Growth characteristics of teak seedling planted on different types of sandy soil in Northeast Thailand

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Abstract

In Northeast Thailand, sandy soil is prevalent, in which the growth of teak (Tectona grandis L. f.) is suppressed. Sandy soil is characterized by low pH, poor fertility, and low water holding capacity. To determine the factors that suppress teak growth, we planted teak seedlings in sandy soil at two sites. One of the sites exhibited suppressed teak growth but the other did not. We compared growth, photosynthetic rate, leaf water potential, and the concentrations of elements in plant organs between the two sites.

The site where teak growth was suppressed showed low concentrations of nutrients in the soil, especially Ca. The average tree height at this site was only 40 cm after 16 months, whereas tree height at the other site was over 300 cm at same time point. The site with low teak growth was characterized by low uptake of nutrients, and especially Ca deficiency. The low growth rates correlated with decreases photosynthetic rate and drought stress in the dry season. Moreover, Mg accumulated in the leaves of teak with low growth, and this accumulation was considered as a factor in the decreased photosynthetic rate and drought stress. We concluded that the concentration of Ca in soil was important for teak growth, and the site with low Ca showed drastic suppression of teak growth and Mg toxicity caused by Ca deficiency.

Keywords: Acrisols, Photosynthesis, Leaf water potential, Nutrients

Introduction

In Northeast Thailand, teak (*Tectona grandis* L. f) plantations have increased as a result of a tree plantation promotion project since 1994 (Furuya et al. 2012). However, there was an area in which the growth of teak was very poor (Tangmitcharoen et al. 2012). In contrast, in an experimental plot only 10 m from that studied by Tangmitcharoen et al. (2012), teak growth was much better (Wichiennopparat et al. 2012). Wichiennopparat et al. (2012) examined the effects of fertilizer on the growth of teak. These experiments showed favorable growth even without fertilization. The representative soil from Northeast Thailand is described as a "light textured sandy soil" (abbreviated to sandy soil) that is categorized in the acrisols (ultisols in USDA soil taxonomy) (Kyuma 2003; Suzuki et al. 2007). The plots of Tangmitcharoen et al. (2012) and Wichiennopparat et al. (2012) had acidic sandy soil (pH <5.5); however, teak growth differed between the two sites. From these previous studies, we could not elucidate the factors that affected teak growth. We predicted that other soil parameters may affect teak growth and caused the observed differences.

The difference in soil texture affected growth of teak, with growth of teak showing a negative correlation with the content of sand, and a plantation with a high content of sand in the soil showed low growth of teak (Tanaka et al. 1998; Salifu 2001). With regard to nutrients, the growth of teak is restricted by nutrient deficiency, especially nitrogen (N), calcium (Ca), and phosphorous (P) (Tewari 1992; Tanaka et al. 1998, Barroso et al. 2005; Zhou et al. 2012). In addition, the concentrations of nutrients in plant organs are important indicators to estimate the effect of any nutrient deficiency (Zech and Drechsel 1991; Gopikumar and Varghese 2004; Barroso et al. 2005). However, little information exists to analyze the concentrations of nutrients in the organs of teak in Thailand (ex. Kayama et al. 2016). Moreover, teak consumes large amounts of water for its growth, and the leaves of teak are sensitive to drought stress (Rao et al. 2008; Cernusak et al. 2009; Kunert et al. 2010). There is a possibility that the plots examined by Tangmitcharoen et al. (2012) and Wichiennopparat et al. (2012) may have differed in their soil texture, nutrients, and water soil content, and as a result the growth levels were different.

The aim of our research was to determine the factors that affect teak growth. We conducted a planting test of teak seedlings in sandy soil in two plots with different sandy soils. We analyzed soil properties and water in soil in the two plots. In addition, we examined the ecophysiological traits of teak seedlings, specifically (1) the growth characteristics of seedlings, (2) leaf water potential, (3) photosynthetic rate, and (4) concentrations of elements in plant organs. Based on these results, we identified factors to affected teak growth in sandy soil in Northeast Thailand.

Materials and methods

Study site

Our experiment was conducted at the Northeast Forest Seed Center located in Khon Kaen Province in northeastern Thailand (16°16′ N, 102°47′ E, 191 m a.s.l.). This center conducts measurements of meteorological data: mean annual precipitation was 1,104 mm, and annual mean, maximum, and minimum temperatures were 28.3 °C, 40° C, and 13 °C, respectively (from 2008 to 2012, Northeast Forest Seed Centre, unpublished data). Precipitation is concentrated from May to October (Northeast Forest Seed Center, unpublished data).

In Khon Kaen Province, we previously published a soil suitability map of teak plantation for farmers (Wichiennopparat et al. 2015). Sandy soil in Khon Kaen Province is distributed over a large area (13.5%). These areas are categorized as moderately suitable for teak planting (“3s” site in a soil suitability map).

Selection of experimental plots and preparations of land and teak seedling

For the selection of experimental plots with sandy soil, we selected two sites at the Northeast Forest Seed Centre based on differences in the herbaceous plant species present. At the more suitable site, grasses were widely distributed over the area, whereas the moderately suitable site was covered with dwarf herbaceous legumes. The moderately suitable plot was the same research site as examined by Tangmitcharoen et al. (2012, “3s” site). The more suitable plot neighbored the research site examined by Wichiennopparat et al. (2012, “2n” site in a soil suitability map). We abbreviated to “moderate” for the moderately suitable site and to “suitable” for the more suitable site, which are used hereafter.

We secured 432 m^2 of land at the moderate and suitable sites for our experiment. The distance between the two sites was ca. 100 m. In the neighborhood of each plot, there were plantations of eucalypt. We made ditches at the border of the plantations of eucalypt in December 2013 to prevent root invasion. The width and depth of the ditch were 2 m and 1 m, respectively. In April 2014, we conducted land preparation. All of trees growing in the two plots were cut down and their roots were removed. In addition, we weeded the two plots. After this work, we ploughed the two plots three times to a depth of 30 cm.

The teak seedlings were prepared by a tissue culture technique. The teak clone was from Mae Hong Son Province (clone number 21), and this clone has been planted in various places (Royal Forest Department, unpublished data). Teak seedlings were raised from March to June 2014 at the Teak Improvement Center, Lampang, Thailand. In July 2014, 252 teak seedlings were transported to the Northeast Forest Seed Center, Khon Kaen.

Establishment of the experiment

We established three blocks each in the moderate and suitable plots. The size of each block was 12 m × 10 m, and there was 4 m between the blocks. On the border between the blocks, teak seedlings were planted for the buffer. After establishment, we buried a concrete pole in the center of two blocks at the two sites. In July 2014, we planted 42 teak seedlings in each block at the two sites. The interval between seedlings was 2 m × 2 m. Twenty-two teak seedlings were planted outside of the blocks and were considered as the buffer trees. We measured various growth characteristics for 20 teak seedlings per block planted within the buffer trees.

After planting, we inserted soil moisture sensors (SM150, Delta-T Devices Ltd., Cambridge, UK) in two blocks at the two sites. The sensors were set near a seedling.

Soil analysis

We measured soil texture, cation exchange capacity (CEC), and chemical properties including pH and concentrations of carbon (C), N, exchangeable P, and base cations. Three soil samples from each block at the two sites were collected in July 2014. To determine the pH of the soil, 25 ml of distilled water was added to 10 g fresh soil to make a homogenized mixture (van Reeuwijk 2002). This mixture was then shaken for 1 h and the pH was measured using a pH meter (SG2, Mettler Toledo, Zürich, Switzerland). Prior to chemical analysis, we conducted the air-drying of soil samples.

The soil texture was determined by the hydrometer method (Klute 1986). In the analysis of CEC, we used a method based on that of Chapman (1965), and developed a rapid method by Fujihira Industry Co. (http://www.fujihira.co.jp/english/soi/Field%20Soil%20Doctor.html). The concentrations of C and N in dried soils were determined using a nitrogen and carbon analyzer (Flash 2000, Thermo Fisher Scientific, Waltham, MA). Exchangeable P was separated using dilute acid fluoride (Sparks et al. 1996) by shaking for 1 minute. P in the extracted solution was determined by the molybdenum blue method (American Public Health Association et al. 1998) using a spectrophotometer (U-1800, Shimadzu, Kyoto, Japan). Exchangeable base cations (Ca, magnesium [Mg], potassium [K], and sodium [Na]) was quantified by mixing 4 g of dry soil with 100 ml of 1 M ammonium acetate solution, and shaking for 1 h (Sparks et al. 1996). Base cations in the extracted solutions were analyzed using an atomic absorption spectrophotometer (AAnalyst 300, Perkin-Elmer, Norwalk, CT).

Measurement of teak seedlings

For the measurement of teak seedlings, 20 seedlings for each block at two sites were used for growth measurements. Total numbers of seedlings were 60 for each site. We measured tree height and basal diameter at six time points (July 2014, October 2014, February 2015, May 2015, July 2015, and November 2015). At these times, we also confirmed the number of dead teak seedlings.

Measurement of photosynthetic rate

We measured area-based photosynthetic rate at light saturation (P_{sat}) and stomatal conductance (gs) for teak leaves located second from the top. For the measurement of photosynthetic rate and leaf water potential, six teak seedlings (two individuals each from three blocks) were used for the measurements. When we measured photosynthetic rate, the leaves of some seedlings were immature or senescent. In addition, the leaves of two-thirds of the seedlings were damaged by worms. To provide uniformly mature and healthy teak leaves, we selected six teak leaves from 60 seedlings. On the maturation of teak leaves, we used them that passed one month after foliation. We measured P_{sat} seven times (October 2014, December 2014, February 2015, May 2015, July 2015, October 2015, and November 2015), and the measurement were always performed between 09:00 and 11:00.

Measurements were made using a portable gas analyzer (LI-6400, LiCor, Lincoln, NE, USA) in steady-state conditions, at an ambient temperature of 28 °C and ambient CO_2 concentration of 38.0 Pa. The LED light source was adjusted to a saturation light level of 1,800 μmol $m^{-2}s^{-1}$ PPF.

Measurement of leaf water potential, concentration of nitrogen, and leaf mass per area

After measurement of photosynthetic rate, we measured the leaf water potential of teak leaves at seven time points (October 2014, December 2014, February 2015, May 2015, July 2015, October 2015, and November 2015). The leaf used to measure water potential was the same as that used to measure photosynthetic rate. In general, leaf water potential was lowest in the afternoon because of transpiration and highest during the night after recovery of water (Larcher 2003). We measured leaf water potential in the afternoon and predawn. Six teak leaves for each treatment were sampled at 13:00–14:00 and 05:30–06:00 the next day. Sampled shoots were placed in a plastic bag that contained a wet filter paper and then kept in a refrigerator. We measured leaf water potential using a pressure chamber (Model 600, PMS Instrument Co., Albany, OR, USA).

After measuring leaf water potential, we analyzed the concentration of nitrogen and leaf mass per area (LMA). Photosynthetic rate is closely related to the concentration of N (Evans 1989; Larcher 2003; Kayama et al. 2007) and leaf thickness (Niinemets 1999; Terashima et al. 2001).

The leaf samples were oven-dried at 70 °C for 3 days. After drying, we samples 3 cm^2 of teak leaf samples and weighed them. LMA (g m^{-2}) was calculated by the method of Larcher (2003). Leaf samples were ground to a fine powder using a sample mill (WB-1; Osaka Chemical Co., Osaka, Japan). The concentration of N was determined using an NC analyzer (Sumigraph NC-220F, Sumika Chemical Analysis Service, Tokyo, Japan). The concentration of N was calculated from the area based on N (N_{area}) from the LMA data.

Analysis of biomass and element concentrations of teak seedlings

To determine the aboveground biomass of teak seedlings, we measured the dry masses of leaves and stems. At the end of November 2015, we collected the aboveground organs of four teak seedlings from each of the three blocks at the two sites. The organs were divided into leaves and stems, and the fresh masses were measured. We collected the largest leaf from the leaf samples and measured its length and width. Leaf area was calculated using equation of the Tondjo et al. (2015). In addition, about 100 g (fresh mass) of leaf and stem samples were collected and their fresh mass measured. Moreover, we collected the leaf located second from the top for analysis. These leaf and stem samples were each placed into separate envelopes and oven-dried at 70 °C for 3 days. When the sample that fresh mass was below 100 g, all of samples were placed into a single envelope. After drying, the dry mass of each component was determined and the water content calculated. We calculated the dry mass of total leaves and stems from this water content data.

We also collected parts of the roots of teak seedling from the same seedlings as used for the aboveground organs. We collected four root samples from each of the three blocks at the two sites. The roots weighed approximately 10 g (fresh mass) and their diameter was less than 2.0 mm. The roots were washed twice with tap water to remove soil and air-dried. The root samples were transport to our laboratory in Japan and washed again with distilled water. Each root sample was placed into a separate envelope and oven-dried at 70 °C for 3 days.

For the analysis of elements in the plant organs, we measured the concentrations of N, P, K, Ca, Mg, and Na in leaves (located second from the top) and roots. Dried samples were ground to a fine powder, and N concentration was determined using the NC analyzer. The remaining samples were digested by the HNO_3-HCl-H_2O_2 method (Goto 1990). Concentrations of K, Ca, Mg, and Na were analyzed using an ICP analyzer (ICPE-9000, Shimadzu, Kyoto, Japan), and the concentration of P was determined by the molybdenum blue method using a spectrophotometer (UV-2500PC, Shimadzu, Kyoto, Japan).

Statistical analysis

Significant pairwise differences for each variable were tested by t-test using Stat View 5.0 (SAS Institute Inc.). Comparisons were made between the moderate and suitable sites. For the data of soil water content, times and sites were examined repeated measures of ANOVA.

Results

Water contents in soil

Average soil water content values at two blocks of two sites were shown in Fig. 1. The water content was low from January to May 2015, but in the rainy season (June to September 2014, and June to August 2015) water content was high. Soil water content was significant difference among months (P<0.001).

Comparing with the data of two sites, soil water content of suitable a showed high values in every months compared with other data. In contrast, the value of soil water content of suitable b was similar with those of moderate a and b. The margin between the suitable and moderate sites was low from December 2014 to May 2015. Soil water content was significant difference between moderate and suitable sites (P<0.001). However, there was no significant interaction between months and sites.

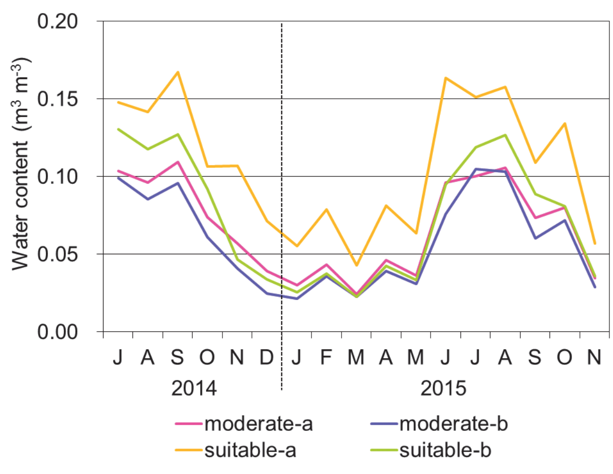

Fig. 1. Average soil water content at the moderate and suitable sites with sandy soil. (from July 2014 to November 2015). There were two data (a and b) at different blocks of two sites.

Soil properties

Regarding soil texture, the content of sand was over 80% for each site (Table 1). Compared the two sites, there was no significance of sand, silt, and clay contents between suitable and moderate sites (P>0.05).

The pH and CEC values were significantly higher for the suitable site than for the moderate site (P<0.001). The concentrations of C, N, Ca, Mg, and K at the suitable site were also significantly higher than those at the moderate site (P<0.01). There was no significant difference in the concentrations of P and Na between the two sites

Growth characteristics

From October 2014, tree height and diameter were significantly larger for the suitable site than for the moderate site (Fig. 2, P<0.001), and differences in teak growth between the moderate and suitable sites were clear (Fig. 3). At the suitable site, the increase in tree height and diameter accelerated from July 2015. In contrast, teak seedlings at the moderate site did not show obvious growth. During the experimental period, the increase in tree height and diameter was 12 cm and 4.6 mm at the suitable and moderate sites, respectively.

Dead seedlings were observed at the moderate site from February 2015. At the end of experiment, 47% of seedlings at the moderate site had died. In contrast, only one seedling died at the suitable site.

Photosynthetic rate

P_{sat} values were significantly higher for the suitable site than that for the moderate site (P<0.05) except for in February 2015 (Fig. 4). P_{sat} was high in October 2014, then the values decreased until May 2015 at each site. In July 2015, P_{sat} increased at both sites, but it then decreased from October 2015 at the moderate site.

gs was also significantly higher at the suitable site than the moderate site (P<0.05) except for in February 2015. The decrease in gs from October 2014 to May 2015 showed a similar trend to P_{sat}. In July 2015, gs increased drastically at the suitable site.

Leaf water potential

Leaf water potential in the afternoon was highest in July 2015 (Fig. 5) for each site. In contrast, leaf water potential was lowest in November 2015 for the suitable site, but at the moderate site it was lowest in February 2015. Comparing the two sites, leaf water potential was significantly higher for the suitable site than that for the moderate site in February 2014, July 2015, and October 2015 (P<0.05).

Table 1. Texture and chemical properties of soils from the moderate and suitable sites with sandy soil (Mean ± SE, n=9). Mean values of each parameter were analyzed by t-test. ** P<0.01, *** P<0.001, and n.s. not significant.

Treatment	Texture (%)			pH
	Sand	Silt	Clay	
moderate	80.2±0.5	14.1±0.7	5.7±0.9	4.53±0.08
suitable	81.5±0.6	13.8±0.4	4.7±0.4	5.95±0.05
Statistical test	n.s.	n.s.	n.s.	***
	CEC ($cmol\ kg^{-1}$)	C ($mol\ kg^{-1}$)	N ($mmol\ kg^{-1}$)	P ($mmol\ kg^{-1}$)
moderate	1.30±0.10	0.58±0.19	21.6±2.5	0.278±0.065
suitable	2.50±0.14	1.35±0.09	6.9±1.1	0.341±0.070
Statistical test	***	**	***	n.s.
	Ca ($mmol\ kg^{-1}$)	Mg ($mmol\ kg^{-1}$)	K ($mmol\ kg^{-1}$)	Na ($mmol\ kg^{-1}$)
moderate	1.31±0.21	0.94±0.12	0.58±0.07	0.103±0.026
suitable	8.37±0.79	2.93±0.20	2.62±0.27	0.184±0.046
Statistical test	***	***	***	n.s.

For the predawn leaf water potential, the value at the moderate site in February 2015 was quite low. In contrast, leaf water potential at the suitable site was not particularly low. Comparing the two sites, leaf water potential was significantly higher for the suitable site than for the moderate site except for in October and November February 2015 (P<0.05).

Concentration of nitrogen and LMA

N_{area} values were highest in December 2014 at the suitable site and in February 2015 at the moderate site (Fig. 6). Comparing the two sites, N_{area} was significantly higher for the suitable site than the moderate site in October 2014, December 2014, and October 2015 (P<0.05). At other time points, there were no significant differences between the two sites.

The trend for LMA at the suitable site showed an increase from October at the start of the dry season. By contrast, this trend was not clear at the moderate site. In May 2015 when new leaves extended, LMA decreased. Comparing the two sites, LMA was significantly higher for the suitable site in December 2014, February 2015, and November 2015 than for the moderate site (P<0.01). In contrast, LMA in October 2014 was significantly higher for the moderate site than that for the suitable site (P<0.05).

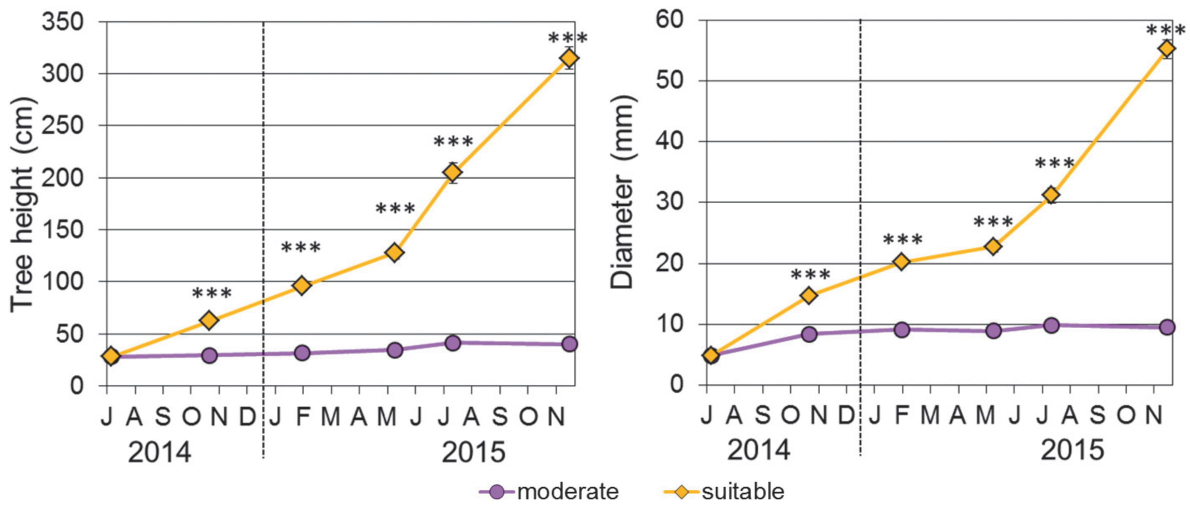

Fig. 2. Tree height and basal diameter of teak seedlings grown at the moderate and suitable sites with sandy soil (mean ± SE, n=60). Mean values of each parameter were analyzed by t-test. *** P<0.01.

Note. Divisions on the horizontal axis over the letters are the first day of each month. The same format is used in subsequent figures.

Fig. 3. Pictures of teak seedling grown at the moderate (left) and suitable (right) sites with sandy soil (October 2015). Teak growth showed obvious differences between the two sites.

Biomass of teak seedling

For the dry masses of aboveground organs in July 2014, leaf and stem dry masses were significantly larger for the suitable site than for the moderate site (Fig. 7, $P<0.001$). In the moderate site, leaf and stem dry masses were only 5.1 g and 26 g, respectively.

In addition, the area of the largest leaf was significantly larger for the suitable site than for the moderate site ($P<0.001$). Comparing the two sites, leaves from the suitable site were 29 times larger than from the moderate site.

Concentration of elements in plant organs

For nutrients in roots, the concentrations were significantly higher for the suitable site than for the moderate site (Table 2, $P<0.01$). Moreover, the concentrations of Ca and P in leaves were also significantly higher for the suitable site than for the moderate site ($P<0.05$). In contrast, the concentration of Mg in leaves was significantly higher for the moderate site than for the suitable site ($P<0.05$). The concentrations of N and K in leaves showed no significant differences between the two sites. In addition, the concentrations of Na in leaves and root did not show any significant difference.

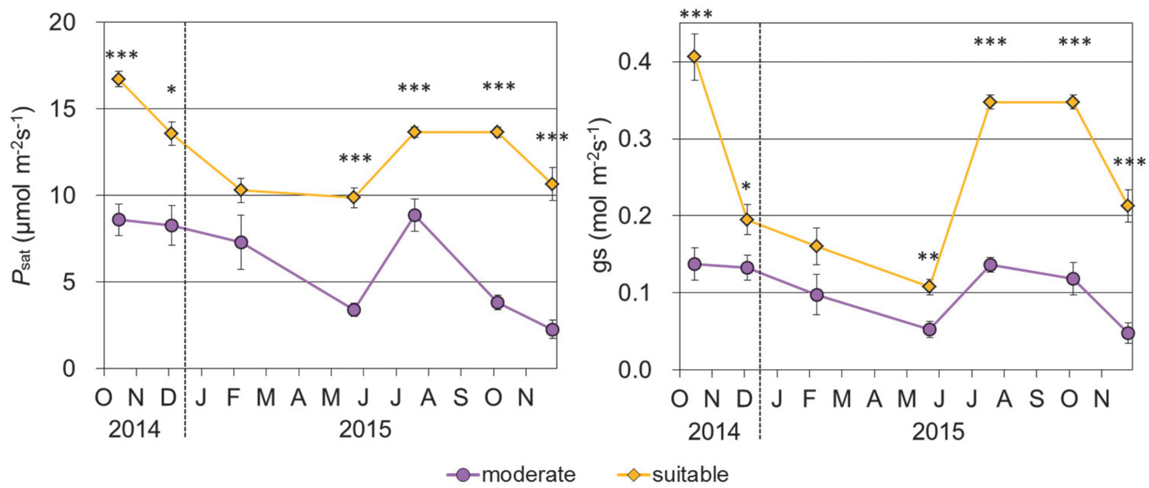

Fig. 4. Photosynthetic rate at light saturation (P_{sat}) and stomatal conductance (gs) for teak seedlings grown at the moderate and suitable sites with sandy soil (9:00-11:00, mean ± SE, n=6). Mean values of each parameter were analyzed by t-test. * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

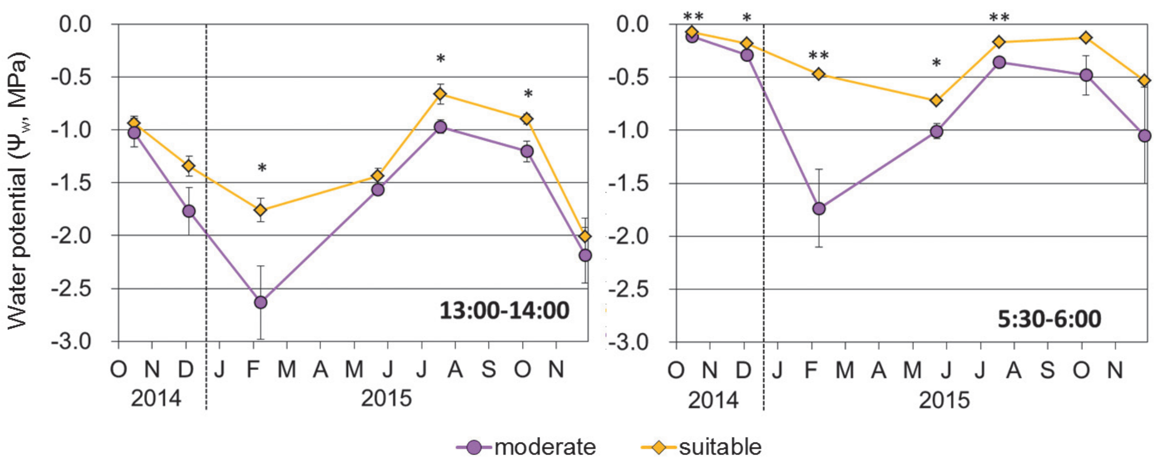

Fig. 5. Leaf water potential in the afternoon (13:00–14:00) and predawn (05:30–06:00) for teak seedlings grown at the moderate and suitable sites with sandy soil (mean ± SE, n=6). Mean values of each parameter were analyzed by t-test. * $P<0.05$, ** $P<0.01$.

Discussion

Based on these results, teak growth was substantially different between the moderate and suitable sites (Fig. 2, 3, 7). At the moderate site, teak growth was suppressed drastically and 47% of seedlings died. With regard to factors that affected teak growth, we predicted that differences of soil texture, nutrients, and water in soil may be contributory factors. The content of sand at the two sites was the same (Table 1); therefore, a difference in soil texture was not the main factor affecting teak growth. Soil water levels were higher at the suitable site; however, the range of its value was wide, and a block of suitable site was similar value of soil water with that of moderate site (Fig. 1). Suitable site showed large growth of teak seedlings for every block compared with moderate site. Thus, differences in soil water were also not a major factor that affected teak growth.

In terms of soil nutrients, various nutrients except for P showed low concentrations at the moderate site (Table 1). In addition, all nutrients in roots and Ca and P in leaves were lower in concentration at the moderate site (Table 2). Thus, teak seedlings grown at the moderate site suffered from the suppression of nutrient uptake, especially of Ca and P.

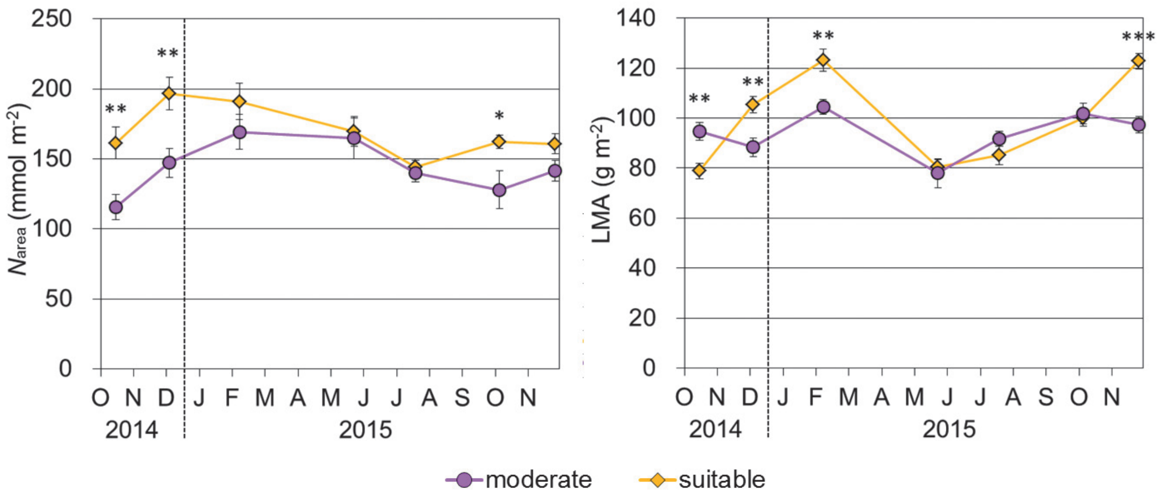

Fig. 6. Concentration of area-based nitrogen (N_{area}) and leaf mass per area (LMA) for teak seedlings grown at the moderate and suitable sites with sandy soil (mean ± SE, n=6).

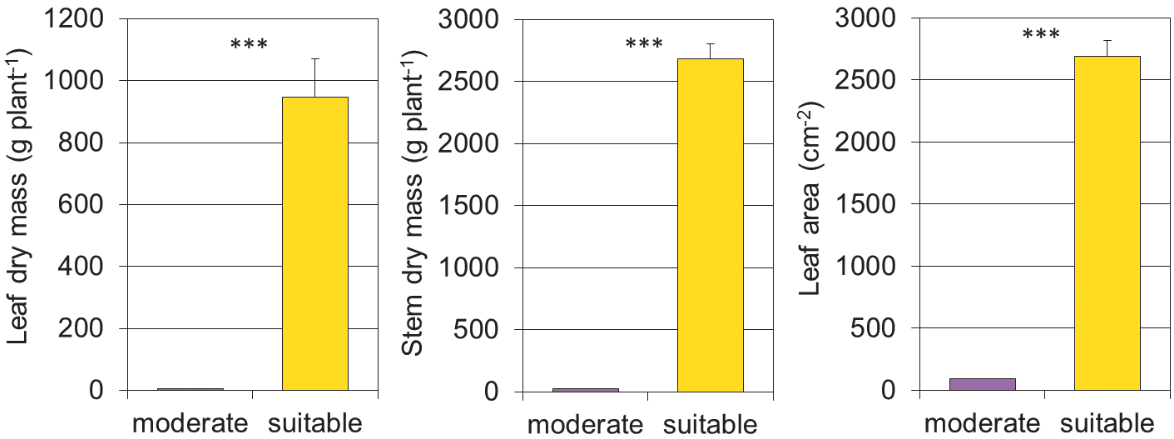

Fig. 7. Leaf and stem dry mass, and the area of the largest leaf for teak seedlings at the end of the experiment (November 2015) at the moderate and suitable sites with sandy soil (mean ± SE, n=12). Mean values of each parameter were analyzed by t-test. *** P<0.001.

Table 2. Concentrations of elements (N, P, K, Ca, Mg, and Na; µmol g^{-1} dry mass) in leaves and roots of teak seedlings grown at the moderate and suitable site with sandy soil (November 2015, mean ± SE, n=12). Mean values of each parameter were analyzed by t-test. * *P*<0.05, ** *P*<0.01, *** *P*<0.001, and n.s. not significant.

Element		Leaf	Root
N	moderate	1423±65	539±22
	suitable	1312±51	705±30
	Statistical test	n.s.	***
P	moderate	165±13	72± 6
	suitable	208±36	109± 7
	Statistical test	*	***
K	moderate	132±15	102± 6
	suitable	101± 8	272±12
	Statistical test	n.s.	***
Ca	moderate	101±20	81± 5
	suitable	249±23	112± 7
	Statistical test	***	**
Mg	moderate	208±15	42± 2
	suitable	157±09	78± 4
	Statistical test	**	***
Na	moderate	26.3±1.4	31.0±2.7
	suitable	25.2±0.9	32.6±1.6
	Statistical test	n.s.	n.s.

In teak, Ca is an important nutrient for growth (Zech and Drechsel 1991; Tanaka et al. 1998; Zhou et al. 2012). When teak seedlings were raised in culture medium excluding Ca, growth was suppressed drastically (Barroso et al. 2005). Comparing with other studies, the nutrient deficiency levels for teak was <138 µmol g^{-1} for Ca and <32 µmol g^{-1} for P (Zech and Drechsel 1991). Based on these data, the concentration of Ca in the leaves of teak at the moderate site (101 µmol g^{-1}) was lower than the deficiency level, and seedlings at this site suffered from Ca deficiency. In contrast, the concentration of P in the leaves at the moderate site (165 µmol g^{-1}) was much higher than the deficiency level. Thus, restriction in the uptake of P was probably not responsible growth suppression of teak compared with Ca. We also calculated the ratio of the moderate site per suitable site for the concentration of each nutrient in soil. The ratio was lowest for Ca, and concentration of Ca in soil at the moderate site was only 16% compared with the suitable site (Table 1). Thus, the main factor affecting teak growth at the moderate site was Ca deficiency.

Moreover, teak seedlings grown at the moderate site suffered from a decrease in photosynthetic rate at many times points (Fig. 4). One of the causes of this decrease in photosynthetic rate was decreased gs (Fig. 4), and low gs decreased the absorption of CO_2 because of stomatal closure. This trend was clear in February and May 2015 (Fig. 4) when the soil water content was low (Fig. 1). Meanwhile, the difference in water content in soil between the moderate and suitable sites was not clear except for in June and October 2014 (Fig. 1). Thus, the difference in gs between the moderate and suitable sites was caused by other factors.

Ca deficiency is not reported to be directly related to decreases in gs (Suárez 2010). However, a low Ca environment decreased N uptake, and lower N levels were associated with decreased photosynthetic rate (Suárez 2010). N_{area} was significantly lower at the moderate site in October 2014, December 2014, and October 2015 (Fig. 6). In these months, photosynthetic rate at the moderate site was probably decreased by the low N_{area}. However, P_{sat} at the moderate site was significantly lower in May, July, and November 2015 when the N_{area} did not differ significantly between the moderate and suitable sites (Fig 4, 6). Thus, there were other causes of the decreases in photosynthetic rate and gs.

In teak leaves at the moderate site, the concentration of Mg was significantly higher than at the suitable site (Table 2). This concentration was quite high and similar to level in woody species grown on high Mg environments such as serpentine (Alexander et al. 2007). Barroso et al. (2005) also confirmed that teak seedlings were raised in culture medium excluding Ca, Mg accumulated in the leaves. In general, when we examine the effects of Mg, we calculated the Ca:Mg ratio in plant organ because Mg toxicity can occur when there is an imbalance between Ca and Mg (Alexander et al. 2007). When this ratio decreases below 0.5, plants can suffer from Mg toxicity (Mizuno 1979; Kayama and Koike 2015). The Ca:Mg ratio for leaves of teak at the moderate site was 0.49, and this level was considered to indicate the plants were suffering from Mg toxicity. In plant species not adapted for Mg tolerance, the accumulation of Mg can readily decrease photosynthetic rate and gs (Palm et al. 2012; Kayama and Koike 2015). Thus, the main cause of the decreased photosynthetic rate and gs in teak seedlings at the moderate site was probably the accumulation of Mg in leaves. Barroso et al. (2005) also indicated negative effects on teak growth from the accumulation of Mg.

Furthermore, teak seedlings grown at the moderate site suffered from drought stress. Leaf water potential was lowest in February 2015, and this value did not increase in the predawn period (Fig. 5). These results were considered to indicate that teak seedlings grown at the moderate site could not recover water during the night time, and as a result they suffered from serious drought stress in February 2015. In addition, the accumulation of Mg is associated with decreased leaf water potential (Rao et al. 1987). Teak seedlings grown at the moderate site may readily suffer from drought stress from the accumulation of Mg.

Finally, we concluded that differences in soil chemical properties affected teak growth. The main factor affecting growth of teak was Ca, with a low concentration of Ca in soil being associated with the suppressed growth of teak. In addition, we confirmed that when teak suffered from Ca deficiency, Mg accumulated in the leaves and various physiological traits were suppressed. To accelerate teak growth at the moderate site, the addition of Ca was essential.

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