strong winds, brought down several trees of *Tetraberlinia* and other species, but not one of *M. bisulcata* (unpublished data). Further, since *M. bisulcata* forms large even-height crowns at high local densities within groves this would tend to minimize canopy-surface turbulence caused by winds, an 'en bloc' effect quite different from that on isolated emergent trees.

Nutrient acquisition

Richards (1996) suggested that the prevalence of buttresses in the tropics depended on the tendency of roots to be concentrated in the better-aerated upper layer of the soil profile, which was often also the one relatively the richest in nutrients. However, in Korup the case for aeration is weak since the soils are sandy and well-drained. This leaves the hypothesis of nutrient exploration, and its corollary that the basic ground plan for buttresses in *M. bisulcata* is set early in tree life according to the surrounding pattern of nutrient supply. (This could in future be tested by following root extension and soil nutrient analysis.) The extent and number of lateral buttresses is seemingly determined by the initial lateral root system. Nevertheless, to achieve greater stability natural selection might have been expected to operate in favor of increasing existing buttresses rather than growing new lateral ones (Henwood 1973), which again points to spatial exploration being important.

Previous work in Korup on nutrient cycling in the groves of high basal area of these three codominant caesalp species has highlighted that they are all ectomycorrhizal (Newbery et al. 1988), that soil phosphorus (P) is generally very low (Gartlan et al. 1986; Newbery et al. 1997), and the fast nutrient cycle (Chuyong et al. 2000) compared with other low-nutrient tropical sites, leads to a ca. 60% increase in P in the top ca. 5 cm of the soil profile (Newbery et al. 1997). This surface organic layer, rich in fine roots and mycorrhizal hyphae, is critical to forest functioning and here most of the nutrients, especially P, are caught and taken up. The organic layer is supplemented by the litter of other species too, so any newly establishing *M. bisulcata* tree would be expected to explore this layer and develop an extensive near-surface fine root mat which would optimize the capture of nutrients. Evidence of these processes help to explain why on *M. bisulcata* the buttresses are so laterally extensive.

Juvenile trees had far fewer and less well-developed side buttresses on *M. bisulcata* than adult trees. The relatively high number on the adults reached almost a 1:1 ratio with the main buttresses (Table 1). Whilst side buttress must also have arisen from previously formed surface roots it seems that they developed only when the tree was much bigger. This leads to the idea the side buttresses might play an important role is stabilizing the tree as an adult. The system of main and side buttresses together (representing the polygon areas), with a diverse set of angles and turns on all sides of the tree, would be effective at giving tensile strength against asymmetrical loads and oblique torque from twisting. Moreover, it would be a flexible strategy of additional support, developing with need over time. The

loss in optimal structural support resulting in a more shallow lateral spread of main buttresses (as opposed to closer and more vertical structures) in *M. bisulcata* appears then to be compensated for by a contribution from these side buttresses.

For *M. bisulcata* the presence of both taproot and buttresses implies that buttresses are additional to the taproot, i.e., the taproot alone is insufficient to provide enough stability for the tree. Given that the buttresses are distributed much more in the lateral than vertical direction, compared with many other tropical tree species, then this buttress shape might not be strong enough for support. Selection of both tap-root and buttresses serves then a set of multiple functions (Kaufman 1988). An outstanding puzzle is why the *Tetraberlinia* spp. do not have lateral roots and buttresses if these help in nutrient exploration and competition. One possible explanation lies in the fact that *Tetraberlinia* as a genus is much more widely distributed than *Microberlinia*, and often on nutrient-richer soils (Letouzey 1968, 1985; Newbery and Gartlan 1996) where nutrient exploitation would be of less selective value.

If a part of a tree's crown tended to be largely supplied with its mineral nutrients via the lateral buttressed roots directly below it (perhaps an explanation for the interesting observations of Whitford 1906, in this respect), then the pattern in buttressing developed in early life (when the tree was in the sub-canopy with minimal structural requirements) would not necessarily be ideally positioned to supply the tension or compression wood for an asymmetry of the crown on the other side as a large canopy/emergent adult (inferred from Richter 1984). This further explains the complicated and varied patterning in buttress sizes and directions. Most buttresses were sinuous, i.e., rarely did a buttress go straight out from a tree; Fig. 1). In early life the course of a lateral root is, according to the hypothesis, determined by nutrient sources. Extensive lateral buttressing would be expected to make seedling establishment and sapling development more difficult with a dense rooting system in place (Black and Harper 1979).

In a recent study in a rain forest in French Guyana, Christensen-Dalsgaard et al. (2007) have shown that at the root–stem interface, buttressed species had fewer and smaller vessels when compared with non-buttressed ones, and correspondingly lower specific conductivities. The buttresses were of the short more-vertical form. At first sight, this might appear not to support the nutrient acquisition idea, except that these measurements were made on very small trees (7–13 cm stem diameter). Vessel anatomy may change with tree growth as demands for water by the canopy increase, and vessel constriction would need to be

shown for spreading buttresses of the form exemplified by *M. bisulcata*. More importantly, the study of Christensen-Dalsgaard et al. (2007) highlights the possible association between increase in structural support and constraints on water flux. The maintenance of a taproot on large trees might overcome this problem.

The nutrient exploration hypothesis, or the "Francis-Petch hypothesis", as first elucidated by Petch (1928), based on work of Francis (1924), and elaborated upon by Henwood (1973), Richter (1984) and especially Richards (1996), gives perhaps the strongest reason why buttresses are common in the tropics and rare in the temperates. Both environments present mechanical stress-and-strain problems but in the tropics the nutrient cycling is such that most (scarce) nutrients are passing through the top 20 cm of the soil profile and here rooting needs to be very effective. This is particularly crucial in early growth when a small tree must establish and compete with others for nutrients. Later the buttressing apparently assumes a structural role to enable the species to complete its life-cycle. Many other species have buttresses which are far more vertical and less lateral in extension, and for these it is postulated that nutrient exploration is not of priority but the buttresses assume the more conventional role of only optimizing mechanical support (Mattheck 1991; Ennos 1993).

Conclusion

Whilst it is clear that buttresses undoubtedly provide structural support to the very large trees of *M. bisulcata* in Korup, the idea advanced in this paper is that additional selection pressure operates with the requirement for high nutrient acquisition in low-nutrient soils, and this radically alters the form, or shape, of buttresses. As a testable operationalist hypothesis (*sensu* Peters 1991) across rain forest sites, an index of buttress lateral spread to buttress height, relating to the parameters of the rectangular hyperbola model, would be expected to be positively correlated with decreasing soil nutrient status.

Appendix

Table 4 Mean and 95% confidence limits to buttress variables of adult and juvenile trees and plantation saplings of *Microberlinia bisulcata* based on logarithmic transformation

	Back-transformed values		
	Mean	Lower limit	Upper limit
Adult trees (n = 20)			
Buttresses			
Number			
Main	5.44	4.85	6.09
Side	1.72	1.40	2.12
Height (m)			
Main	2.87	2.40	3.44
Length (m)			
Main	6.40	4.93	8.31
All	10.55	7.12	15.64
Area (m^2)			
Main	3.39	2.44	4.70
All	4.52	2.96	6.92
Polygon projected areas			
Buttresses (m^2)	112	65	193
Branches (m^2)	98	57	170
Juvenile trees (n = 25)			
Buttresses			
Length (m)			
Sum	3.93	2.57	6.00
Mean	1.09	0.87	1.36
Maximum	1.71	1.30	2.24
Plantation saplings (n = 7)			
Surface roots			
Length (m)			
Sum	2.63	1.33	5.22
Mean	1.08	0.75	1.57
Maximum	1.44	0.93	2.23

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