

# Tree Population Dynamics of Three Altitudinal Vegetation Communities on Mount Cameroon (1989-2004)

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**Abstract:** Changes in permanent sample plots in the lowland, submontane and montane forests on Mount Cameroon (4,095 m above sea level), an active volcano, are described for 15 years from 1989 to 2004. Throughout the study period, the stocking level of trees with a diameter at breast height (DBH)  $\geq 10$  cm in the three forests were lower than in pan-tropical stands suggesting a significant impact of volcanic and human-related activities on the vegetation communities on the mountain. Annual mortality rates in the submontane and montane forests were consistent with those reported for comparable altitudinal ranges in the Blue Mountains of Jamaica. The annual mortality rate was higher in the lowland forest than other lowland sites included. Divergence between recruitment and mortality rates was large suggesting that the three vegetation communities have not reached their climax. The seven-year difference in half-life of large trees (with a DBH  $\geq 50$  cm) in the submontane and montane forests suggests an altitudinal effect on turnover of larger trees that in turn contributes to the frequent small stature of high altitude forests. There was little evidence of an altitudinal effect on species turnover and growth rate. This finding supports generalizations about the zero effect of growth on the stature of high altitude trees. Understanding forest dynamics is crucially important in the management of tropical montane environments

and in this instance particularly so given the recent creation of the Mount Cameroon National Park.

**Keywords:** Growth rates; Recruitment; Mortality; Altitude; Half-life; Mount Cameroon

## Introduction

There is growing recognition of the need for demographic studies of forests in order to evaluate the dynamics of tropical trees (Swaine and Whitmore 1988; Whitmore 1989; Alvarez-Buylla and Martínez-Ramos 1992; Clark and Clark 1992; Zimmermerman et al. 1994). On the African continent, efforts towards characterizing and predicting tree population dynamics using long-term permanent sample plots were initiated in Omo Forest Reserve in Nigeria in the 1920s (Okali and Ola-Adams 1987), Budongo Forest Reserve in the 1930s and 1940s in Uganda (Eggeling 1947; Sheil 1995, 1999) and Kade in Ghana in the late 1960's (Swaine et al. 1987a). Such studies enabled the estimation of recruitment, growth and mortality rates in tropical forests (Alder and Synott 1992). Mount Cameroon, an active volcano which last erupted in 2002, is an important area for plant conservation on account of its rich, diverse, and

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unique vegetation (Hooker 1864; Keay 1955; Richards 1963; Cable and Cheek 1998; Peguy et al. 1999). However, very little is known about the vegetation dynamics of the ecosystem. Previous studies focused on areas below 600 m above sea level (e.g. Ndam et al. 2001; Fonge et al. 2005). Such studies preclude examination of the potential influence of altitude, volcanism, soil, geology and human-related activities on forest dynamics.

Mount Cameroon offers a unique opportunity for the study of variation in forest dynamics with altitude. It is the highest mountain in West and Central Africa, rising directly from sea level to 4,095 m, with forest cover ranging from sea level to 2,500 m. Zonation is a key feature of the vegetation and in common with other massifs on the continent, it is influenced by altitude (Bussmann 2006). Consistency between results from Mount Cameroon and other forests indicates the influence of altitude on forest structure, stature and composition (Proctor et al. 2007). Volcanism, the soil, geology and human-related effects also influence vegetation patterns.

This paper presents data on tree population dynamics from three altitudinal communities on Mount Cameroon – lowland, submontane and montane forests (Payton 1993; Proctor et al. 2007). Two questions are addressed: (1) How do stand characteristics and demographic rates (e.g., basal area, tree growth, mortality, and recruitment) differ between the three communities and with other sites? (2) What is the role of volcanic activity, altitude, soil, geology and human-related causes (such as fire and destructive forest harvesting) on forest dynamics at these sites?

## 1 Material and Methods

### 1.1 Study site

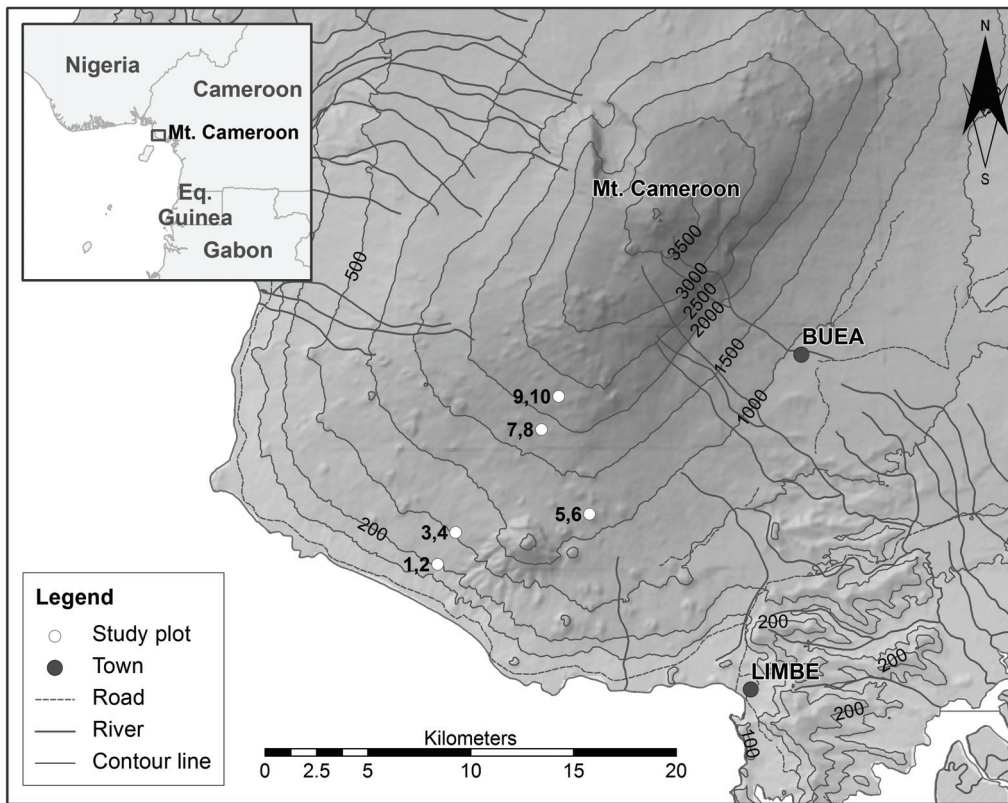
The main massif and foothills of Mount Cameroon cover an area of 1,500 km<sup>2</sup>. The annual rainfall ranges from 12,000 mm in the south-west of the main massif to 2,000 mm in the north-east. Much of the rain is received between June and September. The mean annual temperature is 25° C at sea level and decreases by 0.45° C with every 100 m rise in altitude. Relative humidity averages 70–80% at the coast and the annual sunshine varies

between 900 and 1,200 hours at sea level (Payton 1993).

Mount Cameroon provides a biological mosaic that contributes to extremely high speciation and biological diversity in the Guineo-Congolian regional area of endemism, and is posited as one of the main Pleistocene refugia postulated for Africa (Hooker 1864; Keay 1955; Richards 1963; Gartlan 1989; Cable and Cheek 1998; Peguy et al. 1999; Proctor et al. 2007). The massif and surrounding foothills contain around 4,000 higher plant species and about 50 of these are endemic to Mount Cameroon (Cable and Cheek 1998). This is the last area in Africa where natural vegetation remains unbroken from lowland forest at sea level to the sub-alpine grassland at the summit. The wildlife of the region is rich, with populations of Cercopithecine primates, forest elephant (*Loxodonta africana cyclotis*) and chimpanzee (*Pan troglodytes elliotii*) (Gadsby and Jenkins 1992), and at least two endemic birds (Fotso et al. 2001). The soils are of recent origin, on young volcanic rocks and fertile, though with poor water retention capacity (Hasselo 1961; Proctor et al. 2007). The fertile volcanic soils of Mount Cameroon and its hinterland support extensive oil palm (*Elaeis guineensis*) plantations (Proctor et al. 2007). With continued human migration to the area, the clearance of natural vegetation to provide land for both commercial and subsistence farming poses a serious threat to the forest with much of the lowland forest already converted to industrial plantations. The collection of products from the forest and montane grassland such as honey, medicinal plants, vegetables and spices has a considerable impact on the local economy. Jeanreneaud (1991) reported that many households were selling forest products, including bushmeat. Although some bushmeat is consumed by the households, it is also an important source of cash, supplying a lucrative market in Douala, over 80 km away, and other urban centres (Edderai and Dame 2006).

### 1.2 Data collection

In 1989 the Limbe Botanic Garden and a team of volunteers from Operation Raleigh established ten paired 0.25 ha permanent plots along an altitudinal transect (Figure 1) in undisturbed forest



**Figure 1** Location of study sites on Mount Cameroon in Africa

at approximately 600 m intervals along the southern slopes of Mount Cameroon (Proctor et al. 2007). The lowest plots were established 2 km after the last local agricultural limit and the higher plots were set to avoid existing lava flows. Plots 5 and 6 were set to the east of the transect as there was no closed-canopy mid-elevation forest due to a large landslide that occurred some years previously (Richards 1963). The plots were subdivided into ten 10 × 10 m subplots and all trees and lianas ≥10 cm in diameter at breast height (DBH) were numbered with aluminium tags and measured for DBH. Botanical specimens were collected using a “morphospecies” approach whereby specimens of each taxon were collected once, whether the field botanists knew the individual species or not, to confirm its identity. The identification of the specimens was undertaken at the Limbe Botanic Garden and the Royal Botanic Gardens, Edinburgh. Duplicates were deposited at both the Limbe and Yaoundé herbaria. A Smithsonian Institution-funded team completed the recensus of the plots in 2004. It is hoped that an additional recensus will be completed during 2011. The demographic rates

reported here are derived from the two data sets, 1989 and 2004.

### 1.3 Data analysis

The influence of mortality on the tree population dynamics of each community was established by determining the proportion of the original cohort of trees with a DBH ≥ 10 cm that survived the recensus interval. Mortality rates were computed using the equation:

$$m = 1 - (1 - (N_d / N_o))^{1/t}$$

where  $m$  is the annual mortality,  $N_o$  is the number of trees in the previous census, and  $N_d$  is the number of trees that died by the end of the census interval,  $t$  years (Alder 1995; Sheil et al. 1995). The constant probability of mortality assumption was applied to generate confidence limits using the inverse  $F$ -distribution (Johnson and Kotz 1970; Nelson 1982 cited in Sheil and May 1996) as:

$$m_u = 1 - [1 - 1 / \{1 + F_{inv}[\alpha, 2(N_o - N_t) + 2, 2N_t] N_t / (N_o - N_t + 1)\}]^{1/t}$$

and 
$$m_l = 1 - [1 - 1 / \{1 + F_{inv}[\alpha, 2(1 + N_t), 2(N_0 - N_t)](N_t + 1) / (N_0 - N_t)\}]^{1/t}$$

where  $m_u$  and  $m_l$  are the upper and lower confidence limits of  $m$ ,  $F_{inv}(\alpha, df_{num}, df_{den})$  is the inverse of the  $F$  cumulative probability distribution at confidence level  $\alpha$ . If there are five or more dead trees the confidence limits are computed using the normal approximation to binomial variance based on Dixon and Massey (1969, cited in Condit et al. 1995). The chi-square statistic was used to test for differences in tree mortality in the three forests. The half life of large trees (with DBH  $\geq 50$  cm) was calculated as  $[\ln(0.5)] / (0.01m)$ ; and  $m$  (mortality) expressed as a percentage rate (Swaine et al. 1987b). This is the time it takes for the number of original stems to decrease by 50%.

The recruitment rate ( $r$ ) was computed using the equation:

$$r = 1 - (1 - (N_r / N_0))^{1/t}$$

where  $N_r$  is the number of trees recruited after  $t$  years and  $N_0$  is the number of trees in the previous census (Sheil et al. 2000).

Growth rate was computed as the mean DBH increment per year (Condit et al. 1999) with  $-0.2$  cm yr<sup>-1</sup> and  $+4$  cm yr<sup>-1</sup> used as the limits of “acceptable” DBH change (Sheil 1995). Following Ral (1979) and West (1980), the quadratic function was used to model DBH increment by diameter class for all species:

$$DI = a + b k\text{-DBH} + c k\text{-DBH}^2 + \varepsilon$$

where:

DI = class mean diameter at breast height increment (cm yr<sup>-1</sup>)

$k\text{-DBH}$  = class mean diameter at breast height (cm)

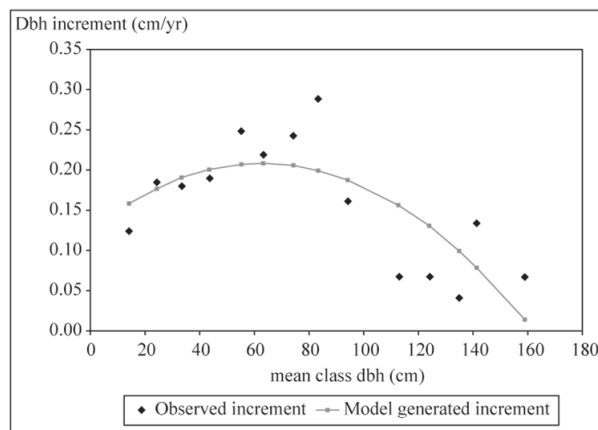
$a, b, c$  are parameters to be estimated and  $\varepsilon$  is independent of  $N(0, \sigma^2)$ .

Positive diameter growth data was pooled across the three communities to model diameter increment, which follows a curvilinear trend (Figure 2) and reasonably approximated by the quadratic equation:

$$DI = 0.125 + 0.00264 k\text{-DBH} - 0.000021 k\text{-DBH}^2$$

Partial tests showed that the constant ( $a$ ) and quadratic term coefficient ( $c$ ) are significantly different from zero ( $p < 0.05$ ) but not the coefficient of the linear term coefficient ( $b, p > 0.11$ )

suggesting the need for a different model. The above model was retained as it explains more of the variation in the data, with an adjusted coefficient of determination ( $R^2$ -adjusted) of 48.5%, than the model with no linear term ( $R^2$ -adjusted 39.5%). The model was used to compute the theoretical maximum growth rate.



**Figure 2** Mean DBH increment of all tree species on Mount Cameroon

Dawkins (1958) suggested a minimum of ten trees for computing demographic rates while Mervart (1972) recommended 100 trees. Thus mortality, recruitment and growth rates are reported here only when there are at least 10 trees with a DBH  $\geq 10$  cm in the initial enumeration.

## 2 Results

The number of species recorded in both censuses decreased with altitude (Table 1). Moreover, there seems to be an altitudinal effect on common species (represented by at least ten individuals) as they differed across the three communities (Table 2). There was little evidence of altitudinal effect on species turnover. During the 15-year census interval the lowland community lost 27 species and gained 15 indicating an average “species turnover” of 1.4% of the 110 species enumerated in 1989. The submontane community lost seven species and gained 11 representing an average “species turnover” of 1.2% of the 56 species recorded in 1989, while the montane community lost nine species and gained four during the same census interval indicating an average “species turnover” of 1.4% of the 34 species recorded in 1989.

**Table 1** Characteristics of plant communities along an altitudinal gradient on Mount Cameroon

Forest type	Plot	1989			2004			Species turnover (%)	Annual BA loss (% yr <sup>-1</sup> )	AM (% yr <sup>-1</sup> )*	AR (% yr <sup>-1</sup> )**	Increment (± 1SE) cm yr <sup>-1</sup>	HL of trees with DBH ≥ 50 cm (years)
		Species (all plots)	N Trees	BA m <sup>2</sup> ha <sup>-1</sup> (± 1 SE)	Species (all plots)	N Trees	BA m <sup>2</sup> ha <sup>-1</sup> (± 1 SE)						
Lowland	P1-4	110	99	9.49 ± 1.16	98	87	5.79 ± 1.11	1.4	3.24	2.47 [2.11, 2.87]	1.39	0.129 ± 0.011	16
Submontane	P5-6	56	94	8.94 ± 0.13	59	78	6.92 ± 0.24	1.2	1.69	2.10 [1.46, 2.69]	0.75	0.183 ± 0.023	22
Montane	P7-10	34	92	22.23 ± 4.51	29	62	12.37 ± 2.18	1.4	3.83	3.71 [3.24, 4.24]	0.79	0.182 ± 0.029	15

**Note:** \* For trees ≥50 cm DBH; \*\*Significant difference in recruitment rate among communities along the altitudinal gradient ( $X^2_1 = 10.06, p < 0.002$ ); BA= Basal Area; AM= Annual Mortality; AR= Annual Recruitment; HL= Half Life DBH= Diameter at Breast Height

**Table 2** Density (stems in 4 ha, Lowland & montane forest; 2 ha in submontane forest) and mortality, recruitment and growth rates of common species on Mount Cameroon. Common species are those that had at least 10 individuals with Diameter at Breast Height (DBH) ≥ 10 cm in the initial enumeration.

Species	Code	Trees 1989	Trees 2004	1989 Stems living in 2004	Dead Trees	Annual mortality (% yr <sup>-1</sup> )		Recruitment (% yr <sup>-1</sup> )		DBH growth (cm yr <sup>-1</sup> )	
						Rate	95% UCL	95% LCL	Rate	± 1SE	Rate
Lowland											
<i>Diogoa zenkeri</i> (Engl.) Mendonca	DIZE	36	31	28	8	1.66	3.28	0.82	0.58	0.057	0.011
<i>Strombosia pustulata</i> Oliv.	STPU	30	21	20	10	2.67	4.72	1.42	0.23	0.107	0.024
<i>Baikiaea insignis</i> Benth.	BAIN	29	28	24	5	1.25	3.09	0.49	0.98	0.131	0.027
<i>Rinorea oblongifolia</i> Marquand ex Chipp	RIOB	25	20	17	8	2.54	4.84	1.24	0.85	0.082	0.020
<i>Chrysophyllum boukokouense</i> & Pellegr.) L. Gaut	GABO	17	33	13	4	1.77	4.66	0.59	189.08	0.082	0.020
<i>Strombosia grandifolia</i> Benth.	STGR	15	15	13	2	0.95	4.13	0.16	0.95	0.108	0.030
<i>Hymenostegia afzelii</i> (Oliv.) Harms	HYAF	14	12	10	4	2.22	5.64	0.73	1.02	0.087	0.027

-Continued-

Species	Code	Trees 1989	Trees 2004	1989 Stems living in 2004	Dead trees	Annual mortality (% yr <sup>-1</sup> )			Recruitment (% yr <sup>-1</sup> )	DBH growth (cm yr <sup>-1</sup> )	
						Rate	95% UCL	95% LCL		Rate	± 1SE
<i>Drypetes</i> sp.	DRSP	10	13	7	3	2.35	6.74	0.61	5.93	0.095	0.036
<i>Chrysophyllum albidum</i> G.Don	GAAL	10		4	6	5.93	10.98	2.38	0.70	0.083	0.042
Submontane											
<i>Aulacocalyx jasminiflora</i> Hook.f.	AUJA	20	17	17	3	1.08	3.55	0.29	0.00	0.125	0.030
<i>Turraeanthus africanus</i> (Welw. Ex C.DC.) P	TUAF	17	12	10	7	3.48	6.68	1.58	0.83	0.213	0.067
<i>Antidesma laciniatum</i> Mull.Arg.	ANLA	12	12	11	1	0.58	4.68	0.03	0.58	0.194	0.058
<i>Chrysophyllum africanum</i> (Baker) Pierre	CHAF	12		7	5	3.53	7.58	1.32	1.21	0.486	0.184
<i>Strombosia scheffleri</i> Engl.	STSC	12		8	4	2.67	6.56	0.87	0.00	0.181	0.064
Montane											
<i>Clausena anisata</i> (Willd.) Hook.f. ex Benth.	CLAN	84	54	48	36	3.66	4.86	2.70	0.49	0.090	0.016
<i>Canthium schimperianum</i> A.Rich.	CASC	51	31	31	20	3.26	4.82	2.14	0.00	0.054	0.017
<i>Allophylus bullatus</i> Radlk.	ALBU	28	16	15	13	4.08	6.51	2.36	0.24	0.200	0.050
<i>Canthium mannii</i> Hiern	CAMA	26	18	14	12	4.04	6.58	2.28	0.00	0.076	0.022
<i>Syzygium rowlandii</i> Sprague	SYRO	26	13	13	13	4.52	7.15	2.60	0.00	0.313	0.122
<i>Syzygium staudtii</i> (Engl.) Mildbr.	SYST	25	14	12	13	4.78	7.53	2.75	0.55	0.161	0.041
<i>Schefflera abyssinica</i> (Hochst). ex. A.Rich	SCAB	19	12	12	7	3.02	5.90	1.37	0.00	0.333	0.256
<i>Pittosporum mannii</i> Hook.f.	PIMA	18		9	9	4.52	7.82	2.27	0.00	0.244	0.109
<i>Nuxia congesta</i> R.Br. ex Fresen.	NUCO	17	17	13	4	1.77	4.66	0.59	1.77	0.226	0.113
<i>Cyathea manniana</i> Hook.f.	CYMA	16	22	12	4	1.90	4.95	0.63	6.33	-0.006	0.017
<i>Rapanea melanophloeos</i> (L.) Mez	RAME	15		5	10	7.06	11.31	3.59	0.46	0.387	0.243
<i>Ilex mitis</i> (L.) Radlk.	ILMI	14	10	8	6	3.66	7.34	1.53	1.02	0.242	0.122

Tree density decreased with altitude and between census periods, and each community experienced a reduction in basal area between the censuses (Table 1). Among trees with a DBH  $\geq$  50 cm, the montane community suffered the largest reduction with a 44.4% loss in basal area, corresponding to an annual basal area loss of 3.83% yr<sup>-1</sup>. About 86% of the basal area loss in the montane forest occurred in trees with a DBH  $\geq$  50 cm. The lowland forest lost 39.0% of its basal area or 3.24% yr<sup>-1</sup> with about 76% of the loss occurring in the DBH  $\geq$  50 cm class, while the submontane community suffered a 22.6% (1.69% yr<sup>-1</sup>) loss, with about 56% of the loss occurring in the DBH  $\geq$  50 cm class.

The analysis shows a community-wide annual mortality rate of 2.47% yr<sup>-1</sup> for the lowland forest, 2.10% yr<sup>-1</sup> for the submontane forest and 3.71% yr<sup>-1</sup> for the montane forest. The annual mortality was significantly higher in the montane forest than in the submontane and lowland communities (Table 1). At the plot level, annual mortality rates were high in the lowland at 250 m above sea level (plots 1-2) and the montane environment between 1,800-2,100 m (plots 7-9) with annual rates exceeding 3% yr<sup>-1</sup> (Table 3). The absence of species in common between communities precludes investigations of species-specific mortality along the altitudinal

gradient. The 95% confidence intervals of annual mortality rate suggest no significant difference in annual mortality among common species in the three communities (Table 2). The half-life of trees with a DBH  $\geq$  50 cm in the submontane is at least five years longer than in the lowland and montane forest (Table 1).

There is evidence of significant differences in recruitment among communities along the altitudinal gradient ( $X^2_1 = 10.06, p < 0.002$ ). The main difference in recruitment rate was between the lowland and the other communities (Table 1). Recruitment was less than mortality in some species and exceeded or closely matched mortality in others (Table 2). For example, the recruitment of *Cyathea manniana* within the montane forest was 6.33% yr<sup>-1</sup> while mortality was 1.90% yr<sup>-1</sup>. In the same community recruitment of *Rapanea melanophloeos* was 0.46% yr<sup>-1</sup> while mortality was 7.06% yr<sup>-1</sup>. At the plot level, recruitment was variable and less than 2% yr<sup>-1</sup>, except in the lowland plots at 500 m above sea level and largely exceeded by mortality (Table 3).

There were no significant differences in stem growth rates along the altitudinal gradient. Stem growth rate was 0.129 cm yr<sup>-1</sup> in the lowland community, 0.183 cm yr<sup>-1</sup> in the submontane and 0.182 cm yr<sup>-1</sup> in the montane. The theoretical

**Table 3** Plot level characteristics of plant communities along an altitudinal gradient on Mount Cameroon

Plot	Altitude (m)	1989		2004		AM (%) & 95% CI	AR (%)	Increment $\pm$ 1SE cm yr <sup>-1</sup>
		Species	LS	Species	LS*			
P1	250	51(5)	111	36(1)	69[10]	3.12 [2.36, 4.07]	0.63	0.141 $\pm$ 0.024
P2	250	35(3)	105	25(1)	63[4]	3.35 [2.53, 4.36]	0.26	0.115 $\pm$ 0.019
P3	500	33	88	29	65[23]	2.00 [1.36, 2.92]	2.00	0.124 $\pm$ 0.024
P4	500	41(11)	93	36(9)	76[38]	1.34 [0.85, 2.12]	3.26	0.134 $\pm$ 0.018
P5	1200	38(6)	94	31(5)	61[7]	2.84 [0.98, 3.85]	0.51	0.208 $\pm$ 0.039
P6	1200	35(7)	93	31(6)	75[13]	1.42 [0.92, 2.22]	0.99	0.163 $\pm$ 0.026
P7	1800	17(5)	88	12(4)	50[8]	3.70 [2.75, 4.87]	0.63	0.416 $\pm$ 0.107
P8	1800	11(3)	131	8(1)	62[7]	4.86 [3.92, 5.93]	0.37	0.147 $\pm$ 0.031
P9	2100	12(3)	70	9(1)	42[15]	3.35 [2.36, 4.64]	1.59	0.056 $\pm$ 0.017
P10	2100	12(4)	78	10(3)	54[11]	2.42 [1.66, 3.49]	1.01	0.102 $\pm$ 0.023
<b>Global</b>		<b>187 (47)</b>	<b>951</b>	<b>149(31)</b>	<b>617 [136]</b>	<b>2.88 [2.59, 3.12]</b>	<b>1.02</b>	<b>0.158 <math>\pm</math> 0.012</b>

**Note:** 1. Figures in brackets ( ) = number of indeterminate species, i.e. 5 of the 51 species in plot 1 in 1989 were indeterminate; [ ] = number of recruits, i.e. there were 10 recruits in plot 1 in 2004;  
 2. LS=Live stems; AM=Annual mortality; CI=confidence intervals; AR=Annual recruitment

maximum stem growth rate of Mount Cameroon was  $0.207 \text{ cm yr}^{-1}$  with 95% confidence interval of  $0.16$  to  $0.25 \text{ cm yr}^{-1}$  and 95% prediction interval of  $0.08$  to  $0.34 \text{ cm yr}^{-1}$  occurring at mean DBH  $62 \text{ cm}$  in the  $65 \text{ cm}$  DBH class. Among the common species, the highest growth rates were  $0.387 \text{ cm yr}^{-1}$  for *Rapanea melanophloeos* and  $0.333 \text{ cm yr}^{-1}$  for *Schefflera abyssinica* in the montane community (Table 2). In the submontane community the fastest growing species were *Chrysophyllum africanum* ( $0.486 \text{ cm yr}^{-1}$ ) and *Turraeanthus africanus* ( $0.213 \text{ cm yr}^{-1}$ ). The fastest growing species of the lowland were *Baikiaea insignis* ( $0.131 \text{ cm yr}^{-1}$ ), *Strombosia grandifolia* ( $0.108 \text{ cm yr}^{-1}$ ) and *Strombosia pustulata* ( $0.107 \text{ cm yr}^{-1}$ ).

### 3 Discussion

Analysis of data from Mount Cameroon shows an inverse relationship between species richness and altitude that corroborates earlier studies (Richards 1963; Payton 1993; Peguy et al. 1999). The analysis also shows a seven-year difference in half-life between the sub-montane and montane forest that supports previous reports of an altitudinal effect on turnover of larger trees (Herwitz and Young 1994) and explains the frequent small stature of high altitude forests. Furthermore, the analysis shows a reduction in basal areas between the two censuses. Meanwhile, community-wide estimates of less than  $100 \text{ stems ha}^{-1}$  and  $23 \text{ m}^2 \text{ ha}^{-1}$  of basal area suggest that the vegetation communities on Mount Cameroon are much less stocked than the pan-tropical stands of Rollet (cited in Phillip 1983) and Dawkins (1958) that support  $168\text{--}197 \text{ stems ha}^{-1}$  and mean basal areas of  $26.77\text{--}36.50 \text{ m}^2 \text{ ha}^{-1}$ . Bellingham and Tanner (2000) reported a  $56 \text{ m}^2 \text{ ha}^{-1}$  basal area in the  $1,640\text{--}1,740 \text{ m}$  altitudinal range on the Blue Mountains of Jamaica. We hypothesize that these differences on Mount Cameroon are influenced by variation in altitude, soil, volcanic and anthropogenic disturbance.

Dilmy (1971) and others reported high basal areas on well drained sites and lower figures on inundated sites and swamps. Mount Cameroon soils are mostly on young volcanic rocks, and though fertile, they have poor water retention capacity that contributes to the poor stocking levels.

By contrast, the surrounding foothills and Mount Etinde at about  $1,715 \text{ m a.s.l.}$  are mostly of older tertiary lava of different composition to the underlying Holocene basalts of the Greater Mount Cameroon (Payton 1993). The low number of stems  $\text{ha}^{-1}$  and basal areas of the lowland forest suggest that soil drainage is not the only factor that influences stocking on Mount Cameroon.

One explanation for the poor stocking levels on Mount Cameroon and the reduction in basal area between censuses is the frequent volcanic disturbance and lava flows that affect regeneration. Eight volcanic events are on record for the last 100 years – 2000, 1999, 1982, 1959, 1954, 1925, 1922 and 1909 (Ndam et al. 2001). Annual mortality in the montane forest ( $3.71\% \text{ yr}^{-1}$ ) was comparable to the  $3.9\% \text{ yr}^{-1}$  reported by Bellingham and Tanner (2000) for the windward slope of the Blue Mountains at  $1,580 \text{ m}$  elevation, and significantly higher than in the submontane and lowland communities on Mount Cameroon. The high mortality in the montane forest plots, and hence disproportionately higher loss in basal area, was certainly caused by the effects of the chemical composition of the larva in 2002 when extensive areas of forest were covered with hot volcanic ash (Proctor et al. 2007). This also explains the high recruitment of tree ferns, opportunistic colonizers of gap vegetation, between census years.

The montane community on Mount Cameroon is poorly developed with discontinuous low canopy of shrubs (Richards 1963; Thomas and Achoundong 1994). It is also much drier and receives lower rainfall than the submontane and lowland forests and consequently very prone to damage by fire that occurs both naturally (lightening and volcanic activity) and deliberately (hunters setting fires to flush out game) in the grassland savanna where trees in plots 7 and 8 showed evidence of fire damage.

While high mortality may be an intrinsic characteristic of high altitude vegetation communities, other factors, notably anthropogenic disturbance such as subsistence farming, explain the higher annual mortalities in the lowland of Mount Cameroon than other lowland tropical forests. Annual mortality in the lowland forest of Mount Cameroon ( $2.47\% \text{ yr}^{-1}$ ) was higher than the  $1\text{--}2\% \text{ yr}^{-1}$  reported for 18 lowland natural tropical forests below  $600 \text{ m}$  altitude (Swaine et al. 1987b).



This was due to the expansion of shifting agriculture up to the perimeter of plots 1 and 2. The felling of two large trees outside of but onto the plot 1 caused significant damage to the residual vegetation. In addition, local harvest of non-timber forest products (Ambrose-Oji 2003) often entails destructive removal of individuals. Stumps of small to mid diameter trees were observed in plots 1 and 2. Annual mortality in the sub-montane forest (2.10% yr<sup>-1</sup>) was consistent with those reported by Swaine et al. (1987b) and the 1.6-1.9% yr<sup>-1</sup> reported by Bellingham and Tanner (2000) for the 1,640-1,740 m altitudinal range in the Blue Mountains of Jamaica.

Discussion of tropical tree population dynamics focus on the division between pioneer and late several species, but small sample sizes frequently render reliable assessment of species-specific difference in mortality difficult (Manokaran and Kochummen 1987). *Chrysophyllum albidum* experienced the highest mortality of 5.9% yr<sup>-1</sup> in the lowland forest. Similarly *Chrysophyllum africanum* and *Turraeanthus africanus* experienced the highest mortality of 3.5% yr<sup>-1</sup> in the submontane community, while *Rapanea melanophloeos* experienced the highest mortality of 7.1% yr<sup>-1</sup> in the montane forest. Sample sizes of these species in the other communities were too small to allow us to assess the extent to which high mortality rate is intrinsic to the species, or is imposed on its population by the local environment (e.g., altitude, volcanic activity). Effective assessment of species-specific mortalities for the few species with overlapping distribution along the altitudinal gradient on Mount Cameroon necessitates the establishment of larger plots.

Recruitment into the lowest enumerated DBH (10 cm) was less than mortality rate in the three communities on Mount Cameroon, unlike other tropical forests (Swaine et al. 1987b). Although recruitment rate is a function of species fecundity, growth and survival of juveniles (seedlings and

saplings) that ideally should be included in studies of population dynamics, the large divergence between recruitment and mortality on Mount Cameroon suggests that all the vegetation communities have not reached their climax. There was an altitudinal effect on recruitment rate. It was higher in the lowland forest than in the two montane forests. There was no evidence of an altitudinal effect on recruitment rate within the two montane positions and growth rate in the three communities. This finding corroborates previous results (Bellingham and Tanner 2000) and discounts the importance of growth in explaining the frequent low stature of high altitude forests. The relative importance of genotype and site factors in determining the growth rates of tropical tree populations is still unknown.

#### 4 Conclusion

Our findings suggest that lower elevation forests are more susceptible to anthropogenic influences from farming and hunting, particularly. Natural regeneration on Mount Cameroon is lower than in other regions and thus communities are more prone to suffer from disturbance in the long term. The vegetation communities at higher elevations exhibit slower growth rates and regeneration and, as such, they are very susceptible to fire damage. The regular fissure type eruptions that occur on Mount Cameroon obviously affect the residual vegetation significantly and the mountain's complex mosaic of vegetation makes it an area of significant conservation value. To that end, a new National Park has recently (March 2010) been decreed that encompasses the majority of the remaining natural vegetation, including the permanent sample plots, reported on here. The intent is to continue to recensus and monitor these plots on a regular basis to ensure we understand the complex dynamics of the forest on Mount Cameroon.

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