
A COMPARISON OF TREE SEEDLING GROWTH IN ARTIFICIAL GAPS OF DIFFERENT SIZES IN TWO CONTRASTING FOREST TYPES

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ABSTRACT

One of the major concerns in forestry in the tropics is the lack of information on the impact of canopy disturbance through logging. The degree of canopy opening that should be allowed during logging to enhance natural regeneration of timber tree species is not known. Information on the seedling ecology of individual species and ecological species groups on which to base management decisions are also lacking. Experiments to determine the ecophysiological responses of seedlings of timber tree species to different irradiances in two forest sites were carried out. The two forest reserves are Nkrabia and Tinte Bepo in the Moist Evergreen and Moist Semi-Deciduous Forest Types, respectively. Eight species, representing three Shade Bearers, four Non-Pioneer Light Demanders and one Pioneer species, were grown in a series of artificially-created gaps in two forest sites differing in annual rainfall. The forest shade received 1-2% irradiance, while the artificial gaps received 5, 10, 15, 30 and 65% irradiance. Seedling growth was greater at Nkrabia Forest Reserve (Moist Evergreen Forest Type) than at Tinte Bepo Forest Reserve (Moist Semi-Deciduous Forest Type). This is probably due to the lower soil moisture stress at Nkrabia as a result of more rainfall. Lower moisture stress at Nkrabia may also explain the greater leaf area and specific leaf area ratios, lower leaf turnover and lower number of small leaves on plants than those at Tinte Bepo. Response of height growth to irradiance of Shade Bearers and Non-Pioneer Light Demanders was similar but different from that of Pioneer species.

Keywords: Forest types; Canopy disturbance; Irradiance; Seedling growth; Ecological species groups

INTRODUCTION

Variation in structure and floristic composition in West African forests are correlated with differences in rainfall and soil conditions. Although parent material may influence soil conditions in some areas (white sands in Cameroon (Newbery *et al.*, 1986), tertiary sediments in the Niger delta (Hall, 1977) and outcropping rocks in dry forest (Hall and Swaine,

1976). Soils over greater part of the region's forest zone are ancient and very deeply weathered so that the long history of leaching dominates soil conditions for plant growth. Soils presently under high rainfall are very acidic, strongly desaturated and infertile (Ahn, 1961).

Superimposed on this regional variation in forest are local differences caused by a variety of environmental influences; most notable and

widespread are the local effects of topography on soil water drainage (swamp forests) and climate conditions (Clinton, 2003), and the natural and artificial openings in the forest canopy caused by natural tree fall and logging operations. These openings often called 'gaps', are important for the development, structure and composition of tropical forests (Brokaw and Busing, 2000; Lima and Moura, 2008). Canopy disturbance causes significant changes in the microclimate of the forest understorey which varies with the size of the opening created (Li *et al.*, 2005) and to some extent with forest type (Agyeman *et al.*, 1999b). These changes can have profound influence on tree seedlings growing in the forest and offer almost the only opportunity for the forester to manipulate forest stocking and composition by controlling the distribution and size of canopy openings caused by logging or silvicultural operations (Lindenmayer and Franklin, 2002).

Tropical forest tree species differ markedly in their tolerance of shade and their ability to respond to changes in irradiance. The responses of species to variation in irradiance can be studied by growth analysis (Fetcher *et al.*, 1983; Mitchel and Woodward, 1988), using shadehouses (Popma and Bongers, 1991, Osunkoya *et al.*, 1994) or gaps created in the forest (Chazdon, 1986; Brown, 1990) or by light response curves in which changes in the rates of photosynthesis and transpiration are measured instantaneously in the same seedling under varying irradiance (Oberbauer and Strain, 1984; Kwesiga and Grace, 1986; Herlory *et al.*, 2007). The latter approach records the rapid responses of existing leaves and photosynthetic apparatus to changes in light (Inman *et al.*, 2007), usually diffuse and neutral in spectral composition (high red:far-red ratio). Growth analysis may be done in shade houses (usually with neutral shade) or in the forest by creating canopy openings of different size, effectively using natural shade where light quality varies with irradiance. In theory, experimental

conditions can be more closely controlled and more precise questions addressed by the approach of measuring photosynthesis, but it is very difficult to use the results to predict outcomes for tree seedlings growing in forests. Forest growth analysis experiments are effective at answering questions about how trees will respond to canopy opening (Aya *et al.*, 2006) but are less effective at determining which of the changed environmental variables are the cause of the seedlings' response.

Based on field experience of tree growth and more particularly the distribution of young seedlings in different forest light environments, it has been possible to define fairly robust classifications of species according to the light requirements (Swaine and Whitmore, 1988; Hawthorne and Musah, 1993), which can be represented by a continuum (Wright *et al.*, 2003; Poorter *et al.*, 2005; Gilberta *et al.*, 2006). The simplest classification divides tree species into pioneers (requiring gaps for seedling establishment and growth) and non-pioneers (able to establish and grow in forest shade). Growth analysis and photosynthesis measurements have shown how these contrasting species guilds differ in growth physiology. Pioneers have high dark respiration, high compensation and saturation points and high quantum efficiency. These characteristics give them substantial flexibility for growth in different light environments, but not sufficient for survival in deep forest shade - shade tolerance appears to be sacrificed for the benefit of very rapid growth in high irradiance. By contrast, non-pioneers have low dark respiration, low compensation and saturation points and show relatively little increase in growth when irradiance increases. Their forte is growth and persistence in deep forest shade. These differences are well exemplified by Kwesiga and Grace (1986).

Differences amongst tree species responses to irradiance as determined by such experiments offer the possibility of predicting seedling growth

in canopy openings in natural forest. However, forest gaps differ not only in irradiance, but also light quality, humidity, air temperatures and water balance - many potential causes to confound the predictions based on light. Thus it is important to test the applicability of experimental results by trials in the forest. Since environmental conditions differ significantly between forest types, we must also test in more than one type.

This paper reports the results of such field trials in two contrasting forest types in Ghana using species which were also tested experimentally in a series of neutral shade houses (Agyeman *et al.*, 1999a). The objectives of this study are; (i) to examine seedling growth response amongst a range of Ghanaian timber tree species to luminance resulting from different sized gaps in a natural forest and (ii) to assess differences in growth of the same species in two contrasting forest types.

MATERIALS AND METHODS

Field Sites and Artificial Forest Gaps

Two field sites with different soil, climate and vegetation were chosen to test the hypothesis that site differences have an effect on the growth performance of tropical tree seedlings. The sites were chosen to represent two forest types, namely; Nkrabia Forest Reserve in the Moist Evergreen Forest Type and Tinte Bepo Forest Reserve in the Moist Semi-Deciduous Forest Type (Agyeman *et al.* 1999b). These two forest types contain the bulk of timber tree species currently being exploited in Ghana. They also constitute the largest forest types in Ghana. Mean annual rainfall in the Moist Evergreen Forest Type is between 1550 and 1750 mm while that of the Moist Semi-Deciduous Forest Type is between 1250 and 1500 mm (Hall and Swaine, 1981).

Experimental plots in the two sites were chosen based on accessibility and extent of canopy closure. Areas in the sites with extensive canopy opening due to logging were avoided because of the potential influence of sidelight and the difficulty of obtaining accurate photosynthetic photon flux density (PPFD) measurements.

Gap creation and measurement followed Brokaw's (1982) procedure and definition (see also Agyeman *et al.* 1999b). The irradiances in the artificial forest canopy gaps were 1.4 (forest shade), 5, 8, 16, 27 and 60% of ambient full sun at Nkrabia Forest Reserve and 2 (forest shade), 5, 10, 13, 31 and 66% of ambient full sun at Tinte Bepo Forest Reserve. Photosynthetic photon flux density (PPFD) was measured in the centre of the gaps using integrating PAR sensors (DIDCOT instruments, DRP2). Red:far-red ratio was measured daily between 12 and 1 p.m. over a period of one week at the centre and edges of all gaps in March 1992.

Experimental Design

Eight forest tree species representing three Guild status of Pioneer (P), Non-Pioneer Light Demanders (NPLD) and Shade Bearers (SB) were selected. The Pioneer species was *Ceiba pentandra* (Linn.) Gaertn (Bombaceae) (Onyina), The NPLD species were *Albizia zygia* Macbride (Mimosaceae) (Okoro), *Entandrophragma angolense* (Welw.) C.DC. (Edinam), *Entandrophragma utile* (Dawe and Sprague) Sprague (Efoobodedwo), and *Mansonia altissima* A. Chev. (Sterculiaceae) (Opronon), while the SB species were *Chrysophyllum albidum* G. Don. (Sapotaceae) (Akasaa), *Celtis mildbraedii*, Engl., (Esa) and *Guarea cedrata* (A. Chev.) Pellegr. (Meliaceae) (Kwabohoro). *Albizia zygia* was used as a standard species in all experiments to enable comparisons to be made between tests. Seeds of this species are readily available and seedlings are adapted to a wide range of light conditions.

Seeds of the test species were germinated in a tray of river sand. Seedlings were transplanted at the two leaf stage, that is four weeks after germination, into polythene bags, 12 cm diameter and 30 cm long, filled with a soil mixture of 33% river sand and 67% loamy soil collected from a well drained Ochrosol (Asiamah 1987). The seedlings were placed under a patch of natural forest at the Mesewam Nursery. The transplanted seedlings were conditioned in 15% irradiance for a period of 2-6 weeks depending upon seedling growth rate. The polythene bags containing the seedlings were half buried in the ground in the forest gaps to prevent them from falling over, the soil drying out and to keep the soil temperature in the pots similar to that of the soil in the gap.

The experiments in the two field sites were run concurrently. Experiments were undertaken in the rainy season from April to July 1993. A complete randomized factorial design was used; the factors assessed were irradiance and species.

The following growth variables: seedling height, stem collar diameter, dry weight of leaves, roots and stems, leaf area, leaf production and mortality were measured at the beginning of the experiment. Seedlings were randomly selected at three weekly intervals for up to 4 months, for destructive sampling. Seedling height was measured using a meter rule and stem diameter using vernier calipers. Dry weight of leaves, roots and shoots was determined after oven drying at 80 °C for 48 hours. Leaf area was determined by a Panasonic digital scanner connected to an IBM (PS2) PC and software (M. D. Swaine) to calculate leaf areas.

Data Analyses

Leaf area ratio (LAR), a measure of efficiency with which a plant deploys its photosynthetic resources, is calculated as photosynthetic surface area per unit dry mass of a plant (Allaby, 1994). Specific leaf area (SLA), a measure of leaf

thickness, is calculated as leaf area per leaf dry mass. Unit leaf rate (ULR), which is the rate of photosynthesis per unit of total leaf area of a plant, can be calculated as growth rate per unit leaf area. These parameters were determined using the final seedling phytomass and leaf area (Beadle, 1993).

Relative growth rate (*RGR*) in collar diameter (*d*) or seedling height (*h*) was calculated as;

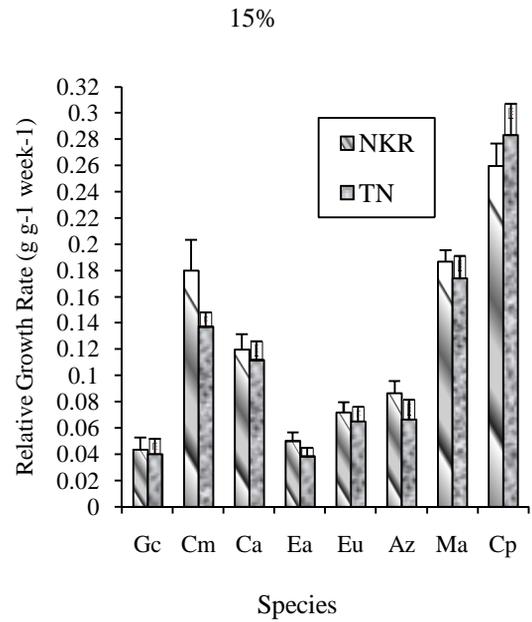
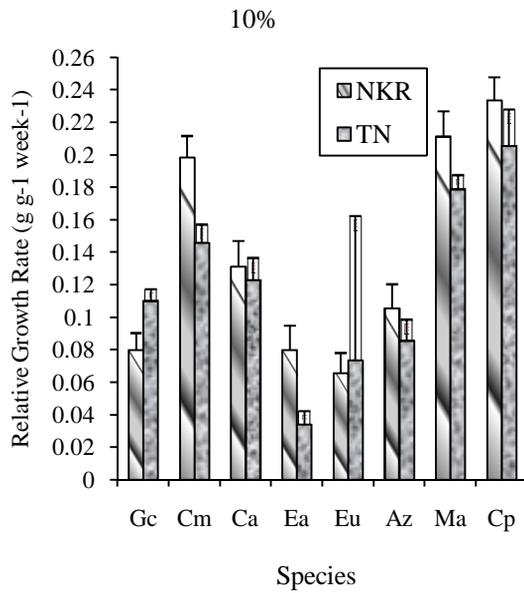
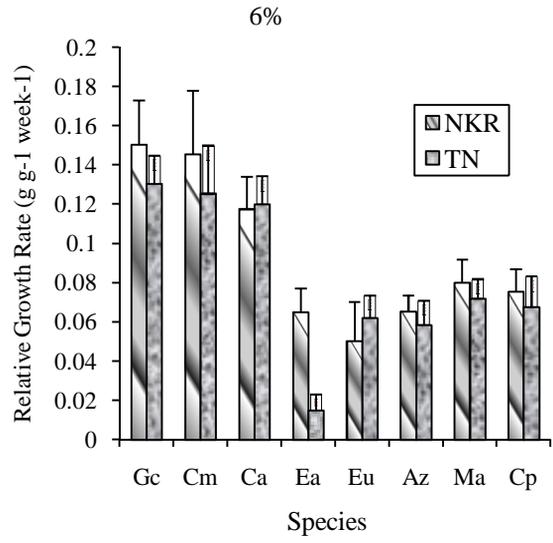
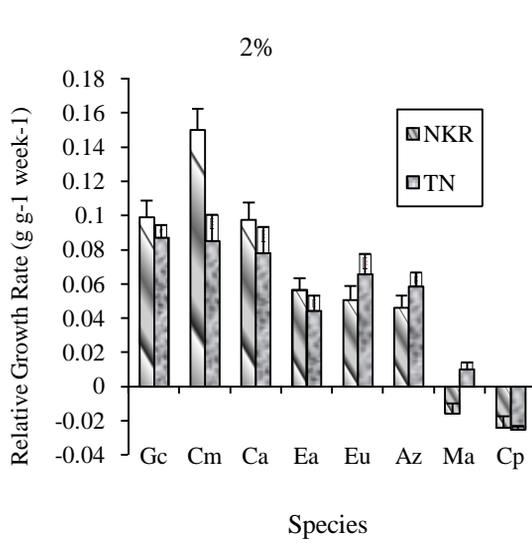
$$RGR = \frac{\ln(x_2) - \ln(x_1)}{t_2 - t_1} \quad (1)$$

where x_1 and x_2 are the initial and final *d* or *h*, and t_1 and t_2 are the beginning and end of period of interest, respectively.

RESULTS

Relative Growth Rate

Phytomass of the seedlings increased for all species growing in 6% to 65% irradiance at both sites. For example, the percentage increase in the phytomass *RGR* of *C. milbraedii*, a shade bearer was 28.6% and 15.4% for Nkrabea and Tinte Bepo, respectively. Similarly, for the same range of irradiance, *C. pentandra*, a pioneer species, recorded 200% and 114.3% increases in phytomass *RGR* at Nkrabea and Tinte Bepo respectively. In 2% irradiance, however, phytomass of *C. pentandra* (*sensu* Hawthorne 1989) decreased while that of all other species increased (Figure 1). Negative *RGR* in phytomass was exhibited by *M. altissima* and *C. pentandra* at Nkrabea with the values being $-0.02 \text{ g g}^{-1} \text{ week}^{-1}$ and $-0.03 \text{ g g}^{-1} \text{ week}^{-1}$, respectively. This suggests that the light compensation points of *C. pentandra* and *M. altissima* lie between 2-6% irradiance while that of all the species was below 2% irradiance.



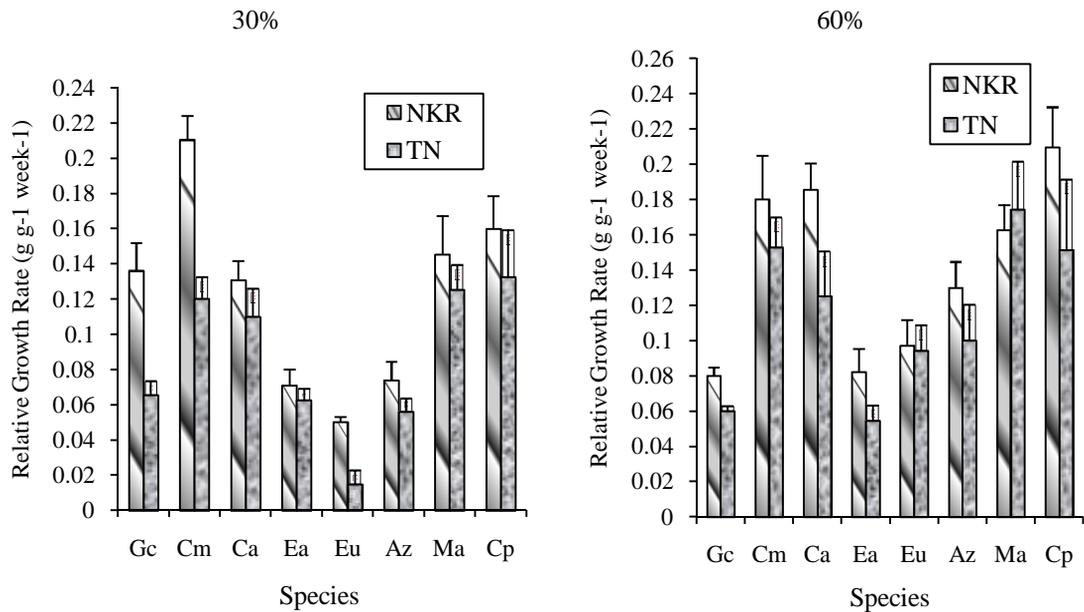


Figure 1: Relative growth rate ($\text{g g}^{-1} \text{ week}^{-1}$) of *Guarea cedrata* (Gc), *Celtis mildbraedii* (Cm), *Chrysophyllum albidum* (Ca), *Entandrophragma angolense* (Ea), *Entandrophragma utile* (Eu), *Albizia zygia* (Az), *Mansonia altissima* (Ma) and *Ceiba pentandra* (Cp) in 2, 6, 10, 15, 30, 60% irradiance. Relative growth rates are presented for Nkrabia and Tinte Bepo. Bars show \pm standard error.

Response surfaces to describe the phytomass accumulation in different irradiances over time of three contrasting species *C. pentandra*, *A. zygia* and *G. cedrata*, grown at Tinte Bepo are shown in Figure 2. *Ceiba pentandra* (pioneer) had a rapid increase in phytomass over time with a faster growth rate at higher irradiances (Figure 2). *Mansonia altissima* had a similar phytomass growth response curve to that of *C. pentandra*. Phytomass accumulation in *A. zygia* (non-pioneer light demander (*sensu* Hawthorne 1989) was slower than *C. pentandra*, with a peak at medium irradiance (Figure 2). Other species showing similar responses are *C. albidum*, *E. angolense* and *E. utile*. *Guarea cedrata* (non-pioneer shade bearer) accumulated phytomass at a slower rate

than the other species (Figure 2). This pattern was also observed in *C. mildbraedii*.

The RGR of three species representing the three major species groups, namely pioneer, light demander and shade bearers, in different environments were compared using Homogeneity of Slopes Test and Analysis of Covariance (Table 1). Shade treatments produced significant differences in species growth at Nkrabia ($P < 0.046$, $df=5,17$) and Tinte Bepo ($P < 0.046$, $df=5,17$) (Table 1). The differences in RGR's between species tested at the two forest sites showed slight differences (Table 2). This is probably because of the short period of time (16 weeks) over which the experiments were run. The RGR was greater at

Nkrabia compared to Tinte Bepo (Table 2).

Relative Height and Diameter Growth

Changes in the Relative Growth Rate (RGR) in height for the seedlings with irradiance (x) followed two different patterns for the species. The Non-Pioneer Light Demanders (NPLD) and Shade bearer (SB) species had a similar pattern, whereas the Pioneer species exhibited a different pattern. For the NPLD and SB species, the RGR in height increased with increasing irradiance up to a peak and thereafter declined with increasing irradiance. However, the decline was steeper with SB species than with NPLD species (Figures 3 and 4). The relationship could be defined by the equation;

$$RGR = \frac{ax^b \times cx^{-d}}{ax^b + cx^{-d}} \quad (2)$$

where a is a measure of the initial magnitude of RGR, b is rate of change of RGR with irradiance, c is a measure of peak value of RGR and d is rate of decline of RGR after the peak value. The parameter values for the height growth models are presented in Table 3. For all the species, the value of the parameter a was greater at the Nkrabea site than at the Tinte Bepo site, signifying better growth performance at low irradiance at the Nkrabea site. With the exception of *Albizia zygia*, the value of parameter b was higher with the Tinte Bepo site than the Nkrabea site for the NPLD species. This trend indicates better growth response to irradiance in the Tinte Bepo site than the Nkrabea site. However, the reverse holds true for the SB species. The Nkrabea site gave higher peak values (parameter c) than the Tinte Bepo site. However, no clear trend was exhibited by the NPLD species. The rate of decline in the RGR after the peak value was greater for the Nkrabea site than the Tinte Bepo site for the SB species, the reverse of which holds true for the NPLD species.

For the Pioneer (P) species the RGR continued to increase with increasing irradiance but the rate of increase declined at higher irradiance and gradually approached an asymptote value (e) (Figure 5). The relationship could be represented as;

$$RGR = \frac{ax^b \times e}{ax^b + e} \quad (3)$$

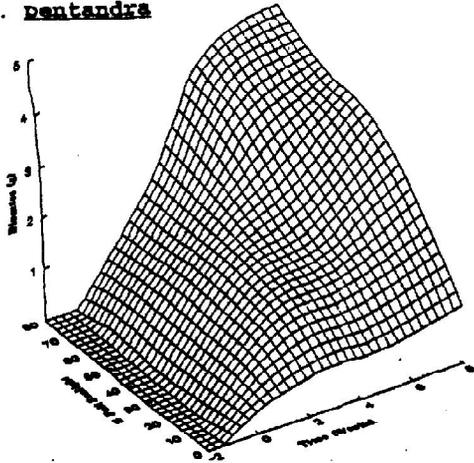
The initial magnitude of the RGR, represented by the parameter a , for the *C. pentandra* at the Nkrabea site was greater than that of Tinte Bepo, indicated by the coefficient value of 0.1222 and 0.0751 cm cm⁻¹ week⁻¹, respectively (Table 3).

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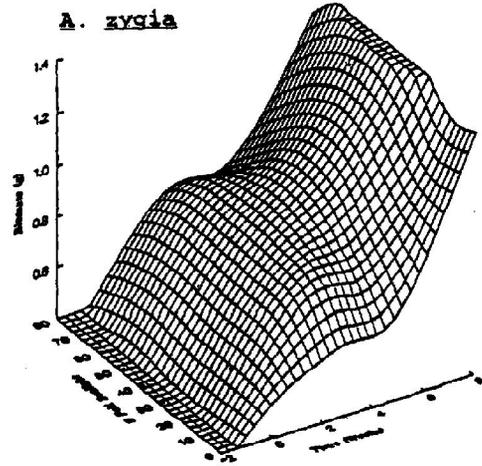
However, the rate of change in RGR in response to increasing irradiance was greater with the Tinte Bepo site than Nkrabea site, represented by the exponent value (parameter b) of 0.9127 and 0.6741, respectively. The asymptotic value (parameter e) was 2.8670 and 2.3238 cm cm⁻¹ week⁻¹ for Tinte Bepo and Nkrabea sites, respectively. The SAS System for Windows 9.0 (SAS Institute Inc., 2002) was utilised in fitting non-linear regression model (PROC NLIN) for Equations 2 and 3.

Most of the species had negative stem diameter growth in 2% irradiance in at least one field site (Table 4). Relative stem diameter growth in 65% irradiance was almost five times higher than that in 2% irradiance. Diameter growth rates of all the species, except *C. mildbraedii* and *E. utile* (non-pioneers) were higher at Nkrabia than Tinte Bepo in low and high irradiance.

C. pentandra



A. zygia



G. cedrata

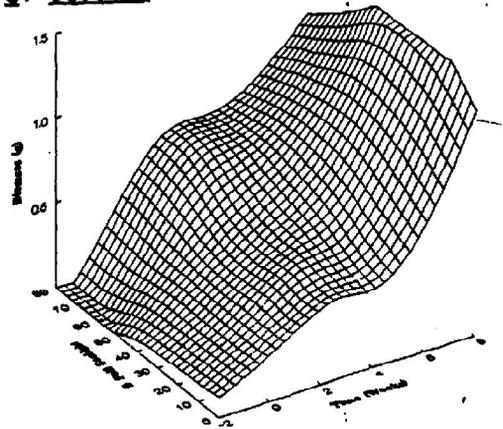


Figure 2: Phytomass growth response surfaces showing increase over time in relation to irradiance in forest gaps for *C. pentandra*, *A. zygia* and *G. cedrata*.

Table 1: Comparison of relative growth rate of three species: *C. pentandra*, *A. zygia* and *G. cedrata* using Analysis of Covariance (ANCOVA). F statistic and levels of significance of growth in individual sites and all the sites combined are presented. The analysis used results from four different readings (3 weekly intervals) of relative growth rate.

Variable	Df	<i>C. pentandra</i> (Pioneer)		<i>A. zygia</i> (Light Demander)		<i>G. cedrata</i> (Shade Bearer)	
		F	P	F	P	F	P
All Sites							
Site	1,45	4.98	0.031*	5.21	0.027*	9.82	0.003*
Shade	1,45	10.02	0.003*	4.35	0.043*	4.79	0.034*
Time	1,45	52.22	<0.001*	143.94	<0.001*	153.58	<0.001*
Site x Shade	1,44	0.98	0.329	0.01	0.931	0.01	0.937
Shade x Time	5,36	2.28	0.061	0.33	0.890	0.02	0.959
Site x Time	1,44	2.08	0.157	0.11	0.919	1.03	0.317
Within Sites:							
(Tinte Bepo)							
Shade	5,17	6.78	0.001*	2.88	0.046*	5.26	0.004*
Time	1,17	72.20	<0.001*	116.85	<0.001*	146.40	<0.001*
Shade x Time	5,12	0.92	0.499	1.65	0.221	2.22	0.120
Within Sites:							
(Nkrabia)							
Shade	5,17	7.03	0.001*	4.77	0.007*	2.85	0.048*
Time	1,17	72.23	<0.001*	119.39	<0.001*	129.45	<0.001*
Shade x Time	5,12	0.43	0.534	0.75	0.601	1.07	0.424

*: Significant at $P < 0.05$

Table 2: Two-way Analysis of Variance (ANOVA) table showing degrees of freedom (df, numerator and denominator), F statistic and significance levels (P) for Height (Ht), stem diameter (SD), relative growth rate (RGR), leaf mortality (LM), leaf area ratio (LAR), specific leaf area (SLA) and unit leaf rate (ULR) of eight species tested in the two field sites. The levels of significance of the above variables between two sites (Nkrabia and Tinte Bepo) using T-Test (*) is presented.

Variables	Test Statistic	Ht	SD	RGR	RSR	LAR	SLA	ULR
	Df	7,336	7,336	7,336	7,336	7,288	7,288	7,288
Species	F	14.2	2.4	12.5	3.1	39.1	18.6	0.7
	P	<0.001	0.025	<0.001	0.004	<0.001	<0.001	0.699
	Df	5,336	5,336	5,336	5,336	5,288	5,288	5,288
Shade	F	4.6	2.9	3.1	1.1	15.7	20.1	1.3
	P	<0.001	0.015	0.010	0.366	<0.001	<0.001	0.259
	Df	35,336	35,336	35,336	35,336	35,288	35,288	35,288
Species x Shade	F	3.2	1.7	1.3	0.9	3.0	6.2	1.0
	P	<0.001	0.010	0.106	0.595	<0.001	<0.001	0.518
	Df	382	382	382	382	334	334	334
Site*	T	-3.2	-2.4	-5.1	-3.3	-2.0	-2.1	-1.1
	P	0.002	0.013	<0.001	0.001	0.047	0.041	0.232

Table 3: Parameters for the height growth models

Site	Guild	Species	Parameters				<i>ef</i>	<i>rmse</i>
			<i>a</i>	<i>b</i>	<i>c/e</i>	<i>d</i>		
Nkrabea	NPLD	Az	0.0686	1.6219	0.8163	-0.4668	0.9600	0.0128
Tinte Bepo	NPLD	Az	0.0316	0.9346	10.0000	-0.9989	0.9665	0.0137
Nkrabea	NPLD	Ea	0.2457	0.2938	3.1275	-0.4654	0.9870	0.0126
Tinte Bepo	NPLD	Ea	0.0762	0.5523	7.3977	-0.8127	0.9275	0.0120
Nkrabea	NPLD	Eu	0.2394	0.1668	10.0000	-0.6068	0.9975	0.0047
Tinte Bepo	NPLD	Eu	0.0857	0.7251	0.3990	-0.2748	0.9976	0.0032
Nkrabea	NPLD	Ma	0.0197	2.1838	1.2313	-0.7294	0.9962	0.0055
Tinte Bepo	NPLD	Ma	0.0168	2.2151	1.0153	-0.7417	0.9833	0.0114
Nkrabea	SB	Ca	0.0472	1.2894	3.0069	-0.9458	0.9997	0.0014
Tinte Bepo	SB	Ca	0.0443	0.7762	0.9978	-0.6896	0.9956	0.0069
Nkrabea	SB	Cm	0.3617	0.8425	1.0699	-0.3353	0.9974	0.0076
Tinte Bepo	SB	Cm	0.1564	0.9088	0.6588	-0.3273	0.9484	0.0077
Nkrabea	SB	Gc	0.1590	0.4022	9.4490	-1.0420	0.9821	0.0082
Tinte Bepo	SB	Gc	0.0277	2.4023	1.9127	-0.8094	0.9501	0.0242

Nkrabea	P	Cp	0.1222	0.6741	2.3238		0.9950	0.0236
Tinte Bepo	P	Cp	0.0751	0.9127	2.8670		0.9903	0.0503

NPLD, Non-Pioneer Light Demander species; SB, Shade Bearer species; P, Pioneer species; Az, *A. zygia*; Ea, *E. angolense*; Eu, *E. utile*; Ma, *M. altissima*; Ca, *C. albidum*; Cm, *C. mildbraedii*; Gc, *G. cedrata*; Cp, *C. pentandra*

Table 4: Stem diameter growth ($\text{mm mm}^{-1} \text{ week}^{-1}$) of *G. cedrata* (Gc), *C. mildbreadii* (Cm), *C. albidum* (Ca), *E. angolense* (Ea), *E. utile* (Eu), *A. zygia* (Az), *M. altissima* (Ma) and *C. pentandra* (Cp) in 2%, 6%, 10%, 15%, 30%, 60% irradiance at Tinte Bepo (TIN) and Nkrabia (NKR) Forest Reserves. Standard errors (SE) of the mean are presented.

SPECIES	SITE	IRRADIANCE (% Full Sun)											
		2	SE	6	SE	10	SE	15	SE	30	SE	60	SE
Gc	NKR	0.04	0.005	0.05	0.003	0.13	0.008	0.1	0.005	0.06	0.006	0.05	0.002
	TIN	0.05	0.007	0.08	0.007	0.07	0.004	0.06	0.007	0.05	0.002	0.05	0.004
Cm	NKR	0.01	0.003	0.04	0.005	0.13	0.007	0.14	0.006	0.1	0.005	0.09	0.003
	TIN	0.05	0.002	0.09	0.007	0.13	0.003	0.09	0.002	0.04	0.003	0.04	0.008
Ca	NKR	0.01	0.004	0.02	0.003	0.04	0.006	0.05	0.004	0.06	0.007	0.06	0.006
	TIN	0.04	0.008	0.02	0.004	0.05	0.004	0.08	0.008	0.07	0.006	0.1	0.001
Ea	NKR	0.02	0.005	0.06	0.008	0.05	0.007	0.07	0.003	0.12	0.009	0.1	0.003
	TIN	0.05	0.007	0.05	0.002	0.05	0.006	0.08	0.007	0.1	0.004	0.13	0.005
Eu	NKR	0.01	0.003	0.06	0.006	0.13	0.003	0.13	0.006	0.18	0.006	0.11	0.009
	TIN	0.05	0.004	0.07	0.008	0.09	0.004	0.15	0.003	0.08	0.007	0.05	0.004
Az	NKR	0.02	0.007	0.05	0.006	0.11	0.002	0.14	0.004	0.16	0.005	0.15	0.002
	TIN	0.05	0.005	0.06	0.004	0.09	0.007	0.1	0.006	0.14	0.004	0.2	0.006
Ma	NKR	0.08	0.004	0.04	0.007	0.13	0.004	0.15	0.007	0.25	0.002	0.24	0.005
	TIN	0.01	0.002	0.05	0.006	0.09	0.006	0.1	0.001	0.14	0.008	0.2	0.003
Cp	NKR	0.01	0.005	0.04	0.003	0.09	0.008	0.18	0.005	0.3	0.006	0.24	0.004
	TIN	0.01	0.003	0.02	0.004	0.06	0.004	0.19	0.009	0.24	0.003	0.33	0.008

Leaf Area Ratio, Specific Leaf Area and Unit Leaf Rate

At the Nkrabea site, with the exception of *E. utile* and *C. mildbraedii* that had peak Leaf Area Ratio (LAR) at 10% irradiance, the rest of the species had the peak LAR at 15% irradiance (Table 5). However, at Tinte Bepo the pattern was different. *Albizia zygia*, *E. utile*, *C. albidum* and *M. altissima* had the peak at 15% irradiance, *C. pentandra* and *C. mildbraedii* had it at 10% irradiance while *E. angolense* and *G. cedrata* had it at 6% and 60%, respectively. In general the highest LAR peak value was exhibited by the P species, followed in a decreasing order by the NPLD and SB species. However the peak value of *C. mildbraedii*, a SB species was similar to those of the NPLD species. The highest peak LAR was given by *C. pentandra*, with values of 12.41 and 15.38 cm²g⁻¹ and the lowest given by *G. cedrata*, with values of 4.51 and 3.72 cm²g⁻¹ for Nkrabea and Tinte Bepo sites, respectively.

In general the response of Specific Leaf Area (SLA) to changes in irradiance followed a bell-shape pattern. The SLA increased with increasing irradiance up to a peak and thereafter declined (Table 6). At the Nkrabea site, three species namely *E. utile*, *C. mildbraedii*, and *G. cedrata* attained their peaks at 10% irradiance, four species namely *A. zygia*, *E. angolense*, *C. pentandra* and *C. albidum* attained their peaks at 15% irradiance, while only *M. altissima* attained its peak at 30% irradiance. At the Tinte Bepo site, only *E. angolense* attained its peak at 6% irradiance, *A. zygia*, *C. albidum* and *C. mildbraedii* attained their peaks at 10% irradiance, whereas *E. utile*, *M. altissima*, *C. pentandra* and *G. cedrata* attained their peaks at 15% irradiance. The highest peak values at both sites were attained by the P species followed in decreasing order by NPLD and SB species. Although *C. mildbraedii* is an SB species, it behaved like an NPLD species.

The highest peak value was given by *C. pentandra*, with peak values of 17.52 and 18.84 cm² g⁻¹ for Nkrabea and Tinte Bepo sites, respectively. The lowest peak value at Nkrabea site was given by *C. albidum* with the value of 6.81 cm² g⁻¹ and at Tinte Bepo by *G. cedrata* with the value of 4.65 cm² g⁻¹. The species exhibited two different patterns with regard to the response of Unit Leaf Rates (ULR) to irradiance.

The ULR of *E. angolense*, *A. zygia*, *E. utile* and *G. cedrata* increased with increasing irradiance up to a peak and thereafter declined with further increase in irradiance. The ULR of four other species, namely *C. pentandra*, *M. altissima*, *C. mildbraedii* and *C. albidum*, continued to increase with increasing irradiance but the rate of increase declined at higher irradiance and gradually approached an asymptotic value. The species that obtained the highest peak value at the Nkrabea site was *C. pentandra*, with a value of 10.92 g cm⁻² week⁻¹ while the lowest peak value was obtained by *E. utile*, with a value of 4.82 g cm⁻² week⁻¹. At the Tinte Bepo site, the highest and the lowest ULR peak values of 10.37 and 3.67 g cm⁻² week⁻¹ were obtained by *C. pentandra* and *E. angolense*, respectively (Table 7).

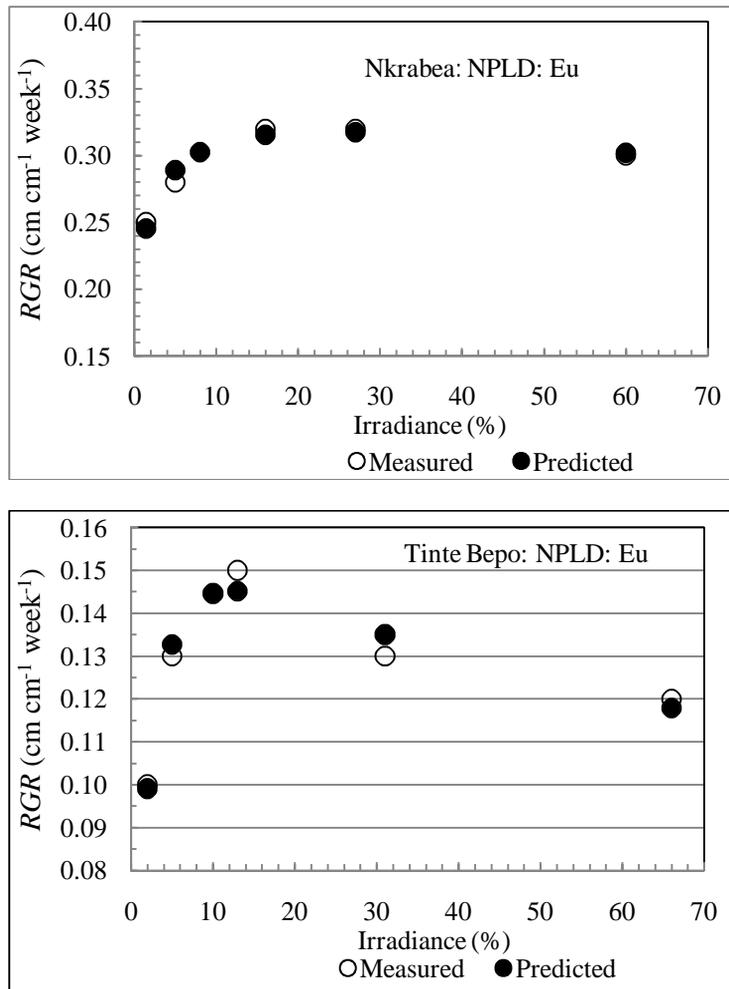


Figure 3: Examples of relative growth rate, RGR, as a function of percentage irradiance for NPLD species. NPLD, Non-Pioneer Light Demander; Eu, *Entandrophragma utile*

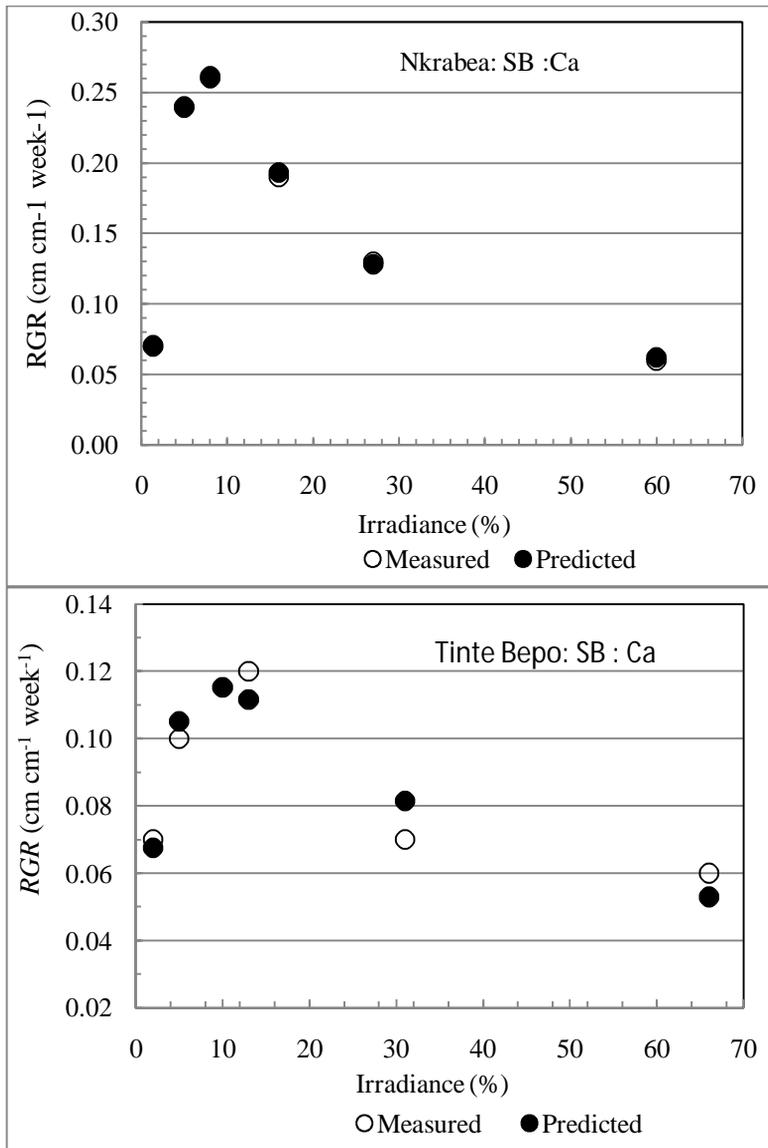


Figure 4: Examples of relative growth rate, RGR, as a function of percentage irradiance for SB species SB, Shade Bearer; Ca, *Chrysophyllum albidum*.

Table 5: Leaf Area Ratio ($\text{cm}^2 \text{g}^{-1}$) of *G. cedrata* (Gc), *C. mildbreadii* (Cm), *C. albidum* (Ca), *E. angolense* (Ea), *E. utile* (Eu), *A. zygia* (Az), *M. altissima* (Ma) and *C. pentandra* (Cp) in 2%, 6%, 10%, 15%, 30%, 60% irradiance at Tinte Bepo (TIN) and Nkrabia (NKR) Forest Reserves. Standard errors (SE) of the mean are presented.

SPECIES	SITE	IRRADIANCE (% Full Sun)											
		2	SE	6	SE	10	SE	15	SE	30	SE	60	SE
Gc	NKR	2.34	0.06	3.15	0.03	4.38	0.07	4.51	0.05	2.38	0.8	2.92	0.4
	TIN	2.19	0.09	3.37	0.07	3.19	0.05	3.27	0.03	3.51	0.6	3.72	0.8
Cm	NKR	4.64	0.06	3.46	0.05	6.28	0.04	5.37	0.07	4.73	0.4	3.51	0.7
	TIN	4.28	0.07	4.38	0.06	7.46	0.08	6.52	0.06	4.52	0.7	4.68	0.4
Ca	NKR	2.37	0.03	2.49	0.09	3.72	0.03	4.83	0.09	3.18	0.5	4.38	0.5
	TIN	2.34	0.04	3.43	0.03	4.46	0.04	6.45	0.03	4.48	0.8	3.19	0.9
Ea	NKR	4.62	0.08	5.72	0.04	7.54	0.06	9.18	1.4	7.92	0.9	7.34	0.7
	TIN	4.53	0.05	6.64	0.05	4.69	0.02	6.48	1.1	6.43	0.4	3.64	0.6
Eu	NKR	3.45	0.06	4.27	0.08	5.67	0.08	4.67	0.06	5.27	0.8	4.51	0.3
	TIN	4.18	0.09	7.18	0.06	8.29	0.09	9.53	0.07	6.58	0.4	6.38	0.9
Az	NKR	3.46	0.04	3.41	0.03	4.62	0.04	7.16	1	5.27	0.9	4.59	0.5
	TIN	2.64	0.02	3.72	0.08	5.83	0.07	7.32	0.06	5.16	0.7	3.49	0.7
Ma	NKR	3.28	0.07	3.46	0.02	7.15	0.03	8.39	0.09	7.64	0.6	7.24	0.9
	TIN	4.67	0.05	5.61	0.09	8.43	0.08	9.73	1.3	8.29	0.8	5.83	0.5
Cp	NKR	2.39	0.04	4.82	0.07	9.72	1.2	12.41	1.8	11.67	1.9	9.37	0.8
	TIN	4.52	0.08	9.46	1.1	15.38	1.5	13.82	0.08	9.75	1.5	7.16	1.2

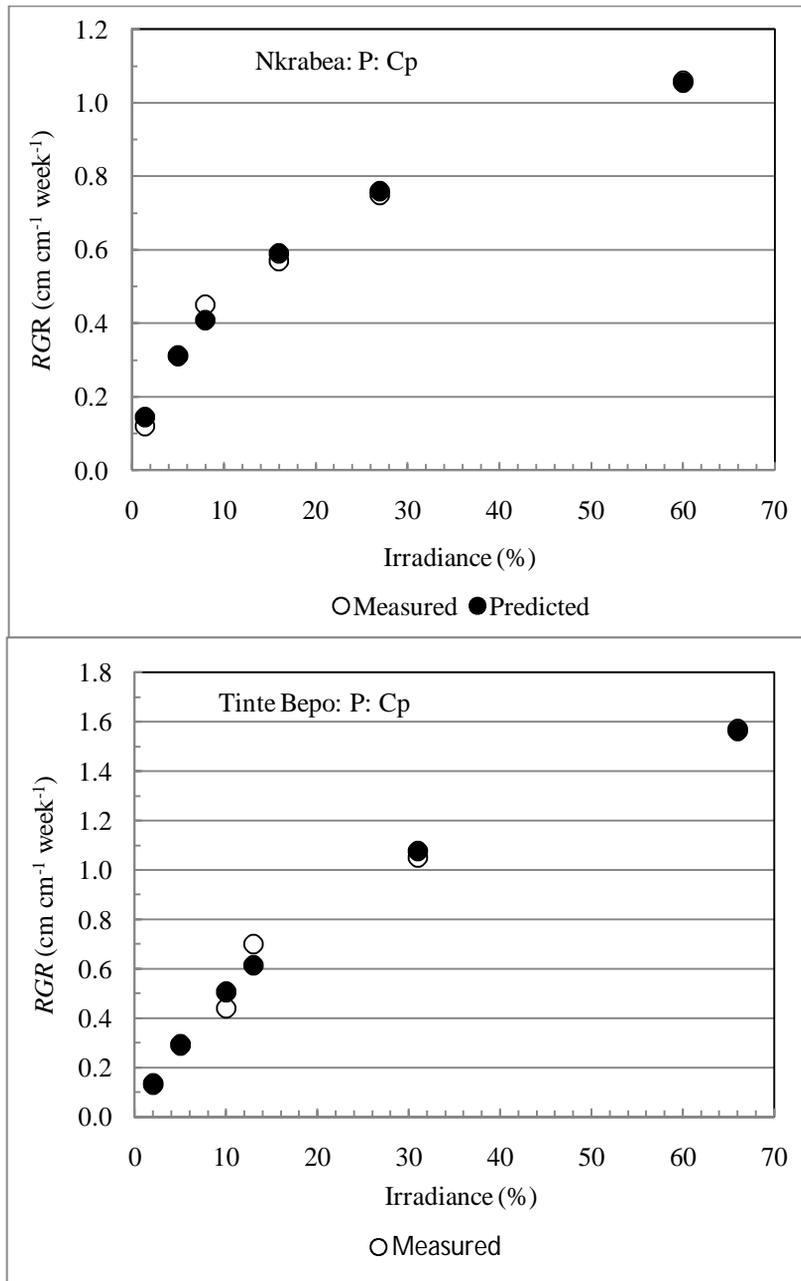


Figure 5: Relative growth rate, RGR, as a function of percentage irradiance for Pioneer species. Cp, *Ceiba pentandra*

Table 6: Specific Leaf Area ($\text{cm}^2 \text{g}^{-1}$) of *G. cedrata* (Gc), *C. mildbreadii* (Cm), *C. albidum* (Ca), *E. angolense* (Ea), *E. utile* (Eu), *A. zygia* (Az), *M. altissima* (Ma) and *C. pentandra* (Cp) in 2%, 6%, 10%, 15%, 30%, 60% irradiance at Tinte Bepo (TIN) and Nkrabia (NKR) Forest Reserves. Standard Errors (SE) of the mean are presented

SPECIES	SITE	IRRADIANCE (% Full Sun)											
		2	SE	6	SE	10	SE	15	SE	30	SE	60	SE
Gc	NKR	3.85	0.5	6.48	0.9	8.27	1.5	5.94	0.7	3.64	0.8	3.82	0.3
	TIN	3.16	0.7	4.12	0.4	4.29	0.7	4.65	0.6	3.19	0.6	3.46	0.8
Cm	NKR	2.54	0.9	4.56	0.6	8.62	0.9	6.85	0.9	4.28	0.3	4.61	0.7
	TIN	5.92	0.6	5.87	0.7	11.57	1.6	8.46	1.1	6.59	0.9	4.92	0.9
Ca	NKR	2.64	0.4	3.65	0.6	4.34	0.8	6.81	1.3	4.92	0.7	5.66	0.4
	TIN	2.18	0.3	4.53	0.9	5.61	0.9	4.37	0.9	5.48	0.4	3.72	0.3
Ea	NKR	5.38	0.8	6.18	0.3	11.68	1.6	13.61	1.9	10.31	0.8	9.47	0.9
	TIN	6.49	0.4	8.95	0.4	8.18	1.2	8.18	0.8	8.59	1	7.64	1.1
Eu	NKR	5.34	0.9	6.52	0.8	7.95	1.4	7.38	1.4	6.34	0.7	5.82	0.8
	TIN	4.62	0.7	8.46	0.6	9.64	0.8	12.39	1.2	8.87	0.5	8.38	0.6
Az	NKR	4.18	0.3	5.67	0.9	7.28	0.7	13.95	1.8	8.29	1.3	6.74	0.5
	TIN	3.28	0.8	8.65	0.7	9.46	0.9	8.69	1.4	8.34	0.7	6.59	0.3
Ma	NKR	3.76	0.4	7.28	0.5	1.68	1.4	10.49	1.6	10.83	1.2	9.48	1.2
	TIN	6.65	0.9	8.54	1.6	1.92	0.7	11.86	1.1	11.37	0.9	8.17	0.8
Cp	NKR	6.48	0.6	7.61	1.4	12.49	1.8	17.52	2.8	14.83	1.4	12.68	1.6
	TIN	5.24	0.7	12.64	1.1	17.65	1.3	18.84	1.7	15.17	1.8	12.43	1.1

Table 7: Unit Leaf Rate ($\text{g m}^{-2} \text{ week}^{-1}$) of *Guarea cedrata* (Gc), *Celtis mildbreadii* (Cm), *Chrysophyllum albidum* (Ca), *Entandrophragma angolense* (Ea), *Entandrophragma utile* (Eu), *Albizia zygia* (Az), *Mansonia. altissima* (Ma) and *Ceiba pentandra* (Cp) in 2%, 5%, 10%, 15%, 30%, 60% irradiance at Tinte Bepo (TIN) and Nkrabia (NKR) Forest Reserves. Standard Errors (SE) of the mean are presented

SPECIES	SITE	IRRADIANCE (% Full Sun)											
		2	SE	6	SE	10	SE	15	SE	30	SE	60	SE
Gc	NKR	6.43	0.8	8.54	0.7	8.73	1.3	8.16	0.7	7.51	0.8	6.72	1.3
	TIN	5.64	0.5	4.38	0.3	4.61	0.5	4.92	0.9	4.62	0.7	3.43	0.5
Cm	NKR	3.28	0.7	4.91	0.4	6.59	0.8	6.73	0.5	5.84	0.6	6.52	0.7
	TIN	2.64	0.3	4.65	0.2	4.37	0.6	4.35	0.8	5.38	0.7	8.73	0.6
Ca	NKR	6.48	1.2	8.42	0.8	5.18	0.4	6.48	0.4	6.72	0.9	6.82	0.9
	TIN	4.37	0.8	4.19	0.6	5.49	1.2	6.17	0.5	6.52	0.2	8.34	1.5
Ea	NKR	4.91	0.5	4.76	0.7	3.43	0.8	4.82	0.9	4.37	0.4	3.57	0.6
	TIN	3.67	0.4	2.37	0.5	2.81	0.3	3.64	0.7	2.94	0.9	1.39	0.7
Eu	NKR	4.82	0.9	4.53	0.4	3.47	0.7	4.72	0.3	4.38	0.7	3.62	0.3
	TIN	3.91	0.5	2.48	0.2	2.64	0.4	4.52	0.5	4.64	0.8	2.48	0.8
Az	NKR	3.42	0.3	3.63	0.6	4.18	0.6	4.16	0.8	5.71	0.6	3.45	0.4
	TIN	1.61	0.4	3.17	0.4	4.57	0.2	3.57	0.9	4.62	0.4	3.28	0.9
Ma	NKR	-1.53	0.5	4.37	0.8	8.67	0.8	8.29	0.4	7.93	1.5	10.38	0.6
	TIN	1.64	0.2	4.79	0.2	6.79	0.6	6.91	0.6	7.24	0.7	8.19	1.3
Cp	NKR	-2.83	0.6	2.54	0.4	7.81	0.7	8.52	0.7	9.43	0.6	10.92	0.8
	TIN	-2.37	0.2	3.72	0.4	5.62	0.3	6.72	0.6	7.31	0.9	10.37	1.7

Table 8: Percentage seedling mortality after 16 weeks in the forest shade and canopy gaps with difference irradiances at Tinte Bepo Forest Reserve

Shade (% FS)	% Mortality							
	Gc	Cm	Ca	Ea	Eu	Az	Ma	Cp
2	4.2	8.3	16.7	16.7	12.5	20.8	25.0	42.0
6	0	4.2	10.4	8.3	4.2	12.5	20.8	30.0
10	8.3	4.2	12.5	12.5	4.2	8.3	12.5	25.0
15	8.3	8.3	12.5	8.3	4.2	8.3	12.5	12.5
30	12.5	12.5	8.3	8.3	4.2	8.3	8.3	4.2
65	8.3	8.3	8.3	8.3	8.3	4.2	8.3	8.3

The legend is the same as in Table 7

Seedling Mortality

With the exception of *G. cedrata* and *C. mildbraedii*, highest mortality occurred at low irradiance at the Tinte Bepo site (Table 8). There was a tendency for decrease in mortality with increasing irradiance. The species with the highest seedling mortality in shade after 16 weeks were *C. pentandra* and *M. altissima*. There was 42% and 25% mortality at 2% irradiance and 30% and 21% mortality at 6% irradiance for *C. pentandra* and *M. altissima*, respectively. However, seedling mortality was similar for all species at 65% irradiance.

DISCUSSION

Tree Seedling Growth Responses under Different Irradiances

Relative Growth Rate, Height and Diameter Growth

Relative growth rate of pioneers was lower in forest understorey shade (2% irradiance) but higher in irradiances greater than 5% compared to non-pioneers. This reflects the higher quantum efficiency of pioneers. The differences in RGR of pioneers and non-pioneers may be a result of evolution in different habitats (Poorter, 1989). A high relative growth rate may enable plants to rapidly occupy a large space, which is an advantage in competitive situations (Lambers and Poorter, 1992), especially in highly disturbed or logged forest.

The higher RGR of pioneers in low irradiance (5-15%) compared to non-pioneers does not mean that pioneers are better adapted than non-pioneers to growing in low irradiance environments. According to Van Andel and Biere (1989), intra- and interspecific differences in RGR are not an indication of adaptation to a certain type of

habitat. This is supported by the fact that, despite having a higher growth rate, pioneers have a higher mortality compared to non-pioneers at low irradiances, suggesting that non-pioneers are better adapted to low irradiance. Therefore, a high potential growth rate does not necessarily confer an ecological advantage, because in a low resource environment, where a high growth rate cannot be realized, a high RGR is a selectively neutral trait (Lambers and Poorter, 1992).

Three reasons may account for the high relative growth rate of pioneers compared to non-pioneers in low irradiance. The first is that under unfavourable conditions a species with a low relative growth rate functions closer to its optimum growth rate than one with a high relative growth rate (Grime *et al.*, 1986). Secondly, non-pioneers make lower demands on available resources and are, therefore, less likely to exhaust these resources in unfavourable conditions. At such low irradiance, shade leaves of non-pioneers have slow respiration and light-saturated photosynthetic rates (Oberbauer and Strain, 1984). Thus, the little physiological activity means smaller maintenance costs, and in this way, carbon losses in the understorey are reduced (Lehto and Grace, 1994). Thirdly, non-pioneers are better able to make and store reserves of photosynthates for later growth (Lambers and Poorter, 1992).

Pioneers had greater height compared to non-pioneers in forest understorey shade and at low irradiances, probably due to etiolation. Jarvis (1964) and Fetcher *et al.*, (1983) reported that etiolation was a general response of pioneers to shade. This may be linked with the competitive advantage of having a greater height in shade (Schulze, 1982). The more stressful conditions (leaf damage and moisture stress) in the field may have suppressed height growth. Response of height growth to irradiance depended on the guild status of the species. Height growth was enhanced at high irradiance for pioneer species but reduced

at very high irradiance. For the Non-Pioneer Light Demanders and Shade Bearer species very high irradiance hampered height growth. The negative impact was more pronounced with the SB species than the NPLD species. Height growth best describes site productive capacity. However, height growth has been found to be erratic especially in small gaps (Kennedy and Swaine, 1992).

Leaf Area Ratio, Specific Leaf Area and Unit Leaf Rate

Pioneers had a higher LAR and SLA compared to non-pioneers in low and high irradiances. The higher LAR of pioneers in low irradiance is an attempt to improve efficiency in sub-optimal conditions by increasing photosynthetic capacity and reducing respiratory burden (Lambers and Poorter, 1992). The higher SLA of pioneers compared to non-pioneers in low irradiance indicates that the leaves of pioneers are thinner. A high SLA is beneficial to pioneers in low irradiance as lower amounts of energy are required to produce thin leaves (Schulze, 1982; Poorter, 1989). The high RGR of pioneers in moderate irradiance (5-16%) may be a result of their high LAR and SLA (Dijkstra, 1989; Poorter, 1989). SLA is considered to be a key factor in explaining growth differences between species (Poorter and Van der Werf, 1998), especially at low irradiances (Poorter, 1999, 2001).

Plants growing in high irradiance develop characteristics to reduce transpiration. The high transpiration, stomatal conductance and leaf temperatures of plants growing in large canopy gaps may be associated with the high irradiance. The low SLA of both pioneers and non-pioneers in high irradiance may be an adaptation to lower transpiration in larger gaps. Lambers and Poorter, (1992) observed that a low SLA is associated with a decrease in transpiration rates.

Unit leaf rate of pioneers was higher than non-pioneers in high irradiance. The high ULR of pioneers compared to non-pioneers in high irradiance may be associated with their higher relative growth rate. Pons (1977) also observed a lower ULR in *Geum urbanum*, a non-pioneer, compared to *Circum palustre*, a pioneer, in high irradiance. Konings (1989) observed that under limiting light and nutrient conditions the differences in RGR between species is mainly governed by ULR. Therefore, non-pioneers are inherently slow growers in low irradiance compared to pioneers because of their higher ULR.

Influence of Site Differences on Plant Growth

Plant growth at Nkrabia was greater than at Tinte Bepo, which is most likely due to the lower moisture stress at Nkrabia. Moisture stress may account for the lower LAR and SLA, greater leaf turnover and the high number of small leaves of plants growing at Tinte Bepo compared to Nkrabia. Hall and Swaine (1976) also reported a decline in the frequency of species with large sized leaves, especially macro and megaphyll leaves, in the dry compared to the wetter forest types in Ghana. This may be due to the tendency of plants to reduce the rate of transpiration and leaf temperature in drier habitats by maintaining smaller leaf areas (Devlin and Witham, 1983 and Von Willert *et al.*, 1992). Leaf expansion is generally influenced by the extent of water uptake (Acevedo *et al.*, 1971) and, therefore, the lower LAR's of plants at Tinte Bepo compared to Nkrabia may be due to the lower soil moisture availability.

The higher photosynthetic photon flux density in gaps at Tinte Bepo, with the same percentage irradiance as in Nkrabia, suggests that growth rate at Tinte Bepo should be higher than at Nkrabia. Fetcher *et al.* (1983), considered PPFD to be the

most important microclimatic variable influencing growth. However, growth rates of almost all the species were higher at Nkrabia than Tinte Bepo. Therefore, rainfall differences between the two forest types may be exerting greater influence on plant growth than differences in PPFD, R:FR and air temperature. Differences in plant growth between the two forest types lends support to the hypothesis that rainfall distribution may be a major influence on forest production and species composition of forests in Ghana (Swaine and Hall, 1988).

Rainfall may be an important factor as the total amount of rainfall at Nkrabia (455 mm) during the period May to June when the field experiments were conducted was 63% higher than at Tinte Bepo (Agyeman *et al.*, 1999b). Nkrabia had a greater amount (1315 mm per annum) and frequency (7-8 wet months) of rainfall, lower PPFD ($18-21 \text{ mol m}^{-2} \text{ day}^{-1}$), lower R:FR (0.14-1.18) and lower maximum air temperature ($29-35^{\circ}\text{C}$) compared to Tinte Bepo. Tinte Bepo had 1107 mm of rain and 4-5 wet months per annum, PPFD of $23-27 \text{ mol m}^{-2} \text{ day}^{-1}$ and maximum air temperature of $28-36^{\circ}\text{C}$ (Agyeman *et al.*, 1999b).

The lower rainfall at Tinte Bepo would cause greater moisture stress than at Nkrabia. The effect of moisture stress is inferred from the amount and distribution of rainfall in the wet season (Kramer, 1983). The soil surface in the polythene bags at Tinte Bepo was often dry, whereas those at Nkrabia generally appeared moist. The amount and more even distribution of rainfall, seems to be exerting a stronger influence on growth rate than differences in photosynthetic photon flux density. Reduced soil moisture content, leading to water stress in plants, may restrict plant growth due to its marked effect on photosynthesis (Lambers and Poorter, 1992). The specific influence of individual microclimatic variables which are likely to have an influence on plant growth are

difficult to determine as these variables are correlated and therefore do not act in isolation (Ford and Milne, 1981).

The pattern of growth response was similar in the two field sites although the quantitative growth rate was higher at Nkrabia compared to Tinte Bepo. This suggests that plant response to light may be genetically controlled and that site differences may only serve to increase or decrease the magnitude of the growth response. The similarity of the irradiances at which maximum growth of individual species was observed at Nkrabia and Tinte Bepo indicates that species growth in artificial canopy gaps may be useful in predicting species performance over a range of different irradiances following logging. However, such a prediction can only be effective if variable factors such as insect attack and drought are either reduced to a minimum or are quantified and included in the model.

Insect attack may also have contributed to the differences in relative growth rates between the two field sites. *Albizia. zygia*, *C. albidum*, *E. utile*, *E. angolense* were particularly prone to insect attack in the field. Defoliation by moth caterpillars was often observed in *A. zygia*. The other three species were attacked by variegated grass hoppers, *Zonocerus* sp. which stripped off the bark. *Mansonia altissima* and *C. pentandra* were also attacked by herbivores, but less frequently. Complete defoliation leading to death was not a major problem at either field site. Less than 2% of all plants died as a result of defoliation. The greatest cause of mortality, especially in pioneers (34%) compared to non-pioneers (16%) was a result of low irradiance.

Almost all the species, including pioneers, had slower growth in high irradiances (above 70% irradiance). This suggests that very large gaps, especially haulage roads and loading bays, created as a result of logging may cause poor regeneration

as a result of the high irradiance and other associated environmental conditions found in such gaps. Poor regeneration of the tree species in loading bays and the middle of logging roads was also observed by Hawthorne (1993) in the Bia-South Game Production Reserve in Ghana. Saptoka and Oden (2009) also found that large gaps, both natural and artificial, were not suitable for growth and regeneration of seedlings examined in a seasonally dry forest in Nepal.

CONCLUSIONS AND RECOMMENDATIONS

Plant growth was greater in the wet compared to dry forest probably as a result of differences in soil moisture availability. Rainfall differences between the two forest types had a greater influence on plant growth than differences in PFD. This result can be largely attributed to the fact that the experiments were carried out in the rainy season, when cloud cover reduces differences in PFD between sites. However, the results are still significant enough to suggest that classification of plants into ecological species groups should not only be based on their response to light but also soil moisture availability/stress. It is recommended that experiments on seedling response to light and moisture stress should be carried out in the dry season when differences in these two microclimatic variables are greatest.

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