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Growth and physiological assessment of chengal seedlings planted under different age groups and fertilizer treatments in logged-over forest

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Abstract

The replanting of chengal or scientifically known as *Neobalanocarpus heimii*, an endemic Malaysian hardwood for rehabilitation purpose in logged-over forests has gained much prominence lately due to its high economic value. In this study conducted in Tekai Forest Reserve, the optimum age and fertilizer requirements on the growth performance of chengal seedlings planted in a logged-over forest were determined using improved planting techniques. Results showed that the growth of the chengal seedlings were significantly affected by different age and fertilizer treatments. It was found that 1 year 8 month (1y 8m) old chengal seedlings, given a combination slow release fertiliser (SRF) and organic fertilizer showed significantly the highest growth

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compared to 6 month (6m) seedlings treated with either SRF or organic fertilizer after 44 months of planting. However in contrast, 6m old seedlings exhibited the highest physiological characteristics namely net photosynthetic rate, transpiration rate, stomatal conductance and Leaf Area Index (LAI) throughout, compared to the 1y 8m old seedlings. The reversed pattern was recorded for Water Use Efficiency (WUE) where 1y 8m old chengal measured higher values compared to 6m chengal. Photosynthetic light response curve were also significantly affected by different age and fertilizer treatments. Chengal at 6m old exhibited higher mean value of photosynthetic components derived from the light response curve specifically maximum photosynthetic rate (A_{max}), light compensation, light saturation, dark respiration and quantum efficiency compared to those in 1y 8m old chengal. All the photosynthetic components except for A_{max} declined significantly under different fertilizer applications. A combination of fertilizers contributed to the highest mean values and the least was in chengal applied with only organic fertilizer. The results from this study has provided new insights on the relationship between the growth performance of chengal and its physiological processes, viz.photosynthetic rate, transpiration rate, stomatal conductance, LAI, WUE and photosynthetic light response curve after outplanting in a logged over forest.

1. Introduction

Chengal, scientifically is known as *Neobalanocarpus heimii* a species of tree from the Dipterocarpaceae family. It produces a heavy hardwood timber which is highly valued for its strength, durability and workability. Chengal is regarded by the timber trade as a 'primary hardwood' and is well known to have a slow growth rate. Earlier reports have suggested that at early seedling stages, chengal is sensitive to over exposure and drought and is naturally absence in open areas. According to Marzalina et al. (2001), the species is much rarer now than it was in the early 20th century. In view of the demand for this and other timber species, the Malaysian government has taken steps to implement conservation measures and sustainable management practices in remaining forest areas. The dipterocarps, including the chengal species, are the main representative timber tree species in Malaysia (Symington 2004, Samsudin 2010). The ability of individual species to tolerate different environmental conditions in its distribution zone generally reflects inherent physiological characteristics of the species.

An important factor that determines plant growth and development is plant nutrition. Apart from carbon, hydrogen and oxygen, which are obtained from the atmosphere, plants require about 17 macro and micronutrients for healthy growth, depending on the plant species. Macronutrients such as nitrogen (N) play the most recognized role in plants for its presence in the structures of chlorophyll and protein molecules. Other important macronutrients are phosphorous and potassium which together with N constitutes N, P, K found in most chemical fertilizers used. It is well known that fertilizer addition typically increases plant growth, but less is known about the optimum amount and ideal type of fertilizer that should be used to affect positively both the growth and physiological attributes of plants under different light availability conditions (Rosati et al., 2000; Turnbull et al., 2007). It has been suggested that plants are able to optimize the allocation of N in order to preserve a balance between the Calvin cycle (i.e., Rubisco) and light-harvesting (chlorophyll) capabilities (Ashton et al., 1988; Warren & Adams, 2001; Delagrange, 2010).

Age is another important factor that determines plant growth. Its physiology and response to environmental changes alter with time. In fact, little has been documented on how age and size of trees are related to their physiology overtime (Niinemets, 2010). Many questions have been raised as to whether the changes in tree physiology are age dependent or altered through physiological and environmental stresses. Correlation analyses using large datasets on tree height and age have suggested that tree size and age highly correlate with foliar modifications (physiological changes) (Niinemets, 2002; Ambrose et al., 2009). A lot of work on age related physiology have been done with angiosperms, but very little has been documented on dipterocarps. It has also been suggested that the age factor affecting the photosynthetic characteristics is only significant during the first year of tree development (Mencuccini et al., 2007; Ambrose et al., 2009). Thus, both age and the environment play a role in the observed decline in photosynthesis in older to young trees. However, clearly more work with different age and size are needed to gain a more conclusive insight into the relative significance of tree size and age in determining the variation in physiological characteristics during tree growth and maturation.

As for dipterocarps, there is scarce information on its physiological parameters, especially regarding its photosynthetic characteristics. In this study, chengal seedlings were planted and rehabilitated in an open and logged area and its physiological characteristics investigated. Thus, the objectives of this study were; 1) to determine the growth and physiological parameters and 2) to analyze the photosynthetic components of chengal seedlings of different age, under different fertilizer treatments in logged-over forest.

2. Materials and Methods

2.1 Study Area

The Tekai Forest Reserve located in Jerantut, central in the state of Pahang was the chosen site for the study. The study plot of 1.73 hectare was located in Plot 4, Compartment 89B, in the Tekai Forest Reserve, Jerantut, Pahang. The topography is with elevations ranging from 80 to 120 m above sea level. The nearest meteorological data collection was at the Weather Station in Batu Embun, Jengka, Pahang, about 20 kilometres from the study plot. Data were also obtained from the Meteorological Department of Malaysia (unpublished data). The annual rainfall of Tekai Forest Reserve, Jerantut as evident from the rainfall data from 2007 to 2011, varied between 2,530 mm and 3,045 mm, with a mean annual rainfall of 2,772 mm. The mean annual temperature for Tekai Forest Reserve was 27.9° C with a daily mean minimum and maximum of 19.0° C and 37.9° C, respectively. As expected of an equatorial region, the area has high humidity. The relative humidity were on the high side towards the end of the year from September to December (84.4% - 87.3%), and lowest during the period of February to July (79.9% - 84.2%).

2.2 Experimental Design and Plot Establishment

A total of 540 chengal seedlings were planted using an improved planting technique developed by Raja Barizan & Shamsudin (2008) which takes into account the hole size, optimum light level and fertiliser application (addition of SRF). The planting site was cleared using a back-hoe tractor. Planting spacing was 3 m x 3 m. Due to improvements in preparing the planting hole and the usage of advanced size of planting stocks, a semi-mechanized planting approach was applied. A vehicle of track tires skid steer loader model 753 or 773 (Bob-Cat) was attached to a hydraulic auger size 36 inches (90 cm) diameter. The size of the planting hole prepared was based on the size of the auger used, ± 90 cm width and ± 90 cm depth, to provide ample space for root growth. Prior to planting, all chengal seedlings were hardened through a slow hardening process at the nursery, FRIM Research Station, Jengka, Pahang. Chengal stocks were placed under 50% light intensity black nets and were exposed to an increment phase of direct sunlight, 2 - 3 months prior to planting. During the hardening periods, the stocks were relieved from transporting shock and the saplings acclimatised to the new open environment in the logged-over forests.

The Randomized Complete Block Design (RCBD) was applied for this study. The experimental design was as follows: 2 Age × 3 Fertiliser Level × 3 Block × 30 Chengal seedlings. The plot was replicated into 3 blocks which consisted of two different ages of chengal seedlings, which were 6m and 1y 8m old. Age of chengal stock under category 1y 8m were 80 - 150 cm in height and 50 - 70 mm in diameter. Whilst the 6m old chengal were 50 - < 80 cm in height and 30 - 50 mm in diameter. Three types of fertiliser treatments were used; 400 g SRF, 500 g goat dung and a combination of SRF (200 g) and goat dung (200 g). The Multicote 12 fertiliser of SRF contains an element nutrient of 19N:10P_2O_5:13K_2O:2MgO and trace elements, whilst organic fertiliser goat dung contains an element nutrient of 11N: 5P_2O_5:11K_2O which was produced and manufactured by Lembaga Pertubuhan Peladang. The fertilisers were applied once at planting. Soil mineral and physical properties at the study site are shown in Table 1.

Table 1: Soil chemical and physical properties at study area

Parameter	Soil chemical properties	Parameter	Soil physical properties
Total N (%)	0.12	pH	4.56
Available P(ppm)	4.48	CEC ($cmol_c kg^{-1}$)	14.40
Mg ($cmol_c kg^{-1}$)	0.30	Clay (%)	24.14
Ca ($cmol_c kg^{-1}$)	0.18	Silt (%)	10.05
K ($cmol_c kg^{-1}$)	0.14	Fine Sand (%)	22.36
Organic C (%)	1.34	Coarse Sand (%)	30.11

source : Forest Research Institue Malaysia (FRIM) Soil Department

2.3 Data Collection

2.3.1 Growth Performance & Physiological Parameters

Net photosynthetic rate, transpiration rate, stomatal conductance and CO_2 concentration (Ci) were measured using a portable photosynthesis system (LI-6400, LICOR, USA). A total of three seedlings from each treatment and three fully matured leaves per seedling were used for the measurements. Measurements were carried out from 900 to 1130 am, when the photosynthetic rate was generally high and to avoid midday photosynthesis depression (Kenzo et al. 2007). For the development of the light response curve, light intensities measured, varied from 2000, 1800, 1500, 1000, 800, 400, 200 and 0 µmol m^{-2} s^{-1}. Net photosynthetic (A_n) at each PPF was recorded when it was stable (usually 3 - 5 min), with CO_2 concentration inside the leaf chamber maintained at 380 µmol mol^{-1}.

During the measurements, the ambient air humidity was 60 - 63% and leaf temperature was about 26 - 27° C. Photosynthetic components were derived from each light response curve by fitting a linear regression line between the 0 - 200 µmol m^{-2} s^{-1} light range, with the light compensation point (µmol photons m^{-2} s^{-1}) determined when y=0 and the dark respiration rate (µmol CO_2 m^{-2} s^{-1}) determined when x=0. Apparent quantum efficiency was calculated as the initial slope of the curve. The A_{max} (µmol m^{-2} s^{-1}) was estimated as the asymptote of the light response curve, while the light level was the light saturation point (µmol photons m^{-2} s^{-1}). Before the photosynthetic light response curve was determined, each plant was maintained at maximum irradiance until net photosynthetic rate became constant, a process requiring 25 to 30 min. The relationship between net photosynthetic and transpiration rate was expressed as WUE. LAI of chengal seedlings were measured using the LAI-2000 Plant Canopy Analyser. All physiology and LAI data collections were done prior to growth parameter measurements at 12th, 22nd and 44th month after planting in the field. A height pole was used to measure height of the chengal from the base of the stem to the highest shoot. Meanwhile, a caliper was used to measure the basal diameter at 5 cm from the base.

2.3.2 Data Analysis and Interpretation

The data collected were analyzed using two-way analysis of variance (ANOVA) and Generalized linear model (GLM) to test the significant difference between the treatments given. As for the fertilizer effect on the above parameters, the Least significant difference (LSD) and Waller-Duncan's Multiple Range Test (DMRT) under GLM were used. While for age treatments, post hoc comparison test could not be performed since there were only two independent variables. Therefore, only the mean values were compared and the significant levels determined based on ANOVA.

3. Results and Discussion

3.1 Growth Performance

The survival rate of chengal seedlings planted in the field was moderately high with 88% survival percentage after 44 months of planting. The survival percentage obtained using improved planting techniques showed that the survival of dipterocarp seedlings can be improved compared to plants planted using the conventional method. A study by Widiyatno et al, 2014 on early performance of 23 dipterocarp species planted in logged-over forest using conventional method recorded only a 70% survival rate after 6.5 years of planting.

Growth and physiology parameters of chengal seedlings in the field, under different age group and fertilizer treatments, showed a significant difference (Table 2). Interactions between both seedling age and fertilizer treatments contributed to a significant effect on growth parameters in terms of height and diameter as well as all the physiological parameters, namely net photosynthetic rate, transpiration rate, stomatal conductance, WUE and LAI at $p < 0.05$ throughout the 44 months of experimental period after planting in the field. All mean values for the observed parameters increased throughout the planting period from 12 to 44 months in the field. It was observed that 1y 8m seedlings showed a higher mean height and diameter compared to 6m old chengal stands for all months. Height and diameter of chengal stands increased gradually by 53 and 51 % from 12 to 44 months respectively after planting in the field (Table 3). Chengal of 1y 8m could be seen to withstand intensive weed growth compared to 6m old seedlings. To reduce the amount of weeding it is preferable to plant seedlings which are large enough to overcome weed competition at an early stage. Similar results were reported in a study by Raja Barizan, 2000 in the Berkelah Forest Reserve, where large *Hopea odorata* seedlings planted resulted in a higher significant increment and a better survival rate compared to small seedlings.

Table 2: Summary of analysis of variance (ANOVA) of physiological parameters for chengal seedlings planted in the field

Source of variance	df	F-value[1]				
		Physiological parameters				
		Net Photosynthetic rate	Transpiration rate	Stomatal conductance	LAI	WUE
MONTH	2	12315*	12264*	1729*	10095*	1729.01*
BLOCK	2	4.27 ns	10.27 ns	2.59 ns	1.19 ns	13.70ns
AGE	1	1447.9*	1995.9*	429.9*	787.7*	385.77*
FERTILIZER	2	1423.5*	3844.7*	547.3*	1559.9*	780.75*
MONTH*AGE*FERTILIZER	4	7.50*	13.99*	19.26*	4.67*	44.38*
BLOCK*AGE*FERTILIZER	4	1.72 ns	0.02 ns	0.99 ns	0.39 ns	0.18ns
AGE*FERTILIZER	2	53.9 *	35.5*	11.1*	10.7*	25.40*

* significant at $p < 0.05$

Table 3: Effects of age treatments on physiological parameters of chengal seedlings planted in the field

	Parameters	Age group	
		1 y 8 m	6 m
12th month			
	Height (cm)	143.20 ± 3.86	132.88 ± 3.51
	Diameter (mm)	15.06 ± 0.53	13.64 ± 0.30
	Net photosynthetic rate (µmol m^{-2} s^{-1})	5.72 ± 0.51	6.20 ± 0.30
	Transpiration rate (µmol m^{-2} s^{-1})	2.45 ± 0.25	2.68 ± 0.21
	Stomatal conductance µmol m^{-2} s^{-1})	0.092 ± 0.007	0.099 ± 0.008
	LAI	5.42 ± 0.27	5.67 ± 0.24
	WUE	2.33 ± 0.04	2.31 ± 0.05
22nd month			
	Height (cm)	191.93 ± 9.02	174.3 8± 3.83
	Diameter (mm)	21.20 ± 1.16	19.55 ± 0.65
	Net photosynthetic rate (µmol m^{-2} s^{-1})	7.50 ± 0.41	8.02 ± 0.33
	Transpiration rate (µmol m^{-2} s^{-1})	2.88 ± 0.29	3.14 ± 0.24
	Stomatal conductance µmol m^{-2} s^{-1})	0.118 ± 0.031	0.148 ± 0.256
	LAI	5.88 ± 0.26	6.16 ± 0.25
	WUE	2.60 ± 0.04	2.55 ± 0.03
44th month			
	Height (cm)	305.18 ± 25.27	287.09 ± 13.20
	Diameter (mm)	30.68 ± 2.88	28.49 ± 2.09
	Net photosynthetic rate (µmol m^{-2} s^{-1})	8.16 ± 0.41	8.66 ± 0.26
	Transpiration rate (µmol m^{-2} s^{-1})	3.42 ± 0.36	3.88 ± 0.39
	Stomatal conductance µmol m^{-2} s^{-1})	0.172 ± 0.027	0.196 ± 0.026
	LAI	7.08 ± 0.39	7.38 ± 0.33
	WUE	2.39 ± 0.03	2.23 ± 0.05

Means values are ± SD with $n = 27$ from each treatments

Chengal seedlings applied with SRF and organic fertilizer recorded the highest mean for both height and diameter throughout the 44 months of planting followed by application with only SRF, while the lowest mean was recorded in chengal applied with only organic fertilizer. After 44 months, the height and diameter of chengal stands given SRF and organic fertiliser increased by 67 and 65 % respectively (Table 4). SRF with a nutrient content of 19:10:13 % nitrogen:phosphorus:potassium and goat dung with 11:5:11 % nitrogen:phosporus:potassium contributed to the highest increment for height and diameter. This showed that an addition of extra nutrients could improve the growth performance of chengal stands in logged-over forest. Fertilizer studies on dipterocarp species in the logged forests, where the fertiliser were applied in the field, produced different results (Wan Razali & Ang 1991; Ang et al. 1992; Nussbaum et al. 1995; Turner et al. 2006). The few field experimental studies that have been conducted suggest that nutrient limitation may be common in enrichment planting conditions. Nussbaum et al. (1995) and Hattori et al. (2013) reported strong growth responses to nutrient addition on very low fertility, heavily compacted, log-landing sites with no topsoil.

Table 4: Effects of fertilizer treatments on physiological parameters of chengal seedlings planted in the field

	Physiological parameters	Fertilizer treatments		
		SRF	Organic	SRF + Organic
12th month				
	Height (cm)	138.62 ±4.03 **b**	133.82 ±5.52 **c**	141.95 ±6.38 **a**
	Diameter (mm)	14.20 ±0.71 **b**	14.09 ±0.64 **c**	14.79 ±0.95 **a**
	Net photosynthetic rate (μmol m^{-2} s^{-1})	5.88 ± 0.26 **b**	5.53 ± 0.39 **c**	6.47 ± 0.17 **a**
	Transpiration rate (μmol m^{-2} s^{-1})	2.51 ± 0.12 **b**	2.34 ± 0.19 **c**	2.84 ± 0.15 **a**
	Stomatal conductance μmol m^{-2} s^{-1})	0.093 ± 0.005 **c**	0.089 ± 0.004 **b**	0.106 ± 0.005 **a**
	LAI	5.45 ± 0.18 **c**	5.31 ± 0.13 **b**	5.88 ± 0.13 **a**
	WUE	2.34 ± 0.04 **b**	2.36 ± 0.05 **a**	2.27 ± 0.04 **c**
22nd month				
	Height (cm)	184.87 ± 12.58 **b**	175.18 ± 4.49 **c**	189.22 ± 9.57 **a**
	Diameter (mm)	20.13 ± 0.42 **b**	19.55 ± 0.82 **c**	21.49 ± 1.36 **a**
	Net photosynthetic rate (μmol m^{-2} s^{-1})	7.54 ± 0.33 **b**	7.40 ± 0.27 **c**	7.78 ± 0.22 **a**
	Transpiration rate (μmol m^{-2} s^{-1})	3.23 ± 0.15 **b**	3.14 ± 0.20 **c**	3.30 ± 0.13 **a**
	Stomatal conductance μmol m^{-2} s^{-1})	0.122 ± 0.021 **b**	0.107 ± 0.016 **c**	0.171 ± 0.011 **a**
	LAI	5.92 ± 0.15 **c**	5.78 ± 0.17 **b**	6.35 ± 0.15 **a**
	WUE	2.33 ± 0.05 **b**	2.35 ± 0.05 **a**	2.35 ± 0.04 **a**
44th month				
	Height (cm)	299.42 ±13.38 **b**	265.99 ± 6.22 **c**	311.48 ± 21.39 **a**
	Diameter (mm)	30.25 ± 0.48 **b**	26.45 ± 0.85 **c**	32.23 ± 2.09 **a**
	Net photosynthetic rate (μmol m^{-2} s^{-1})	8.19 ± 0.28 **b**	8.18 ± 0.35 **b**	8.65 ± 0.18 **a**
	Transpiration rate (μmol m^{-2} s^{-1})	3.75 ± 0.43 **b**	3.51 ± 0.18 **c**	3.99 ± 0.16 **a**
	Stomatal conductance μmol m^{-2} s^{-1})	0.174 ± 0.015 **b**	0.159 ± 0.011 **c**	0.220 ± 0.012 **a**
	LAI	7.13 ± 0.22 **b**	6.87 ± 0.17 **c**	7.71 ± 0.11 **a**
	WUE	2.18 ± 0.04 **b**	2.33 ± 0.03 **a**	2.16 ± 0.03 **c**

Means in each column not sharing same letter letter are significantly different at $p < 0.05$, values are ± SD with $n = 27$ from each treatments

3.2 Physiological Parameters

The study also found that 6m old chengal seedlings contributed the highest mean net photosynthetic rate, transpiration rate, stomatal conductance and LAI throughout, compared to the 1y 8m old seedlings. However a reversed pattern was recorded for WUE where 1y 8m old chengal stands exhibited higher values compared to 6m chengal, with an increment of 7% after 44 months planting (Table 3). Ishida et al. (2006) reported a similar observation whereby the photosynthetic, transpiration, stomatal conductance of *Dryobalanops aromatica* (medium growing) recorded higher rates in younger seedlings by 70% compared to older seedlings. The higher WUE values observed in the older chengal planted seedlings are in accordance with a study on chengal and *Pouteria* species, both are shade tolerant, by Kenzo et al. (2008). They reported that WUE negatively correlated with all other physiological characteristics such as net photosynthetic rate, transpiration rate and stomatal conductance. High stomatal conductance species generally exhibit high water consumption via transpiration and photosynthetic activity (Larcher, 2003 & Maruyama et al., 2005). Thus chengal may require large amounts of water uptake to maintain their photosynthetic performance regardless of light, age group and fertilizer treatments. On the other hand, Eichhorn et al. (2007) reported that young and expanded leaves of *Shorea leprosula* seedlings planted in secondary logged-over forest in Sabah recorded a higher LAI compared to the old leaves. Reich et al. (2009) also concurred with the results where he noted that gradual changes in photosynthetic capacity and transpiration were observed to be influenced by age in trees. Higher values of photosynthesis and transpiration rates observed in younger leaves of seedlings compared to older ones might be due to leaf thickness. Extra mesophyll layers in older leaves could have contributed to the lower values observed in the physiology of chengal planted seedlings. Lower photosynthetic rates could also account for the lower stomatal conductance (Langenheim, 2003). Ishida et al. (2006) reported that leaf chlorophyll content differences in younger and older leaves of seedlings could be associated with the variance in photosynthetic activities. The young leaves were light green and had a lower chlorophyll content, but high chlorophyll a/b ratio compared to the old leaves which had a higher chlorophyll content but lower chlorophyll a/b ratio. This has been well documented in plants or leaves that are shaded or growing under lower light irradiances and higher a/b ratios are normally observed in sun plants and is associated with higher photosynthetic capacity (Nasrulhaq Boyce et al., 2011).

The combination of fertilizers treatment showed the highest physiology value compared to the application of SRF only, while the lowest was observed in seedlings applied with organic fertilizer for all months. In contrast, the trend recorded for WUE values varied, whereby organic fertilizer application contributed to the highest WUE compared to the application of SRF and the application of SRF and organic fertilizer in combination, by an increment of 6% and 7% respectively. The difference in values recorded did not vary much at the earlier phase of growth, from 12 to 22 months after planting (Table 4). All the physiological parameters determined were observed to decrease throughout planting regardless of both age and fertilizer treatments. A study by Kenzo et al. (2007) also observed a lower net photosynthetic rate for *Shorea ovata* species planted in a degraded forest of Niah Forest Reserve, Sarawak. Hazandy et al. (2011), who studied *Shorea platyclados*, *Shorea assamica* and *Anisoptera marginata* also recorded lower rates of transpiration and stomatal conductance in seedlings given controlled release fertilizer. Okuda et al. (2003) working on *Shorea platyclados* and *Shorea assamica* given NPK and organic fertilizer reported similar findings of WUE as was observed with chengal in this study, while Mun et al. (2011) recorded similar LAI values in *Shorea dasyphylla, Shorea leprosula* and *Shorea ovata*. The higher N mineral supply improved the physiological activity of chengal planted seedlings and in turn the increase in photosynthetic activity led to an increase in LAI (Saldana, 2005). These findings are in agreement with that of Irino et al. (2005) who reported that application of controlled release fertilizer showed the most favorable results in terms of survival and growth of dipterocarps in the field, suggesting it enhanced photosynthetic activity and nutrient status of the plants.

3.3 Light Response Curve

A significant difference was observed for all photosynthetic components derived from the light response curve experiments, which included A_{max}, light compensation point, light saturation point, dark respiration, and quantum efficiency in seedlings of different age groups and fertilizer regimes at the 12^{th}, 22^{nd} and 44^{th} months after growing in the field (Table 5). The A_{max} of planted chengal seedlings increased from the 12^{th} to the 44^{th} month as photosynthetic photon flux (PPF) increased from 0 to 2000 μmol m^{-2} s^{-1} for both chengal seedlings treated under different light and fertilizer treatments.

Table 5: Summary of analysis of variance (ANOVA) of light response curve derived parameters for chengal seedlings planted in the field

Source of variance	df	F-value[1]				
		Maximum photosynthetic rate	Dark respiration	Light compensation point	Light saturation point	Quantum efficiency
MONTH	2	18.65*	7.86*	204.03*	922.31*	505.97*
BLOCK	2	18.65ns	7.86ns	1.65ns	23.81ns	1.48ns
AGE	1	412.25*	529.01*	369.34*	183.86*	195.31*
FERTILIZER	2	460.93*	77.74*	739.75*	336.36*	235.90*
MONTH*AGE*FERTILIZER	4	1.19*	2.77ns	8.66*	1.00ns	3.39*
BLOCK*AGE*FERTILIZER	4	2.19ns	0.37ns	1.92ns	0.75ns	1.29ns
AGE*FERTILIZER	2	25.21*	0.06ns	2.22ns	31.77*	22.42*

* significant at $p < 0.05$

Age of chengal seedlings significantly affected A_{max}, light compensation point, light saturation point, dark respiration and quantum efficiency, where the younger and smaller size chengal seedlings (6m old) exhibited maximum mean values compared to the older 1y 8m old seedlings (Table 6). Chengal seedlings aged 6m exhibited the highest A_{max} and dark respiration with an increment of 3.3 and 10.9 % respectively compared to 1y 8m seedlings throughout the experimental period (Figure 1). Bruce et al. (2005) reported similar findings in *Phaseolus vulgaris* and *Acacia auriculariformis*, where he observed an A_{max} and dark respiration in younger leaves higher by nearly 60 and 55 % compared to older leaves regardless of treatment given. The difference in dark respiration between older and younger leaves is believed to be largely due to younger leaves of those plants developing an alternative oxidase system which inhibits the alternative pathway of electron transport in mitochondria (Bruce et al., 2005). The older leaves underwent a slower hardening process at the nursery whereby the exposure to sunlight was gradually done and planting in the field might have caused a complete elimination of the cytochrome path that returned with a recovery phase in the light (Bruce et al., 2005). Age related changes in light compensation, light saturation and quantum efficiency were also similar to those previously reported by Langenheim (2003) for other species of Amazonian rainforest tree species namely *Hymenaea courbaril* and *Hymenaea parvifolia*. They reported rates of young leaves were higher by 47 and 31 % compared to older leaves for *Hymenaea courbaril* and *Hymenaea parvifolia* respectively. In this study, the light compensation point of 6m old chengal seedlings was significantly higher by 6.4% compared to 1y 8m old planted chengal. The light saturation point of 6m old chengal seedlings was also higher by 2.6% compared to the old chengal seedlings. Similar results were also reported by Langenheim (2003) on *Agathis robusta* which recorded a light saturation point between 200 - 500 µmol m^{-2} s^{-1} 2-fold higher in young leaves compared old leaves grown under full sunlight. The young leaves of the chengal seedlings had higher stomatal conductance and higher intercellular CO_2 concentrations than mature leaves. The physiological attributes of light compensation point and light saturation were at their maximum in young leaves and declined with increasing age. The effect of age on all these characteristics can probably be explained by the higher dark respiratory rates with minimal quantum efficiency (Langenheim, 2003).

Table 6: Effects of age group on of light response curve derived parameters of chengal seedlings planted in the field

	Physiology parameters (μmol m^{-2} s^{-1})	Age group	
		1 y 8 m	6 m
12th month			
	Maximum photosynthetic rate	8.65 ± 0.32	9.67 ± 0.23
	Dark respiration	0.96 ± 0.04	1.06 ± 0.03
	Light compensation point	4.17 ± 0.32	4.45 ± 0.22
	Light saturation point	581 ± 17	600 ± 11
	Quantum efficiency	0.024 ± 0.09	0.027 ± 0.09
22nd month			
	Maximum photosynthetic rate	9.70 ± 0.41	11.07 ± 0.28
	Dark respiration	0.79 ± 0.03	0.89 ± 0.04
	Light compensation point	3.89 ± 0.37	4.13 ± 0.31
	Light saturation point	544 ± 26	559 ± 16
	Quantum efficiency	0.022 ± 0.18	0.024 ± 0.10
44th month			
	Maximum photosynthetic rate	11.67 ± 0.34	13.60 ± 0.22
	Dark respiration	0.65 ± 0.05	0.74 ± 0.04
	Light compensation point	3.86 ± 0.23	4.15 ± 0.33
	Light saturation point	522 ± 23	536 ± 15
	Quantum efficiency	0.020 ± 0.15	0.023 ± 0.09

Means values are ± SD with n = 27 from each treatments

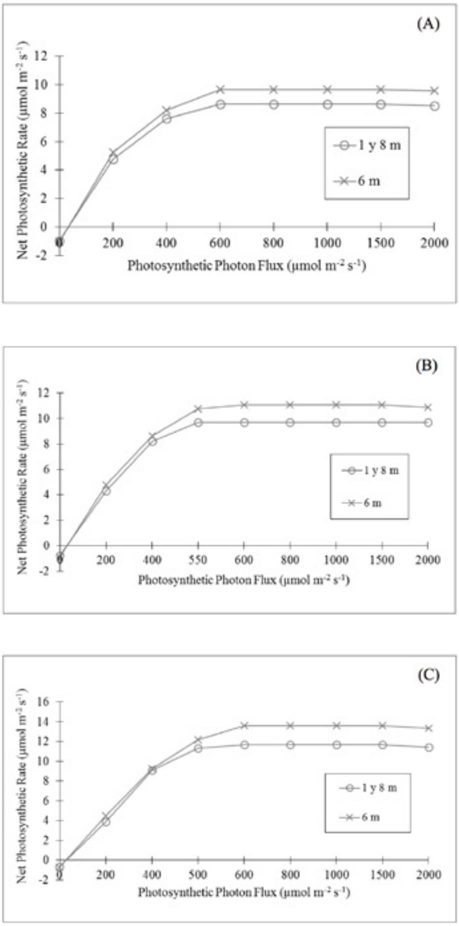

Figure 1: Photosynthetic light response curve for chengal seedlings under different age treatments. (A) 12 month. (B) 22 months. (C) 44 months after planting in the field. The relationship between net photosynthetic rate and photosynthetic photon flux were fitted by non-linear regression equation with n = 27 from each treatments.

Fertilizer application significantly affected the physiological characteristics of the planted chengal seedlings in the field (Table 7). All the physiological parameters with the exception for A_{max} declined significantly throughout the experimental period in the field with seedlings given a combination of SRF and organic fertilizers showing the highest mean followed by application of SRF and the lowest was recorded with the application of organic fertilizer singly. All derived parameters were observed to decrease throughout 44 months of planting in the field regardless of age group and fertilizer applications. In the field, chengal seedlings treated with a combination of

SRF and organic fertilizers showed the highest A_{max} with an average increment of 4.2 and 5.8 % compared to SRF and organic fertilizer applied singly respectively (Figure 2). Irino et al. (2005) reported the same results with *Dryobalanops lanceolata* where application of higher amounts of controlled release fertilizer increased the A_{max} and dark respiration of both seedlings in field by 9.6 and 10.0% respectively compared to the control (without fertilizer).

Table 7: Effects of fertilizer treatments on of light response curve derived parameters of seedlings planted in the field

	Physiology parameters (μmol m^{-2} s^{-1})	Fertilizer treatments		
		SRF	Organic	SRF + Organic
12th month	Maximum photosynthetic rate	9.32 ± 0.24 **b**	9.18 ± 0.24 **c**	9.74 ± 0.14 **a**
	Dark respiration	1.01 ± 0.05 **ab**	0.99 ± 0.06 **b**	1.03 ± 0.05 **a**
	Light compensation point	4.27 ± 0.17 **b**	4.02 ± 0.21 **c**	4.64 ± 0.12 **a**
	Light saturation point	591 ± 16 **b**	578 ± 17 **c**	603 ± 10 **a**
	Quantum efficiency	0.023 ± 0.07 **b**	0.021 ± 0.09 **c**	0.026 ± 0.08 **a**
22nd month	Maximum photosynthetic rate	10.06 ± 0.30 **b**	9.20 ± 0.29 **c**	11.91 ± 0.16 **a**
	Dark respiration	0.84 ± 0.05 **b**	0.81 ± 0.06 **c**	0.86 ± 0.04 **a**
	Light compensation point	3.87 ± 0.18 **b**	3.69 ± 0.19 **c**	4.45 ± 0.11 **a**
	Light saturation point	550 ± 13 **b**	530 ± 16 **c**	575 ± 10 **a**
	Quantum efficiency	0.021 ± 0.12 **a**	0.020 ± 0.11 **b**	0.023 ± 0.08 **a**
44th month	Maximum photosynthetic rate	12.28 ± 0.19 **b**	11.44 ± 0.30 **c**	14.07 ± 0.17 **a**
	Dark respiration	0.70 ± 0.05 **b**	0.65 ± 0.06 **c**	0.74 ± 0.05 **a**
	Light compensation point	3.89 ± 0.19 **b**	3.77 ± 0.14 **c**	4.35 ± 0.25 **a**
	Light saturation point	522 ± 13 **b**	512 ± 12 **c**	553 ± 6 **c a**
	Quantum efficiency	0.020 ± 0.10 **ab**	0.19 ± 0.11 **b**	0.021 ± 0.06 **a**

Means in each column not sharing same letter letter are significantly different at $p < 0.05$, values are ± SD with $n = 27$ from each treatments

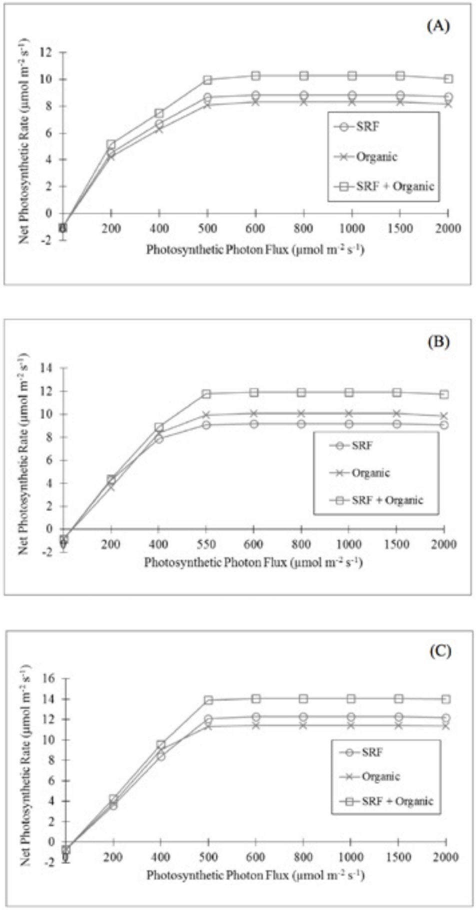

Figure 2: Photosynthetic light response curve for chengal seedlings under different fertilizer treatments. (A) 12 month. (B) 22 months. (C) 44 months after planting in the field. The relationship between net photosynthetic rate and photosynthetic photon flux were fitted by non-linear regression equation with n = 27 from each treatments.

A study by Kenzo et al. (2008) reported similar results with chengal planted in the field given extra nutrition where, it was observed that larger chlorophyll content and chlorophyll to nitrogen ratio in the leaves are related to lower light compensation, light saturation and dark respiration values and permitted better acclimation of the seedlings towards optimal light conditions (Table 7). An increased susceptibility to photoinhibition in plants grown with low N compared to those given higher N was reported by Bungard et al. (2000) and Feng (2008).

4. Conclusion

This study has shown that improved planting techniques can boost the survival and improve the growth performance of the shade tolerant chengal species which has a very slow growth rate. The result of the study also suggests that age and fertilizer treatment had a significant influence on the growth performance and physiological parameters of chengal seedlings planted in logged-over forest, where the older and bigger seedling enhanced growth compared to a younger seedlings. In contrast, younger and smaller chengal seedlings exhibited higher physiological characteristics compared to older chengal seedlings. A combination of SRF and organic fertilizer treatment gave better growth performance and increased the physiological characteristics compared to only application of SRF and organic fertilizer singly. It can be concluded that the adoption of improved planting techniques using older seedlings supplied with a combination of SRF and organic fertilizers can lead to an increased in growth and survival of the planted chengal seedlings in logged over forest.

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