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RESPONSES OF GROWTH AND CHLOROPHYLL FLUORESCENCE OF *GMELINA ARBOREA* ROXB. EX SM. TO LIGHT ARE NOT INFLUENCED BY MILD MOISTURE STRESS IN NON-NITROGEN-LIMITED SOIL

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ABSTRACT

To examine the combined effects of soil moisture and nitrogen availability on the responses of growth and chlorophyll fluorescence to light, seedlings of *Gmelina arborea* were grown under full sunlight or 50% sunlight, four moisture regimes (M1: 20-30%; M2: 40-50%; M3: 60-70%; M4: 80-90% field capacity) and four nitrogen levels (N1: 3 g/kg; N2: 3.75 g/kg; N3: 4.5 g/kg; N4: 5.25 g/kg) for six months. Full sunlight suppressed height and stem volume whereas it increased biomass production. Moisture elevation augmented morphological traits and biomass production while reducing root: shoot. Height, leaf count, stem diameter and volume were decreased by nitrogen increase. A 2-factor interaction indicated that the increase in height by shading was limited to M2, M3, and M4. Similarly, M1 counteracted the beneficial effect of full sunlight on root biomass. Another interaction revealed that only seedlings in N1 and/or N2 experienced the increase in morphology induced by moisture elevation. Minimum fluorescence yield, maximum quantum yield of PSII and maximum primary yield of photochemistry of photo system II were insensitive to treatments. No 3-way interaction was detected, suggesting that the responses of *Gmelina arborea* to light may not be constrained by the M×N interaction.

INTRODUCTION

The world's climate has been changing outside its limits of natural variability over the decades due to natural and man-made causes. Global temperatures have increased by 1°C since the onset of the industrial revolution and are predicted to further rise by 1.5°C to 4.8°C by the end of this century (Harris *et al.*, 2017). Although studies have shown a 2% overall increase in global land precipitation, rainfall characteristics vary considerably among regions with the outcome that some areas are becoming wetter and others drier (Huho *et al.*, 2012). On the other hand, anthropogenic activities keep on increasing atmospheric and, hence, soil nitrogen contents (Clark and Tilman, 2008). With current rate of emission of greenhouse gases, more drastic changes in temperature, rainfall and soil nitrogen availability may be experienced in the future. Alterations in these environmental conditions can have important implications on the growth and development of forest plants. Soil nitrogen availability is one of the most important factors driving growth. An elevation of soil nitrogen increases the rate of plant growth and physiological processes like photosynthesis.

From an investigation on the long-term effects of simulated nitrogen deposition on *Pinussylvestris*, for instance, it was concluded that soil nitrogen enrichment can augment many growth parameters (Valinger, 1992). Similarly, elevating soil nitrogen and phosphorus levels have been found to positively impact photosynthesis and growth of *Betula pendula* and *Helianthus annuus* (Ekwe, 2015). The amount of water needed for proper growth and development varies across plant species and its availability often depends on other factors like temperature, wind current, evapo-transpiration rate and soil texture, among others (Lambers *et al.*, 2013). The importance of water to plant growth and functioning cannot be over emphasized. For example, the processes of photosynthesis and translocation of photosynthetic assimilates are strongly dependent on plant water status. Moreover, soil nutrients are often dissolved in water before being taken up by plants. Excess or limited soil moisture availability may affect the plant negatively with visible stress indicators like withering, low biomass production and stunted growth. Similarly, severe low soil moisture stress can cause the death of the entire plant or suppress growth through its damaging effects on the

photosynthetic machinery (Lambers *et al.*, 2013). As a sessile and autotrophic organism, the entire life cycle of a plant is strongly influenced by an ever-changing light environment (Kami *et al.*, 2010). Light is the main energy source for photosynthesis. In addition, it is an environmental signal that controls morphogenesis, growth and differentiation of plant cells, tissues and organs (Abidi *et al.*, 2013). Growth and physiological responses of forest plants to light are influenced by nitrogen and moisture availability (Cai *et al.*, 2010; Tripathi and Raghubanshi, 2014). It is, however, important to recognize that nitrogen and moisture may interact with each other in affecting the plants responses to light in ways that are yet unelucidated (Abayomi and Adefila, 2008).

Gmelinaarborea Roxb.ex Sm. (Gmelina) is an important tree of the western Cameroon highland forests. There are several economic and ecological attributes associated with the species. The wood properties and potential size make them ideally suitable for timber. Due to its lightweight, stability, and durability, timber of large sizes and high grade is sawn for construction of window frames, doors, staircases, floors, panels and musical instruments (Adam and Krampah, 2005). The tree is also of high medicinal value (Ashalatha and Sankh, 2014). Owing to these uses and an upsurge in human population in the forest area, the tree's population is drastically declining in some parts of its range. To offset an imminent imbalance between the demand for the aforementioned and other services offered by the species and the supply, it is imperative to put in place management practices that can ensure high performance on regeneration sites. This is only possible if an existing knowledge void on its growth and physiological responses to ecosystem conditions is filled. The aim of this study was to investigate the interactive effects of soil moisture and nitrogen availability on growth and chlorophyll fluorescence dynamics of Gmelina to light.

MATERIALS AND METHODS

Plant material: Seeds of Gmelina were germinated in a seedbed at the Reforestation Task Force nursery situated at Mile 6 Nkwen, Bamenda (5.9586/10.1475 latitude/longitude; 1250 m*asl*), North West Region, Cameroon under ambient conditions. After twelve weeks, seedlings of similar size were transplanted individually into polythene bags filled with soil that had been collected from a Bamenda Highlands forest site and analyzed for nitrogen. The polythene bags were then placed in a greenhouse constructed from wood and sealed with a transparent polythene sheet.

Experimental design: Treatments were comprised of two light levels (full sunlight and 50% sunlight), four moisture regimes (M1: 20-30%; M2: 40-50%; M3: 60-70%; M4: 80-90% field capacity) and four nitrogen levels (N1: 3 g/kg; N2: 3.75 g/kg; N3: 4.5 g/kg; N4: 5.25 g/kg). The experiment followed a split-split plot design with light as the whole plot, moisture as the split-plot, and nitrogen as the split-split plot. There were five plants per treatment combination in two replicates, making a total of 320 plants for the trial. The 50% light treatment was achieved by putting the seedlings under a forest green knitted shade fabric with 50% UV block (Coolaroo, USA). As for the moisture regimes, the water content of the substrate was measured daily with a soil moisture meter (Vegetronix VG-METER-200) and then water was added to keep the moisture level in the polythene bag within the target limit. The nitrogen treatments were obtained by determining the soil nitrogen

concentration (N1 = 3 g/kg) and then amending with 25%, 50%, and 75% of the basal value using urea (NPK 46:0:0). The pre-determined fertilizer quantities were weighed and dissolved in water before being applied to the plants at the respective nitrogen levels. The fertilization was done fortnightly. The treatments were commenced in September 2018 and terminated in February 2019.

Data collection: At the end of the experiment, three seedlings were randomly chosen from each treatment and replication. Chlorophyll fluorescence was measured with a Hansatech FMS-2 portable pulse modulated fluorometer on the third leaf from the apex. Before measurement, leaves were dark adapted for 60 minutes with leaf clips. F_m was obtained by illuminating the leaf with a pulse of strong light ($\sim$14,000 μmol m^{-2} s^{-1}) for 800 ms. Variable fluorescence ($F_v = F_m$-F_o), maximum quantum yield of PSII (F_v/F_m), and maximum primary yield of photochemistry of photo system II (F_v/F_o) were then computed from the maximum (F_m) and minimum (F_o) fluorescence yields. The height, stem diameter, and number of leaves of each of the seedlings were then recorded after which they were decapitated at the root-shoot junction with the use of secateurs. The root system was rinsed free of soil and the weights of the oven-dried shoot and root fractions were determined with an electronic balance. Stem volume (*SV*) was computed from the height (*H*) and diameter (*D*) measurements ($SV = D^2H$; Aphalo and Rikala, 2003).

Data analysis: All the data were examined graphically for normality using probability plots and homogeneity of variance using histograms. The effects of light, nitrogen, moisture availability and their interactions on the growth and chlorophyll fluorescence parameters were then tested with split-split plot ANOVA. When the main effect of a factor with more than two levels or an interaction was significant for a given parameter, Scheffe's test was used for means separation. All the analyses were conducted using the statistical package Data Desk 6.01 at α = 0.05.

RESULTS

Height: The ANOVA detected a significant effect of light, moisture and nitrogen availability on the height. In addition, there was an interaction between light and moisture availability for this parameter (Table 1). The height declined from N1 to N4. Similar to the situation for N1 and N2, however, the difference in height between N3 and N4 was not significant at any moisture level (Fig.1).
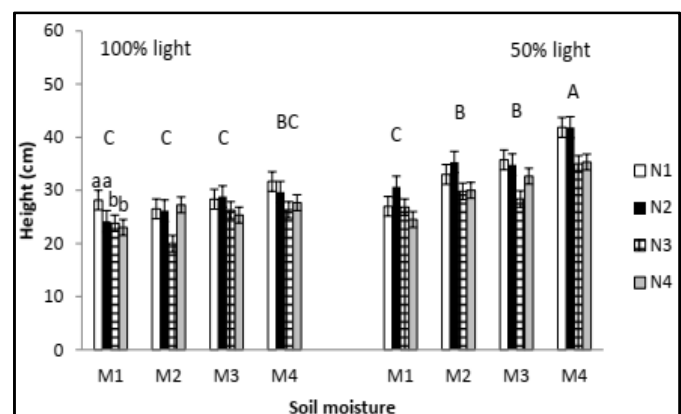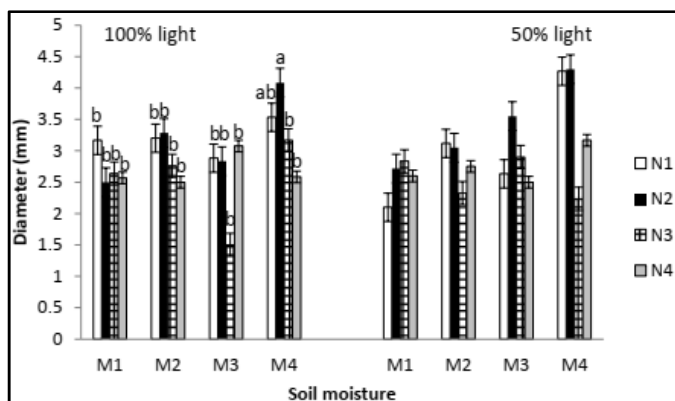

Fig. 1. Effects of light (L), moisture (M) and nitrogen (N) availability on height. The upper- and lower-case letters above the bars indicate the effect of L×M and N, respectively

Table 1. ANOVA p-values for the effect of treatments on growth and chlorophyll fluorescence

| Source	L	M	N	L×M	L×N	M×N	L×M×N	Rep
H	≤ 0.0001	≤ 0.0001	0.0003	0.0276	0.2751	0.8415	0.7643	0.0671
D	0.5836	0.0002	0.0007	0.5040	0.5636	0.0252	0.0589	0.4048
SV	0.0069	0.0001	0.0001	0.0712	0.3596	0.0033	0.0610	0.1353
Leaves	0.2336	0.0001	0.0053	0.4675	0.3853	0.0342	0.8641	0.0587
SM	≤ 0.0001	≤ 0.0001	0.0023	0.5337	0.4995	0.9692	0.3997	0.8712
RM	≤ 0.0001	0.0060	0.0676	0.0145	0.4549	0.9007	0.8984	0.8576
TM	≤ 0.0001	≤ 0.0001	0.0006	0.2973	0.3137	0.9158	0.9157	0.8999
R:S	0.0719	≤ 0.0001	0.4101	0.0024	0.3687	0.9894	0.1693	0.7586
F_o	0.1885	0.9544	0.5459	0.8347	0.6982	0.9837	0.5068	0.0736
F_v/F_m	0.9686	0.6376	0.4357	0.3563	0.9109	0.9706	0.6067	0.1008
F_v/F_o	0.9889	0.6516	0.454	0.3794	0.8963	0.9581	0.6162	0.0630

L – light, M – moisture, N – nitrogen, Rep – replication, *H* – height, *D* – stem diameter, *SV* – stem volume, SM – shoot biomass, RM – root biomass, TM – total biomass, R:S – root-to-shoot ratio, F_o– minimum fluorescence yield, F_v/F_m– maximum quantum yield of PSII, F_v/F_o– maximum primary yield of photochemistry of photosystem II.
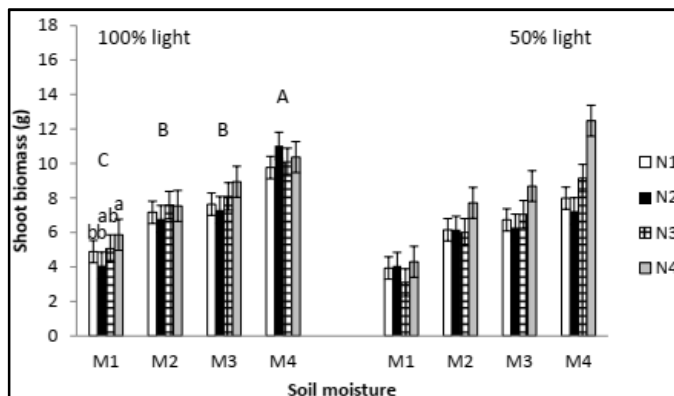

Fig. 2. Effects of light, moisture (M) and nitrogen (N) availability on diameter. The letters above the bars indicate the effect of M×N
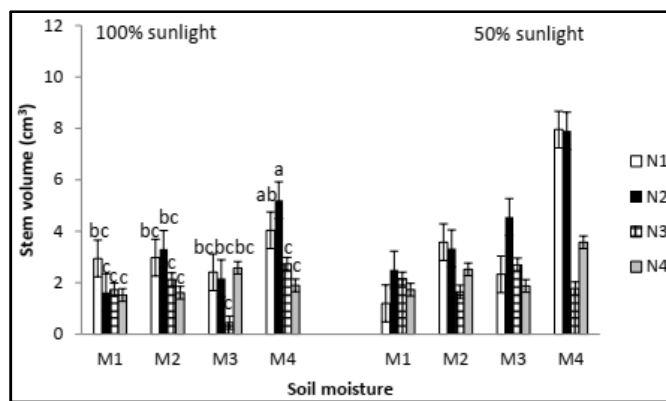
Fig. 3. Effects of light, moisture (M) and nitrogen (N) availability on stem volume. The letters above the bars indicate the effect of M×N
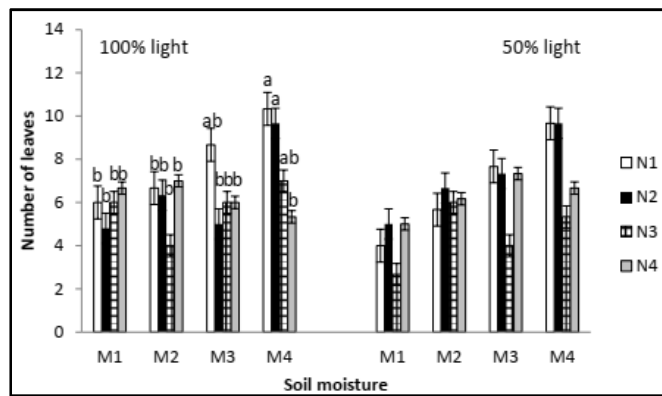
Fig. 4. Effects of light, moisture (M) and nitrogen (N) availability on number of leaves. The letters above the bars indicate the effect of M×N

Fig.5. Effects of light, moisture and nitrogen availability on shoot biomass. The upper- and lower-case letters above the bars indicate the effect of moisture and nitrogen availability, respectively

In terms of the L×N interaction, height was unaffected by moisture under 100% light whereas the values were lowest at M1 and highest at M4 under 50% light. Responses of height to M2 and M3 were similar in the shaded treatment. None of the moisture levels in 100% light differed with M1 at 50% light for height. Similarly, the parameter responded to M2 and M3 under 50% light in a comparable manner to M4 under 100% light (Fig. 1).

Stem diameter: Stem diameter was influenced by moisture and nitrogen supply as wells their interaction (Table 1).On the other hand, no significant effects of light or light related interaction was observed. Values were highest in N2 atM4 and lowest in N3 at M3 (Fig. 2). However, the difference between N2 and N1 was not statistically significant at M4.

Stem diameter declined from N2 to the N3 and N4 treatments which did not differ with each other or any other treatment (Fig. 2).

Stem volume: The main effect of each of the factors tested was significant for stem volume (Table 1). It was augmented by 50% light (Fig. 3). In addition, moisture interacted with nitrogen supply in affecting this parameter following the same pattern described previously for stem diameter. There was no other significant interactive effect of treatments on stem volume (Table 1).

Number of leaves: Leaf count was affected by moisture, nitrogen, and their interaction (Table 1). There was neither a significant effect of light nor any other interaction of

treatments on number of leaves (Table 1). Although absolute values of the trait were highest in N1of M4, the post-hoc test detected as comparable the responses between the said nutrient treatment and either N2 and N3 in M4 or N1 in M3 (Fig. 4). Number of leaves declined from N1 and N2 to N4 at M4 but not in the other moisture treatments where it was unresponsive to nitrogen supply. M4 significantly increased number of leaves only at N2 (Fig. 4).

Shoot biomass: A significant main effect of light, moisture and nitrogen supply was observed for shoot biomass (Table 1). There wasno significant interaction among the treatments for this trait. Shoot biomass was suppressed by 50% light. On the other hand, it increased from M1 to M4 with a notable absence of a significant difference between M2 and M3. The response to nitrogen availability was such that it increased from N1 to N4. However, N1 and N2 had a similar effect on this biomass component. Furthermore, differences between N3 and either N4 or the other two nitrogen treatments were insignificant (Fig. 5).

any of the moisture treatments in 50% light. The other three moisture treatments in 100% light resulted in similar responses of root biomass (Fig. 6).

Total Biomass: Each of the factors examined significantly affected total biomass production (Table 1). They did not, however, interact in affecting this trait. Total biomass responded to light, moisture and nutrient availability following the trend described for shoot biomass above (Fig. 7).

Root-to-shoot biomass ratio: There was a significant effect of moisture availability on root:shoot. In addition, moisture availability interacted with light in affecting this parameter (Table 1). The M1 treatment significantly increased root:shoot under 50% light. Root:shoot did not differ among the other three moisture treatments under shade (Fig. 8). The scenario was different under 100% light where no significant differences existed between moisture regimes. Furthermore, root:shoot did not change between light treatments at any moisture level (Fig. 8).
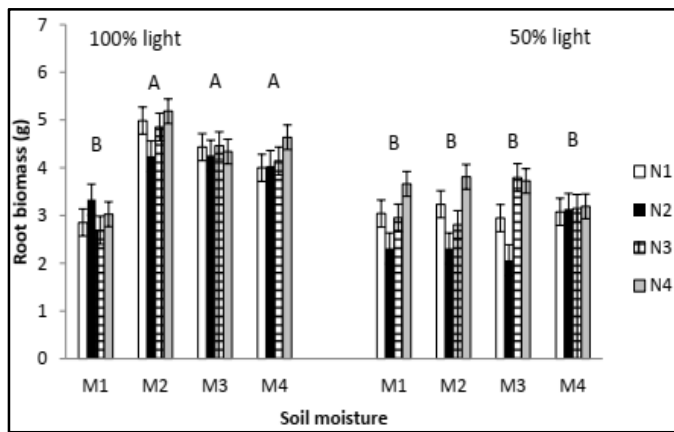

Fig. 6. Effects of light (L), moisture (M) and nitrogen availability on root biomass. The letters above the bars indicate the effect of L×M
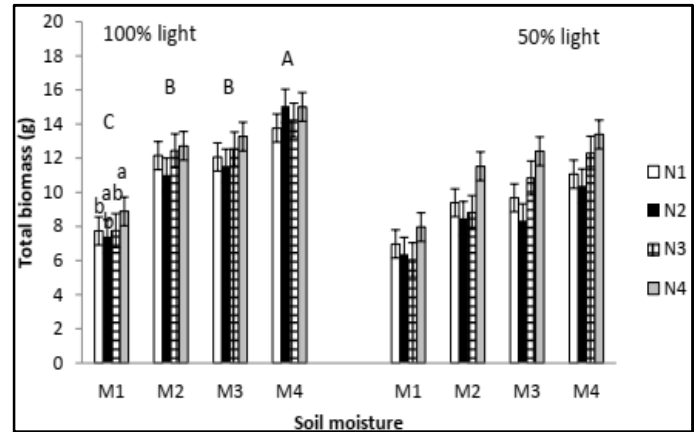

Fig. 7.Effects of light, moisture and nitrogen availability on total biomass. The upper- and lower-case letters above the bars indicate the effect of moisture and nitrogen availability, respectively
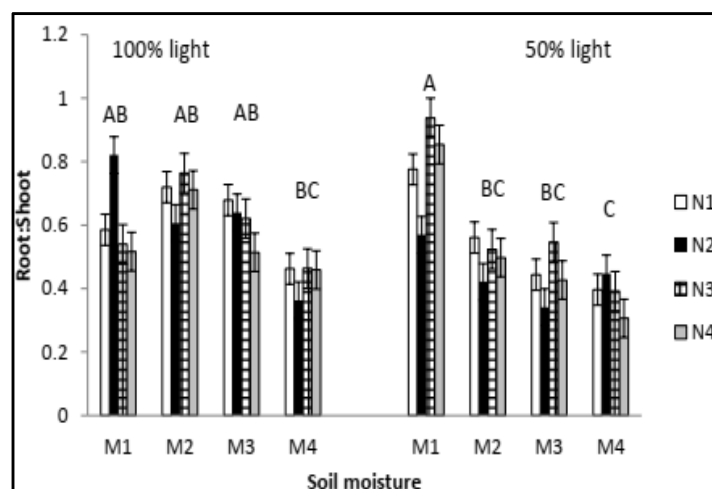
Fig. 8. Effects of light (L), moisture (M) and nitrogen availability on root-to-shoot biomass ratio. The letters above the bars indicate the effect of L×M

Root biomass: Root biomass was influenced by light, moisture, and light×moisture interaction (Table1). Under 50% light, root biomass was unaffected by moisture treatments (Fig. 6). On the other hand, it declined under the M1 treatment in 100% light which did not show a significant difference with

Chlorophyll fluorescence: There was no significant main or interactive effect of treatments on minimum (F_o) fluorescence yield, maximum quantum yield of PSII (F_v/F_m), and maximum primary yield of photochemistry of photosystem II (F_v/F_o) (Tables1 and 2).

Table 2. Effects of light, moisture and nitrogen availability (Mean±SE) on chlorophyll fluorescence parameters

Parameter	Light	Moisture	Nitrogen			
			N1	N2	N3	N4
F_o	100% light	M1	360.00±11.88	342.33±12.74	356.00±13.00	316.33±28.17
		M2	356.33±29.27	407.67±17.21	400.00±11.01	392.00±05.01
		M3	314.33±10.93	413.33±11.05	404.56±09.31	390.67±07.13
		M4	349.67±07.21	391.67±13.22	365.01±14.17	376.67±18.87
	50% light	M1	346.00±10.26	360.67±11.08	340.11±11.11	374.67±09.19
		M2	377.33±15.13	428.00±13.93	399.00±12.47	400.33±01.65
		M3	292.00±13.47	342.00±13.68	318.70±13.27	360.00±08.13
		M4	349.00±10.63	324.00±07.21	348.03±10.00	358.00±07.19
F_v/F_m	100% light	M1	0.79±0.01	0.80±0.01	0.80±0.00	0.82±0.01
		M2	0.80±0.08	0.80±0.07	0.79±0.03	0.78±0.00
		M3	0.82±0.01	0.78±0.00	0.80±0.01	0.78±0.01
		M4	0.83±0.00	0.81±0.00	0.81±0.00	0.80±0.01
	50% light	M1	0.83±0.00	0.82±0.00	0.80±0.01	0.81±0.01
		M2	0.82±0.01	0.80±0.00	0.81±0.01	0.80±0.00
		M3	0.81±0.00	0.79±0.01	0.79±0.00	0.78±0.00
		M4	0.82±0.00	0.82±0.00	0.80±0.00	0.81±0.00
F_v/F_o	100% light	M1	3.98±0.20	4.03±0.14	4.01±0.16	4.78±0.48
		M2	4.05±0.21	3.65±0.15	3.61±0.08	3.57±0.06
		M3	4.60±0.27	3.63±0.12	3.60±0.15	3.57±0.21
		M4	5.03±0.15	4.18±0.07	4.07±0.10	4.10±0.13
	50% light	M1	5.02±0.09	4.58±0.13	4.10±0.11	4.23±0.16
		M2	4.44±0.21	3.90±0.09	3.91±0.09	3.93±0.05
		M3	4.34±0.05	3.72±0.15	3.63±0.07	3.58±0.06
		M4	4.60±0.07	4.56±0.01	4.40±0.10	4.35±0.05

DISCUSSION

Morphology: Light has been highlighted as one of the main abiotic factors controlling the growth and functioning of plants in natural ecosystems. In this study, the shade treatment simulated the light climate beneath a forest canopy. Phenotypic adjustments to light range from physiological changes at the level of the photosynthetic apparatus in the leaf to whole-plant changes in morphology and biomass (Lüttge, 2013). The augmentations of height by shade observed in Gmelina are consistent with findings on other species including *Passiflora* spp., *Nothofagus leonii*, *Cordyline fruiticosa*, and *Entandrophragma angolense* (Zanella *et al.*, 2006; Pires *et al.*, 2012; Santelices *et al.*, 2015, Krishnakanth *et al.*, 2017, Minang and Ambebe, 2019). Stem elongation is a typical morphogenetic response to shade that is caused by an increase in endogeneous auxin levels (Ford, 2014). As rays of sunlight pass through the canopy, the selective absorption of red light by foliage can result in a major increase in the far-red to red light ratio in the forest understory environment, which favours *de novo* synthesis of auxins (Tao *et al.*, 2008). Mechanistically, the hormone initiates loosening of the cell wall matrix with the outcome that increased turgor against the wall results in the elongation (Ray and Ruesink, 1962). However, the low water availability and, hence, tissue water content due the lowest moisture treatment level likely made it impossible for the shaded seedlings to take advantage of the auxin effect at this moisture regime. Better height performance of seedlings raised under shade resulted in the higher stem volume in this treatment than under full sunlight.

Beneficial effects of nitrogen fertilization on growth and net photosynthesis have been attributed to an increase in the amount and activity of the key photosynthetic enzyme, ribulose-1,5-bisphosphate carboxylase/oxygenase (Guo*et al.*, 2016). Furthermore, nitrogen application on nutrient limited sites often results in leaf expansion and increased foliar contents of the enzymatically active substrate, ribulose-1,5-

The finding of this study that height, stem diameter, number of leaves, and stem volume did not increase with nitrogen addition is an indication that tissue nitrogen concentrations due to the lowest nitrogen treatment level was already sufficient for the growth of the seedlings. A plant's response to mineral nutrition is such that growth increases initially with an increase in nutrient supply up to the so called ' adequate zone' where nutrient addition does not result in an increase in growth, but is reflected in increased tissue concentrations (Taiz and Zeigler, 2010). Beyond, this point is the 'toxicity zone' where any further increase in nutrient concentration will lead to a decline in growth due to toxicity. The decline in height at N3 and N4 and the tendency for a decline in diameter and stem volume at these nutrient levels may be ascribed to the toxic nitrogen levels in the seedlings as reported previously for *Elaeis guineensis* (Mohidin *et al.*, 2014). Visible nitrogen toxicity symptoms of necrosis of leaves that eventually led to the death of some of the seedlings were observed. An increase in soil moisture availability has been found to augment height of *Achyranthes japonica*, height and number of leaves of *Helianthus annus*, and height, leaf area, number of leaves, leaf chlorophyll content, root length, and number of branches of *Dracocephalum moldavica* (Lee and Park, 2005; Abayomi and Adefila, 2008; Alaei *et al.*, 2013). However, researchers have detected two-factor interactions suggesting that the positive effect of the moisture increase is limited to plants growing under favourable nutrient conditions (Lee *et al.*, 2017). The finding of the present study that the highest moisture level augmented stem diameter, volume, and number of leaves only at the non-toxic nitrogen levels concurs with the latter view.

Biomass: The responses of biomass to treatments were as expected. The decline in total biomass production and biomass of plant components under shade may be attributed to a lower availability of light for photosynthesis and, hence, carbohydrate formation. This trend is consistent with the outcome of research by other investigators (Guenni *et al.*, 2008). In contrast to our data, however, biomass accumulation of *Menthapiperita* was not influenced by a manipulation of the

intensity of sunlight (Virzo de Santoand Alfani, 1980). Such discrepancy between studies highlights varying adaptive capabilities of the species due to differences in evolutionary history and other environmental conditions. The beneficial effect of increasing moisture and nitrogen availability on the biomass traits was an expected result since nitrogen is fundamental to the process of photosynthesis and biomass accumulation on the one hand, and water is essential for nutrient uptake and translocation of photosynthetic assimilates on the other (Lambers *et al.*, 2013). The unresponsiveness of root biomass to light at M1 is indicative of stronger low moisture stress than light effect at this moisture regime.

According to the theory of functional balance, a plant would respond to limited availability of a given resource with a relative increase in the flow of assimilates to the plant part that is responsible for its acquisition (Brouwer, 1963). The marked increase in root:shoot by the lowest moisture level in shade is in accord with Brouwer's hypothesis. In contrast, however, the inability of a decrease in moisture supply to augment biomass allocation under full sunlight may be linked to soil warming due to the direct solar radiation reaching the soil. The increase in soil temperature should have been greatest at M1 where soil moisture content was least. The rate of root respiration increases exponentially with temperature and up to half of the daily carbon gain by photosynthesis can be lost through root respiration (Pregitzer *et al.*, 2000). The finding that root biomass allocation was unaffected by nitrogen supply was justified by the fact that none of the nitrogen treatment levels imposed low nitrogen stress on the seedlings.

Chlorophyll fluorescence: The very important role of the chlorophyll fluorescence technique in the measurement of PSII activities and screening of photosynthetic processes related to the plant status is well established (Ivanov and Bernards, 2016). Commonly used chlorophyll fluorescence parameters, such as F_o, F_v/F_o, and F_v/F_m, are considered to be the most useful in evaluating the stability and functioning of the photosynthetic machinery under variable environmental conditions. This study's findings that the chlorophyll fluorescence parameters were generally insensitive to treatments and that all the values of F_v/F_m and F_v/F_o were within the normal range for a healthy plant, is an indication that the stress imposed by the treatments did not cause damage to the photosynthetic apparatus.

Conclusion

As expected, light had an effect on growth of Gmelina. In addition, augmentations of growth by moisture addition were dependent on nitrogen availability. However, the complete absence of a 3-way interaction suggests that the responses to light may not be constrained by the interaction of the moisture and nutrient treatments tested.

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