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Variation in Photosynthetic Traits and Correlation with Growth in Teak (*Tectona grandis* Linn.) Clones

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Abstract: In order to interpret the patterns of genetic variation of photosynthesis and the relationships with growth traits within gene resources of teak (*Tectona grandis* Linn.), gas exchange, and chlorophyll fluorescence parameters, growth traits of plants in nursery and field trials were measured for 20 teak clones originated from different countries. The results show that there was abundant genetic variation in gas exchange, chlorophyll fluorescence, and growth among the teak clones. The measured traits were found to have generally high heritability (h^2) except for intercellular concentration of carbon dioxide (CO_2) (C_i). The net photosynthetic rate (P_n), seedling height, and individual volume of wood were significantly correlated with each other, and seedling height was significantly correlated with plant height in field trials, suggesting that P_n and seedling height can be useful in teak breeding. Teak clones 7029, 71-5, 7219, 7412, and 7122, and provenances 3070, 3074, and 3071 had higher photosynthetic rates, and can be regarded as a key resource in teak improvement programs. This work provides useful information for teak breeding and germplasm resource management.

Keywords: gas exchange; chlorophyll fluorescence; growth trait; genetic variation; early selection

1. Introduction

Teak (*Tectona grandis* Linn.) is naturally distributed in India, Thailand, Myanmar, and Laos [1,2]. Its desirable hardwood properties, fine grain, and durability have made teak the luxury timber for furniture making, carving, and building around the world [3,4]. Due to its economical importance, teak has been introduced widely in the tropical regions since the 19th century, especially in Asia, Africa, Central America, and South America [5].

As one of the most valuable wood species in international markets, teak plantations have developed rapidly in the recent decade. Developing high productivity and uniform clones that can be used for plantations in different regions has become an important objective of teak breeding. Information on variation of photosynthetic parameters and their relationship with growth traits help us understand underlying processes and responses, and will be useful in tree improvement programs. During the growth process of plants, organic compounds are generated by photosynthesis, and gradually accumulate in trunks. The photosynthetic characteristics are the main measurable indicators of plant growth rates [6]. Numerous studies on breeding for high photosynthetic ability in crops have been conducted, to improve the yield [7–9], but studies on forest trees are limited [10–12]. Chu et al. 2010 [10] studied gas exchange and chlorophyll fluorescence parameters, as well as their relationship with the growth of *Populus nigra*, and found that the species originating in Serbia, southern and east Europe can be regarded as a resource with high light-use efficiency for future breeding. Teak has broad leaves and prefers warmth and sunlight, and developing clones with high productivity and uniformity by evaluating photosynthetic characteristics can be an important goal in teak breeding. In the past, teak breeding was mainly focused on the analysis of growth indices in field experiments [13,14], and studies on photosynthetic physiology of teak are limited to those on photosynthetic responses of a single clone to simulated acid rain stress [15], photosynthetic physiological characteristics under different disturbance intensities among teak plants [16], and diurnal and seasonal photosynthetic characteristics in teak clones [17]. However, studies on teak germplasm or clones, which systematically estimate photosynthetic characteristics and correlation with growth, have not been reported.

The purpose of this study was (1) to investigate the genetic variation of photosynthetic parameters and growth traits of teak clones, (2) to reveal the correlation, if any, between photosynthetic characteristics and growth traits within the gene resources of teak, and (3) to evaluate and select superior teak resources possessing high photosynthetic efficiency for breeding.

2. Materials and Methods

2.1. Materials

A total of 20 widely cultivated teak clones propagated through tissue culture were investigated in this study. The 20 clones were selected from international provenance trial planted at Jianfeng, Hainan, China, by the Research Institute of Tropical Forestry of Chinese Academy of Forestry (RITF-CAF). A complete list of accessions with descriptions and origins is given in Table 1. Among these accessions, 10 were clones originating from India, 9 were from Myanmar sources and 1 from Nigeria.

Table 1. Information of 20 commercial teak clones investigated in the study.

Clone Name	Provenance Name	Longitude Latitude	Altitude (m)	Annual Rain Fall (mm)
Clones from India provenances				
7013	3070	77°20′ E 08°00′ N	700	1270
7029	3070	77°20′ E 08°00′ N	700	1270
71-5	3071	76°47′ E 10°30′ N	640	2030
7114	3071	76°47′ E 10°30′ N	640	2030
7122	3071	76°47′ E 10°30′ N	640	2030
7146	3071	76°47′ E 10°30′ N	640	2030
7137	3071	76°47′ E 10°30′ N	640	2030
7210	3072	76°10′ E 11°55′ N	823	1270
7219	3072	76°10′ E 11°55′ N	823	1270
7412	3074	74°28′ E 15°12′ N	43	2032
Clones from planted provenances in China (Myanmar source but no detailed records of origin)				
Z408	20001	110°14′ E 21°07′ N	60	1650
7509	8204	108°42′ E 18°51′ N	60	1600
7514	8204	108°42′ E 18°51′ N	60	1600
7531	8204	108°42′ E 18°51′ N	60	1600
7544	8204	108°42′ E 18°51′ N	60	1600
7549	8204	108°42′ E 18°51′ N	60	1600
7555	8204	108°42′ E 18°51′ N	60	1600
7559	8204	108°42′ E 18°51′ N	60	1600
8301	8204	108°42′ E 18°51′ N	60	1600
Clone from Nigeria provenance				
3078-5	3078	03°52′ E 07°10′ N	700	1900

2.2. Experimental Design and Growth Parameter Measurement

The young in vitro plantlets of teak clones were transplanted to a sterilized sand bed in the greenhouse at the Research Institute of Tropical Forestry, Chinese Academy of Forestry (RITF-CAF), in Guangzhou (113°18′ E, 23°06′ N). One month later, healthy and uniform seedlings (Ramets derived from each clone) about 6 cm in height were transplanted into plastic pots filled with a mixture of lateritic red soil, black peat, vermiculite, and perlite (2:2:1:1, v/v/v/v)—one seedling per pot. A completely randomized block design was used in this nursery experiment with 5 seedlings in one row per plot, 6 repeats in total with 40 cm × 40 cm pot space. Seedling height and collar diameter of all seedlings in the nursery were measured at the age of one year.

Field trial was carried out at Dingan in Hainan Island (110°19′ E, 19°39′ N) and a completely randomized block design was used with 6 plants in one row per plot, 6 repeats in total, with 2.5 m × 4 m space. Plant height (H) and diameter at breast height (DBH) of each plant in field trial were measured at the age of four years.

2.3. Physiological Parameter Measurement

Three seedlings in the nursery were randomly selected for each clone, 1 seedling per plot, 3 repeats in total, in a completely randomized block design (to make sure the test was random for all 60 selected seedlings) and 3 functional leaves per seedling exposed to sunlight were chosen for study. The gas exchange parameters including net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (Tr) were measured on sunny days between 8:45 and 11:30 in August 2013 with a Li-6400 portable photosynthetic apparatus (LI-COR Co. Lincoln, NE, USA) at the nursery of RITF-CAF, in Guangzhou. A leaf chamber automatic light (800 $\mu mol \cdot m^{-2} \cdot s^{-1}$) was used when testing, with CO_2 concentration 380 ± 15 $\mu mol \cdot mol^{-1}$, temperature of the leaf chamber 30–38 °C, and a relative humidity 58%–68% recorded by the photosynthetic apparatus under natural conditions. Three stable values were recorded for each leaf. Chlorophyll fluorescence characteristics were measured at the same time using the German PAM-2500 Walz portable fluorescence spectrometer, the saturation pulse intensity was 4500 $mol \cdot m^{-2} \cdot s^{-1}$, and actinic intensity was 1000 $mol \cdot m^{-2} \cdot s^{-1}$. The actual quantum yield PSII (Yield), non-photochemical quenching (NPQ) and maximum photochemical efficiency of PSII (F_v/F_m) were also measured [18,19]. The calculation formula for Yield is Yield = $(F_m' - F_t)/F_m'$, where F_m' is referred to maximum fluorescence under light adaptation, and F_t denotes real fluorescence at any given time. The formula of NPQ = $F_m/F_m' - 1$; $(F_v/F_m) = (F_m - F_o)/F_m$, and F_o, F_m, and F_v refer to dark-adapted initial fluorescence, maximum fluorescence, and variable fluorescence, respectively. Before testing, 20 min shading treatment was carried out with a blade holder to ensure selected leaves had dark adaptation for a long enough period of time.

2.4. Data Analysis

Water use efficiency (WUE) was calculated by the formula $WUE = P_n/Tr$ [20], and the coefficient of variation was calculated by the formula C = S/X, where S is the standard deviation, and X is the overall average value of each index. Clone heritability was calculated with the formula $h^2 = 1 - 1/F$ [21], where F is test statistic of clones in variance analysis. Individual volume of wood was calculated by the formula $V = 0.4787D^2H$, where D is DBH, and H is plant height of field trial [22]. Variance and Duncan's multiple comparison analyses were conducted for each parameter, and correlation analyses (using Pearson's product-moment correlations) between photosynthetic parameters, water use efficiency, and growth index, were performed using SAS software (version 8.1).

3. Results

3.1. Gas Exchange, Chlorophyll Fluorescence, and Growth Traits of Different Teak Clones

Variance analysis of gas exchange, chlorophyll fluorescence, and growth parameters among teak clones are shown in Table 2. There is a significant difference in the photosynthetic parameters, water use efficiency, and growth index but not for intercellular CO_2 concentration (C_i). In addition, apart from C_i ($h^2 = 0.145$) and NPQ ($h^2 = 0.168$), other parameters had high heritability ($h^2 = 0.670$–0.903), with actual quantum yield PSII (Yield) having the highest heritability (h^2 = 0.903), suggesting a strong genetic influence on the function, and that it is less affected by environment.

Table 2. Variance analysis (ANOVA) of gas exchange, chlorophyll fluorescence, water use efficiency, and growth parameters among teak clones.

Category	Parameter	*F*	*p*	Heritability (h^2)	Variation Coefficient
Gas exchange	P_n	5.46	<0.0001 ***	0.817	0.401
	G_s	4.53	<0.0001 ***	0.779	0.474
	C_i	1.17	0.3213 ^{ns}	0.145	0.111
	Tr	3.38	0.0004 ***	0.704	0.349
Chlorophyll fluorescence	NPQ	5.93	<0.0001 ***	0.168	0.447
	Yield	10.32	<0.0001 ***	0.903	0.294
	F_v/F_m	3.03	0.0011 **	0.670	0.028
Water use efficiency	*WUE*	10.32	<0.0001 ***	0.903	0.474
Seedling growth at 1 year	Seedling height	3.39	<0.0001 ***	0.705	0.116
	Collar diameter	3.29	<0.0001 ***	0.696	0.102
Field growth at 4 years	H	7.88	<0.0001 ***	0.873	0.092
	DBH	6.74	<0.0001 ***	0.852	0.167
Individual volume at 4 years	V	7.24	<0.0001 ***	0.863	0.327

Note: P_n: net photosynthetic rate, G_s: stomatal conductance, C_i: intercellular CO_2 concentration, Tr: transpiration rate, NPQ: non-photochemical quenching, Yield: the actual quantum yield PSII, F_v/F_m: maximum photochemical efficiency of PSII, *WUE*: water use efficiency, H: height of field growth at 4 years, DBH: diameter at breast height of field growth at 4 years, V: individual volume at 4 years. ** indicate highly significant difference at $p < 0.01$ level of probability, *** more highly significant difference at $p < 0.001$ level of probability, and ^{ns} no significance.

Duncan's multiple comparison analysis of photosynthetic and growth traits are listed in Tables 3–5. The ranges of the main parameters, such as P_n and F_v/F_m, were 4.45 ± 1.62–14.47 ± 0.32 μmol·m^{-2}·s^{-1}, 0.67 ± 0.02–0.75 ± 0.01, respectively. Water use efficiency (*WUE*) was between 1.02 ± 0.36 and 6.38 ± 1.25. Apart from the maximum photochemical efficiency of PSII F_v/F_m (0.028), the variation coefficients of other parameters (0.092–0.474) were great, suggesting that the teak genotypes possessed extensive variation in these traits. Results indicated that there are suitable germplasm resources for breeding of teak for high photosynthetic efficiency. Teak clones 7029, 71-5, 7219, 7412, and 7122 were selected as clones with high net photosynthetic rate based on the results.

Table 3. Values of gas exchange parameters among teak clones from different countries.

Clone	P_n (μmol·m^{-2}·s^{-1})	G_s (mol·m^{-2}·s^{-1})	C_i (μmol·mol^{-1})	Tr (mmol·m^{-2}·s^{-1})
7013	8.09 ± 3.76 defgh	0.14 ± 0.09 cdefgh	263.98 ± 7.95 ab	3.34 ± 1.58 abcde
7029	14.19 ± 1.17 ab	0.23 ± 0.04 abcde	261.92 ± 7.42 ab	2.69 ± 0.28 cdefg
71-5	13.50 ± 2.34 abc	0.28 ± 0.07 ab	290.25 ± 5.21 ab	3.04 ± 0.70 abcdef
7114	9.87 ± 4.09 abcdefg	0.18 ± 0.10 bcdefg	237.06 ± 18.08 b	3.81 ± 1.61 abc
7122	11.58 ± 2.02 abcd	0.25 ± 0.07 abcde	287.70 ± 8.14 ab	3.91 ± 0.71 abc
7146	9.59 ± 1.30 bcdefgh	0.20 ± 0.03 abcdef	280.00 ± 3.58 ab	4.02 ± 0.59 abc
7210	6.16 ± 0.77 efghij	0.08 ± 0.02 fgh	219.18 ± 28.34 b	2.07 ± 0.56 cdefg
7219	14.47 ± 0.32 a	0.32 ± 0.02 a	287.80 ± 6.16 ab	3.97 ± 0.25 abc
3078-5	9.66 ± 2.87 abcdefgh	0.22 ± 0.07 abcde	292.56 ± 4.91 ab	3.80 ± 0.66 abc
7412	11.01 ± 2.66 abcde	0.29 ± 0.09 ab	298.57 ± 18.78 ab	4.73 ± 0.97 a
7509	7.04 ± 2.62 efghi	0.09 ± 0.05 fgh	220.30 ± 45.30 b	1.34 ± 0.80 fg
7514	10.19 ± 0.66 abcdef	0.25 ± 0.03 abcd	295.67 ± 20.91 ab	3.33 ± 0.41 abcde
7531	5.23 ± 3.07 ghij	0.12 ± 0.08 efgh	281.11 ± 3.07 ab	3.05 ± 1.80 abcdef
7544	7.74 ± 2.27 defgh	0.17 ± 0.09 bcdefgh	284.34 ± 18.03 ab	2.97 ± 1.01 abcdef
7549	4.92 ± 3.96 ij	0.07 ± 0.06 h	345.30 ± 199.15 a	0.95 ± 0.72 g
7555	4.45 ± 1.62 j	0.06 ± 0.04 h	270.91 ± 41.52 ab	2.21 ± 0.89 cdefg
7559	5.68 ± 4.55 fghij	0.12 ± 0.12 efgh	272.62 ± 33.65 ab	2.72 ± 2.32 bcdefg
8301	7.40 ± 1.80 defgh	0.15 ± 0.04 cdefgh	268.42 ± 10.16 ab	3.55 ± 0.71 abcd
Z408	8.78 ± 0.78 cdefgh	0.25 ± 0.03 abcde	310.87 ± 2.85 ab	4.30 ± 0.28 ab
7137	10.04 ± 3.10 abcdefg	0.14 ± 0.09 cdefgh	224.10 ± 59.08 b	1.80 ± 0.87 defg

Note: P_n: net photosynthetic rate, G_s: stomatal conductance, C_i: intercellular CO_2 concentration, Tr: transpiration rate. Values followed by the different letter of each group were significantly different at $p < 0.05$ level of probability.

Table 4. Values of chlorophyll fluorescence parameters and *WUE* among teak clones.

Clone	NPQ	Yield	F_v/F_m	*WUE*
7013	0.773 ± 0.256 def	0.42 ± 0.07 bcd	0.69 ± 0.02 bcdef	2.43 ± 0.06 def
7029	1.547 ± 0.397 abcde	0.35 ± 0.09 cdefg	0.72 ± 0.01 abcd	5.29 ± 0.12 ab
71-5	1.785 ± 0.268 abc	0.21 ± 0.05 hi	0.70 ± 0.03 bcdef	4.48 ± 0.30 bc
7114	0.891 ± 0.192 cdef	0.47 ± 0.01 ab	0.75 ± 0.01 a	2.60 ± 0.03 de
7122	0.585 ± 0.104 ef	0.44 ± 0.01 bc	0.70 ± 0.01 bcdef	2.96 ± 0.03 de
7146	0.834 ± 0.172 cdef	0.40 ± 0.03 bcde	0.70 ± 0.02 bcdef	2.39 ± 0.08 def
7210	0.800 ± 0.285 def	0.41 ± 0.05 bcde	0.68 ± 0.01 def	3.05 ± 0.45 de
7219	2.165 ± 0.147 a	0.25 ± 0.01 ghi	0.72 ± 0.03 abcd	3.66 ± 0.30cd
3078-5	1.528 ± 0.060 abcde	0.32 ± 0.01 defgh	0.71 ± 0.02 bcde	2.51 ± 0.31 def
7412	0.421 ± 0.179 f	0.56 ± 0.04 a	0.72 ± 0.02 abcd	2.33 ± 0.34 def
7509	2.079 ± 0.258 a	0.20 ± 0.05 i	0.67 ± 0.03 f	6.38 ± 2.82 a
7514	1.978 ± 0.582 ab	0.20 ± 0.07 i	0.70 ± 0.01 bcdef	3.09 ± 0.37 de
7531	1.006 ± 0.547 cdef	0.41 ± 0.10 bcde	0.71 ± 0.01 bcde	1.78 ± 0.30 ef
7544	1.997 ± 0.531 ab	0.23 ± 0.04 hi	0.70 ± 0.01 bcdef	2.66 ± 0.36 de
7549	1.646 ± 0.730 abcd	0.25 ± 0.10 ghi	0.73 ± 0.02 ab	5.16 ± 1.04 ab
7555	1.578 ± 0.046 abcd	0.32 ± 0.03 defgh	0.69 ± 0.01 cdef	1.02 ± 0.36 f
7559	1.737 ± 0.446 abcd	0.26 ± 0.06 fghi	0.67 ± 0.02 f	2.03 ± 0.49 ef
8301	1.085 ± 0.166 bcdef	0.37 ± 0.05 bcdef	0.70 ± 0.02 bcdef	2.07 ± 0.19 ef
Z408	1.215 ± 0.732 abcdef	0.36 ± 0.12 cdefg	0.71 ± 0.01 bcde	2.04 ± 0.08 ef
7137	1.398 ± 0.212 abcde	0.31 ± 0.04 efghi	0.73 ± 0.03 abc	5.98 ± 1.25 a

Note: NPQ: non-photochemical quenching, Yield: the actual quantum yield PSII, F_v/F_m: maximum photochemical efficiency of PSII, *WUE*: water use efficiency. Values followed by the different letter of each group were significantly different at $p < 0.05$ level of probability.

Table 5. Values of growth traits among teak clones from different countries.

Clone	Seedling Height (cm)	Collar Diameter (mm)	H (m)	DBH (cm)	Individual Volume (dm^3)
7013	48.67 ± 8.16 cdefg	10.19 ± 2.18 bcdef	4.35 ± 1.03 cdefg	4.38 ± 1.40 bcde	6.25 ± 4.50 efghi
7029	61.13 ± 15.51 a	11.12 ± 2.39 abcd	4.87 ± 0.92 ab	5.37 ± 1.58 ab	11.01 ± 7.56 ab
71-5	53.63 ± 6.85 abcd	10.32 ± 1.79 bcde	3.98 ± 0.66 fghi	4.44 ± 1.59 bcde	6.79 ± 4.80 defghi
7114	44.33 ± 12.64 defg	9.53 ± 2.37 def	4.43 ± 0.68 bcdefg	5.03 ± 1.27 abc	9.12 ± 5.04 bcde
7122	59.53 ± 13.65 ab	12.63 ± 3.03a	4.88 ± 0.60 ab	5.32 ± 1.10 ab	9.97 ± 4.21 bcd
7146	48.87 ± 11.21 cdefg	10.97 ± 2.63 abcde	4.24 ± 1.02 defgh	4.78 ± 1.76 bcd	8.01 ± 6.75 bcdefg
7210	52.07 ± 10.82 abcde	8.65 ± 1.58 f	4.19 ± 0.81 efgh	3.88 ± 1.25 cdef	6.39 ± 3.29 efghi
7219	51.07 ± 10.03 bcdef	9.97 ± 2.23 cdef	3.97 ± 0.61 fghi	4.48 ± 1.48 bcde	8.26 ± 6.95 bcdef
3078-5	49.80 ± 9.40 cdef	9.95 ± 1.53 cdef	5.07 ± 0.99 a	6.05 ± 1.91 a	13.59 ± 7.06 a
7412	44.53 ± 11.45 defg	9.95 ± 2.08 cdef	4.28 ± 0.77 defgh	4.68 ± 1.53 bcde	8.63 ± 7.49 bcdef
7509	41.07 ± 10.71 gf	9.75 ± 2.00 def	4.41 ± 1.13 bcdefg	5.96 ± 5.79 a	8.26 ± 5.85 bcdef
7514	44.93 ± 15.40 defg	9.28 ± 1.43 def	4.71 ± 0.84 abcd	4.79 ± 1.27 bcd	10.75 ± 6.18 abc
7531	39.40 ± 12.33 g	9.35 ± 2.42 def	3.65 ± 1.11 ij	3.53 ± 1.52 ef	2.81 ± 2.05 j
7544	46.80 ± 9.84 cdefg	10.76 ± 2.47 abcde	4.36 ± 0.89 cdefg	4.20 ± 1.43 bcdef	5.71 ± 3.46 fghij
7549	42.20 ± 17.77 efg	9.40 ± 3.57 def	4.18 ± 0.80 efgh	4.34 ± 1.17 bcde	5.38 ± 3.39 fghij
7555	46.60 ± 7.40 cdefg	11.84 ± 1.45 abc	4.38 ± 0.63 cdefg	4.36 ± 0.83 bcde	6.18 ± 3.14 efghi
7559	55.60 ± 12.16 abc	12.33 ± 2.54 a	4.59 ± 1.00 bcde	5.09 ± 1.77 abc	9.18 ± 5.61 bcde
8301	50.47 ± 15.18 bcdef	10.30 ± 2.81 bcdef	4.79 ± 1.07 abc	4.18 ± 1.11 bcdef	8.00 ± 5.43 bcdefg
Z408	45.87 ± 10.12 defg	12.01 ± 2.37ab	3.97 ± 0.82 fghi	3.62 ± 1.22 def	4.06 ± 2.66 ij
7137	45.00 ± 8.60 defg	9.95 ± 2.26 cdef	4.33 ± 0.82 cdefg	4.23 ± 1.57 bcdef	8.33 ± 3.83 bcdef

Note: H: height of field growth at 4 years, DBH: diameter at breast height of field growth at 4 years. Values followed by the different letter of each group were significantly different at $p < 0.05$ level of probability.

3.2. Characteristics of Gas Exchange and Chlorophyll Fluorescence of Teak Resources from Different Regions

As shown in Table 6, net photosynthetic rate (P_n), stomatal conductance (G_s), transpiration rate (Tr), and non-photochemical quenching (NPQ), and actual quantum yield (Yield) of PSII were significantly different among teak provenances.

Table 6. Variance analysis of photosynthetic parameters among teak clones from different provenances.

Category	Parameter	Among Provenances	
		F	p
Gas exchange	P_n	3.52	0.0033 **
	G_s	3.19	0.0062 **
	C_i	1.13	0.3667 ^{ns}
	Tr	5.40	0.0001 ***
Chlorophyll fluorescence	NPQ	3.38	0.007 **
	Yield	5.59	<0.0001 ***
	F_v/F_m	1.95	0.0758 ^{ns}

Note: P_n: net photosynthetic rate, G_s: stomatal conductance, C_i: intercellular CO_2 concentration, Tr: transpiration rate, NPQ: non-photochemical quenching, Yield: the actual quantum yield PSII, F_v/F_m: maximum photochemical efficiency of PSII. ** indicate highly significant difference at $p < 0.01$ level of probability, *** more highly significant difference at $p < 0.001$ level of probability, and ^{ns} no significance.

Among the teak provenances (Table 7), 3070, 3074, and 3071 had higher P_n, 3074 had higher G_s and Tr, while 20001 and 3074 had a higher C_i value. While 8204, 3078, and 3072 showed high NPQ value (Table 8), 3074, 3071, and 3070 had higher Yield and F_v/F_m values. These results suggest that different teak provenances have different photosynthetic physiological characteristics. Provenances 3070, 3074, and 3071 can be considered to have high photosynthetic rates.

Table 7. Values of gas exchange parameters among teak clones from different provenances.

Provenance	P_n (μmol·m^{-2} s^{-1})	G_s (mol·m^{-2} s^{-1})	C_i (μmol·mol^{-1})	Tr (mmol·m^{-2} s^{-1})
20001	8.775 ± 0.776 ab	0.248 ± 0.032 abc	310.865 ± 2.848 a	4.296 ± 0.280 ab
3070	11.142 ± 4.169 a	0.187 ± 0.075 abc	262.948 ± 6.970 a	3.014 ± 1.075 bc
3071	10.914 ± 2.769 ab	0.210 ± 0.084 abc	263.820 ± 37.149 a	3.317 ± 1.189 abc
3072	10.316 ± 4.583 ab	0.196 ± 0.133 abc	253.485 ± 41.822 a	3.022 ± 1.112 bc
3074	11.011 ± 2.663 a	0.287 ± 0.091 a	298.570 ± 18.778 a	4.730 ± 0.967 a
8204	6.333 ± 3.189 bc	0.129 ± 0.084 cd	279.833 ± 67.715 a	2.515 ± 1.303 cd
3078	9.657 ± 2.869 ab	0.223 ± 0.072 abc	292.562 ± 4.907 a	3.798 ± 0.657 abc

Note: P_n: net photosynthetic rate, G_s: stomatal conductance, C_i: intercellular CO_2 concentration, Tr: transpiration rate. Values followed by the different letter of each group were significantly different at $p < 0.05$ level of probability.

Table 8. Values of chlorophyll fluorescence parameters among teak clones from different provenances.

Provenance	NPQ	Yield	F_v/F_m
20001	1.215 ± 0.732 a	0.359 ± 0.120 b	0.706 ± 0.007 ab
3070	1.160 ± 0.519 a	0.385 ± 0.085 b	0.709 ± 0.022 ab
3071	1.098 ± 0.478 ab	0.368 ± 0.102 b	0.714 ± 0.028 a
3072	1.483 ± 0.775 a	0.329 ± 0.090 b	0.703 ± 0.028 ab
3074	0.421 ± 0.179 b	0.564 ± 0.045 a	0.718 ± 0.022 a
8204	1.638 ± 0.550 a	0.281 ± 0.087 b	0.695 ± 0.025 b
3078	1.528 ± 0.060 a	0.318 ± 0.012 b	0.707 ± 0.016 ab

Note: NPQ: non-photochemical quenching, Yield: the actual quantum yield PSII, F_v/F_m: maximum photochemical efficiency of PSII. Values followed by the different letter of each group were significantly different at $p < 0.05$ level of probability.

3.3. Correlations between Photosynthetic and Growth Traits

Correlation analyses (Table 9) of teak clone parameters showed that P_n had significant positive correlation with G_s, Tr, F_v/F_m, seedling height and individual volume, respectively. P_n values can therefore be regarded as a critical parameter in teak breeding, indicating potential for faster growth.

Table 9. Correlation analysis among photosynthetic characteristics, growth traits, and ecological factors of teak clones.

	P_n	G_s	C_i	Tr	NPQ	Yield	F_v/F_m	*WUE*	Seedling Height	Collar Diameter	H	DBH	V
P_n													
G_s	0.891 **												
C_i	0.057	0.345											
Tr	0.568 **	0.802 **	0.286										
NPQ	0.062	−0.009	0.090	−0.426									
Yield	0.135	0.228	0.030	0.580 **	−0.944 **								
F_v/F_m	0.430 *	0.405	0.254	0.318	−0.164	0.391							
WUE	0.380	0.030	0.254	0.469 *	0.404	−0.396	0.143						
Seedling Height	0.463 *	0.343	0.029	0.219	−0.061	0.038	−0.184	0.015					
Collar diameter	−0.048	0.039	0.162	0.112	−0.04	−0.114	−0.319	−0.262	0.498 *				
H	0.156	0.058	0.104	0.067	0.007	−0.003	−0.096	0.029	0.486 *	0.258			
DBH	0.294	0.15	0.154	−0.004	0.197	−0.139	−0.111	0.314	0.294	0.136	0.707 **		
V	0.491 *	0.369	0.133	0.208	0.103	−0.036	0.074	0.183	0.456 *	0.061	0.832 **	0.830 **	

Note: P_n: net photosynthetic rate, G_s: stomatal conductance, C_i: intercellular CO_2 concentration, Tr: transpiration rate, NPQ: non-photochemical quenching, Yield: the actual quantum yield PSII, F_v/F_m: maximum photochemical efficiency of PSII, *WUE*: water use efficiency, Seedling Height: height of seedling growth at nursery at 1 year, Collar Diameter: collar diameter of seedling growth at nursery at 1 year, H: height of field growth at 4 years, DBH: diameter at breast height of field growth at 4 years, V: individual volume at 4 years. ** indicate highly significant difference at $p < 0.01$ level of probability, * significant difference at $p < 0.05$ level of probability.

In addition, seedling height was positively correlated with collar diameter, plant height (H), and individual volume. *WUE* was significantly negatively correlated with *T*r, suggesting that teak clones with high transpiration could show low *WUE*; G_s was positively correlated with *T*r, indicating that high stomatal conductance contributed to higher transpiration; *T*r was positively correlated with the actual quantum yield of PSII, suggesting that the higher the transpiration rate, higher the actual quantum yield of PSII would be.

4. Discussion

Plant growth and yield depend largely on photosynthesis [23,24]. Plant photosynthesis is not only affected by environmental factors, but also affected by plant genetic characteristics. It is the complex process of interaction between plant genetic and environmental factors that influences photosynthetic activity [25]. To date, ecophysiological studies on photosynthesis in forest trees were those that examined the effects of stress on photosynthetic physiology [26–29], and the photosynthetic responses to light intensity [30] and CO_2 concentration [31]. The present study chiefly focused on systematically measuring photosynthetic gas exchange and chlorophyll fluorescence parameters, correlating the photosynthetic characteristics with growth, and providing a means of rapid evaluation of teak germplasm, for introduction, utilization, and improvement of teak resources in future breeding programs.

Our study showed that teak clones had high variation and high heritability (h^2) for many growth and physiological traits. The results were generally consistent with the findings reported for *Populus trichocarpa* by McKown [32]. The gas exchange, chlorophyll fluorescence, and growth parameters of teak clones were highly controlled by genetic factors, especially for the actual quantum yield (Yield) of PSII. Therefore, such a parameter has high practical significance and can be effectively used for improving the efficiency of teak breeding. However, it is worth emphasizing that intercellular CO_2 concentration (C_i) and non-photochemical quenching (NPQ) were greatly influenced by the environment.

Further analysis showed that teak clones and resources from different regions vary in their photosynthetic characteristics. In this study, teak clones 7029, 71-5, 7219, 7412, 7122, and provenances 3070, 3074, 3071, which had higher P_n, can be regarded as the key resource in future breeding and management programs. However, more teak clones from different provenances and countries need to be included in this kind of study in the future. Huang et al., 2016 [33] had suggested, after SSR molecular marker testing, that the Nigerian provenance 3078, investigated in this paper, may have originated from India. The present studies, that reveal their similar photosynthetic characteristics, further corroborates this conclusion.

The significantly positive correlation that the net photosynthetic rate has with seedling height, individual volume, F_v/F_m, G_s, and *T*r, is an interesting finding of this study. In addition, seedling height was significantly and positively correlated with plant height and individual volume. Both results indicate that teak clones of high P_n and high seedling height result in fast-growing clones. However, it is known that photosynthetic processes are influenced by environmental conditions such as light, temperature, water, and nutrients [25]. Photosynthetic rate is not the only limiting factor for growth [34]. These factors may affect growth differently for different clones, resulting in no significant relationship between P_n and plant height or DBH of field growth at 4 years, the result being similar to previous reports [12,35].

Correlation analysis also revealed that water use efficiency was significantly but negatively correlated with *T*r, suggesting that teak clone *WUE* may decrease when transpiration rate is high in daytime. Such results were consistent with the study by Huang et al., 2016 [17], in that diurnal variation possessed a double peaked curve, with a "midday depression" phenomenon in summer, when strong sunshine often accompanied by high temperature produces excessive transpiration, followed by decline of water use efficiency. There was no significant correlation between seedling collar diameter and other parameters, except for seedling height, consistent with the results of the study on photosynthesis and growth of *Populus nigra* [10]. At the same time, the coefficient of genetic variation of C_i and F_v/F_m were lower than other photosynthetic indices in the present study, similar to photosynthetic characteristics of the clones [10]. The variation coefficients of F_v/F_m were small in this study (0.028) and in *Populus nigra* clones (0.024) [10]. This may be due to CO_2 concentration, leaf temperature, and relative humidity fluctuating significantly under natural conditions, reducing the F_v/F_m compared to conditions where they remain constant [25].

Farquhar et al., 1982 [36] concluded that photosynthetic rate was controlled by stomatal factors when P_n, C_i, and G_s increased or decreased at the same time. In this study, correlation analysis indicates that there was significant positive correlation between P_n and G_s, a positive but not significant correlation between P_n and C_i, G_s, and C_i, suggesting that the photosynthetic rate of teak was mostly controlled by stomatal factors. Plant dynamic photosynthesis was affected by many environmental factors such as light intensity, CO_2 concentration, leaf temperature, and relative humidity. Fluctuating environments would have a large impact on photosynthesis. Plants have a highly responsive regulatory system to make rapid photosynthetic responses to fluctuating environments, and a number of photoprotective mechanisms allow plants to maintain photosynthesis under stressful fluctuating environments [25].

For further research, the following points need to be considered in the future studies on teak. Firstly, it is desirable that more clones from different provenances be included in this kind of study in order to analyze variation among teak resources of different provenances more efficiently. Secondly, the differences in P_n among teak clones in this study was greater than that seen in *Populus nigra* [10] and *Populus deltoides* clones [11]. It is to be ascertained whether such a difference was caused by inherent differences in photosynthetic characteristics between the tree species, or if is due to other reasons. Thirdly, further evaluation of differences in leaf area between teak clones is needed since tree growth is restricted not only by photosynthetic efficiency, but also by photosynthetic leaf area [37,38]. Lastly, we found that photosynthetic rates of teak plants in the field trial measured at the age of 2 years were higher than that of the potted seedlings and, therefore, correlation analysis among photosynthetic parameters, photosynthetic leaf area, and growth traits in field trials need to be executed in future teak breeding programs.

5. Conclusions

Our findings have at least three important implications. First, photosynthetic parameters other than intercellular CO_2 concentration (C_i) are highly controlled by genetic factors. In addition, photosynthetic parameters and growth traits in different clones revealed abundant genetic variation. Second, the net photosynthetic rate (P_n), seedling height, and individual volume of wood significantly correlated between each other, and seedling height was significantly correlated with plant height in field trials, suggesting P_n and seedling height can help us in teak breeding. Third, teak clones 7029, 71-5, 7219, 7412, and 7122, and provenances 3070, 3074, and 3071, revealed to have higher photosynthetic rate, can be regarded as key resources for future breeding and germplasm resource management.

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