

Associations between tree growth, soil fertility and water availability at local and regional scales in Ghanaian tropical rain forest

Timothy R. Baker¹, David F. R. P. Burslem and Michael D. Swaine

Department of Plant and Soil Science, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, UK
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Abstract: Relating patterns of species abundance to the processes that determine them at local and regional spatial scales is one of the central aims of ecological research. To examine the relationship between distribution and growth in tropical rain forest, seasonal and annual changes in tree diameter of two tree species with contrasting distribution patterns, *Celtis mildbraedii* and *Strombosia glaucescens*, were monitored across topographic gradients in moist semi-deciduous and moist evergreen forest in Ghana over 2 years, 1997–9. Concurrent measurements were made of soil water availability, and during 1997/8, of rainfall, nutrient availability and photosynthetically active radiation (PAR). The two sites received similar, low, total rainfall during 1997/8, but soil water availability in the dry season at the evergreen site exceeded that at the semi-deciduous forest site. Soil water availability was higher during 1998/9 at both sites. During 1997/8, PAR was similar at the two sites. The evergreen site had soils of lower pH, available P, Mg, Ca and K concentrations than the semi-deciduous forest site. Water availability and the sand content of the soil increased and concentrations of total N and C decreased, from summit to valley positions at both sites. *Celtis mildbraedii* had significantly faster growth rates than *S. glaucescens*, and growth of both species was greater at the semi-deciduous than the evergreen forest site during the wet year (1998/9) but not during the dry year (1997/8). *Celtis mildbraedii* in semi-deciduous forest grew less in valley than summit and slope positions. We conclude that in the absence of a severe dry season, growth is higher in semi-deciduous than evergreen forest, and is related to the higher soil fertility in more seasonal forest. The patterns are consistent with the hypothesis that concentrations of available P and/or cations in the soil limit growth in evergreen forest, while concentrations of N in valley soils limit growth of *C. mildbraedii* in semi-deciduous forest. There was no evidence that variation in PAR influenced growth rates in these forests. A reduction in growth rate on less fertile soils may be a factor determining the distribution limit of dry forest species, such as *C. mildbraedii*, in evergreen forest.

Key Words: Ghana, nutrient limitation, soil water availability, spatial scale, species distribution, tree growth

INTRODUCTION

A central aim of ecological research is to understand the processes that maintain gradients of species composition at different spatial scales. In tropical forests, much research has focused on describing spatial variation in species composition, and from this work it is well known that tree species distribution and abundance varies at regional (10^5 – 10^6 m) and local (10 – 10^3 m) scales and that these patterns often correlate with edaphic variation in soil nutrient availability and drainage (Ashton & Hall 1992, Austin *et al.* 1972, Baillie *et al.* 1987, Basnet 1992, Clark *et al.* 1998, Newbery & Proctor 1984, Newbery *et al.* 1986, Swaine & Hall 1986). However, little is known about the mechanisms that maintain these patterns. Most work in this area has concentrated on seedling ecology

and the potential of high seedling mortality rates to determine future canopy composition (Gunatilleke *et al.* 1997, Ortiz-Arrona 1999, Veenendaal *et al.* 1996b). By contrast, there has been little research examining how adult tree performance varies across environmental gradients. Variation in growth rates could, however, prove critical for species distribution and abundance if slow growth is linked to high mortality or low recruitment rates. For example, the slowest-growing trees showed the highest rates of mortality in a semi-deciduous forest in Ghana (Swaine *et al.* 1987).

Associated with a lack of information on the spatial patterns of tropical tree growth, it is also unclear which environmental variables limit tree growth over different temporal and spatial scales. This information is important not only for understanding the mechanisms that determine species distributions, but also for predicting how tropical forests will respond to climate change. Soil water

¹ Corresponding author: School of Geography, University of Leeds, Leeds, LS2 9JT, UK.

availability, irradiance, and soil nutrient status may all be important factors that determine rates of tropical tree growth. For example, in some studies, variation in rainfall correlates with patterns of tropical tree growth (Bullock 1997, Whigham *et al.* 1990, Worbes 1999). Gradients in annual rainfall are also associated with patterns of species composition at regional scales (Swaine 1996) and changes in species composition over local scales are often attributed to variation in the drainage regime (Sollins 1998). In addition, the seasonal pattern of rainfall determines vegetative phenology in both seasonal and relatively aseasonal climates (Reich 1995). However, irradiance may also determine vegetative and reproductive phenology (Wright & van Schaik 1994), community-wide tree growth rates (Clark & Clark 1994) and the seasonality of primary productivity of tropical evergreen forest in South America (Raich *et al.* 1991). The potential importance of nutrient supply has been demonstrated by fertilizer experiments that have shown that adult trees respond to increased nutrient supply in tropical forests in Venezuela, Jamaica and Hawaii (Tanner 1992, Tanner *et al.* 1990, 1998; Vitousek *et al.* 1993). In addition, in descriptive studies, the availability of one or more soil nutrients has been found to correlate with the distribution of tropical tree species (Gartlan *et al.* 1986, Sollins 1998, Swaine 1996). This study takes a novel approach by assessing the effect of all these environmental variables on tree growth simultaneously, and by measuring soil water availability directly to include the variation caused by changes in soil texture and topographic position.

The high-forest zone of Ghana represents an appropriate system for examining the relationships between growth, distribution and environmental conditions, as different forest types occur across a broad rainfall and soil fertility gradient, and the distribution patterns of forest tree species are well known (Chipp 1927, Hall & Swaine 1981, St. Clair Thompson 1936, Taylor 1952, Thompson 1910).

The specific questions addressed by this study were as follows: (1) Is there a significant difference in annual and seasonal growth rates of common forest tree species between the moist evergreen and moist semi-deciduous forest types in Ghana? (2) How does topographic position influence growth rates within each forest type? (3) What environmental variables are associated with the patterns of growth at each site?

STUDY SITES AND SPECIES

The study sites were Tinte Bepo Forest Reserve (7°04'N, 2°06'W) in the moist semi-deciduous forest type and Bonsa River Forest Reserve (5°20'N, 1°51'W) in the moist evergreen forest type (Hall & Swaine 1981). Tinte Bepo is at approximately 300 m asl, and in the study area overlies fine-grained, non-micaceous hornblende granite

(Adu 1974). Common canopy tree species, which may exceed 60 m in height, are *Triplochiton scleroxylon* K. Schum. (Sterculiaceae), *Celtis mildbraedii* Engl. (Ulmaceae) and *Nesogordonia papaverifera* R. Capuron (Sterculiaceae). Common understorey species are *Cleidion gabonicum* Baill. (Euphorbiaceae), *Microdesmis puberula* Hook.f. *ex* Planch. (Pandaceae) and *Baphia nitida* Lodd. (Fabaceae) (Hall & Swaine 1981). There are approximately equal proportions of evergreen and deciduous canopy trees in moist semi-deciduous forest (Hall & Swaine 1981). Mean annual rainfall, 1971–1993, recorded at the nearest Ghana Meteorological Service station at Bechem, 15 km north-east of the site, is 1288 mm. There is a strong dry season from December to March, when soil matric potential typically declines below -1.5 MPa, and a second, less severe dry season from July to September (Veenendaal *et al.* 1996a). Bonsa River is at approximately 250 m asl and overlies sandstone (Boateng 1993). The tallest trees in moist evergreen forests are shorter on average than those in semi-deciduous forest, up to 40 m height, and deciduous species comprise only a small fraction of the canopy (Hall & Swaine 1981). Typical canopy species are *Strombosia glaucescens* J. Leonard (Olacaceae) and *Lophira alata* Banks *ex* Gaertn. (Ochnaceae). Mean annual rainfall at the nearest Ghana Meteorological Service station at Tarkwa, 20 km south-west of the site, from 47 y of data collected 1939–1993, is 1993 mm. As in semi-deciduous forest, monthly rainfall is bimodal in moist evergreen forest, but the main dry season, from December to March, is less pronounced (Veenendaal *et al.* 1996a).

The topography at both sites is undulating with maximum slopes of approximately 20°. At both sites, the altitudinal difference between summits and valleys is 30–50 m over horizontal distances of 300–500 m. The soils become redder and finer textured with depth, but paler in colour and increase in sand content downslope. This pattern is typical across West Africa (Ahn 1970). At Tinte Bepo, the topsoils are reddish brown sandy clays on the summits, yellowish brown sandy clays on the slopes and yellowish brown sandy clay loams and sandy loams in the valleys (Adu 1993). At Bonsa River, the topsoils range from red sandy clays on the summits to greyish brown sands in the valleys (Boateng 1993). Chemical characteristics for these soils are presented below (Table 1).

The study species were *Celtis mildbraedii* Engl. (Ulmaceae) and *Strombosia glaucescens* J. Leonard (Olacaceae). *Celtis mildbraedii* is an evergreen, non-pioneer species found throughout the Guineo-Congolian forest zone and in East African coastal forests (Hawthorne 1995). It is very common in semi-deciduous forests in Ghana: in five, 1-ha plots at Tinte Bepo, it comprises 22.9% of all stems greater than 20 cm dbh (T. Baker, unpubl. data). Its abundance declines as the landscape becomes wetter, both at regional, climatic and local, topo-

Table 1. Soil chemical characteristics across topographic gradients for soils 5–10 cm depth beneath moist semi-deciduous and moist evergreen forest in Ghana. Values are means \pm 1 SE.

Variable	Position	n	Tinte	Bonsa	
			Bepo Semi-deciduous	River Evergreen	
pH	Summit	15	6.9 \pm 0.2	6	3.8 \pm 0.03
	Slope	8	6.6 \pm 0.2	15	4.0 \pm 0.08
	Valley	7	6.6 \pm 0.3	4	4.4 \pm 0.08
Total N (%)	Summit	15	0.47 \pm 0.06	6	0.37 \pm 0.06
	Slope	8	0.28 \pm 0.09	15	0.29 \pm 0.05
	Valley	7	0.33 \pm 0.09	4	0.14 \pm 0.01
Total C (%)	Summit	15	5.3 \pm 0.8	6	4.5 \pm 0.7
	Slope	8	3.3 \pm 1.6	15	3.2 \pm 0.7
	Valley	7	3.4 \pm 1.2	4	1.4 \pm 0.3
Available P ($\mu\text{g g}^{-1}$)	Summit	15	8.2 \pm 1.5	6	3.0 \pm 0.8
	Slope	8	5.2 \pm 1.4	15	2.3 \pm 0.5
	Valley	7	10.1 \pm 3.6	4	0.9 \pm 0.2
Exchangeable K (cmol kg^{-1})	Summit	15	0.48 \pm 0.07	6	0.10 \pm 0.01
	Slope	8	0.27 \pm 0.05	15	0.09 \pm 0.01
	Valley	7	0.36 \pm 0.14	4	0.05 \pm 0.002
Exchangeable Ca (cmol kg^{-1})	Summit	15	23.0 \pm 4.7	6	0.23 \pm 0.09
	Slope	8	12.5 \pm 4.7	15	0.26 \pm 0.07
	Valley	7	15.0 \pm 5.7	4	0.30 \pm 0.07
Exchangeable Mg (cmol kg^{-1})	Summit	15	4.7 \pm 1.1	6	0.32 \pm 0.05
	Slope	8	2.6 \pm 0.6	15	0.34 \pm 0.06
	Valley	7	2.6 \pm 0.8	4	0.25 \pm 0.06

graphic, scales, and it is absent from the forests with the highest rainfall (Figure 1a; Hawthorne 1995, Swaine & Hall 1986). It is an important economic species and a favourite wood for fuel, charcoal production and making pestles. *Strombosia glaucescens* is found throughout the Guineo–Congolian region, and is a common evergreen, non-pioneer species in Ghana. For example, this species comprised 5.8% of the stems greater than 20 cm dbh in seven, 1-ha plots in moist evergreen forest (T. Baker, unpubl. data). Its distribution in Ghana is biased toward wet, infertile sites (Figure 1b; Swaine 1996) and it is currently important for manufacturing telegraph poles. Both species occur at both sites, but only *C. mildbraedii* at the semi-deciduous forest site and *S. glaucescens* at the evergreen site were sufficiently common to allow comparisons between trees growing in all topographic positions.

METHODS

Topographic definitions

Three topographic positions, summit, valley and slope, were defined within each forest reserve on the basis of soil colour (cf. Clark *et al.* 1998). Soil colour was assessed using a Munsell Soil Colour chart at 15 cm depth, 2 m away on the western side of each selected tree (see below) and at 5-m intervals along transects from the bottom to the top of the watershed. An important determinant of colour in tropical soils is the content and form of the predominant iron oxide present, which is influenced both by the soil parent material and the water regime. Haemitite, which gives the soil a bright red colour, is the

form typical of well-drained areas and soil parent materials that have relatively high iron contents, whilst the formation of goethite is favoured under wetter conditions (Schwertmann & Taylor 1989). In the evergreen forest site the most well-drained positions have paler colours than at equivalent positions in the semi-deciduous forest site. This pattern is a result both of the higher rainfall and the presence of the more iron-rich hornblende granite at the semi-deciduous forest site, compared with the sandstone at the evergreen forest site (Ahn 1970). At both sites there were clear and consistent changes in soil colour downslope, with contiguous areas of different colour from summit to valley positions. Soil colour could therefore be used within each site to define different topographic positions, reflecting within-site variation in water supply. Different landscape positions were defined on the basis of the hue (Oyama & Takehara 1991). At the semi-deciduous forest site, summit topsoils were red, 5 YR 4-6/6-8, slope topsoils yellow/red, 7.5 YR 5/6-8 and valley topsoils pale brown/grey, 10 YR 5-6/3-6. At the evergreen forest site, summit topsoils were yellow/red, 7.5 YR 5/6-8, slope topsoils pale brown/grey, 10 YR 4-6/4-8 and valley topsoils grey, 2.5 Y 5/4.

Dendrometer bands

Following classification of the landscape into different topographic positions, trees of the two species greater than 20 cm dbh whose crowns received at least some direct overhead light, i.e. Dawkins crown classification of 4 or 5 (Dawkins 1958), were selected for study. Dawkin's

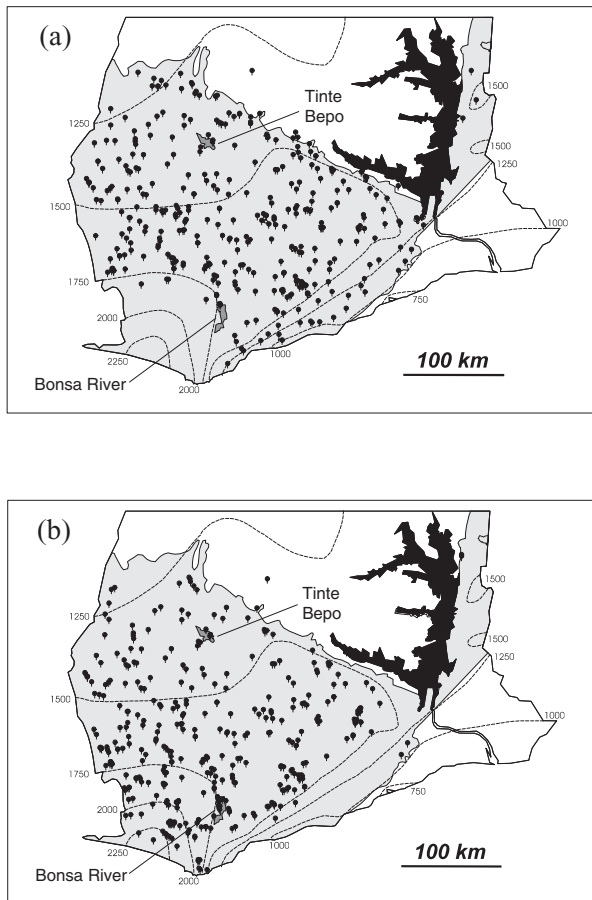


Figure 1. Distribution maps for (a) *Celtis mildbraedii* and (b) *Strombosia glaucescens* in Ghana. Species location points refer to their presence in Forestry Department botanical surveys 1980–1995. The study sites, 250 mm isohyets, extent of the forest zone (shaded area) and Lake Volta (black) are also shown.

classification of crown position has been widely used to classify the amount of light received by tree crowns (Clark & Clark 1992, Davies *et al.* 1998). In addition, both Clark & Clark (1993) and Davies *et al.* (1998) demonstrated that differences in crown position score amongst saplings correlate with estimates of canopy openness obtained using hemispherical photographs.

All suitable trees were selected over approximately 12-ha at both sites, over several watersheds. Seasonal changes in tree girth were monitored using dendrometer bands (cf. Daubenmire 1973, Reich & Borchert 1982). These were constructed from 20 mm width, 150 μ m thickness, hard-tempered aluminium and held in place with a stainless steel spring. Shoe eyelets were used to strengthen the holes where the spring held the band. Measurements to 0.1 mm were made using Vernier calipers of the distance between scribe marks on the overlapping front and rear ends of the band. In a comparison of three different operators, 58% of repeated measurements were within 0.1 mm, and 81% within 0.2 mm. Bands were placed at 1.3

m height or 50 cm above the top of any fluting or buttress. Trunk climbers were cut prior to fixing the band. Between 23 July and 6 August 1997, bands were applied to 28 *C. mildbraedii* and three *S. glaucescens* trees at the semi-deciduous forest site. One *S. glaucescens* was added to the sample on 22 August 1997, two *C. mildbraedii* on 1 October 1997 and one *S. glaucescens* on 17 October 1997. At the evergreen forest site bands were applied to 18 *S. glaucescens* on 12 and 13 August 1997. Eight *S. glaucescens* were added to the sample on 25 September 1997 and ten *C. mildbraedii* on 26 October 1997. In total, 30 *C. mildbraedii* and five *S. glaucescens* were studied at the semi-deciduous forest site, and 10 *C. mildbraedii* and 26 *S. glaucescens* at the evergreen forest site. Measurements of tree girth were made at approximately monthly intervals until December 1999.

One problem with the use of dendrometer bands is that some settling may occur (Keeland & Sharitz 1993). Repeated measurements at the start of the study indicated that a short period was required before reliable readings were obtained from the bands, therefore readings taken less than 30 d following the attachment of a band were discarded (cf. Pélissier & Pascal 2000). A control band placed on one individual of *Celtis mildbraedii* in the semi-deciduous forest site, that had a badly damaged crown, showed no change in girth over the 2 y of the study, suggesting that the results are not confounded by long-term settling of the bands. To minimize the influence of diurnal fluctuations in tree girth due to changes in tree water status (Kozłowski 1972), all measurements were performed during the morning. However, significant diurnal changes in tree diameter were never found when re-measurements of the dendrometer bands were made during the afternoon, on several occasions, for either species at either site. Diurnal fluctuations in tree girth may be particularly small in these shade-tolerant species with relatively high-density wood.

Soil matric potential

Measurements of soil matric potential were made concurrently with measurements of tree girth at approximately monthly intervals. The filter paper method described by Deka *et al.* (1995) was used as it gives reliable results down to very low matric potentials of approximately -2 MPa, sampling is rapid and it is inexpensive. A standard filter paper is equilibrated in a sealed container with a soil sample over 6 d, the water content of the filter paper determined and then related to the matric potential using calibration equations given by Deka *et al.* (1995). At the semi-deciduous forest site, preliminary sampling at depths of 15, 35 and 55 cm was carried out 2 m from the southern side of nine *C. mildbraedii* on 28 August and 18 September 1997. On the second and subsequent measurement occasions, samples were taken 50 cm from the eastern and

western sides of the original sample point, and then three sets of three sample points, each 50 cm behind the previous set. This systematic sampling pattern was then repeated, moving clockwise, and assumes there is no systematic variation in soil matric potential within a 3.5 m radius around each tree. From 11 October 1997, samples were taken around 14 *C. mildbraedii* at the semi-deciduous forest site across the range of landscape positions at these three depths. To simplify sampling, it was investigated whether measurements at 15 cm depth were good predictors of soil matric potential at 35 and 55 cm depth. Significant linear, positive regressions were obtained between log-transformed soil matric potential at the three depths ($r^2 = 80\text{--}92\%$). Following this, from 5 November 1997 until 4 December 1999, samples were taken at just 15 cm depth around all 35 trees.

At the evergreen forest site sampling was initially confined to three trees of *S. glaucescens* in each landscape position at 15, 35 and 55 cm depth. Again significant linear, positive regressions were obtained between log-transformed soil matric potential at the three depths ($r^2 = 91\text{--}97\%$), and from 22 November 1997 until July 1999 sampling continued at the 15 cm depth only, but around all 36 trees.

Phenology and environmental data

Other studies have shown a relationship between the production of new leaves and short-term patterns of stem girth change as a result of increased transpirational water loss (Boaler 1963, Reich & Borchert 1984). To enable this to be tested for these species, the presence of new leaves was recorded for each tree on each measurement occasion from July 1997 using a numerical scale as follows: 0, no new leaves; 1, some new leaves; 2, new leaves distributed evenly over canopy.

Photosynthetically active radiation (PAR) was logged at 1 m height, at 30 min intervals, averaging per-minute records using sensors attached to a logger (DataHog2, Skye Instruments Ltd, UK). These were sited in an open area less than 5 km from each site. Six gaps in the data were caused by battery failure. For the semi-deciduous forest site, daily rainfall data were obtained from the Ghana Meteorological Service station at Bechem. During the course of the study, at the evergreen forest site, daily rainfall was recorded at Wassu Bremia, 4 km west of the site using an identical rainfall gauge.

Wet-season water supply

Wet-season water supply was investigated in valley positions in the semi-deciduous forest site by direct measurement of soil anoxia, fine-root length densities and leaf water potential. The presence of anoxic zones in the soil was examined using 2,2 dipyrindyl indicator (Batey &

Childs 1982). Approximately 10 g soil samples were placed in vials containing the 20 ml of test solution and shaken. A positive result was indicated by the colourless solution turning red. Samples were taken at various locations and depths on 25 June and 13 September 1998 at the semi-deciduous forest site. Fine-root length densities and biomass were measured during May 1998 at both sites. In each site, five trees were randomly selected in each topographic position and a pit dug 2 m away on the northern side of each tree; 125-cm³ metal cups were used to excavate samples from the side of each pit centred at three depths of 7.5, 15 and 35 cm. The roots in each sample were washed out and the length of roots < 2 mm in diameter using the Tennant method (Tennant 1975). Dawn (06h00–09h00) leaf water potential was measured for summit and valley trees of *C. mildbraedii* on 23 August and 13 September 1998 using a pressure bomb (Scholander *et al.* 1965). Leaves were shot down from the canopy using a catapult, bagged and leaf water potential determined immediately.

Soil sampling and analysis

Soil samples were collected from 5–10 cm depth, 2 m from the western side of each tree at both sites during October 1998. Samples were air-dried, crushed and transported to Aberdeen University for chemical analysis. pH was determined in suspensions of 1 part soil to 2.5 parts deionized water. Total N and C was measured by flash combustion at 1050 °C (NA 1500 NCS autoanalyser, Fison's Instruments, USA). Available P was measured by an automated colorimetric technique (FIAstar 5010 Analyser, Tecator, USA) following chloride-saturated resin bag extraction (Anderson & Ingram 1989). To determine the concentrations of exchangeable cations, samples were extracted with 1 M ammonium acetate (Allen 1989) and the amounts of Ca and Mg in the solution measured using atomic absorption spectrophotometry (Alpha 4, Baird, USA). K concentrations in the leachate were measured using flame photometry (PFPI Flame photometer, Petracourt, UK).

Data analysis: environmental data

Multivariate analysis of variance was used to test the effect of site and topographic position on the changes in soil matric potential during 1997/8. Individual measurement occasions were used as response variables, with site and topographic position as factors in a factorial design. Second, the patterns of soil matric potential in summit positions were compared between 1997/8 and 1998/9. Measurements in the first year of study were paired with measurements made at the most similar date during the second year, and differences tested using pairwise t-tests.

Total annual PAR was calculated during 1997/8.

Missing values were determined by linear interpolation between 7-d means at the start and end of each period without data.

Data analysis: patterns of tree girth change

Repeated-measures ANOVA using a factorial, species \times site, design was used to test for differences between species, sites and years in annual diameter increment. 'Year' was specified as a within-subjects factor, and 'species' and 'sites' as between-subject factors. Repeated-measures ANOVA was also used to test for the effect of the same factors on diameter change during the main dry season and the rest of the year, termed 'wet' season, although including the drier period between July and September. Annualized diameter increments over 1997–9 were calculated for the periods 18 September 1997 to 18 September 1999 at Tinte Bepo, 6 November 1997 to 6 November 1999 for *C. mildbraedii* at Bonsa River and 25 October 1997 to 25 October 1999 for *S. glaucescens* at Bonsa River. Main dry-season diameter change was calculated 21 November to 18 March, and wet-season diameter change was calculated 18 September to 21 November and 25 April to 17 September for both years. The period 18 March–25 April was omitted from the calculation of wet-season diameter change, as the first wet-season measurement incorporates significant rehydration following the dry season.

The effect of topographic position on diameter change was tested separately. One-way ANOVA was used to test the effect of topographic position on annual diameter increment for *C. mildbraedii* in semi-deciduous forest and *S. glaucescens* in evergreen forest. In addition, repeated-measures analysis of variance was used to assess the effect of topographic position on the monthly records of changes in tree girth for the same species/site combinations. 'Measurement occasion' was used as a within-subjects factor, and 'position' as a between-subjects factor.

Data analysis: controls on tree girth change

Finally, the relationship between the rate of girth change, soil matric potential and PAR on monthly changes in tree girth was investigated for *C. mildbraedii* in semi-deciduous forest and *S. glaucescens* in evergreen forest using multiple regression. For *C. mildbraedii* mean rates of girth change for each position were regressed against soil matric potential and site PAR, with topographic position an additional factor. As there was no influence of topographic position on the monthly rate of girth change for *S. glaucescens*, all records were pooled and topographic position was not included in the analysis. Time

periods with missing PAR values were omitted from the analysis.

Repeated-measures ANOVA was carried out using the General Linear Model command in SPSS 10 which accounts for differences in class sizes. All other analyses were carried out using MINITAB. If necessary, prior to analysis, the data were Box–Cox transformed to ensure that the residuals were normally distributed and the variance was not significantly different between factor levels. The stepwise regression approach in GLIM (Crawley 1993) was used for analysing the relationship between girth change and environmental variables. All second- and third-order interactions were initially included in the model and the significance of individual terms assessed using F-tests of the increase in variance caused by their deletion compared with the previous error variance (Crawley 1993). Starting with the least significant, highest order interactions, insignificant terms were progressively deleted from the model.

RESULTS

Climatic differences between sites during 1997/8

Total annual rainfall during 1997/8 (1 August 1997–31 July 1998 for Tinte Bepo; 16 August 1997–15 August 1998 for Bonsa River) was very similar at the two sites: 1087 mm at the semi-deciduous site and 1139 mm at the evergreen forest site. However, there was a significant difference in the seasonal pattern of soil water availability between the two sites (Table 2). Higher soil matric potentials were maintained at the evergreen forest site during the late dry season (March–April). More early wet-season rainfall at the semi-deciduous forest site led to higher matric potentials there during May–June (Table 2, Figure 2). Significantly, at the evergreen forest site, soil matric potential did not fall to -1.5 MPa, the value generally accepted below which water is unavailable to plants (Kramer & Boyer 1995).

Total annual PAR was very similar at both sites, approximately 8500 and 8100 mol m⁻² in the evergreen and semi-deciduous forest sites respectively. Seasonal fluctuations in irradiance were also similar across forest types (Figure 2). Both sites had periods of generally low PAR during the dry season in January, probably caused

Table 2. Results of MANOVA on spatial patterns of soil matric potential at 15 cm depth, 1997/8, comparing the main effects of site (semi-deciduous/evergreen), topographic position (summit/slope/valley) and their interaction.

Variable	Effect	F	P
Soil matric potential	Site	331	<0.005
	Position	3	<0.005
	Site \times Position	3	<0.005

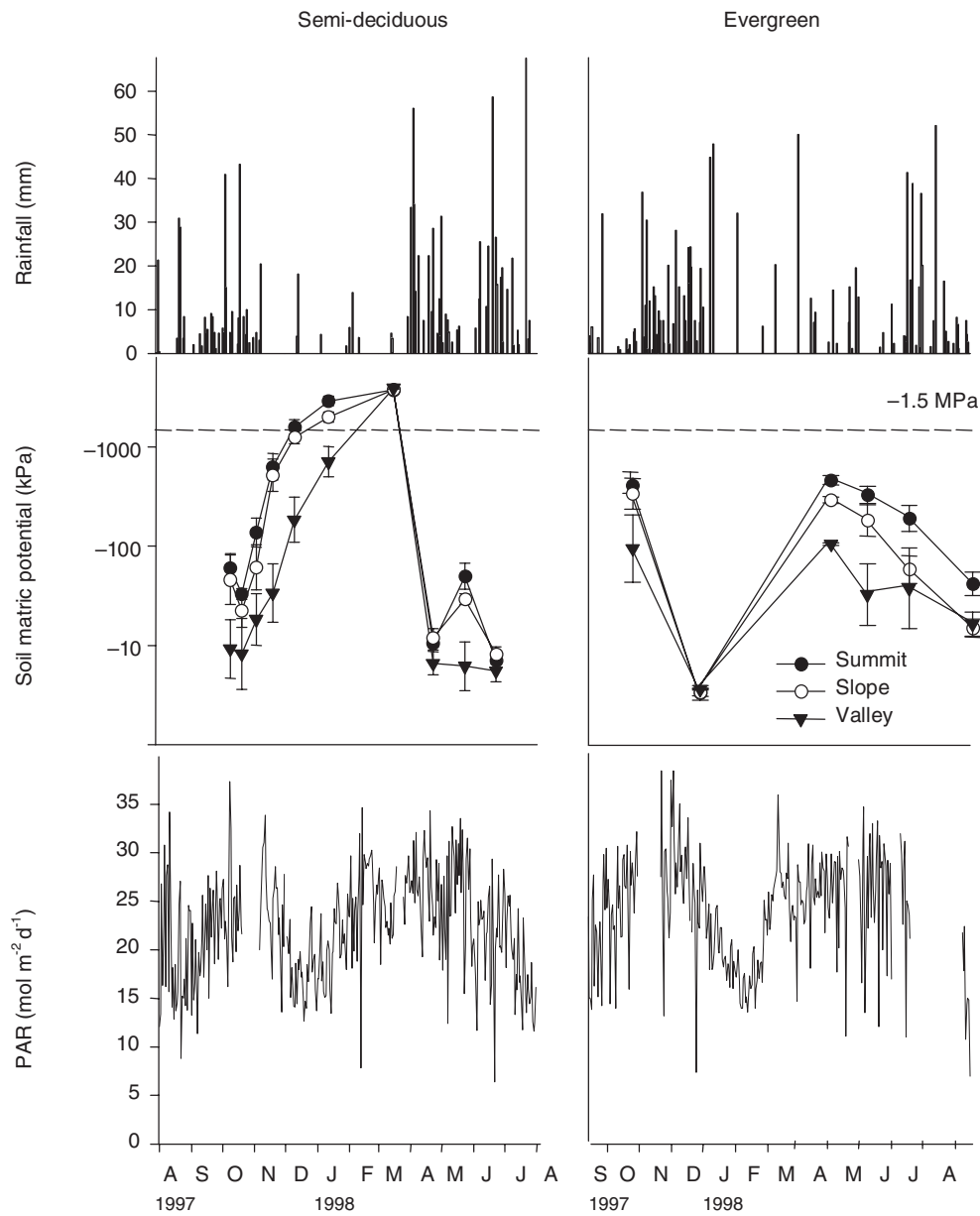


Figure 2. Daily rainfall, photosynthetically active radiation (PAR) and mean (\pm SE) of untransformed values of soil matric potential at 15 cm depth in three topographic positions during 1997/8 for semi-deciduous and evergreen forest sites in Ghana. Gaps in the PAR record were caused by battery failure.

by smoke haze, and during the middle of the wet season in August, which is typically a cloudy time of year. PAR was approximately 50% greater during November and April/May.

Edaphic differences between sites

Concentrations of exchangeable Ca were 50–100 times greater and the other exchangeable cations and available P significantly greater in soil at 5–10 cm depth taken from the semi-deciduous forest (Tables 1 and 3). Total N and

C concentrations did not differ significantly between sites (Table 3).

Edaphic differences within sites during 1997/8

Valley sites had higher soil matric potentials and a less severe dry season than summit sites (Table 2, Figure 2). This effect was more marked at the semi-deciduous forest site, where valley sites maintained higher soil matric potentials until the very end of the 1997/8 severe dry season. Total N and C concentrations declined

Table 3. Results from two-way analysis of variance on chemical characteristics of soil from 10–15 cm depth taken from three topographic positions (summit/slope/valley) from each of two forest types (semi-deciduous/evergreen) in Ghana. No significant interaction terms were found. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

	Site	Position
pH	***	
Total N		**
Total C		**
Available P	***	
Exchangeable K	***	*
Exchangeable Ca	***	
Exchangeable Mg	***	

significantly downslope (Table 3). Of the other nutrients, only exchangeable K showed a significant topographic effect, again a decline downslope, although the other cations showed the same, non-significant, trend (Tables 1 and 3).

Interannual differences in soil water availability

Water availability was significantly higher in summit positions, during the dry season in the semi-deciduous forest site and during the wet season in the evergreen forest site in 1998/9 compared with 1997/8 (Figure 3, August–March, pairwise t-test, $n = 5$, $t = 4.96$, $P < 0.01$ and May–September, $n = 4$, $t = 5.01$, $P < 0.05$, respectively). Slope and valley positions showed similar patterns (see Figure 5 for semi-deciduous forest site).

Annual patterns of growth

Repeated-measures ANOVA demonstrated that there was a significant effect of year ($F = 104$, $P < 0.005$), and site ($F = 4.9$, $P < 0.04$) on annual diameter increment. Generally, growth was higher in 1998/9 compared with 1997/8, and higher in semi-deciduous compared with evergreen forest (Figure 4). However, there was also a significant year/site interaction term (Figure 4, $F = 18$, $P < 0.005$). The general patterns described above are only true for three out of the four species/site combinations. Whereas growth increased markedly for both species in the second year of study in the semi-deciduous forest site, in evergreen forest, growth rates were only marginally greater for *S. glaucescens* and declined for *C. mildbraedii* (Figure 4). There was also a significant effect of species on annual growth rate ($F = 6.8$, $P < 0.02$). In all comparisons between equivalent years and sites, *C. mildbraedii* had higher growth rates than *S. glaucescens* (Figure 4). A significant year/species interaction ($F = 5.0$, $P < 0.03$) highlights that mean growth rates increased in the second year of study for *S. glaucescens* in both sites, but only increased for *C. mildbraedii* in semi-deciduous forest (Figure 4).

When summit and slope categories were combined for *C. mildbraedii* at the semi-deciduous site, topographic position had a significant effect on annualized growth during 1997–9, as trees in valley positions grew less (Figure 5, $F = 6.3$, $P < 0.02$). Topographic position did

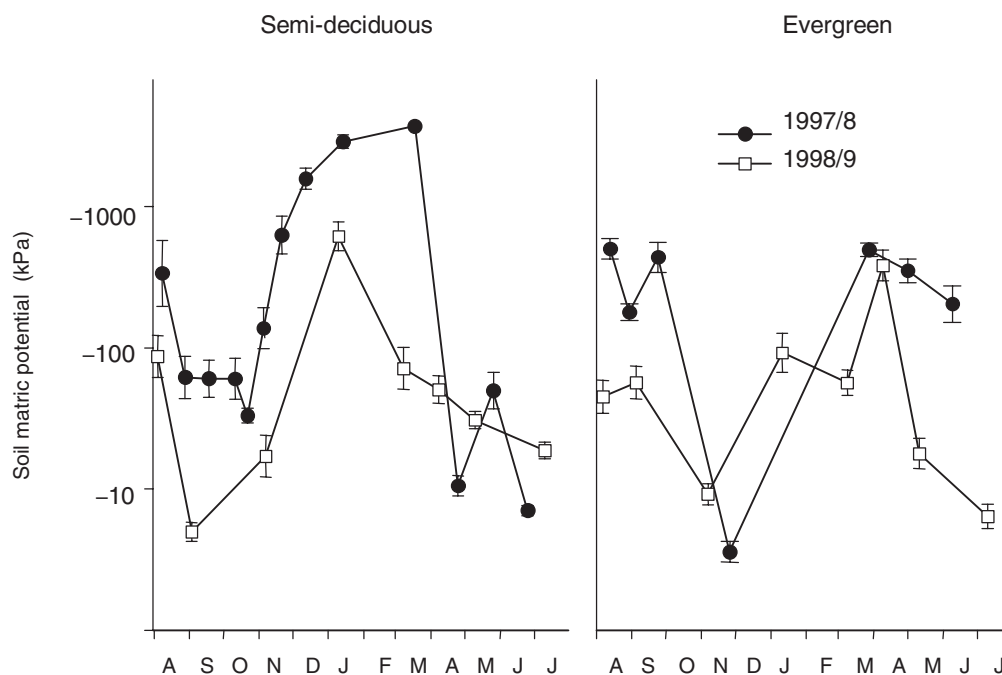


Figure 3. Mean (\pm SE) untransformed values of soil matric potential at 15 cm depth in summit position of semi-deciduous and evergreen forest during 1997/8 and 1998/9.

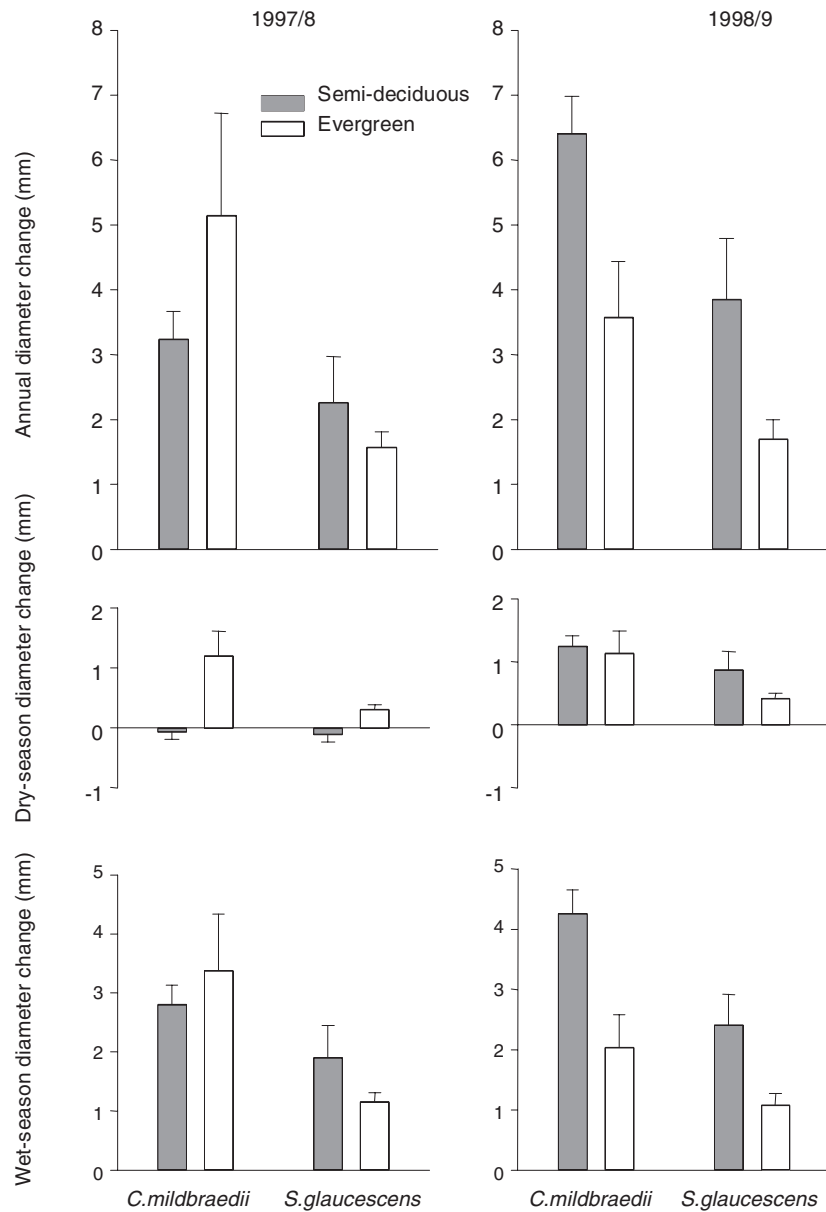


Figure 4. Mean (\pm SE) untransformed values of annual diameter increment, dry- and wet- season diameter change (mm) over 2 years (1997/8 and 1998/9) for trees of *C. mildbraedii* and *S. glaucescens* in semi-deciduous and evergreen forest types in Ghana. Dry-season diameter change was calculated 21 November–18 March and wet-season diameter change 18 September–21 November and 25 April–17 September.

not have a significant effect on annual diameter increment for *S. glaucescens* at the evergreen forest site.

Tree diameter showed no relationship with annual diameter increment for *C. mildbraedii* in the semi-deciduous forest in either year (1997/8, $F = 0.02$, $P < 0.88$; 1998/9, $F = 3.08$, $P < 0.09$) or *S. glaucescens* in the evergreen forest (1997/8, $F = 0.20$, $P < 0.66$; 1998/9, $F = 0.36$, $P < 0.62$).

Seasonal patterns of tree diameter change

There was a significant effect of year ($F = 840$, $P < 0.005$) and site ($F = 26$, $P < 0.005$) on dry-season diameter

change. Overall, diameter change was higher during 1998/9 than 1997/8 and in evergreen compared with semi-deciduous forest (Figure 4). However, a significant year/site interaction ($F = 24$, $P < 0.005$) highlights that the increase in diameter change between years was confined to the semi-deciduous forest site. There was little difference between years in dry-season diameter change for either *C. mildbraedii* or *S. glaucescens* at the evergreen forest site (Figure 4). There was also a significant difference between species ($F = 9.1$, $P < 0.005$). *Celtis mildbraedii* had higher rates of dry-season diameter change than *S. glaucescens* for all comparisons of equivalent year/site combinations (Figure 4).

Diameter change during the wet season showed similar patterns to those for annual diameter increment. Diameter change was significantly greater for *C. mildbraedii* compared with *S. glaucescens* (Figure 4, $F = 5.7$, $P < 0.03$) and during 1998/9 compared with 1997/8 (Figure 4, $F = 14$, $P < 0.005$) but there was no significant difference between sites, and no significant interaction terms.

Repeated-measures analysis of variance demonstrated that there was significant temporal variation in the monthly rate of diameter change for *C. mildbraedii* in semi-deciduous forest, but no overall effect of topographic position (Table 4). However, there was a significant position/time interaction (Table 4) indicating that diameter change for this species at this site varied between positions at particular times of year. Univariate F tests for each measurement period gave a significant ($P < 0.05$) effect of topographic position on six occasions, during the late wet season in 1997 and 1998 and during the early wet season in 1998 (Figure 5). *Strombosia glaucescens* at the evergreen forest site showed a similar, significant temporal pattern of girth change to *C. mildbraedii* at the semi-deciduous forest site, with the lowest rates from January to March and highest rates from June to August (Table 4), but there was no significant effect of topographic position or significant position/time interaction (Table 4).

Environmental variables and tree growth

For *C. mildbraedii* in semi-deciduous forest, regression analysis showed significant main effects of soil matric potential and topographic position on weekly rates of tree diameter change (Table 5, Figure 6). PAR and all interaction terms were non-significant. Adding the proportion of trees flushing into the model did not give a significant effect ($F = 3.5$, $P < 0.07$).

For the evergreen forest site, neither soil matric potential nor PAR explained a significant proportion of the variation in weekly rates of diameter change for *S. glaucescens*.

There was no evidence that an excess or deficiency of water was limiting tree expansion rates of *C. mildbraedii* in valley positions in semi-deciduous forest during the wet season. Repeated testing for the presence of anoxic zones in the soil profile in the valley bottom never revealed evidence of waterlogging in these soils. There was a significant effect of depth on fine-root (< 2 mm diameter) length,

fresh and dry mass. For example, over all samples, root length density decreased from 1.6 ± 0.1 to 0.4 ± 0.05 cm cm⁻³ and dry mass from 2.2 ± 0.3 to 0.3 ± 0.05 mg cm⁻³ between 7.5 and 35 cm depth. However, site, topographic position and all interactions were non-significant.

Measurements of dawn leaf water potential did not differ between three valley and three summit trees on either 23 August or 13 September 1998. The non-significant trend was for the valley trees to have higher leaf water potential values (-450 ± 50 and -700 ± 100 kPa, compared with -750 ± 90 and -730 ± 100 kPa respectively). These results suggest that they are better supplied with water and that statistical significance might be confirmed with greater replication.

DISCUSSION

This study demonstrates that there is significant intraspecific variation in tree growth rates over both temporal and spatial scales in Ghanaian forest. Specifically, growth was greater in semi-deciduous compared to evergreen forest during the second year of the study (Question 1) and growth rates of *Celtis mildbraedii* were lower in valley compared with summit positions in semi-deciduous forest (Question 2). Analysis of the environmental variation over these scales allows us to identify the factors that contribute to the patterns of growth in these species (Question 3).

Regional and interannual variation in irradiance, soil matric potential and nutrient availability

Annual rainfall was unusually low, and similar at the two sites, during the first year of this study. Rainfall at the nearest long-term meteorological station to the evergreen forest site, at Tarkwa, from 16 August 1997–15 August 1998 was only 1242 mm, which is a 40% reduction on the 1939–1993 average of 1993 mm (Swaine *et al.* 1997). This reduction was caused largely by low early wet-season rainfall during April–June 1998. For the semi-deciduous forest site, rainfall measured at Bechem was 1087 mm during 1997/8, which is a 15% reduction on the 1971–1993 average of 1288 mm. The seasonal pattern of rainfall was, however, different at the two sites (Table 2), with no period at the evergreen forest site when water was apparently unavailable for growth. Significant amounts of

Table 4. Results of repeated-measures ANOVA to test the effect of different topographic positions on monthly rates of tree diameter change.

Site	Species	Effect	F	P
Semi-deciduous	<i>C. mildbraedii</i>	Time	19.0	< 0.005
		Position	1.5	ns
		Time × Position	3.4	<0.005
Evergreen	<i>S. glaucescens</i>	Time	5.2	<0.005
		Position	1.5	ns
		Time × Position	1.4	ns

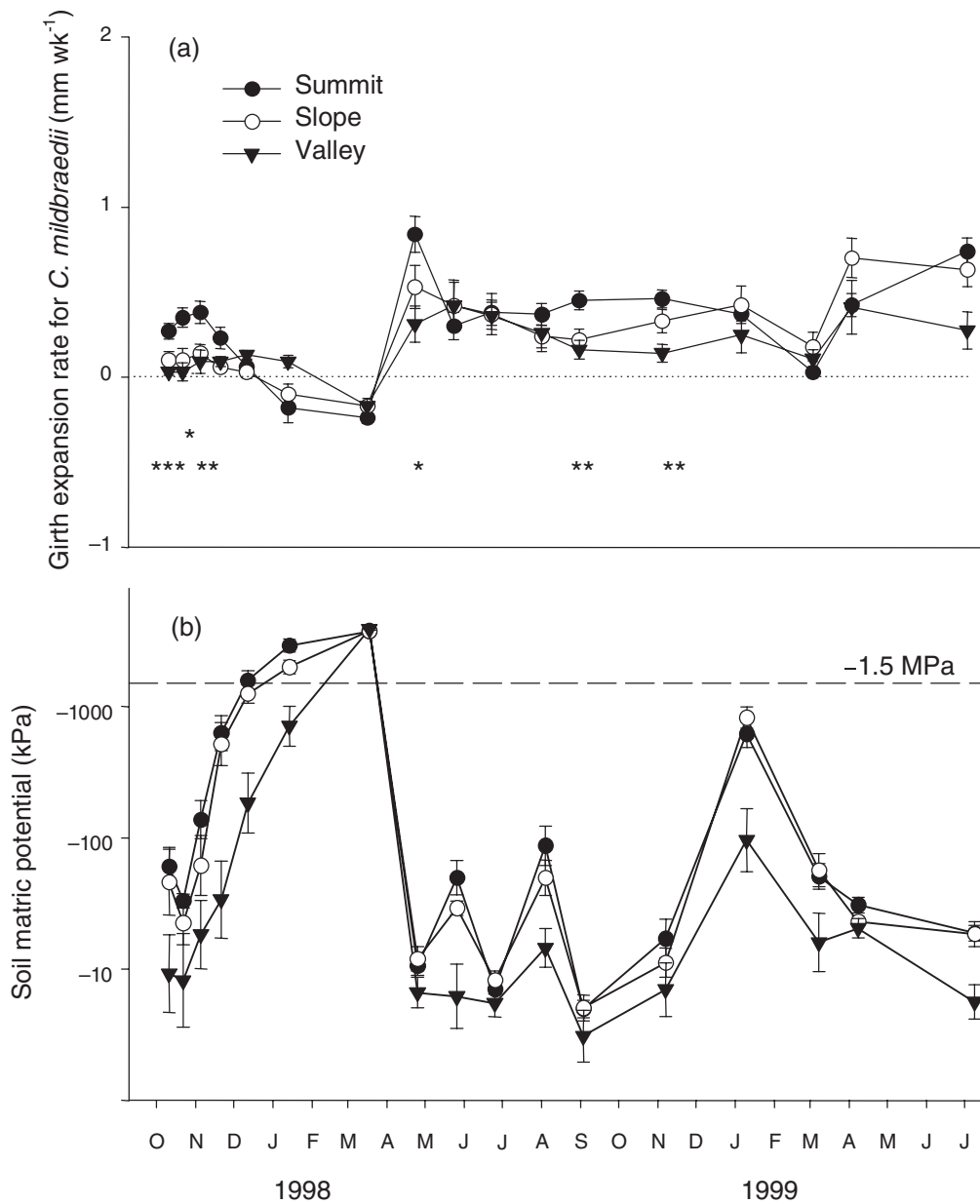


Figure 5. (a) Rates of girth change for *Celtis mildbraedii* in different topographic positions in semi-deciduous forest. Significance of univariate ANOVA at each measurement occasion shown: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$. (b) Mean (\pm SE) of soil matric potential in semi-deciduous forest in three topographic positions.

Table 5. Results of GLIM analysis of rate of girth change of *Celtis mildbraedii* in semi-deciduous forest using soil matric potential, irradiance and topographic position as explanatory variables. All interaction terms were found to be non-significant. F-values presented are for the increase in variance resulting from the deletion of that term from the model.

Response variable	F	P
Soil matric potential	32.4	< 0.005
Topographic position	6.71	< 0.01
PAR	2.66	ns

rainfall maintained relatively high soil matric potentials during the dry season (Figure 2). These patterns are similar to those described by Veenendaal *et al.* (1996a), in a 2-y comparison of the soil water regime in moist semi-deciduous and wet evergreen forest in Ghana, 1992–1994. The dry conditions during 1997/8 coincided with an El Niño Southern Oscillation (ENSO) event. In contrast to this very dry year, soil water availability remained generally higher during 1998/9. Specifically, the dry season at the semi-deciduous forest site was less severe, similar in intensity to that in the evergreen forest site.

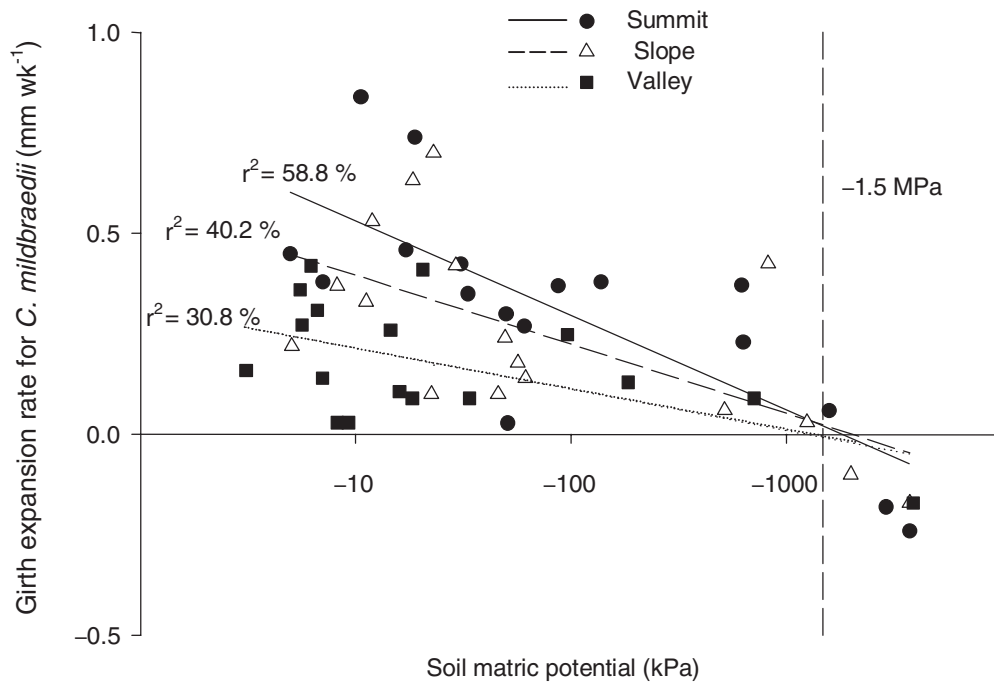


Figure 6. Relationship between soil matric potential and rate of change of girth for *C. mildbraedii* in semi-deciduous forest in Ghana. Individual regression lines were fitted separately for each topographic position. Summit: Girth change (GC) = $0.752 - 0.227 \times \text{Log}(\text{Soil matric potential (SMP)})$; Slope: GC = $0.495 - 0.147 \times \text{Log}(\text{SMP})$; Valley: GC = $0.229 - 0.0991 \times \text{Log}(\text{SMP})$.

Soils in semi-deciduous forest had higher pH and concentrations of available P and exchangeable cations, but equivalent values of total N and C compared with evergreen forest soils, confirming the patterns described by Hall & Swaine (1981). The higher concentrations of available P and cations at Tinte Bepo are due both to the lower long-term rainfall and more nutrient-rich granite, compared with sandstone, parent material (Ahn 1970).

In 1997/8 there was little difference in PAR between the sites in Ghana, which might be explained by the unusually low and similar total annual rainfall in both forest types. Data are not available for PAR for 1998/9, but the higher soil water availability compared with the previous year indicates that lower values would be expected due to increased rainfall and cloudiness (Clark & Clark 1994), although whether regional differences in PAR would be detected during a wetter year remains unknown. However, as both sites had very similar patterns of soil water availability during 1998/9, values for annual PAR are unlikely to have been dissimilar.

Regional variation in tree growth

Comparing the regional variation in growth for these species with variation in soil water and nutrient availability and irradiance, suggests that the observed patterns of growth depend on the relative importance of the opposing trends in water and nutrient availability. As irradiance did not differ between sites, the important question is whether

growth rates are higher on the more fertile soils of semi-deciduous forest that are susceptible to severe seasonal drought, or on the less fertile soils of evergreen forest that do not dry out during the dry season. The significantly lower rate of dry-season diameter change at the semi-deciduous forest site during 1997/8, shows that the dry season can limit the growth of semi-deciduous much more than evergreen forest trees (Figure 4). However, during the second year of the study when there were no differences in the degree of dry-season diameter change between sites, annual growth rates were greater at the semi-deciduous forest site. Therefore, even though reduced soil water availability can shorten the growing season in semi-deciduous forest, the effect is limited to drier years, such as 1997/8. Over a long timescale, it is likely that the growth rates of these species will be lower in evergreen forest. In addition, the regional patterns in specific soil nutrients suggests that the concentrations of P and/or exchangeable cations may be the critical factors limiting growth in evergreen forest, when water availability is high.

In contrast to this work on adult tree growth, results from seedling experiments have emphasized the importance of soil water availability, rather than soil fertility, on growth. Seedlings of *Celtis* and *Strombosia* were found to be insensitive to soil fertility when they were grown in well-watered pots containing soil from either semi-deciduous or evergreen forest (Veenendaal *et al.* 1996b). In addition, in a field transplant experiment of six species,

including *C. mildbraedii*, into semi-deciduous and evergreen forest types (Swaine *et al.* 1997), all species, regardless of origin, grew better in the wetter forest type where there were less fertile soils, but also a less severe dry season. These results indicate that low soil fertility was not the factor limiting growth of these species in the field as young plants. By contrast this study concerns adult tree growth and suggests a more important role for variation in soil fertility. It is possible that nutrient limitation only becomes apparent when the trees are larger and possess higher demand for nutrients, or when they are large enough for the size of their root systems to buffer them against seasonal water shortage.

Topographic variation in nutrient and water availability

Topographic position had a significant effect on the soil water regime, with increased soil water availability and a shorter effective dry season at lower positions in the topography (Figure 2), an effect that was particularly marked at the semi-deciduous forest site. The pattern of soil nutrient concentrations differs from that at the regional scale, with only total C, total N and exchangeable K concentrations showing a significant decline downslope. In contrast, in other studies, soil fertility typically increases lower down the catena, presumably as a result of accumulation of leached nutrients downslope and alluvial deposition (Gunatilleke *et al.* 1997, Ortiz-Arrona 1999). However, the gradient of soil nutrients found here reflects the particular topographic changes in soil texture found in West Africa. Ahn (1970) describes a forest catena overlying granite in Ghana, similar to the sequence of soils found at the semi-deciduous forest site, where the mid- to lower-slope soils are formed from colluvium. This material is sorted to leave mid-slope sandy clays grading into loamy sand and sandy loams on the lower slopes, with the clay from these lower-slope soils transported further down the watershed. The valley positions for both of the study sites comprise this sandy colluvial material. Furthermore, examination of the soil characteristics collected by Hall & Swaine (1981), shows that although concentrations of total N do not differ between the moist semi-deciduous and moist evergreen forest types, N concentrations across the forest zone of Ghana do vary with the sand content of the soil ($r^2 = 25.6\%$, $P < 0.005$, $n = 100$). The principal variation in soil texture in this region occurs across topographic gradients, so it may be that the reduction in N concentrations on sandier, lower-slope soils is a common phenomenon in the forest zone of Ghana. This pattern could potentially limit growth across topographic gradients.

Topographic variation in growth

After 2 y, a significant effect of topography was found on diameter increment of *C. mildbraedii* in semi-deciduous

forest, caused by the reduced expansion rates in valley trees in the late wet seasons of both 1997 and 1998 (Figure 5). Three explanations are possible, related to excess water supply, reduced irradiance or low nutrient availability in valley positions. There is no evidence that waterlogging is the cause of this pattern. Although we acknowledge the limited spatial resolution of the direct tests for anoxic conditions in the soil profile, there was no evidence that anoxic conditions did develop, even when the wettest soils were sampled. For waterlogging to be an important factor influencing root survival during the late wet season in valley trees, root length density would be expected to decline downslope at this time. However, there were no differences in root length density or biomass between summit and valley positions. Fine-root density and biomass do appear low in the semi-deciduous forest site, particularly in the upper layers. However, roots were not sampled in the top 5 cm of soil, and the values at greater depths are comparable to other work. For example, in another semi-deciduous forest in Ghana, Lawson *et al.* (1970) found fine-root biomass, 0–10 cm depth, to vary from approximately 37 to 104 mg cm⁻², but at 30–40 cm depth to be approximately 0.25 mg cm⁻² (values read from their graph). Finally, the late wet-season leaf water potentials demonstrate that the valley, compared with the summit, trees were not short of water at this time. The values obtained are of the same magnitude as those for seedlings at the start of the dry season in the same forest (Veenendaal *et al.* 1996c). When water stressed, during the middle of the dry season, these values may drop to -2.5 MPa.

It is also possible that there is a topographic effect on light availability so that the trees in the valley receive an effectively shorter day. However, several reasons suggest this is not the case. First, the depression of valley tree expansion rates is not seen until the late wet season. Second, the difference in day length is very small over the undulating landscape and only concerns the period of the day with low PAR, and, third, for these large, adult trees, the very uneven forest canopy is likely to mask any topographic difference in light availability. The remaining explanation is that the reduction in nutrient concentrations, particularly N, in the sandy valley soils, limits growth. The lack of a detectable difference in growth rate between topographic positions for *S. glaucescens* at the evergreen site may be due to the slow growth rate of this species or limiting availabilities of P and cations at this site.

Environmental determinants of tree growth

This study indicates that soil matric potential rather than PAR determines some of the variation in growth of mature trees of two important species in Ghanaian forest. Other research examining the environmental factors that

control tropical tree growth suggests that soil water availability is important in seasonal forests and PAR has a more significant role as the climate becomes wetter and less seasonal. For example, Bullock (1997) and Whigham *et al.* (1990), working in dry forest in Mexico where annual rainfall is typically < 1000 mm, found positive correlations between growth and rainfall. Worbes (1999) reported positive correlations between wet-season growth and rainfall for three species in a semi-deciduous forest in Venezuela with an annual rainfall of 1700 mm. In addition, marked seasonal variation in monthly changes in tree girth was found in wet evergreen forest in India, which has a high total annual rainfall of more than 4000 mm, but a strong 3–3.5-mo dry season (Pélissier & Pascal 2000). The intra-annual variation in growth was related to the alternation of wet and dry periods during the year. In contrast, clear correlations have not emerged between tree growth and rainfall, and an important role for PAR has been suggested, though not demonstrated, for the growth of evergreen forest at La Selva, in Costa Rica (Breitsprecher & Bethel 1990, Clark & Clark 1994). This site is far wetter than the dry forest sites in Mexico and Venezuela with mean annual rainfall of 3859 mm. It has a relatively aseasonal climate where all months have, on average, at least 100 mm of rain (Clark & Clark 1994). In the context of these sites, both of the forests studied here have relatively dry, seasonal climates and would therefore be expected to be limited by water supply, as is suggested by the higher rates of annual and wet season growth during 1998/9. The significant regression (Table 5) between the rate of weekly diameter change for *C. mildbraedii* in semi-deciduous forest and soil matric potential, but not PAR, also supports this. The lack of any relationship between soil matric potential or PAR and weekly diameter change for *S. glaucescens* in the evergreen forest is likely to be caused by its slow growth rate, the lack of a severe dry season at this site and presumably total rainfall still too low to increase cloudiness to the extent that growth is limited by irradiance.

Alternatively, independent variation in other environmental factors, such as temperature or air humidity, not measured here may be important determinants of the seasonal variation in growth. Monthly mean temperature varies less than 5 °C in semi-deciduous forest in Ghana (Lawson *et al.* 1970) but variation in humidity could be important. For example, it explained much of the variation in daily patterns of CO₂ exchange in tropical forest near Manaus (Grace 1999). However, the influence of these variables on diameter growth rates remains untested.

The spatial patterns in the results presented here can be explained by soil fertility interacting with soil water availability to determine growth rates. Recent work on the same environmental gradient in Ghana at the species and stand level (Affum-Baffoe 1999), supports the finding that growth rates are higher in forests growing on more fertile

soils. In contrast, other researchers have failed to find an effect of soil fertility on tree growth within tropical forests. Clark *et al.* (1998) concluded that there was no difference in growth rate for adults of nine species of canopy or emergent trees on two contrasting soils in Costa Rica. In addition, Ashton & Hall (1992) found no correlation between proportional diameter growth and soil nutrient status for large (> 30 cm dbh) trees in 13 plots across Borneo from 1965–1985. It is possible that the effects of soil fertility were masked by limitation by soil water availability during these studies. Alternatively, the forest zone of Ghana represents a particularly wide environmental gradient where it is easier to detect the effect of soil fertility. For example, there are up to 15-fold differences in the concentrations of available K and Mg between sites (Table 1). In addition, the difference in available P concentrations in the soil between the two sites in Ghana, 2.2 µg g⁻¹ to 7.8 µg g⁻¹, is three times greater than the difference of 1.6–2.6 µg g⁻¹ to 3.9 µg g⁻¹ between the soil types described by Clark *et al.* (1998).

It is also significant that different soil nutrients appear to limit growth at different spatial scales. The possibility that concentrations of P limit growth at regional scales is in agreement with the conventional view, from studies of concentrations of nutrients in leaves and litterfall, that growth is typically limited by available P in tropical lowland forests (Vitousek 1984). In addition, fertilizer experiments on seedlings have shown that both P (Burslem *et al.* 1994) and cations (Denslow *et al.* 1987) can be important for limiting growth. However, in field experiments, mycorrhizal plants have shown a lack of response to added P (Turner *et al.* 1993), and in a fertilization experiment of a forest stand in Indonesia, neither P, nor N fertilization produced a significant difference in diameter growth rates after 5 y (Mirmanto *et al.* 1999). This forest has a far wetter climate (annual rainfall *c.* 3600 mm) than the sites studied here: a fertilization experiment in comparable forest is required to test the hypothesis that the growth of mature trees is limited by concentrations of P or cations in Ghanaian evergreen forest.

By contrast, the local-scale patterns suggest variation in N concentrations may have an important role across topographic gradients. Nitrogen limits tropical tree growth in montane environments (Tanner 1992, Tanner *et al.* 1990). In montane, compared with lowland forest, a higher proportion of the total N is in the soil compared with the above-ground biomass (Edwards & Grubb 1982), and N availability is limited by low rates of mineralization (Marrs *et al.* 1988, Tanner 1977). In addition, N limitation to growth has also been demonstrated on young, N-deficient, soils of volcanic origin in Hawaii (Vitousek *et al.* 1993). We speculate that the high concentrations of available P and exchangeable cations in the semi-deciduous forest soils in this study, result in limitation to growth by N on the sandy valley soils, even though concentrations

of N are themselves high compared with the range, 0.09–0.52% (Hall & Swaine 1981), found across the forest zone in Ghana. The late wet-season pattern of low girth expansion on the sandy valley soils could reflect the seasonal availability of N as a result of rapid leaching of nutrients released from the decomposition of the previous year's litterfall, or a reduction in N mineralization as the wet season progresses.

Synthesis

This study demonstrates intraspecific spatial variation in tree growth rates for two species along local and regional environmental gradients. Does this spatial variation in growth correspond to variation in species distribution and abundance? There is no evidence that the limit to the distribution of the wet-forest specialist, *Strombosia glaucescens*, in dry forest is caused by a reduction in adult growth rates. Sensitivity to seasonal drought at the seedling stage may therefore be more important for this species (Swaine *et al.* 1997). However, the distribution limit in evergreen forest of the dry-forest specialist, *C. mildbraedii*, and its reduced abundance lower down catenas, may in part be determined by a reduction in growth rate on less fertile soils.

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