

## ORIGINAL ARTICLE

# Leaf functional traits in relation to growth performance in Malaysian teak (*Tectona grandis* L.f.)

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Received: November 10, 2023 Accepted: May 20, 2024 J-STAGE Advance published date: July 20, 2024

**ABSTRACT** Leaf functional traits such as leaf mass per area (LMA) and nitrogen and chlorophyll content are potential indicators of tree growth performance because they reflect leaf physiological traits including photosynthetic capacity and are influenced by environmental stress. However, our knowledge of the leaf traits associated with growth is limited in teak (*Tectona grandis*). We investigated the relationship between leaf functional traits and growth rate in four Malaysian teak stands varying from 14 to 46 years of age. We measured the height and diameter of 11–13 teak individuals in each stand. Sun-exposed leaves from each tree were collected and assessed for nitrogen content, LMA, single leaf area, and SPAD value, which is an indicator of chlorophyll content. SPAD values were positively correlated with diameter growth in all stands, with height increases found in three of four stands. Nitrogen content and single leaf area were positively correlated with height and diameter growth in one forest stand each, whereas LMA did not exhibit a significant relationship. After pooling the data for all stands, we examined the relationship between leaf functional traits and stand age, diameter and height via multiple regression analysis and found a significant positive correlation with SPAD value, but weaker correlations with the other three leaf traits. Because leaf chlorophyll content decreases with environmental stresses such as reduced soil nutrient availability and drought, trees with lower SPAD values may decrease their photosynthetic production and thus grow more slowly. Our results suggest that the SPAD value is a simple growth indicator of teak, regardless of their age and size.

**Key words:** chlorophyll, leaf area, photosynthesis, nitrogen, SPAD value

## INTRODUCTION

Leaf functional traits such as nutrient content and morphology are closely related to physiological functions, and respond to environmental conditions such as drought and light (Garnier et al. 2016; Kattge et al. 2020). Leaf photosynthesis is the primary process by which plants fix carbon (C), and is therefore strongly correlated with several leaf functional traits, including leaf mass per area (LMA) and nitrogen (N), and chlorophyll content (Koike 1988; Reich et al. 1994; Wright et al. 2010; Osone et al. 2021; Ellsworth et al. 2022; Kenzo et al. 2022). Thus, leaf functional traits associated with photosynthesis directly reflect C fixation and may be used as growth rate indicators across a range of species (Sterck et al. 2006; Wright et al. 2010; Garnier et al. 2016; Guimarães et al. 2018).

While leaf morphological and chemical traits relate to photosynthetic and growth rates, the patterns of intra- and inter-specific variations slightly differ. Interspecific variations in leaf traits such as photosynthesis are explained by negative correlations between LMA and the mass-based photosynthetic rate, as well as mass-based leaf N concentration ( $N_{\text{mass}}$ ), whereas the area-based photosynthetic rate is not correlated with LMA across species (Wright et al. 2004). For example, tree species with higher  $N_{\text{mass}}$  often exhibit faster growth than those with lower  $N_{\text{mass}}$  (Cornelissen et al. 1997; Poorter and Bongers 2006). Therefore, when comparing leaf traits between species, mass-based values are more important than area-based values such as nitrogen content per unit area ( $N_{\text{area}}$ ). In contrast, intraspecific variation in leaf traits is also observed under different environmental conditions, particularly light gradients, as well as size, ontog-



eny, or genetic variation (Lambers et al. 1998). Intraspecific variation caused by light gradients is mainly explained by the positive correlation between LMA, and the area-based photosynthetic rate and  $N_{\text{area}}$ , whereas differences in mass-based photosynthetic rates and  $N_{\text{mass}}$  between leaves in sun and shade are generally small (Poorter et al. 2019). Under weak light conditions, LMA is generally reduced to increase light interception per unit of leaf mass, and  $N_{\text{area}}$  is simultaneously lowered to avoid excess investment of N in photosynthetic apparatus components such as rubisco (Walters et al. 1993; Lambers et al. 1998). In addition, LMA generally increases with tree size and ontogeny, in association with changes in physiological functions such as area-based photosynthesis, whereas weak responses are observed for mass-based values such as  $N_{\text{mass}}$  and the mass-based photosynthetic rate (Kenzo et al. 2006, 2015; Kitajima and Poorter 2009; Iida et al. 2014). Thus, there appear to be intraspecific differences in the traits of sun-exposed leaves across individuals of similar age or sizes, possibly caused by genetic variations and/or environmental conditions other than light. In other words, such differences in leaf traits between individuals could potentially be used to select suitable planting sites or breeding varieties, through indicators of environmental stress on the tree, such as drought, or as indicators of superior growth traits (Xu et al. 2000; Marron and Ceulemans 2006; Ichie et al. 2019). However, in Asian seasonal tropical forests, variation in intraspecific leaf traits that correlate with tree growth vary among species; for example, *Mallotus garrettii* displays a positive relationship between growth rate and leaf chlorophyll content, whereas the growth rates of *Castanopsis echidnocarpa* and *Knema tenuinervia* are positively related to LMA and/or leaf thickness but not to chlorophyll content (Yang et al. 2021). Furthermore, the growth of *Falcataria falcata*, an early successional species, showed no relationship with six leaf functional traits (LMA, stable carbon isotope ratio, dry matter content,  $N_{\text{area}}$ , osmotic potential at full turgor, and leaf area) in even-aged stands (Kawai et al. 2023). Thus, the intraspecific relationship between leaf traits and growth rate is complex even in plants of the same age under the same light conditions, and it is necessary to consider which leaf traits best reflect growth on a species-by-species basis.

Teak (*Tectona grandis* L.f.) is an economically valuable tree species native to the tropical seasonal forests of Southeast Asia and India (Tewari 1999; Kenzo et al. 2020). Therefore, it has been widely planted beyond its original distribution, including in Africa and Central and South America (Kollert and Kleine 2017; Pinnschmidt et al. 2023). Teak has also been planted in Malaysia for more than 100 years, with many plantations on the Malay Peninsula and in the state of

Sabah, Borneo (Wyatt-Smith 1957; Vincent 1964; Tang and Jaafar 1979; Tee 1995; Gotoh et al. 2003). However, growth varies substantially among individuals even within the same stand (Tee 1995; Siddiqui and Abod 1998; Noor et al. 2005; Yahya et al. 2011; Yoneda et al. 2018). Within-stand growth differences may be related to internal and external variations in genotype and environments, such as the availability of soil water and nutrients to individual plants. Furthermore, these differences may also cause differences in leaf traits. For example, soil N availability is positively related to the SPAD value, leaf  $N_{\text{mass}}$ , and  $N_{\text{area}}$  in various tree species (Chang and Robison 2003; Ordoñez et al. 2009). An understanding of teak tree growth based on leaf functional traits could simplify forest management and potentially support selective breeding. Furthermore, if growth-related leaf functional traits can be detected based on leaf optical characteristics such as chlorophyll content, remote sensing technology could be used to predict growth over larger areas, aiding the selection of suitable planting sites (Hosoi et al. 2019; Liu et al. 2021).

Several studies on teak seedlings found that their growth and/or photosynthesis were significantly correlated with leaf traits such as N content and LMA, and these leaf traits not only responded to the light gradient, but also reflected other environmental stresses and genetic traits (Jayasankar et al. 2003; Leksungnoen et al. 2021; Huang et al. 2019). For example, drought stress decreased both leaf chlorophyll levels and photosynthesis rates (Husen 2010; Hassan et al. 2021; Maisuria et al. 2023), whereas limitation of soil nutrients such as nitrogen was negatively related with both leaf nitrogen and chlorophyll levels, as well as growth (Kaul et al. 1972). However, little is known of the relationship between leaf functional traits and growth rate in older planted teak trees, despite the fact that leaf traits and stress responsiveness are known to vary with age and size in other tree species (Kenzo et al. 2006, 2016; Meinzer et al. 2011). In addition, the relationship between leaf traits and growth in plantations of varying age is poorly understood, particularly in Malaysia. Therefore, it is necessary to examine planted teak forests of varying age to determine which leaf traits are associated with growth. To address this question, we examined growth and leaf functional traits related to leaf photosynthesis in four Malaysian plantations ranging in stand age from 14 to 46 years. In this study, by comparing the leaf traits of sun-exposed crowns within the same forest stands, we partially controlled for intraspecific variation in terms of ontogeny and light gradient, and therefore expected that differences in leaf traits and growth might reflect other environmental factors such as individual soil nutrient and water availability. Although genetic variation

also affects growth and leaf traits, such effects may be small because the seeds and cuttings planted in the study sites were derived from only a few mother trees.

## MATERIALS AND METHODS

### *Study site and plant materials*

We examined four teak plantations varying in age from 14 to 46 years (Table 1) in four states on the Malay Peninsula (Malacca, Negeri Sembilan, Pahang, and Selangor). The average diameter at breast height (DBH) and height (H) also differed among stands (Table 1, Yoneda et al. 2018). All sites have a humid tropical climate, with no distinct wet and dry seasons. Annual precipitation varied from about 2,140 to 2,700 mm. The mean and maximum annual temperatures varied slightly from 24.1 °C to 26.5 °C and 28.0 °C to 29.8 °C, respectively. All sites were located in lowland areas with gentle slopes below an altitude of 250 m and the soil consisted of highly weathered ultisols, which are found in most regions of Malaysia.

### *Measurements of leaf functional traits*

We selected 11–13 teak trees of varying sizes from each study site and measured their DBH and H. We selected only individuals that were free of shading or suppression by other trees. The DBH and H of each individual were divided by stand age to obtain the mean annual increments (MAI) of DBH and H (MAID and MAIH). MAID and MAIH are useful parameters for comparing growth rates among planted trees within stands of the same age, although these parameters usually change with stand age (Karmacharya and Singh 1992; Appanah and Weinland 1993). We assumed that leaf functional traits would be relatively homogenous within the sun-exposed canopies of each tree, as traits such as N content

do not differ significantly among sun-exposed canopy positions (Husni et al. 1996, Jayamadhavan et al. 2000). Thus, we collected 3–5 mature leaves free from severe damage or senescence from the sun-exposed canopy of each tree using a 20-m-long pole with a sickle. Leaves were immediately transported to the laboratory and single leaf area was measured using a scanner. Leaf chlorophyll content, indicated by the SPAD value (Ichie et al. 2002), was determined as an average of 30 measurements taken throughout each leaf blade using a SPAD meter (SPAD-502, Konika-Minolta, Tokyo, Japan). To determine LMA, we cut several portions of the leaf, measured their areas, and then dried them at 65 °C for 3 days to determine the dry leaf mass. Leaf  $N_{\text{mass}}$  and C concentrations were determined using an NC analyzer (Sumigraph NC-900, Sumika Chemical Analysis Service, Osaka, Japan) after grinding the dry leaf to powder. We calculated  $N_{\text{area}}$  by multiplying  $N_{\text{mass}}$  and LMA.

### *Statistical analyses*

We analyzed the mean leaf trait values for each forest stand using one-way analysis of variance (ANOVA) and post hoc Tukey's honest significant difference (HSD) tests (Sokal and Rohlf 1995). Regression analysis was performed for MAID and MAIH vs. the five traits (LMA, SPAD value,  $N_{\text{area}}$ ,  $N_{\text{mass}}$ , and leaf area) for each stand. We also performed multiple regression analysis to determine the relationships between leaf functional traits and growth (Sokal and Rohlf 1995), using MAID and MAIH as dependent variables and the four traits (LMA, SPAD value,  $N_{\text{area}}$ , and leaf area) and stand age as explanatory variables;  $N_{\text{mass}}$  was not included as an explanatory variable to avoid multicollinearity (Sokal and Rohlf 1995). In addition to these analyses based on raw parameter values, we developed parallel regression models based on standardized parameter values (Yang et al. 2021). We standardized MAID and MAIH by dividing each tree value by the maximum MAID or MAIH for each stand

Table 1. Age after planting, average diameter at breast height (DBH), tree height (H), stand density (SD) at study period, altitude, annual rainfall and annual average ( $T_{\text{ave}}$ ) and maximum temperature ( $T_{\text{max}}$ ), slope gradient and soil type in four study stands in Malaysia. Different letters indicate significant differences between stands [ $P < 0.05$ ; analysis of variance (ANOVA) followed by Tukey's honest significant difference (HSD) test]. Data are means  $\pm$  standard error (SE).

Stand location	Age (y)	DBH (cm)	H (m)	SD (trees ha <sup>-1</sup> )	Altitude (m)	Rainfall (mm y <sup>-1</sup> )	$T_{\text{ave}}$ (°C)	$T_{\text{max}}$ (°C)	Gradient (°)	Soil type
Selangor	14	18.0 $\pm$ 0.9 <sup>b</sup>	12.0 $\pm$ 0.6 <sup>b</sup>	300	60	2700	26.1	29.8	2	Ultisol
Malacca	18	23.6 $\pm$ 1.8 <sup>ab</sup>	14.4 $\pm$ 0.9 <sup>b</sup>	420	40	2140	26.5	29.4	2	Ultisol
Pahang	27	18.5 $\pm$ 2.7 <sup>b</sup>	14.5 $\pm$ 1.7 <sup>b</sup>	1100	250	2160	24.1	28.0	4	Ultisol
Negeri Sembilan	46	26.4 $\pm$ 1.6 <sup>a</sup>	21.1 $\pm$ 0.9 <sup>a</sup>	1100	200	2300	24.9	28.7	8	Ultisol

(RMAID, RMAIH) to reduce any aging effect on growth rates among sites. We also standardized leaf traits by subtracting the mean value for each stand from the value for each individual. RMAID and RMAIH were used as dependent variables and the four standardized leaf traits and stand age as explanatory variables. Each regression model was assessed for goodness of fit using the adjusted coefficient of determination (adjusted  $R^2$ ). All statistical analyses were performed with SPSS v27.0 for Windows (IBM Corp., Armonk, NY, USA).

## RESULTS

### *Tree size and leaf functional traits among stands*

DBH was highest in Negeri Sembilan at 26.4 cm, which was significantly greater than in Selangor (18.0 cm) or Pahang (18.5 cm, Table 1). Mean tree height was also significantly higher in Negeri Sembilan (21.1 m) than in the other three stands, which varied from 12.0 m in Selangor to 14.5 m in Pahang (Table 1).

We found no significant differences in  $N_{\text{area}}$  or leaf area among stands ( $P > 0.05$ , Table 2), although  $N_{\text{mass}}$  was significantly higher in Malacca than at other sites ( $P < 0.05$ , Table 2). Leaf mass-based carbon concentrations were also similar

among stands, with a very small range from 49.0% in Pahang to 49.7% in Malacca ( $P > 0.05$ , data not shown). In contrast, SPAD values were significantly higher in Negeri Sembilan (44.9) than in Selangor (34.7), and those for Malacca (39.8) and Pahang (39.7) were intermediate ( $P < 0.05$ , Table 2). The LMA of Negeri Sembilan ( $87.5 \text{ g m}^{-2}$ ) was significantly higher than those of Pahang ( $58.7 \text{ g m}^{-2}$ ) and Malacca ( $62.7 \text{ g m}^{-2}$ ), whereas that of Selangor was intermediate ( $77.6 \text{ g m}^{-2}$ ,  $P < 0.05$ , Table 2). Leaf area was similar among stands, but varied by more than three-fold even within the same stand (Table 2, Fig. 1).

### *Relationship among leaf functional traits*

Leaf  $N_{\text{area}}$  was positively correlated with both SPAD value and LMA ( $P < 0.01$ , Table 3). SPAD value was also positively correlated with  $N_{\text{area}}$  and LMA ( $P < 0.01$ , Table 3). Leaf area was negatively correlated with  $N_{\text{mass}}$  ( $P < 0.05$ , Table 3).

### *Relationships between leaf functional traits and growth for each stand*

We found significant positive correlations between SPAD values and both DBH and height growth rates (MAID,



Fig. 1. Example of teak leaf variation at the Selangor site. Each leaf was collected from a different individual.



Table 2. Number of trees sampled (No), mean annual increments of DBH (MAID) and H (MAIH), leaf-area and -mass based nitrogen ( $N_{\text{area}}$  and  $N_{\text{mass}}$ ), SPAD value, leaf area, and leaf mass per area (LMA) of sampled trees in four study stands in Malaysia. Different letters indicate significant differences between stands ( $P < 0.05$ , ANOVA followed by Tukey's HSD test). ns, means not significant. Data are means  $\pm$  SE.

Stand location	No	MAID (cm year <sup>-1</sup> )	MAIH (m year <sup>-1</sup> )	$N_{\text{area}}$ (g m <sup>-2</sup> )	$N_{\text{mass}}$ (%)	SPAD	Leaf area (cm <sup>2</sup> )	LMA (g m <sup>-2</sup> )
Selangor	13	1.22 $\pm$ 0.14 <sup>a</sup>	0.79 $\pm$ 0.09 <sup>a</sup>	1.31 $\pm$ 0.06 <sup>ns</sup>	1.74 $\pm$ 0.11 <sup>b</sup>	34.7 $\pm$ 1.3 <sup>b</sup>	783 $\pm$ 77 <sup>ns</sup>	77.6 $\pm$ 5.3 <sup>ab</sup>
Malacca	11	0.94 $\pm$ 0.17 <sup>ab</sup>	0.60 $\pm$ 0.08 <sup>ab</sup>	1.61 $\pm$ 0.12 <sup>ns</sup>	2.55 $\pm$ 0.12 <sup>a</sup>	39.8 $\pm$ 1.5 <sup>ab</sup>	551 $\pm$ 42 <sup>ns</sup>	62.7 $\pm$ 3.1 <sup>b</sup>
Pahang	11	0.70 $\pm$ 0.13 <sup>b</sup>	0.53 $\pm$ 0.08 <sup>ab</sup>	1.20 $\pm$ 0.13 <sup>ns</sup>	2.06 $\pm$ 0.07 <sup>b</sup>	39.7 $\pm$ 2.4 <sup>ab</sup>	593 $\pm$ 98 <sup>ns</sup>	58.7 $\pm$ 6.5 <sup>b</sup>
Negri Sembilan	12	0.58 $\pm$ 0.05 <sup>b</sup>	0.47 $\pm$ 0.02 <sup>b</sup>	1.45 $\pm$ 0.12 <sup>ns</sup>	1.69 $\pm$ 0.14 <sup>b</sup>	44.9 $\pm$ 1.5 <sup>a</sup>	654 $\pm$ 124 <sup>ns</sup>	87.5 $\pm$ 54.9 <sup>a</sup>

Table 3. Pearson's correlation coefficients for leaf functional traits. \* $P < 0.05$ , \*\* $P < 0.01$ .

	$N_{\text{area}}$ (g m <sup>-2</sup> )	$N_{\text{mass}}$ (%)	SPAD value	Leaf area (cm <sup>2</sup> )	LMA (g m <sup>-2</sup> )
$N_{\text{area}}$					
$N_{\text{mass}}$	0.493**				
SPAD	0.492**	0.001			
Leaf area	-0.224	-0.360*	0.094		
LMA	0.517**	-0.469**	0.500**	0.123	

MAIH, RMAID, RMAIH) for all stands ( $P < 0.05$ ), except for the relationship with MAIH and RMAIH in Selangor (Figs. 2 and 3, Appendix 1). We found no significant relationship between LMA and growth rate in any stand (Figs. 2 and 3, Appendix 1). Leaf  $N_{\text{area}}$  and  $N_{\text{mass}}$  were positively correlated with both diameter and height growth in Malacca ( $P < 0.05$ , Figs. 2 and 3, Appendix 1). There was a significant positive correlation between leaf area and both diameter and height growth in Selangor, but not in the other three stands ( $P < 0.05$ , Figs. 2 and 3, Appendix 1).

### Leaf functional traits associated with tree growth

Multiple regression analysis revealed significant relationships between leaf functional traits, especially the SPAD value, and both DBH and height growth (Table 4). Although stand age was negatively correlated with MAID and MAIH, there was little or no correlation between stand age and parameters that attenuate the age effect (RMAID or RMAIH). When standardized leaf traits and RMAIH were combined, stand age exhibited a positive correlation ( $P < 0.05$ ), but this correlation was much weaker than that of the SPAD value ( $P < 0.0001$ , Table 4). When using standardized leaf trait values, only SPAD values were positively correlated with DBH growth (MAID and RMAID) among all leaf traits (Table 4). SPAD values also showed significant positive

correlations with MAID and RMAID when raw leaf trait values were used, as well as a positive correlation with leaf area when MAID was the dependent variable (Table 4). The adjusted  $R^2$  was higher when standardized leaf trait values were used as the explanatory variables than when raw leaf trait values were used for regression of DBH growth (MAID and RMAID).

Tree height growth parameters (MAIH and RMAIH) were also positively correlated with standardized SPAD values and negatively correlated with standardized LMA values, although SPAD values ( $P < 0.001$ ) were more strongly correlated with height growth parameters than LMA ( $P < 0.05$ ). When raw leaf trait values were used, SPAD values were also significantly correlated with MAIH and RMAIH, and leaf area was positively correlated with MAIH (Table 4). The adjusted  $R^2$  values for MAIH and RMAIH were also higher when standardized leaf trait values, not raw leaf trait values, were used (Table 4).

## DISCUSSION

### Leaf functional traits and tree growth

The SPAD value was the best leaf functional trait for predicting teak growth rate, likely because chlorophyll content effectively indicates photosynthetic capacity and environmental stress. Generally, photosynthetic capacity under strong light is indicated by the rubisco level, which usually explains inter-specific differences in terms of photosynthesis; however, within the same species, chlorophyll content can also explain differences in photosynthesis between individuals or leaves (Lambers et al. 1998). Leaf chlorophyll absorbs the light energy that drives C-fixing reactions in photosynthetic systems (Hikosaka and Terashima 1996; Lambers et al. 1998). Therefore, photosynthetic ability is directly related to chlorophyll abundance, and leaf greenness as indicated by the SPAD value is closely related

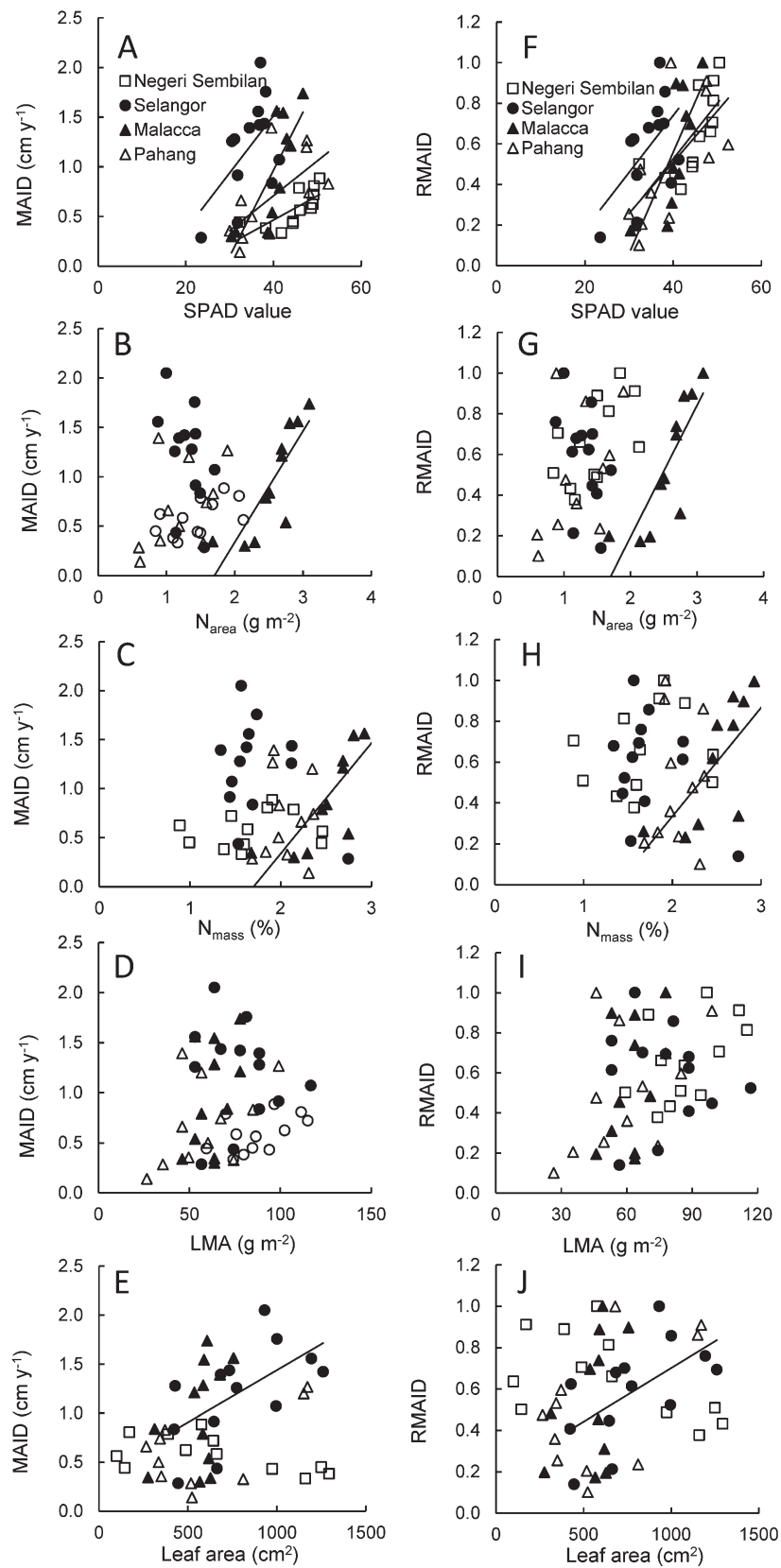


Fig. 2. Relationship between mean annual increment of diameter at breast height (MAID) or relative MAID (RMAID) and (A, F) SPAD value, (B, G) leaf area-based nitrogen content, (C, H) leaf mass-based nitrogen concentration, (D, I) leaf mass per area (LMA), and (E, J) single leaf area. Regression lines indicate significant relationships within each stand ( $P < 0.05$ ). Values of correlation coefficients appeared in Appendix 1. The value of correlation coefficient was same between MAID and RMAID.

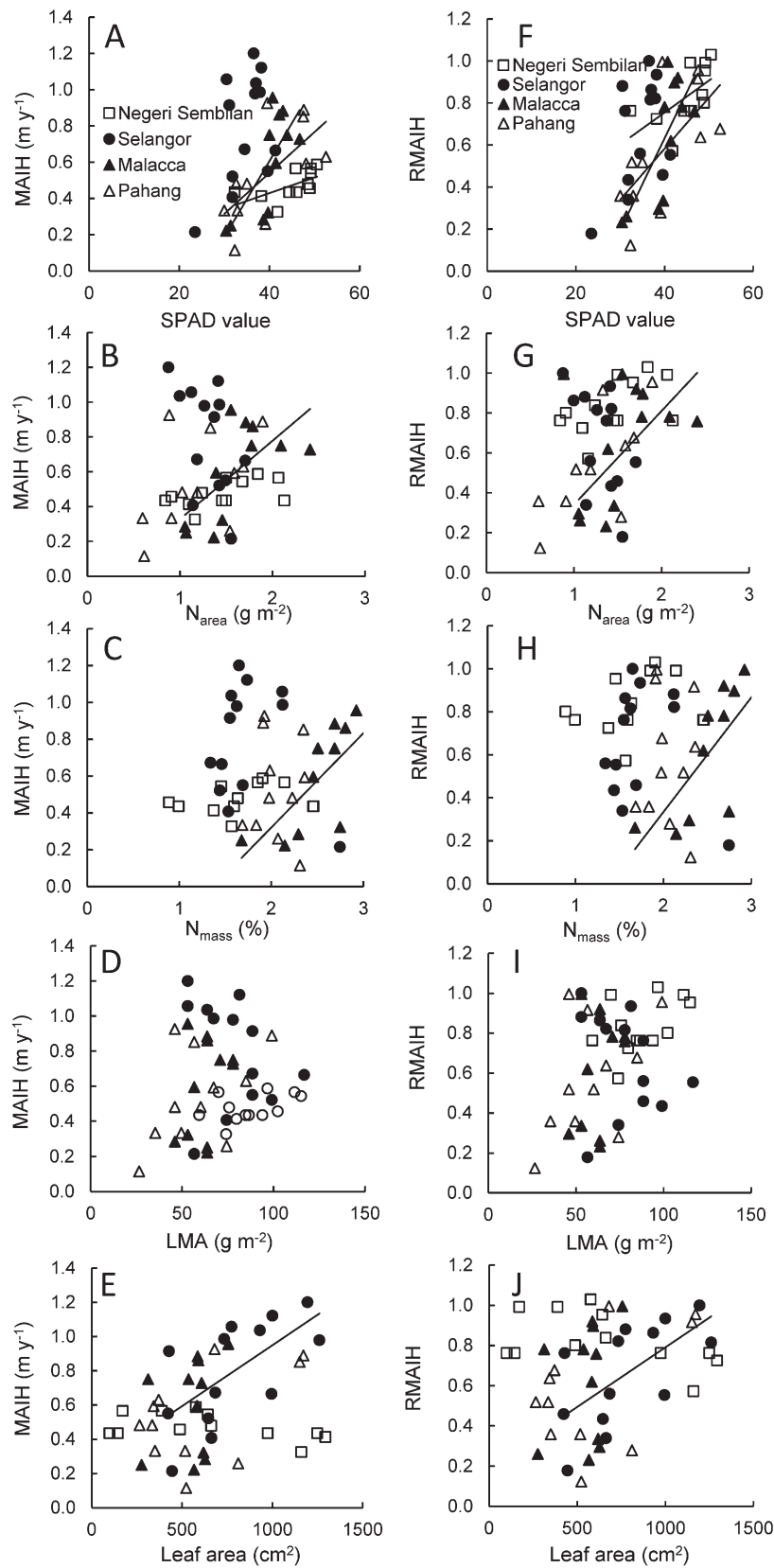


Fig. 3. Relationship between mean annual increment of height (MAIH) or relative MAIH (RMAIH) and (A, F) SPAD value, (B, G) leaf area-based nitrogen content, (C, H) leaf mass-based nitrogen concentration, (D, I) LMA, and (E, J) single leaf area. Regression lines indicate significant relationships within each stand ( $P < 0.05$ ). Values of correlation coefficients appeared in Appendix 1. Value of correlation coefficient was same between MAIH and RMAIH.

Table 4. Results of multiple regression analysis including both relative (standardized) and raw values of four leaf functional traits (nitrogen content,  $N_{\text{area}}$ ; SPAD value; leaf area; LMA) and stand age as explanatory variables of the mean annual increment of growth for diameter (MAID) and height (MAIH), and relative mean annual increments of growth for diameter (RMAID) and height (RMAIH). Data are standardized regression coefficients. \*\*\*\* $P < 0.0001$ , \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ .

Explanatory variables	Explanatory variables are standardized leaf trait values				Explanatory variables are raw leaf trait values			
	MAID	RMAID	MAIH	RMAIH	MAID	RMAID	MAIH	RMAIH
$N_{\text{area}}$	0.237	0.272	0.198	0.239	0.148	0.184	0.069	0.177
SPAD value	<b>0.520**</b>	<b>0.646***</b>	<b>0.561***</b>	<b>0.601****</b>	<b>0.397*</b>	<b>0.561**</b>	<b>0.417*</b>	<b>0.475**</b>
Leaf area	0.177	0.092	0.195	0.151	<b>0.267*</b>	0.174	<b>0.295*</b>	0.249
LMA	-0.288	-0.283	<b>-0.355*</b>	<b>-0.344*</b>	0.007	-0.001	-0.018	-0.044
Stand age	<b>-0.450**</b>	0.129	<b>-0.384**</b>	<b>0.277*</b>	<b>-0.643**</b>	-0.153	<b>-0.577***</b>	0.057
Intercept	1.33	0.51	0.82	0.53	-0.17	-0.48	0.05	-0.33
Adjusted $R^2$	0.48	0.42	0.43	0.40	0.41	0.35	0.34	0.33
$P$ -value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.001

to photosynthetic performance (Murchie et al. 1997; Fu et al. 2013; Boussadia et al. 2023). A significant positive correlation between SPAD values and photosynthetic capacity, determined as the maximum photosynthetic rate of the leaf at light saturation, has been observed in various species such as olive (Boussadia et al. 2011) and litchi trees (Fu et al. 2013). In addition, the SPAD value is related to leaf nutrient status, particularly N content (Ichie et al. 2002; Loh et al. 2002), as N is found in both chlorophyll molecules and photosynthetic proteins, which account for more than half of leaf N (Evans 1989; Hikosaka 2004). Our finding that leaf SPAD values were positively correlated with N content is consistent with previous reports for various plant species, including tree species (Ichie et al. 2002; Netto et al. 2005; Fritschi and Ray 2007; Xiong et al. 2015). In addition, environmental stresses such as soil N shortage, drought, salt stress, and excess light often lead to leaf chlorophyll loss and limited photosynthesis and growth (Olsen et al. 2002; Swiader and Moore 2002; Kenzo et al. 2007, 2021; Esfahani et al. 2008; Da Silva-Pinheiro et al. 2016); thus, SPAD values have been used to diagnose tree health under stressful conditions, such as in urban trees (Smiley et al. 2006; Scattolin et al. 2013). Similarly, decreased SPAD values and limited growth have been observed in teak seedlings subjected to drought treatment (Husen 2010; Sneha et al. 2012; Maisuria et al. 2023). Overall, the strong relationship we observed between SPAD values and growth rates may be attributed to the sensitivity of SPAD values to various stresses encountered by teak trees, even under stands differing age and size class. Furthermore, SPAD values can be determined for large areas using drones equipped with spectral cameras and/or satellite remote-sensing techniques (Bausch and Duke 1996; Hosoi et al. 2019; Garza et al.

2020; Morley et al. 2020; Liu et al. 2021), and growth prediction using SPAD values is more rapid and easy than other methods such as leaf nitrogen determinations. Therefore, these findings may improve the selection of suitable planting sites for Malaysian teak, and accurately predict growth.

Aside from SPAD values, leaf functional traits and leaf nitrogen in particular were not always correlated with teak tree growth, despite a positive correlation detected between leaf nitrogen ( $N_{\text{mass}}$  and  $N_{\text{area}}$ ) and growth in the Malacca stand. Although we were unable to establish the cause of this weak relationship between N and growth, it is possible that the differences in N allocation to non-photosynthetic proteins, such as those in the cell wall, and photosynthetic proteins, among sites or individuals may relate to this weak relationship, as the N allocation within the leaf affects the photosynthetic N use efficiency (photosynthetic rate per unit leaf N) (Onoda et al. 2004, 2017; Takashima et al. 2004). Consistent with our results, the Malaysian tropical canopy species *Dyera costulata* exhibited significantly reduced growth and SPAD values when subjected to drought and strong light stress, whereas leaf N content remained unchanged (Kenzo et al. 2021). In addition, leaf size is an indicator of environmental stress in various plant species; for example, drought and strong winds often lead to smaller leaves and reduced growth (Turner 2001; Larcher 2003; Kenzo et al. 2019). Teak seedlings exposed to drought stress respond by reducing their leaf size or total leaf area, which may lower transpiration loss (Hassan et al. 2021). Although larger leaves have been reported in unstressed potted teak seedlings (Hassan et al. 2021) and other tree seedlings (Jiang et al. 2022), the relationship between leaf size and growth was limited in our study,



except in the Selangor stand. In Selangor, larger leaves were correlated with higher growth rates, suggesting a potential link between growth and environmental stress such as drought, or may be related to light acquisition strategy across the canopy (Terashima et al. 2005; Migita et al. 2023). However, further studies such as soil nutrient and moisture monitoring are necessary to better understand the factors influencing this relationship.

### Model comparison

Standardizing leaf functional traits improved the accuracy of teak growth prediction, especially the SPAD value was an effective explanatory variable in all models. Standardizing the increments of annual growth (RMAID and RMAIH) also markedly reduced the effect of stand age on growth. The MAID and/or MAIH of teak may decline with stand age, although variation in average tree size and other site conditions may also affect MAID and MAIH (Appanah and Weinland 1993; Tewari 1999; Auykim et al. 2017). Age- and size-dependent changes in MAID and/or MAIH have been observed in various tree species, with the annual growth of teak usually decreasing with age (Nwoboshi 1983; Karmacharya and Singh 1992; Appanah and Weinland 1993; Hashim and Noor 2002; Noor 2003; Auykim et al. 2017). These previous findings are consistent with those of the present study. Overall, using standardized parameters improved the predictive accuracy of our model when comparing leaf traits and growth among forest stands, which aligns with the results of another study on seasonal trees in tropical Asian forests (Yang et al. 2021).

### CONCLUSIONS

We found that leaf SPAD values can be used to indicate both diameter and height growth in Malaysian teak trees of various ages and sizes. Additional studies in different regions and on trees with varying genotypes, as well as physiological experiments to explore environmental conditions such as the stress level in each tree, would allow us to elucidate the relationships among SPAD values (chlorophyll content), photosynthesis, drought tolerance, and other factors controlling teak growth.

**ACKNOWLEDGEMENTS** The authors thank to the Universiti Putra Malaysia and Forest Research Institute Malaysia, and to Prof. NM. Majid, Dr. Z. Yahya and Mr. SK Amir for their kind support of this study. This research

was partly supported by Grant-in-Aid for scientific research (No. 15K07488, 17H04623, 20K06153, 23K05323) from the Ministry of Education, Science and Culture, Japan, and an Adaptive Forestry research program from the Japan International Research Center for Agricultural Sciences.

**Author contributions** TK, RY conceived and designed the experiment. TK, RY and MAA performed the experiment. TK wrote the main manuscript text. All authors reviewed the manuscript.

### DECLARATIONS

**Competing of interest** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix 1. Values of correlation coefficients by regression analysis between growth and leaf traits in each stand. Mean annual increment of diameter (MAID) and height (MAIH) are dependent variables and leaf traits are explanatory variables. \* $P < 0.05$ , \*\* $P < 0.01$ . ns, not significant. The values of slope and intercept appear below the correlation coefficients if the regression is significant.

Stand location	$N_{\text{area}} (\text{g m}^{-2})$		$N_{\text{mass}} (\%)$		SPAD		Leaf area ( $\text{cm}^2$ )		LMA ( $\text{g m}^{-2}$ )	
	MAID	MAIH	MAID	MAIH	MAID	MAIH	MAID	MAIH	MAID	MAIH
Selangor	-0.20 <sup>ns</sup>	-0.25 <sup>ns</sup>	-0.12 <sup>ns</sup>	-0.04 <sup>ns</sup>	<b>0.31*</b>	0.22 <sup>ns</sup>	<b>0.35*</b>	<b>0.41*</b>	-0.01 <sup>ns</sup>	-0.09 <sup>ns</sup>
Slope	-	-	-	-	0.06	-	0.001	0.001	-	-
Intercept	-	-	-	-	-0.79	-	0.38	0.24	-	-
Malacca	<b>0.69**</b>	<b>0.44*</b>	<b>0.65**</b>	<b>0.48*</b>	<b>0.63**</b>	<b>0.55**</b>	0.17 <sup>ns</sup>	0.08 <sup>ns</sup>	0.19 <sup>ns</sup>	0.12 <sup>ns</sup>
Slope	1.13	0.45	1.13	0.51	0.09	0.04	-	-	-	-
Intercept	-1.92	-0.12	-1.92	-0.71	-2.51	-1.07	-	-	-	-
Pahang	0.22 <sup>ns</sup>	0.23 <sup>ns</sup>	0.01 <sup>ns</sup>	0.00 <sup>ns</sup>	<b>0.42*</b>	<b>0.44*</b>	0.29 <sup>ns</sup>	0.26 <sup>ns</sup>	0.20 <sup>ns</sup>	0.23 <sup>ns</sup>
Slope	-	-	-	-	0.04	0.02	-	-	-	-
Intercept	-	-	-	-	-0.70	-0.36	-	-	-	-
Negri Sembilan	0.32 <sup>ns</sup>	0.27 <sup>ns</sup>	0.04 <sup>ns</sup>	0.04 <sup>ns</sup>	<b>0.50**</b>	<b>0.35*</b>	0.33 <sup>ns</sup>	-0.25 <sup>ns</sup>	0.25 <sup>ns</sup>	0.21 <sup>ns</sup>
Slope	-	-	-	-	0.02	0.01	-	-	-	-
Intercept	-	-	-	-	-0.50	0.08	-	-	-	-