

SPECIES DIFFERENCES IN SEEDLING GROWTH AND LEAF WATER RESPONSE TO LIGHT QUALITY

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ABSTRACT

For the majority of forest species slight canopy opening reduces light limitations suggesting that light quality often measured as red:far red ratio (R:FR) plays a significant role in the development of seedlings. The effect of different levels of R:FR was studied on seedlings of four Ghanaian timber species of different ecological guilds to assess their growth and leaf water response to changes in R:FR. The experiment was conducted in shade houses of varying light qualities (0.30, 0.46 and 0.76 R:FR) achieved with the use of bamboo slats, green filter and white cotton cloth. Relative height growth of all species declined in high R:FR with *Guarea cedrata* and *Celtis mildbraedii*, shade bearers, having a slower decline of height growth with increasing R:FR than *Terminalia ivorensis*, pioneer, and *Albizia zygia* non-pioneer light demander. Relative diameter growth on the other hand increased in higher R:FR treatments except for *G. cedrata*. Relative biomass growth was not significantly affected by R:FR. Leaf area ratio did not vary in different R:FRs for *G. odorata* but for the other species it was lower in higher R:FRs. Specific leaf area was also not affected by R:FR except in *G. cedrata* where it dropped with increase in R:FR. The diurnal pattern of change in stomatal conductance and leaf water potential of *T. ivorensis* and *G. cedrata* were similar in lower R:FR ratio but opposite in higher R:FR. This results show that the response of seedlings to changes in R:FR is different for different species and is more of morphological change rather than growth (biomass accumulation). Pioneers are more sensitive to these changes than non-pioneers.

Keywords: Red:far-red ratio, light quality, seedlings growth response, leaf water status, morphological change

INTRODUCTION

The canopy of tropical rain forests often creates poor light conditions on the forest floor (Sasaki and Mori, 1981). The light intensity reaching the forest floor ranges from 0.5 to 2% of full sun (Chazdon and Fetcher, 1984) while light quality ranges from 0.03 to 0.05 red:far-red ratio (Smith, 1982). The low red:far-red ratio (RFR) associated

with the forest understorey is due to the absorption of the red wavelength of light, which is 660 nm, whilst transmitting the far-red wavelength, which is 730 nm (Smith, 1982).

Although the creation of canopy gaps results in the improvement in light conditions in the forest, (Chazdon and Fetcher, 1984; Brown, 1990) seedlings may spend considerable length of time

in shade before canopy opening opportunity arrives (Swaine, 1996). While the total quantity of light, of which approx. 51% is photosynthetically active radiation, controls the micro-climate and plant growth, it is the wavelength composition difference, for example R:FR, that has a considerable influence on plant developmental response (Kwesiga and Grace, 1986; Smith, 1982; Hart, 1988), understory photosynthesis and photoperiod response (Feferer and Tanner, 1966).

In addition to its influence on plant developmental response, R:FR also influences stomatal opening (Hsiao *et al.*, 1973; Hsiao, 1976). The stomata control the balance between water loss and carbon gain (Beadle *et al.*, 1993) and maintains leaf temperature below lethal limits through the regulation of water loss (Taylor and Sexton, 1972). This implies that R:FR may affect assimilation and transpiration through its influence on stomatal opening.

However, despite the importance of R:FR in controlling stomatal opening, very little work has been done on its effect on leaf water status of plants (Kwesiga and Grace, 1986). Where studies have compared plant growth response to neutral and filtered light, (Mitchell and Woodward, 1988; Turnbull, 1991), the upper limit of R:FRs used in these trials was in most cases greater than 1.2. However, the range of R:FRs found in the forest understory and gaps lies between 0.03 and 1.12 (Smith, 1982; Ross *et al.*, 1986) and between 1.7 and 1.8 under a secondary forest regrowth (Dike, 2009) and therefore most of the experiments that have been conducted are of little practical applicability. The influence of R:FR on the leaf water status of forest tree seedlings has implications for seedling tolerance to shade as well as the ability to adjust to elevated light levels associated with forest disturbance. A study of the

subject will therefore improve our understanding of the natural forest's response to logging and other disturbances.

Light limitation is removed in the majority of species in conditions of only slight canopy opening suggesting light quality effect. Species differ in the way they respond to environmental variables (Swaine *et al.*, 1997) and these differences may account for their relative successes in coping with changes in the ecosystem. Whilst species differences in seedling growth response to irradiance and a lesser extent R:FR ratio is widely known, mechanisms driving this have not been properly studied. Besides how the differences in species ecology influence the mechanisms are poorly understood.

The objective of this study is to assess seedling growth and leaf water response of four common West African timber species to changes in R:FRs. The species occupy distinct positions on the shade tolerance gradient.

MATERIALS AND METHODS

Experimental Design

A two-factorial completely randomised design was used with species and light quality as the factors. Four species, namely; *Terminalia ivorensis* A. Chev. (Combretaceae), pioneer, *Albizia zygia* Macbride (Mimosaceae), non-pioneer light demander, *Celtis mildbraedii* and *Guarea cedrata* (A. Chev.) Pellegr. (Meliaceae), non-pioneer shade bearers (*sensu* Hawthorne 1992), were assessed in the seedling growth trial. However, only *T. ivorensis* and *G. cedrata*, chosen to represent the two main ecological species groups, pioneer and non-pioneers (*sensu* Swaine and Whitmore, 1988), were assessed in the

the leaf water status trial.

Seeds of all the four species were germinated in a tray filled with river sand. Seedlings were transplanted at the two leaf stage, i.e. 4 weeks after germination, into polythene bags of 20 cm diameter and 30 cm depth filled with a soil mixture of 33% river sand and 67% loamy soil from a well drained Ochrosol (Asiamah, 1987) under a patch of natural forest close to Kumasi. The polythene bags had holes on the sides and bottom to prevent water-logging. The positions of seedlings within the shade house were periodically rearranged to avoid the shading of slow growing seedlings by fast growing ones. Plants were watered three times a week. These seedlings were conditioned under a shed with low irradiance, 15% full sun, for 2 weeks and then transferred into four different shade houses (different light qualities).

Shade House Characteristics

Shade houses of different light qualities (0.30, 0.46 and 0.76 R:FR) were constructed using bamboo slats, green filter and white cotton cloth. The bamboo slats were used to produce a dappled light effect. Filtered shade was provided by Strand Lighting pea green filter (No. 421) which had a R:FR value of 0.60. White cotton cloth which transmitted almost the same percent PAR as the green filters was used for neutral shade.

Two layers of green filter and a layer of mosquito netting were placed together to produce 0.30 R:FR. The irradiance under this shade treatment ranged from 12-17% full sun. The mosquito netting was to reduce the irradiance under the pea green filter to similar levels as that under the cotton cloth. The resultant photosynthetically active radiation was in the range of 10 to 15% full sun. A layer of green filter and one of cotton cloth

produced 0.46 R:FR while two layers of cotton cloth produced 0.76 R:FR. A higher R:FR could not be achieved without a further increase in irradiance due to the close association between irradiance and R:FR.

Light Measurements

Photosynthetically photon flux density (PPFD) was measured monthly using DIDCOT Integrating PARSUM sensors (DRP 02). Daily totals, from sunrise to sunset, spanning a period of 5 days were measured monthly. The daily totals were calculated as a percentage of full sunlight. Red:far-red measurements were also taken biweekly using a SKYE Red: Far-red meter. These biweekly R:FR measurements were carried out to assess the extent of deterioration of the filters with time. The differences in irradiance readings of the different shade treatments using the AP4 Porometer were similar to those measured independently, using DIDCOT Integrators, during the setting up of the shade treatments. The range of leaf temperatures for both species through the day was similar in the different R:FR treatments however; at mid-day leaf temperatures of *T. ivorensis* were higher than *G. cedrata*.

Seedling Growth and Leaf Water Status Measurements

Seedling height was measured using a metre rule and root collar diameter using Vernier callipers. Dry weight of leaves, roots and shoots were 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 areas from PCX image files. Height, stem diameter, and dry biomass assessments were carried out every three weeks.

Stomatal conductance, leaf temperature and light intensity incident on the leaf were measured using the Delta-T AP4 Transit-Time Porometer (Beadle *et al.*, 1993). The youngest two fully expanded leaves were used for all measurements on leaf water status. This is because leaf age or maturation affects its water status (Tyree *et al.*, 1978; Roberts *et al.*, 1980). In each of the shade treatments, five seedlings each of *G. cedrata* and *T. ivorensis* were randomly chosen for measurements. The stomatal conductance on the abaxial leaf surfaces were measured throughout the day (7.30 a.m. to 5 p.m.). The leaf water status of plants was assessed in June, during the wet season, after 12.5 weeks of seedling growth in the various treatments.

The pressure chamber method was used to determine the leaf water status of the seedlings (Scholander *et al.*, 1965). The precautions recommended by Turner (1981) in order to obtain reliable leaf water status results from the pressure chamber method were used. The leaves were cut neatly with a sharp blade and placed immediately in the Whitney Pressure Chamber and measurements taken quickly. After measurements on leaf water potential had been recorded, the leaves were quickly placed in plastic bags, weighed and used for measurements of relative water content. Three seedlings were randomly selected from each shade house for these measurements.

Relative water content was determined by weighing after hydrating the leaf samples until constant weight was achieved (usually within 48 hours). This was followed by oven drying at 85 °C for 48 hours (Beadle *et al.*, 1993). Relative water content and leaf water potential of seedlings were measured in the early morning (07.30-08.30 GMT) and afternoon (12.00-13.00 GMT).

Statistical Analysis

The seedling growth data and analyses presented involve only those for surviving seedlings. The functional approach to plant growth analysis in Hunt (1990) was used in data analysis. Most of the analyses were done using SYSTAT V5.0 (Statistical and Graphics Analysis Package).

Leaf area ratio ($\text{m}^2 \text{kg}^{-1}$), specific leaf area ($\text{m}^2 \text{kg}^{-1}$) and root:shoot ratio (g g^{-1}) were determined using only the final seedling biomass and leaf area. However, unit leaf rate ($\text{g m}^{-2} \text{week}^{-1}$) was determined using both the final and initial seedling biomass and leaf area (Beadle *et al.*, 1993). The final reading is suitable for growth analysis because the plants will have reached a phase of equilibrium with the individual polythene bags (Blackman and Wilson, 1951). The formulae used are as follows:

$$\text{LAR} = s_2/W_2, \text{SLA} = s_2/w_2, \text{ULR} = ((W_2 - W_1)(\text{Ln } s_2 - \text{Ln } s_1))/((s_2 - s_1)(t_2 - t_1)).$$

Where s_2 = Final plant leaf area,

s_1 = Initial plant leaf area,

W_2 = Final plant dry weight,

W_1 = Initial plant dry weight,

w_2 = Final leaf dry weight,

t_2 = Final time (Weeks),

t_1 = Initial time (Weeks)

Relative growth rates were obtained by modeling the changes in absolute growth over a period of time (Hunt, 1990). This method is useful when comparing seedlings which had different initial sizes. A graph of the mean values of the 3-weekly readings was plotted to determine the model to use in analysis. Linear, Logarithmic or power function regression models which best fit the growth of each species in the different pot sizes were determined. The responses with time of all the growth variables measured, with the exception

of biomass, were linear. Biomass accumulation, however, was best fitted by a natural logarithmic function. The regression lines or models generated for each of the response variables in the different pot sizes were tested for "homogeneity of slopes" (Snedecor and Cochran, 1967; Edwards, 1979).

Table 1: Mean and range of percent full sun (%FS) and range of photosynthetic photon flux density (PPFD) in different red:far-red ratios (R:FR). Measurements were taken twice a month between April and July 1993 (during the rainy season) when the experiment was carried out

R:FR	Mean % FS	Range of % FS	PPFD (mol m ⁻² day ⁻¹)
0.30	15	12-17	1.73 – 2.45
0.46	12	9-15	1.30 – 2.16
0.76	10	8-12	1.15 – 1.73

RESULTS

Effects of Different R:FRs on Stomatal Conductance

Photosynthetically photon flux density (PPFD) measurements in each of the three Red-far-red ratio (R:FR) measurements are presented in Table 1. The PPFD in 0.30R:FR ranged from 1.73-2.45 mol m⁻² day⁻¹, while that of 0.76R:FR ranged from 1.15-1.73 mol m⁻² day⁻¹ (Table 1). It is worth noting that in order to be able to test the effects of R:FRs, deliberate effort was made to ensure that the PPFDs in the three R:FRs were not different.

The diurnal pattern of changes in stomatal conductance of *G. cedrata*, non-pioneer (Figure 1), and *T. ivorensis*, pioneer (Figure 2), in the three R:FR levels were similar. Early morning conductances of *G. cedrata* (Figure 1) and *T.*

ivorensis (Figure 2) were high and decreased to a minimum between 12-14 hours GMT. Stomatal conductance of both plants was higher in the early evening compared to mid-day but lower than that of early morning (Figures 1 and 2).

Stomatal conductance levels ranged between 100µmol m⁻² s⁻¹ and 300µmol m⁻² s⁻¹ for both *G. cedrata* and *T. ivorensis* in 0.30 R:FR (Figure 1). Stomatal conductance at 0.76 R:FR throughout the day for the two species was significantly higher (about 1.5 times higher) than the stomatal conductance at 0.30 R:FR (Figures 1 and 2). The quantitative response of stomatal conductance of *G. cedrata* at 0.46R:FR was not significantly different from that of 0.30R:FR in the morning but was however significantly different in the afternoon and early morning (Figure 1). On the other hand, stomatal conductance of *T. ivorensis* growing in 0.46 R:FR was significantly different in the early morning and evening but not at mid-day (Figure 2).

In a comparison of stomatal conductance of the two species growing in the three R:FRs (Figure 3), it was observed that stomatal conductance of *T. ivorensis* in 0.76 R:FR was significantly higher than that of *G. cedrata*. However, there were no significant differences between the stomatal conductance of the two species at the 0.30R:FR and 0.46R:FR (Figure 3).

It is also noted that stomatal conductances of the two species in the mornings were almost 50% higher than that of the evenings (Figure 3).

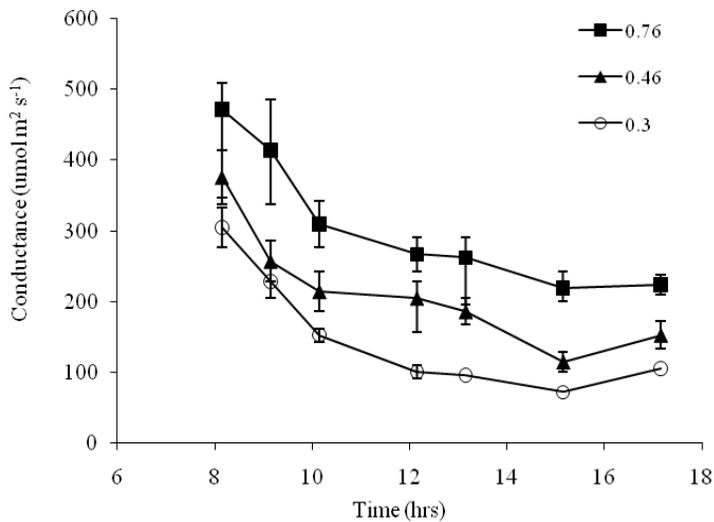


Figure 1: Diurnal course of stomatal conductance of *G. cedrata* in 0.30, 0.46 and 0.76RFR

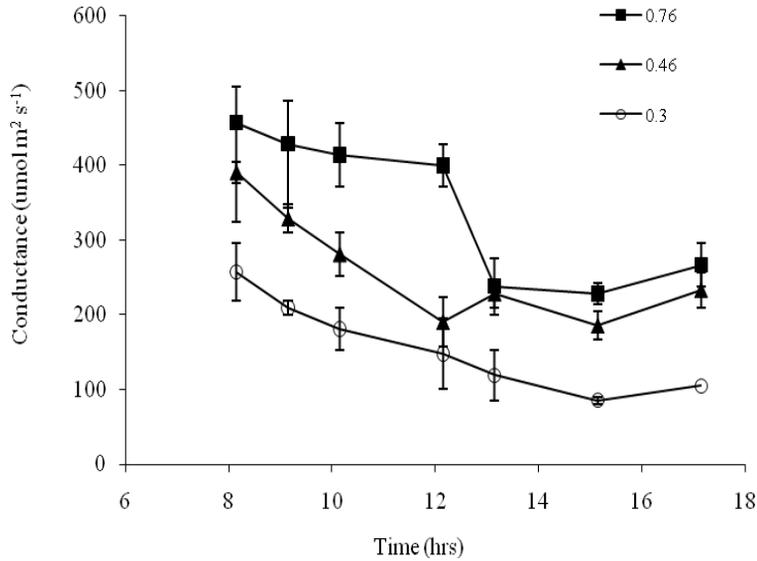


Figure 2: Diurnal course of stomatal conductance of *T. ivorensis* in 0.30, 0.46 and 0.76R:FR

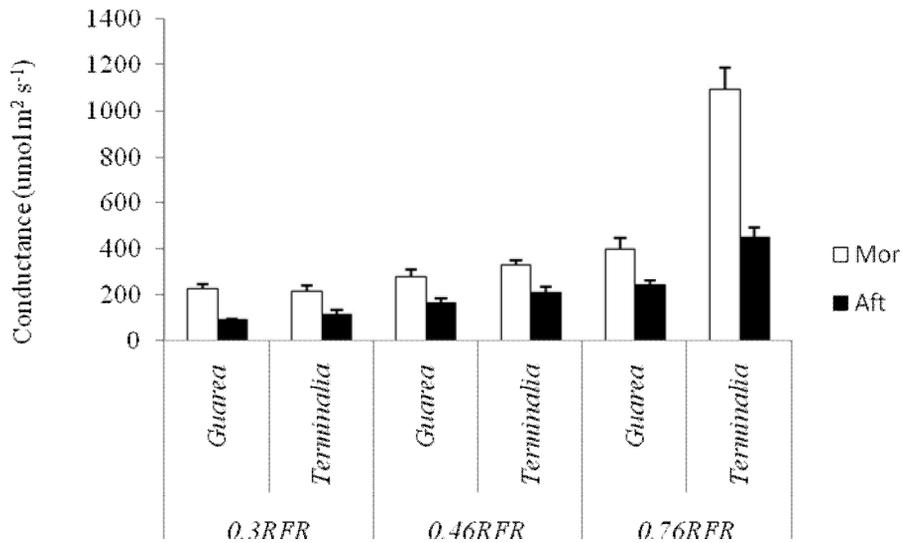


Figure 3: Morning (mor) and afternoon (aft) stomatal conductances of *G. cedrata* (Guarea) and *T. ivorensis* (Terminalia) in 0.30, 0.46 and 0.76R:FR

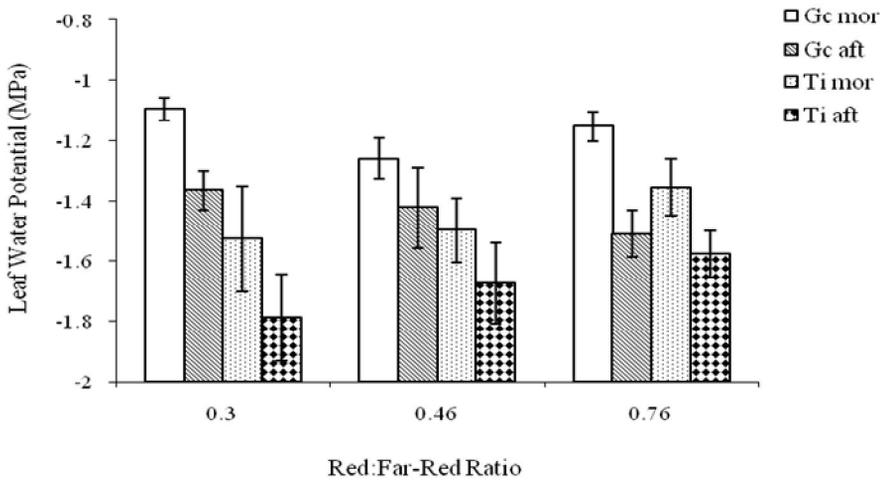


Figure 4: Leaf water potential (MPa) of *G. cedrata* in the morning (Gc mor) and afternoon (Gc aft) and *T. ivorensis* in the morning (Ti mor) and afternoon (Ti aft) in 0.30, 0.46 and 0.76R:FR.

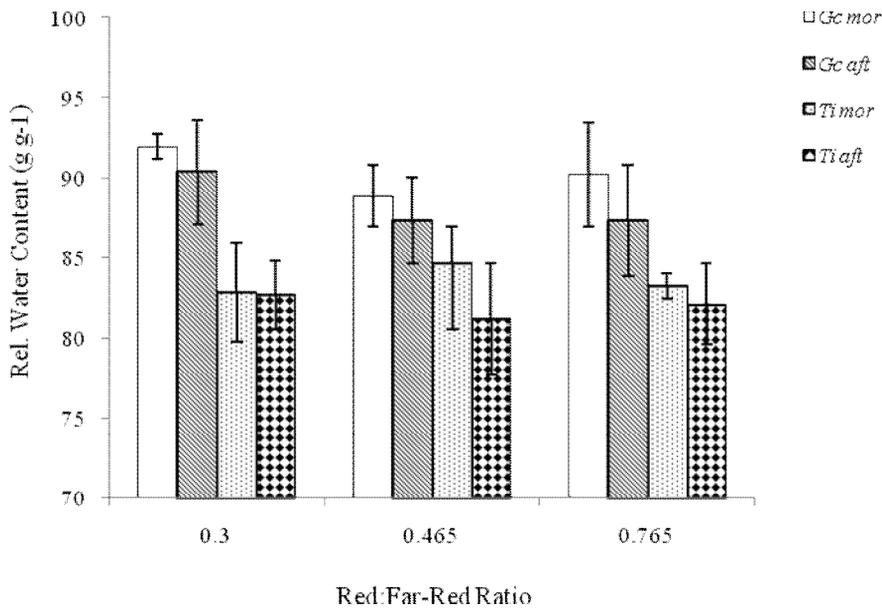


Figure 5: Relative water content (g g⁻¹) of *G. cedrata* in the morning (Gc mor) and afternoon (Gc aft) and *T. ivorensis* in the morning (Ti mor) and afternoon (Ti aft) in 0.30, 0.46 and 0.76R:FR

Response of Leaf Water Potential (LWP) and Relative Water Content (RWC) to Different Red: Far-Red Ratios

In the mornings, leaf water potential (LWP) was greater, less negative, for both species compared to the afternoons (Figure 4). LWP levels for *G. cedreta* in the morning and afternoon were higher than the corresponding values of *T. ivorensis* in the different R:FRs. Leaf water potential of *T. ivorensis* appears to increase, less negative, from 0.30R:FR to 0.76R:FR, however for *G. cedrata* the LWPs decreased, more negative, with increasing R:FRs. The only exception was for the morning LWP of *T. ivorensis* which increased from 0.46R:FR to 0.76R:FR (Figure 4).

The pattern of relative water content (RWC) of the two species in different RFRs (Figure 5) was similar to that of LWP (Figure 4). There were no differences between morning and afternoon RWCs for both *G. cedrata* and *T. ivorensis*. In *T. ivorensis* however, relative water content levels rose with increasing levels of R:FR and was also lower in the afternoons except at the 0.3 R:FR. (Figure 4). At low R:FR (0.3-0.46) relative water content of *G. cedrata*, was higher compared to *T. ivorensis*, but at 0.76R:FR a reverse situation was observed due to the different ways in which the two species respond to increases in R:FR (Figure 5).

Seedling Growth Response to Different Red: Far Red Ratios

Relative height, diameter and biomass growth rates of four species in different R:FRs are presented in this section. The species are *T. ivorensis*, pioneer, *A. zygia*, non-pioneer light demander, *G. cedrata* and *C. mildbraedii*, non-pioneer shade bearers (*sensu* Hawthorne, 1992). Absolute leaf area ratio, specific leaf area, unit

leaf rate and biomass allocation response are also shown.

Relative Height, Diameter and Biomass Growth

Relative height growth (RHG) was higher for *T. ivorensis* (pioneer) and *A. zygia* (light demander) compared to *G. cedrata* and *C. mildbraedii* (shade bearers) at all the R:FRs (Figure 6). Relative height growth (RHG) of all species declined from 0.30R:FR to 0.76R:FR. However *G. cedrata* and *C. mildbraedii*, shade bearers, had a slower decline of height growth with increasing R:FR than *T. ivorensis*, pioneer, and *A. zygia*, light demander, (Figure 6).

Unlike RHG, relative diameter growth (RDG) of all species increased with higher R:FR treatments (Figure 7). *T. ivorensis* (pioneer) had the highest RDGs in all R:FRs followed by *G. cedrata* (shade bearer) and *A. zygia* (light demander) respectively. Differences in relative biomass growth were not significantly affected by R:FR. There were also no differences in relative biomass growth between species in the different R:FRs (DF = 3,55; F = 0.677; P = 0.57) Table 2).

Leaf Area Ratio (LAR), Specific Leaf Area (SLA), Unit Leaf Rate (ULR) and Biomass Allocation

Leaf Area Ratios (LARs) of *T. ivorensis*, *C. mildbraedii* and *A. zygia* was almost 5 times higher than that of *G. cedrata* in all the different R:FRs (Figure 8). Two patterns of leaf area ratio response to different R:FR ratios were observed among species. In the first response pattern, the LARs of *T. ivorensis*, *C. mildbraedii* and *A. zygia* were higher in 0.30R:FR compared to 0.76R:FR. However, LARs in 0.46R:FR did not seem to be different from that of 0.30R:FR and 0.76R:FR

(Figure 8). In the second response pattern shown by *G. cedrata*, leaf area ratio did not vary in different R:FR ratios (Figure 8).

Specific leaf area (SLA) was highest for *T. ivorensis* and least for *G. cedrata*. All species had higher specific leaf area at 0.3R:FR compared to 0.76R:FR ratio (Figure 9). The response pattern of SLA of the various species in different R:FR ratios was similar to that of LAR except in *G. cedrata* where this time round the SLA in 0.30R:FR was higher than that of 0.30R:FR and 0.46R:FR (Figure 9). The response in SLA of the various species per unit increase in R:FR ratio was however, higher compared to LAR.

There was a general pattern of increase in Unit Leaf Rate (ULR) with increasing R:FR. The ULR of all the four species were higher in 0.76R:FR compared to 0.30R:FR (Figure 10). With the exception of *G. cedrata*, the ULRs of the species in 0.46R:FR were not different from that of 0.30R:FR, neither from that of 0.76R:FR (Figure 10). Biomass allocation, in the form of root:shoot ratio (RSR), for the four species was not different for the three R:FRs (Figure 11). *G. cedrata* had a higher RSR than the other three species. However, there were no differences in the RSRs of *T. ivorensis*, *C. mildbraedii* and *A. zygia* in the three R:FRs (Figure 11).

Table 2: F values and levels of significance (P) using Analysis of Covariance (ANCOVA) to test the differences between the relative biomass growth of four species in the three red:far-red ratio (R:FR) treatments (0.30, 0.46 and 0.76R:FR). The degrees of freedom (df) are shown.

	ANCOVA		
	DF	F	P
Species	3,55	0.677	0.570
R:FR	1,55	0.230	0.633
Time	1,56	233.67	<0.001
Species x Time	3,52	0.006	0.999
Shade x Time	2,54	0.065	0.937

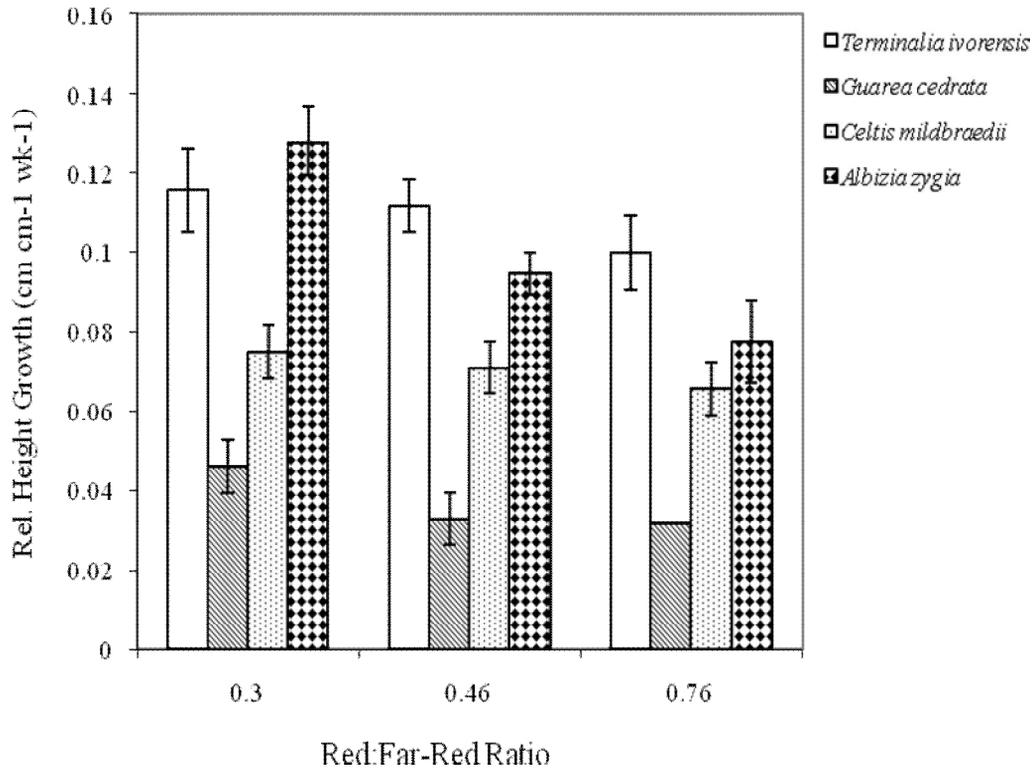


Figure 6: Relative height growth ($\text{cm cm}^{-1} \text{ week}^{-1}$) of *T. ivorensis*, *G. cedrata*, *C. mildbraedii* and *A. zygia* in 0.30, 0.46 and 0.76R:FR

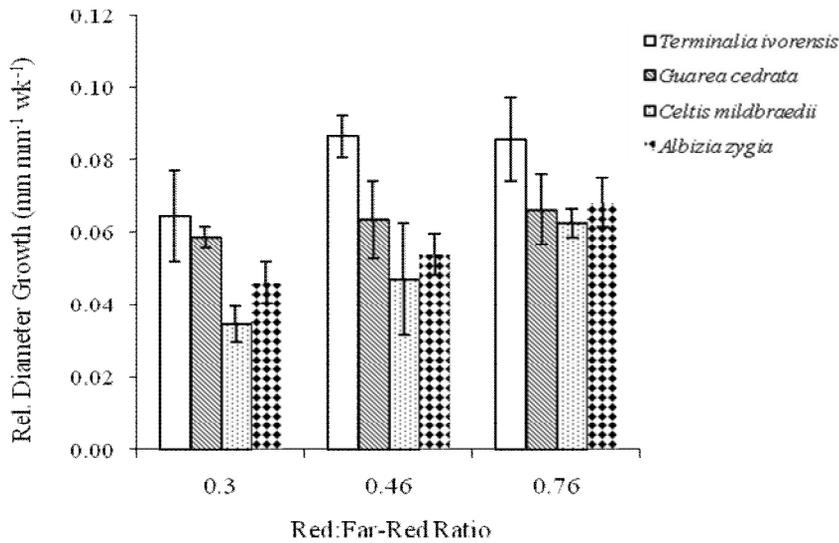


Figure 7: Relative diameter growth ($\text{mm mm}^{-1} \text{ week}^{-1}$) of *T. ivorensis*, *G. cedrata*, *C. mildbraedii* and *A. zygia* in 0.30, 0.46 and 0.76R:FR

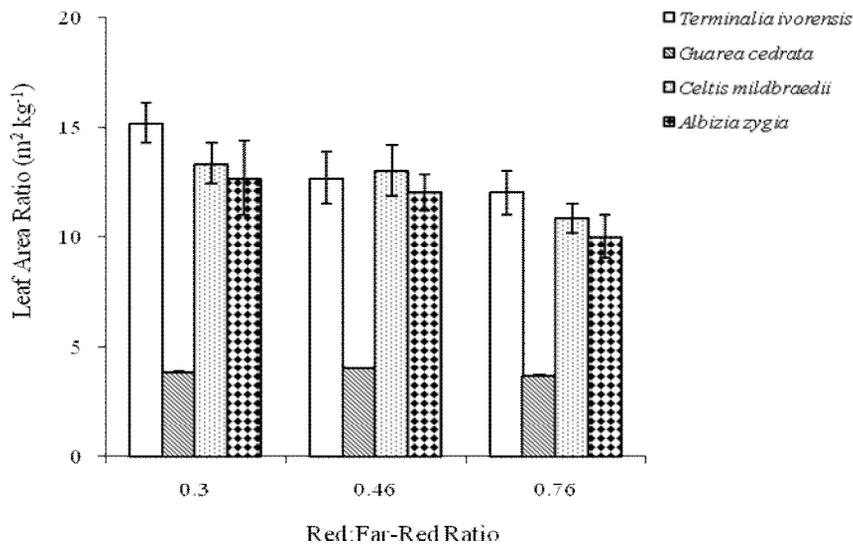


Figure 8: Leaf area ratio ($\text{m}^2 \text{ kg}^{-1}$) of *T. ivorensis*, *G. cedrata*, *C. mildbraedii* and *A. zygia* in 0.30, 0.46 and 0.76RFR.

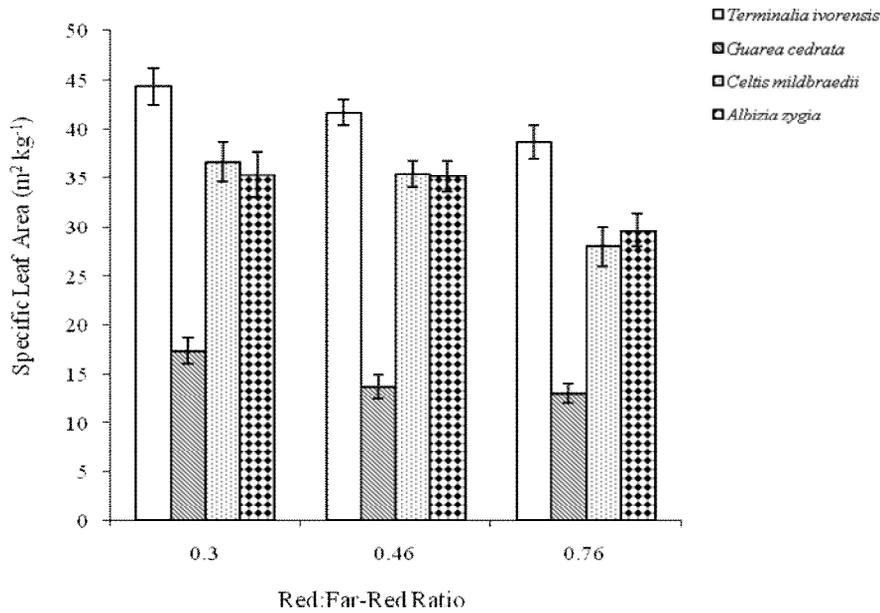


Figure 9: Specific leaf area (m² kg⁻¹) of *T. ivorensis*, *G. cedrata*, *C. mildbraedii* and *A. zygia* in 0.30, 0.46 and 0.76R:FR.

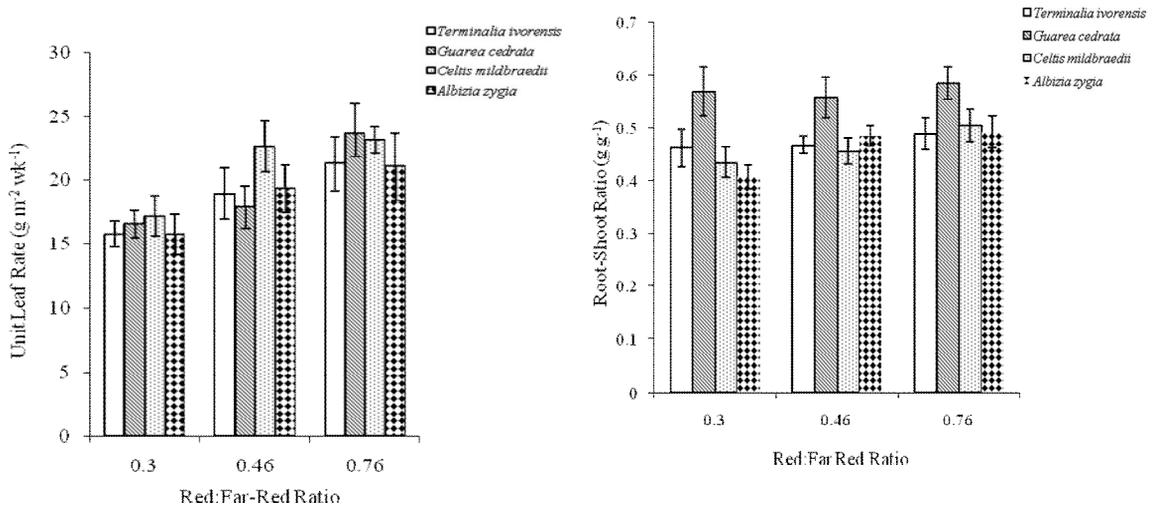


Figure 10: Unit leaf rate (g m² wk⁻¹) of *T. ivorensis*, *G. cedrata*, *C. mildbraedii* and *A. zygia* in 0.30, 0.46 and 0.76R:FR.

Figure 11: Root-shoot ratio (g g⁻¹) of *T. ivorensis*, *G. cedrata*, *C. mildbraedii* and *A. zygia* in 0.30, 0.46 and 0.76R:FR.

DISCUSSION

Variation of Leaf Water Status with Changes in Red Far-Red Ratio

Stomatal Conductance

Stomatal conductance of *T. ivorensis*, pioneer, was higher at low RFR ratios and vice versa. However, stomatal conductance of *G. cedrata*, non-pioneer, was similar in the different RFR ratio treatments. Turnbull (1991) also observed a higher stomatal conductance in pioneer species in higher RFR ratios. According to Jefferson and Muri (2007) response of *Psathyrostachys juncea* seedlings were reduced by declining red:far-red light ratio. Many species, especially pioneers, show strong responses to a depression in RFR ratio (Morgan and Smith, 1976; Casal *et al.*, 1987). The higher stomatal conductance of pioneers in high R:FR ratios may be due to the effect of the red light wavelength (660 nm) on stomatal opening (Hsiao *et al.*, 1973).

The influence of red light on stomatal conductance is generally observed above 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Hsiao, 1976). This is equivalent to mid-day irradiance underneath the forest canopy in the field or almost 2%. Goldberg and Klein (1980) observed that the influence of R:FR ratio on stomatal opening depends not only on the level of irradiance, but also on the light compensation point. They reported that R:FR ratio influences stomatal opening only after the compensation point of the plant has been reached. The irradiance, 10-15% full sun, under which the RFR ratio experiment was undertaken was higher than the light compensation point of the two species (Agyeman, 1994).

The influence of R:FR ratio on stomatal conductance may be more pronounced pre-dawn,

provided the light compensation point has been reached. This is because stomatal conductance is highly sensitive to pre-dawn irradiance which has a higher R:FR ratio than irradiance throughout the rest of the day (Smith, 1982). However, pre-dawn stomatal conductance readings could not be taken due to the high relative humidity, > 80%, during the period of the measurements (wet season). Nevertheless, high stomatal conductances were still observed in the early morning. This may be due to the early morning opening of stomata which results in a rapid increase in stomatal conductance (Grantz *et al.*, 1987).

The mechanism by which R:FR ratio controls stomatal opening and therefore, stomatal conductance is still not clear (Hsiao *et al.*, 1973). However, it might be due to the action of phytochrome whose primary function is the reception of R:FR (Smith, 1982). A small variation in RFR is accompanied by large changes in phytochrome photoequilibrium resulting in various plant responses (Smith and Holmes, 1977; Morgan and Smith, 1976). The magnitude of the response is influenced by the sensitivity of the phytochrome adaptation mechanism of the plant (Smith, 1982; Casal and Smith, 1989). Therefore, the higher stomatal conductance of *T. ivorensis*, pioneer, compared to *G. cedrata*, non-pioneer, in high R:FR may be due to the higher sensitivity of pioneers to phytomorphogenetically induced stomatal activity.

According to Beadle *et al.*, (1993), stomata are highly sensitive to changes in environmental conditions. Therefore, differences in stomatal conductance between the two species may also be due to the higher sensitivity of stomata on *T. ivorensis* to changes in light quality and other environmental conditions especially irradiance, air temperature and atmospheric pressure deficit.

The number and size of stomata influences stomatal conductance (Turnbull, 1991). Therefore the higher stomatal conductance of pioneers compared to non-pioneers in high R:FR may be due to their higher stomatal density.

Stomatal conductances of *T. ivorensis* and *G. cedrata* were 3-10 times higher than those of temperate tree species, for example *Pica stichensis* and *Pinus slyvestris* (Turner and Jarvis, 1975, Beadle *et al.*, 1985). The high stomatal conductances amongst the tropical tree species may be an adaptive mechanism which ensures an adequate rate of transpiration and low aerodynamic conductance (Grace *et al.*, 1982) in order to prevent their leaf temperatures from rising to lethal levels (Taylor and Sexton, 1972). This adaptive mechanism may be especially important to West African tropical plants due to the high temperatures in which they grow (20-36°C).

Leaf Water Potential and Relative Water Content

Leaf water potential and relative water content of *T. ivorensis* and *G. cedrata* were within the range recorded for tropical tree seedlings growing in the field (Okali, 1972; Whitehead *et al.*, 1981). Leaf water potential and relative water content of *T. ivorensis*, pioneer, were lower than those of *G. cedrata* in 0.3 R:FR. The lower sensitivity of the stomata of non-pioneers coupled with their high degree of tolerance to shade compared to pioneers (Okali, 1972) may explain their higher or less negative leaf water status in low (0.30) R:FR ratio. For *G. cedrata* leaf water potential seems to reduce with increasing R:FR whilst the opposite is the case for *T. ivorensis*.

Leaf water status of plants is influenced by relative growth rate (Dijkstra and Lambers, 1989;

Poorter and Bergkotte, 1992), root size and leaf area of plants (Calkin and Percy, 1984; Sarmiento *et al.*, 1985). Pioneers generally have higher relative water content compared to non-pioneers due to their faster growth. Therefore the higher leaf water status of *T. ivorensis* compared to *G. cedrata* in high (0.76) R:FR may be due to its higher growth rate, leaf area ratio and specific leaf area. However, the higher leaf water status of *G. cedrata* in low (0.3) R:FR may be related to its high root: shoot ratio.

Influence of Red-Far-Red Ratio on Seedling Growth

Height, Diameter and Relative Biomass Growth Rate

Pioneers and non-pioneers had more etiolated stems and smaller diameters in the 0.3 R:FR treatment compared to 0.76 R:FR. According to Smith (1982), stem elongation is the most conspicuous developmental response to low R:FR. Etiolation in low R:FR is related to the ecological niche of species (Morgan and Smith, 1979) and tends to be higher in pioneers compared to non-pioneers (Mitchell and Woodward, 1988; Casal and Smith, 1989). The effects of red:far-red light (FR) and nutrient supply on the growth and nitrogen accumulation of silver birch (*Betula pendula*) seedlings indicate that stem elongation rate was increased by red:far-red light (Aphalo and Lehto, 2001).

Etiolation may be important as an adaptive response to avoid shade in the tropical forest, explaining why pioneers, which are less tolerant of shade than non-pioneers, have greater stem elongation rate in low R:FR. In a study on the effect of the ratio of red:far red light (R:FR) on seed germination of 27 herbaceous species from northern temperate deciduous forest, Jankowska-

Blaszczyk and Daws (2007) observed that for pioneers there was a significant negative relationship between R:FR and germination rate. The results suggested that small-seeded species only germinate in micro-sites with a high R:FR which signals the absence of over-topping vegetation or leaf litter.

Biomass accumulation at 12.5 weeks of *T. ivorensis* was 30% higher in 0.76 R:FR treatment than in 0.3 RFR. Biomass accumulation of *G. cedrata* was however, 20% lower in 0.76 compared to 0.3 R:FR. Differences in the final dry biomass of several species grown under different R:FRs have been observed (Kwesiga and Grace, 1986; Morgan *et al.*, 1983) and Warrington *et al.*, 1988). However, biomass accumulation at the final reading is a poor indicator of growth response. This is because differences in the initial plant sizes and duration of experiments do not always allow for realistic comparison of data from different experiments (Evans, 1972; Hunt, 1982). The use of final dry weights to determine the response of R:FR is inappropriate because whereas it was significantly different for *T. ivorensis* and *G. cedrata* in 0.3 and 0.78 R:FR, the relative biomass growths were not significant ($df = 3,55$; $P < 0.05$; Table 2).

Relative growth rate of seedlings did not vary with R:FR (Figure 6). Increase in growth rate of tree seedlings is not always associated with changes in R:FRs (Smith, 1982). For example, Kwesiga and Grace (1998) observed an increase in the growth rate of *T. ivorensis* (pioneer) with decrease in R:FR. However, they did not observe any significant change in *Khaya senegalensis* (Desr.) A.Juss. (non-pioneer light demander).

The role of R:FR in plant growth is still not clear. Results of studies by Grace *et al.*, (1982), Warrington *et al.*, (1988) and Mitchell and

Woodward (1989) seem to suggest that, among other functions, R:FR also supplements the effects of irradiance in plant growth. In a study on the effects of parental light deprivation on distinct reproductive structures in the *Polygonum hydropiper* Lundgren and Sultan (2005) observed that under low red:far-red conditions where resources are limiting, *P. hydropiper* plants appear to prioritize terminal achenes through increased provisioning as well as specific growth changes.

The responses to low red:far-red light (R/FR) ratios simulating dense stands were evaluated in wheat (*Triticum aestivum* L) cultivars released at different times in the 20th century and consequently resulting from an increasingly prolonged breeding and selection history. While tillering responses to the R:FR ratio were unaffected by the cultivars, low R:FR ratios reduced grain yield per plant (primarily grain number and secondarily grain weight per plant) particularly in modern cultivars. Low R:FR ratios also delayed spike growth and development, reduced the expression of spike marker genes, accelerated the development of florets already initiated, and reduced the number of fertile florets at anthesis. It is noteworthy that low R:FR ratios did not promote stem or leaf sheath growth and therefore the observed reduction of yield cannot be accounted for as a consequence of divergence of resources towards increased plant stature. It is proposed that the regulation of yield components by the R/FR ratio could help plants to adjust to the limited availability of resources under crop conditions (Ugarte *et al.*, 2010).

R:FR response may be an adaptation to warn the plant of impending or actual competition by other plants (Smith, 1982). It does this through the action of phytochrome which is so sensitive to R:FR ratio that it allows the plant to detect actual

shading before it begins to exert an effect on growth (Ballare *et al.*, 1987; Jiao *et al.*, 2007). The primary function of phytochrome or R:FR detection may therefore be to elicit a fast development response in the plant to avoid the effects of shading (Rockwell *et al.*, 2009; Wagner *et al.*, 2009). Because of the strong influence of changes in canopy, climatic and cloud conditions on R:FR (Holmes and Smith, 1977), its detection would enable the plant to respond quickly to actual or potential changes in light.

Leaf Area Ratio and Specific Leaf Area

Leaf area ratio and specific leaf area of all species except *G. cedrata*, non-pioneer, varied with different R:FRs. *T. ivorensis* and *A. zygia* had a higher, (10-15%) leaf area ratio and specific leaf area in 0.3 compared to 0.76 R:FR. Higher increases of the order of about 5-10 fold have been observed in some pioneer species at lower R:FRs (Hoddinott and Hall, 1982; Kwesiga and Grace, 1986; Warrington *et al.*, 1988). The higher leaf area ratio and specific leaf area response of *T. ivorensis* observed by Kwesiga and Grace (1986) compared to results of the same species in this paper may be due to the higher R:FR used (1.7 R:FR).

The response of specific leaf area to changes in R:FR tends to be species specific (Morgan and Smith, 1981; Corre, 1983), with large variation among pioneers compared to non-pioneers (Mitchell and Woodward, 1988). Specific leaf area and leaf area ratio also tend to influence interspecific variation in relative growth rate (Potter and Jones, 1977; Poorter, 1989; Poorter and Remkes, 1990). This suggests that the non-significant change ($P < 0.05$) in relative growth rate with R:FR observed in both pioneers and non-pioneers may be due to the lower rates of change of leaf area ratio and specific leaf area

compared to results of Kwesiga and Grace (1986).

Ecological Significance of R:FRs on Plant Development

The experiment to test the influence of R:FR was conducted under unnatural light conditions using filters because of the difficulty of varying R:FR while keeping other variables constant in the field. Nevertheless the results have important implications for tropical forest management since it shows the potential differences that exist in species in their responses to conditions that may prevail in different shaded parts of the forest.

The similar relative growth of pioneers and non-pioneers in low R:FR does not mean that their adaptation to growing under the forest canopy is the same. According to Lambers and Dijkstra (1987) non-pioneer are better adapted to low irradiances despite having lower relative growth rate compared to pioneers due to the lower selection pressure on growth rate compared to the other variables.

The higher leaf area ratio and specific leaf area together with a lower root: shoot ratio of pioneers compared to non-pioneers in low RFR may be an adaptive response for the pioneers to increase its photosynthetic capacity while reducing its respiratory system. According to Poorter (1989), there is a high selection pressure for leaves with high specific leaf area in dense vegetation. This selection pressure is more pronounced in pioneers than in non-pioneers. This may be due to the consequences of their adaptation to growing under high RFRs.

The lower leaf water status of pioneers compared to non-pioneers in 0.3 RFR suggests that they are less adapted to growing under the forest canopy. According to Schulze and Hall (1982), in an

environment of low evaporative demand and high water supply, plants appear to lose water only at a rate which is correlated with the capacity of the mesophyll for fixing CO₂. Therefore, the lower stomatal conductance of pioneers compared to non-pioneers in low RFR treatment, 0.30, suggests that they have a lower capacity to fix CO₂ in such conditions and may therefore be less adapted to growing under the forest canopy.

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