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ORIGINAL ARTICLE



Effects of tree density and size symmetry of competition on diameter growth in the early stages of growth in planted teak (*Tectona grandis*) trees in northern Thailand

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ABSTRACT

Teak (*Tectona grandis*) is among the most valuable tropical hardwoods, but silvicultural guidelines are needed to improve the growth and quality of trees in teak plantations, particularly those owned by smallholders in Asia. We analyzed the diameter growth of individual trees to determine the effects of density control in the early stages of growth in a teak plantation in northern Thailand. Site water conditions estimated using the topographic index (TI) affected initial tree size at 10 years after planting, before the first thinning was conducted. Thinning comprised three levels: high, low, and none (control). Five years after thinning, we assessed the effects of thinning, diameter at thinning, TI, and neighborhood competition on tree diameter growth using generalized linear mixed models. We found two significant factors on diameter growth: negative effect of neighborhood competition and positive effect of initial diameter at thinning. We used two indices of neighborhood competition: size-asymmetric (one-sided) and symmetric (two-sided) competition. The two-sided competition model predicted diameter growth more accurately. The results indicate that inter-tree competition in even-aged teak plantations is size-symmetric or two-sided. In addition, the presence of size-symmetric competition implies that teak trees compete not only for light but also for below-ground resources, such as water and nutrients.

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Density control; thinning; topographic index; competition for light; competition for water

Introduction

Teak (*Tectona grandis*) is among the most valuable tropical hardwoods, but natural sources have declined due to over-exploitation. Teak is planted in more than 60 countries (Kollert and Kleine 2017) with the expectation of high market returns. The global area of teak plantations was reported to be 4.3 Mha in 2010, 83% of which was in Asia. Most plantations are owned and managed by government entities (Kollert and Cherubini 2012). By contrast, teak plantations owned by smallholders are currently a minor component of the global teak estate, comprising 19% of the plantation area in Asia, but production by smallholders nevertheless represents a potentially important source of teak (Kollert and Cherubini 2012; Kollert and Kleine 2017).

There have been several prescriptions of teak plantation management in different countries around the world, which on average suggest 4–5 times of thinning for a final stocking of 230 trees ha⁻¹, and final harvest at 35 years old (Pachas et al. 2019a). In Thailand and Laos, teak may be among the forest resources exploited by smallholder families to generate income (Kollert and Kleine 2017). However, smallholder teak plantations in these countries are often depicted as overcrowded and slow-growing, as a result of poor silvicultural practices (Mittelman 2000). Thai forestry laws restricting the harvest and transport of teak have historically constrained smallholders from implementing appropriate forest management practices, such as thinning (Mittelman 2000), but these regulations were relaxed in 2019. Limited demonstrative information and poor understanding of teak

silviculture are additional contributing factors (Mittelman 2000; Midgley et al. 2007; Newby et al. 2012), and have created reluctance among smallholders to remove trees during the early stages of plantation growth. It is critical to provide silvicultural guidelines to improve the growth and quality of teak grown in smallholder plantations (Pachas et al. 2019a, 2019b); these guidelines may vary significantly according to local environmental and silvicultural objectives (Pandey and Brown 2000; Kollert and Kleine 2017).

Teak is a light-demanding tree (Krishnapillay 2000; Pandey and Brown 2000) and proper density control in plantations is essential for maintaining diameter growth (Briscoe and Ybarra-Cornado 1971; Krishnapillay 2000; Sousa et al. 2012; Budiadi et al. 2017; Pachas et al. 2019b). Therefore, thinning is critical to ensure adequate light availability (Ugalde Arias and Monteuiis 2013; Sadono 2014; Budiadi and Ishii 2017). Effects of neighborhood competition on the growth of light-demanding species are primarily size-asymmetric, or one-sided, i.e. larger trees suppress the growth of surrounding smaller trees, whereas smaller trees hardly affect the growth of larger trees (Weiner 1986; Kohyama 1992, 1994; Ogawa and Hagihara 2003). However, size structures are typically more homogeneous in even-aged plantations than in uneven-aged forests; in such cases, inter-tree competition in the stand may be size-symmetric or two-sided (Thomas and Weiner 1989). Although the degree of size asymmetry in competition is a critical factor for developing appropriate density control guidelines for plantation forests, it has not been sufficiently implemented in teak stands. In addition, size-symmetric

competition has been reported in cases where competition for water and nutrients has greater importance than the competition for light (Thomas and Weiner 1989; Schwinning and Weiner 1998). This may apply to teak plantations because several reports have indicated that deficits in soil nutrients and water restrict teak growth (Zech and Drechsel 1991; Watanabe et al. 2010; Chia 2011). In Thailand, monsoon climates with dry seasons (Kaosa-ard 1989; Kollert and Kleine 2017) result in soil water deficits that have serious effects on the diameter growth of teak (e.g. Yoshifuji et al. 2006, 2011). However, aside from a mention by Krishnapillay (2000), thinning has not been explored as a means to release competition for below-ground resources among teak trees in plantations.

To determine whether one- or two-sided neighborhood competition is predominant in young teak plantations, we assessed factors affecting diameter growth in individual trees in a teak plantation in northern Thailand 5 years after the first thinning.

Material and methods

Study site

The study site was located 20 km east of the provincial capital of Uttaradit in northern Thailand (17° 41' N, 100° 17' E, 220 m a.s.l.). The mean daily maximum temperature ranges from 28°C in December to 36°C in March and April, and the mean daily minimum temperature ranges from 17°C in December to 26°C in April and May, as estimated based on meteorological data recorded in Uttaradit (68 m a.s.l.). The study region is characterized by rainy summers and dry winters. Monthly precipitation, based on data which were collected in Uttaradit and provided by Thai Meteorological Department, is approximately 200 mm between May and October, and <100 mm between November and April (Figure 1). Mean and standard deviation of annual precipitation of 5 years from 2014 to 2018 was 1270 ± 272 mm.

Experimental design and field surveys

A teak plantation of approximately 8 ha was established at the study site in 2004, with an initial planting density of 625 seedlings per ha (4 × 4-m spacing). Nine study plots were established at the site in May 2014. Each plot was assigned to

one of the three levels of thinning intensity, and each treatment was replicated three times. The plot dimensions were 40 × 40 m. The diameter at breast height (DBH, cm) and height (m) of all trees in each plot were measured (denoted as DBH₂₀₁₄ and H₂₀₁₄, respectively), and thinning was conducted based on the percentage of stand basal area (m²) of the plot prior to the operation, as follows:

$$\text{stand basal area} = \sum_i D_i^2 \pi / 40000$$

where D_i is the DBH (cm) of the i th tree within the plot as of March 2014. Thinning intensity levels included heavy (60% removal of standing crop; denoted as HI), light (40% removal; denoted as LO), and none (or control; 0% removal, denoted as CO; Table 1). Trees were selected for removal based on defects, trunk damage, or poor growth, as determined by visual assessments. In June 2019, the DBH and height of all trees in each plot were remeasured; however, height measurement was omitted for approximately half the trees in the CO plots for labor-related reasons. Height was measured using a Haglof Vertex IV ultrasonic hypsometer (Haglof Inc., Torsang, Sweden). DBH was measured using a diameter tape.

The study site is characterized by moderately undulating topography. We measured the position and relative elevation of the base of each tree in all plots in 2016 using a laser rangefinder to calculate the topographic index (TI). The TI is used as an index of topographical effects on hydrological processes based on TOPMODEL (Beven and Kirkby 1979; Noguchi et al. 2014), and is calculated following Quinn (1995):

$$TI = \ln(a/\tan b)$$

where a is the upslope area (m²) per unit contour length, and b is the local slope angle. Contour length was set to 5 m and calculations were conducted in Grass 7.8 (Open Source Geospatial Foundation Project; <http://grass.osgeo.org>). The mean $\pm$ standard deviation TI of the nine plots was 6.2 ± 1.6 and ranged from 2.9 to 13.5.

Analyses

To evaluate the effects of topography on initial tree size prior to thinning, we assessed whether TI was correlated with DBH₂₀₁₄ and H₂₀₁₄ after thinning.

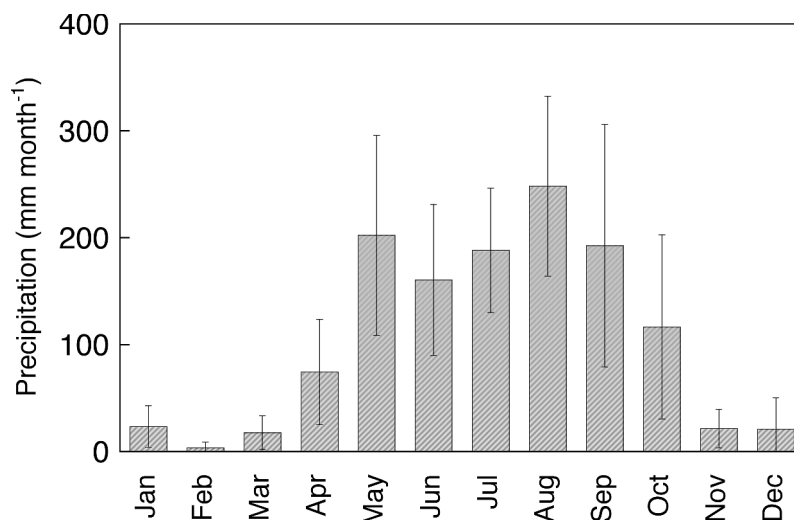


Figure 1. Seasonal variations in precipitation at the study site. Values represent mean monthly precipitation over 5 years (2014–2018); vertical bars indicate SD. Data were provided by the Thai Meteorological Department.

Table 1. Parameters of study plots by thinning intensity and measurement period. Values represent the arithmetic mean $\pm$ standard deviation of plots subjected to the same thinning intensity. Note that height data for the CO plots in 2019 represent approximately half the trees in the plot.

Parameter	Time of measurement		Thinning intensity		
			LO	HI	CO
Number of trees (trees ha ⁻¹)	2014	before thinning	585.4 $\pm$ 20.1	579.2 $\pm$ 34.4	614.6 $\pm$ 9.6
	2014	after thinning	310.4 $\pm$ 25.3	197.9 $\pm$ 26.0	614.6 $\pm$ 9.6
	2019		285.4 $\pm$ 25.3	181.3 $\pm$ 27.2	445.8 $\pm$ 68.6
Stand basal area (m ² ha ⁻¹)	2014	before thinning	12.3 $\pm$ 1.3	11.4 $\pm$ 1.7	11.0 $\pm$ 0.6
	2014	after thinning	7.8 $\pm$ 0.7	4.8 $\pm$ 0.9	11.0 $\pm$ 0.6
	2019		10.8 $\pm$ 1.7	7.4 $\pm$ 1.2	12.6 $\pm$ 1.9
Mean DBH (cm)	2014	before thinning	16.1 $\pm$ 1.0	15.6 $\pm$ 0.7	14.9 $\pm$ 0.5
	2014	after thinning	17.8 $\pm$ 1.2	17.5 $\pm$ 1.2	14.9 $\pm$ 0.5
	2019		21.7 $\pm$ 1.4	22.6 $\pm$ 1.1	18.8 $\pm$ 0.8
Mean height (m)	2014	before thinning	15.9 $\pm$ 0.6	15.3 $\pm$ 0.7	14.8 $\pm$ 0.7
	2014	after thinning	16.5 $\pm$ 0.7	16.2 $\pm$ 0.6	14.8 $\pm$ 0.7
	2019		18.0 $\pm$ 1.6	17.0 $\pm$ 0.8	16.4 $\pm$ 0.3

DBH increments of individual trees 5 years after thinning (G_{DBH} , cm) were calculated as follows:

$$G_{DBH} = (DBH_{2019} - DBH_{2014})$$

where DBH_{2014} and DBH_{2019} represent DBH (cm), as measured in 2014 and 2019, respectively. Competitive effects with neighboring trees were evaluated based on the basal area (denoted as BA , m² ha⁻¹):

$$BA = \sum D_i^2 \pi / (4 \times 48\pi)$$

where D_i is the DBH of the i th tree within a given radius from the focal tree. BA represents the sum of the basal area of trees remaining after thinning operations in May 2014, excluding the basal area of the focal tree. Based on other studies (Kohyama 1992; Kikuzawa and Umeki 1996; Masaki et al. 2006), we examined competitive effects among neighboring trees using two different BA metrics. The first was the total BA (BA_T , m² ha⁻¹), which was the sum of the BA of all trees within a given radius; BA_T is an indicator of the magnitude of symmetric competition. The second was the total BA of trees with a diameter larger than that of the focal tree (BA_L , m² ha⁻¹), and was calculated as the sum of the BA s of trees with D_{2014} larger than the focal tree. BA_L is an indicator of the magnitude of asymmetric competition between neighboring trees. We consider that focal trees compete with their immediate neighbors only in the early stages of stand development. Thus, we chose 48π (m²) as the calculation area for BA s, which is the average area of a circle with a radius of $4\sqrt{2}$ m (the distance to the second adjacent trees) and a circle with a radius of 8 m (the distance to the third adjacent trees). Trees in the outer two rows in each plot were classified as buffer trees and used only in BA calculations. The remaining trees were classified as focal trees and were used in G_{DBH} analyses (Table 2). Data on focal trees that died between 2014 and 2019 were omitted from the analyses.

Effects of initial tree size, thinning, TI, and neighborhood competition on G_{DBH} were evaluated using the following generalized linear mixed model (GLMM):

$$G_{DBH} = a_0 + a_i(x_i) + r$$

where a_0 and a_i are unknown parameters, r represents a random effect, x_i represents the i th explanatory variable, and a_i represents the i th unknown parameter. The following parameters were used as explanatory variables:

Thinning: a categorical factor representing density control operations. *Thinning* was assigned a value of 0 in the CO plots and 1 in the HI and LO plots.

DBH_{2014} : a factor representing initial tree size.

TI: a factor representing site suitability.

BA_T and BA_L : factors representing neighborhood competition.

We first assessed a full model that included all explanatory variables. We then built and tested additional models, in which variables were removed in a round-robin test of all combinations to determine the best model. We used Akaike's information criterion (AIC) to compare models, with the lowest AIC value representing the best model. Collinearity among explanatory variables was assessed in the final model to evaluate the suitability of the variable selection. We tested two full models using both BA_T and BA_L as explanatory variables of neighborhood competition.

Analyses and final model selection were conducted using the R packages *nlme* (Pinheiro 2020) and *MuMIn* (Burnham and Anderson 2002), and R version 3.6.2 (R Development Core Team 2020).

Table 2. Parameters of focal trees and explanatory variables used in the analyses of G_{DBH} . Aside from the number of trees, values represent the arithmetic mean $\pm$ standard deviation of plots subjected to the same thinning intensity. Note that the sample size for height data in the CO plots in 2019 was 28.

Parameters and explanatory variables	Time of measurement		Thinning intensity		
			LO	HI	CO
Number of focal trees	2014	after thinning	57	34	83
	2019		53	31	63
DBH (cm)	2014	after thinning	17.7 $\pm$ 2.5	17.0 $\pm$ 1.9	15.1 $\pm$ 2.5
	2019		22.0 $\pm$ 3.1	22.2 $\pm$ 2.6	18.9 $\pm$ 3.0
H (m)	2014	after thinning	16.9 $\pm$ 1.2	16.0 $\pm$ 1.1	14.8 $\pm$ 1.4
	2019		18.6 $\pm$ 1.7	16.8 $\pm$ 2.1	16.1 $\pm$ 1.5
G_{DBH} (cm)	2019		4.2 $\pm$ 1.3	4.9 $\pm$ 1.4	3.3 $\pm$ 1.1
BA_T (m ² ha ⁻¹)	2014	after thinning	5.9 $\pm$ 2.2	3.7 $\pm$ 2.1	6.7 $\pm$ 1.5
BA_L (m ² ha ⁻¹)	2014	after thinning	3.1 $\pm$ 3.6	2.1 $\pm$ 3.1	3.5 $\pm$ 3.4
TI	2016		7.0 $\pm$ 2.5	6.0 $\pm$ 1.1	5.7 $\pm$ 1.2

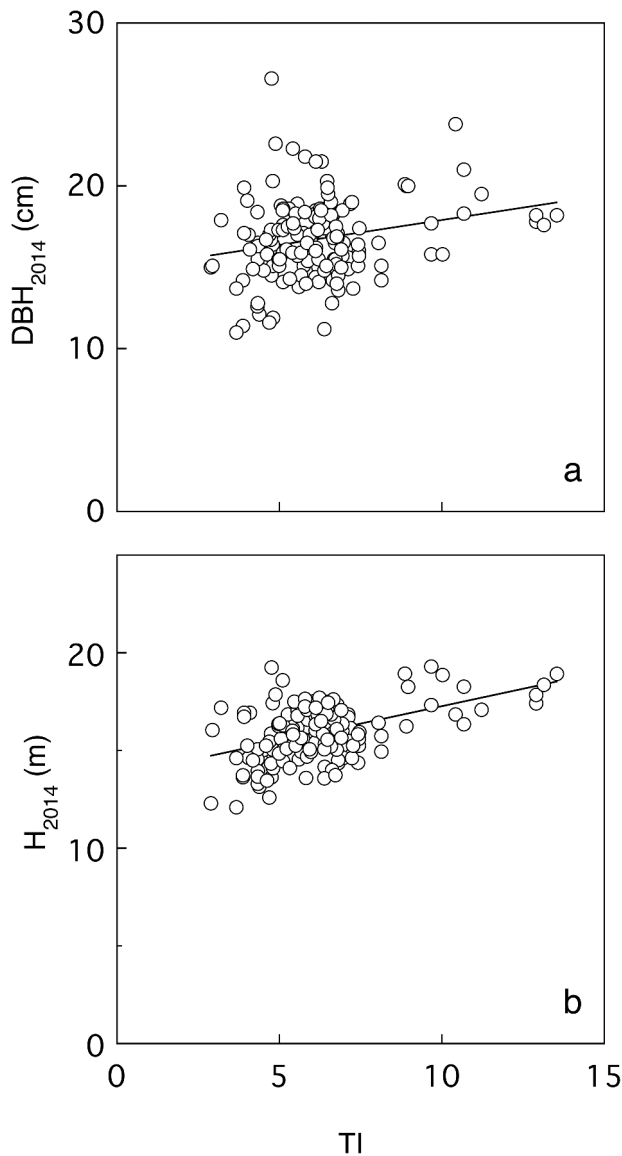


Figure 2. Relationships between TI and initial diameter (DBH_{2014} , (a)), and between TI and initial height (H_{2014} , (b)) 10 years after planting but before thinning. Open circles represent individual trees and lines represent Pearson's linear regression.

Results

Effects of topography on initial tree size prior to thinning

The mean DBH 10 years after planting, but before thinning, ranged from 14.9 to 16.1 cm (Table 1). The mean values for initial height ranged from 14.8 to 15.9 m. TI was significantly positively correlated with DBH_{2014} ($r^2 = 0.06$, $p < 0.01$; Figure 2a) and H_{2014} ($r^2 = 0.23$, $p < 0.01$; Figure 2b).

Factors affecting DBH growth after thinning

Model B (final model with BA_T , Table 3) had the lowest AIC value, of 426.5; the next lowest AIC value was 428.5 for Model A (full model with BA_T). In Models A and B, significant effects of DBH_{2014} in positive direction and of BA_T in negative direction ($p < 0.001$) on G_{DBH} were exhibited, respectively. Neither *Thinning* nor TI exhibited significant effects on G_{DBH} ($p = 0.265$ and 0.681 , respectively) in Model A.

The AIC values for models with BA_L were ≥ 444 and were higher than the values of models that included BA_T . In Model C (full model with BA_L), G_{DBH} was significantly affected negatively by BA_L and positively by *Thinning* ($p < 0.001$ and $p < 0.05$, respectively), but not by DBH_{2014} or TI ($p = 0.315$ and 0.512 , respectively). In Model D (final model with BA_L), BA_L and *Thinning* were included as explanatory variables and exerted similar significant effects to Model C on G_{DBH} ($p < 0.001$ and $p < 0.01$, respectively).

In Model B, the correlation between DBH_{2014} and BA_T was significant ($r^2 = 0.06$, $p < 0.01$). In Model D, the correlation between BA_L and *Thinning* was not significant ($p = 0.08$).

Discussion

Effects of topography on initial tree size before thinning

Significant positive correlations between TI and DBH_{2014} , and between TI and H_{2014} ($r^2 = 0.06$ and 0.23 ; Figure 2a and 2b), indicate that initial diameter and height 10 years after planting were positively affected by variations in soil water conditions, as estimated by TI. As numerous reports have demonstrated that teak growth is affected and constrained by soil water conditions (Priya and Bhat 1999; Rajendrudu et al. 2000; Yoshifuji et al. 2006, 2011; Husen 2010), it is likely that differences in tree size prior to thinning are attributable to variations in TI. The correlation coefficients suggest that TI affected initial tree size, as reported in other studies, but the effect was not dominant. The higher correlation coefficient between TI and H_{2014} compared to that between TI and DBH_{2014} suggests that TI affected initial height more than the initial diameter. It is reasonable that drier soil condition causes hydraulic constraints in teak tree and leads to restrained height growth rather than diameter growth. This is consistent with other studies reporting that water stress reduces height growth relative to radial growth (Callaway et al. 1994; Trouvé et al. 2015).

Factors affecting DBH growth after thinning

Both indices of neighborhood competition had a significant negative effect on G_{DBH} in the final models (Models B and D; Table 3). These results indicate that neighborhood competition constrains diameter growth in teak, indicating that density control to reduce competition effectively enhanced the diameter growth of teak trees 10 years after planting. In this study, we assumed two models of local competition: size-asymmetric (one-sided competition) and size-symmetric (two-sided competition). Smaller AIC values for Model B compared to Model D indicate that the model assuming size-symmetric competition has greater predictive power for G_{DBH} .

Previous studies have described teak as a light-demanding tree (Krishnapillay 2000; Pandey and Brown 2000). Properly timed density control operations at suitable intensities are important for maintaining diameter growth (Briscoe and Ybarra-Cornado 1971; Krishnapillay 2000; Sousa et al. 2012; Budiadi and Ishii 2017; Pachas et al. 2019b). As such, density control in teak plantations has focused on optimizing a single aboveground resource, i.e. light, in the stand. For example, Sadono (2014) evaluated the competitive status of teak plantations using the radii of crown projection and crown height. Ugalde Arias and Monteuuis (2013) and Budiadi et al. (2017) noted that canopy

Table 3. Effects of model components on G_{DBH} .

Model A. Full model with BA_T				
Model component	Estimate	Std. Error	t value	p value
Intercept	2.236	0.666	3.355	0.001
DBH_{2014} (cm)	0.202	0.037	5.504	< 0.001
BA_T ($m^2 ha^{-1}$)	-0.324	0.038	-8.464	< 0.001
TI	0.018	0.044	0.413	0.681
Thinning	0.223	0.184	1.213	0.265
AIC	428.54			
Model B. Final model with BA_T				
Model component	Estimate	Std. Error	t value	p value
Intercept	2.230	0.652	3.419	< 0.001
DBH_{2014} (cm)	0.221	0.034	6.556	< 0.001
BA_T ($m^2 ha^{-1}$)	-0.338	0.036	-9.312	< 0.001
AIC	426.48			
Model C. Full model with BA_L				
Model component	Estimate	Std. Error	t value	p value
Intercept	3.208	0.938	3.421	< 0.001
DBH_{2014} (cm)	0.052	0.052	1.008	0.315
BA_L ($m^2 ha^{-1}$)	-0.259	0.043	-6.061	< 0.001
TI	0.035	0.053	0.658	0.512
Thinning	0.896	0.256	3.500	< 0.05
AIC	446.87			
Model D. Final model with BA_L				
Model component	Estimate	Std. Error	t value	p value
Intercept	4.317	0.214	20.128	< 0.001
BA_L ($m^2 ha^{-1}$)	-0.287	0.032	-8.927	< 0.001
Thinning	0.995	0.237	4.189	< 0.01
AIC	444.56			

closure resulted in a decline in teak growth, and that canopy closure may be a good indicator of thinning during the early stages of plantation growth. Generally, competition for light is considered size-asymmetric or one-sided, because the shade provided by larger trees is greater than that provided by smaller trees (Weiner 1986; Kohyama 1992, 1994; Ogawa and Hagiwara 2003). At the present study, the range of heights of focal trees in 2014 (14.8–16.9 m; Table 2) implies that height differences among the study plots were small. Under such conditions, smaller trees shade the lower part of the crown of larger trees, which may induce size-symmetric, two-sided competition for light, as previous studies indicated (Thomas and Weiner 1989; Schwinning and Weiner 1998; Inoue et al. 2008).

In addition, our finding that competition in the teak plantation was size-symmetric indicates that competition may occur not only for light but also for below-ground resources, such as water and nutrients. Soil water conditions at the study site may frequently become critical due to the seasonality of precipitation in monsoon climates (Figure 1). Under these circumstances, neighborhood competition for below-ground resources (particularly water) can be as intense as that for above-ground resources (i.e. light), which is consistent with existing studies indicating that inter-tree competition is size-symmetric in cases where competition for water and nutrients has greater importance (Thomas and Weiner 1989; Schwinning and Weiner 1998). There are many reports of soil nutrient and water status being a limiting factor in teak growth (Zech and Drechsel 1991; Yoshifuji et al. 2006; Watanabe et al. 2010; Chia 2011). However, competition for below-ground resources among even-aged teak trees has scarcely been discussed in the literature, aside from a suggestion that proper management improves the productivity of teak on problem soils (Krishnapillay 2000). Our finding showed that TI did have a positive effect on tree height and diameter 10 years after planting but before thinning (Figure

2a and 2b), whereas it was not useful in predicting DBH growth after thinning (Table 3). This result suggests that relief of neighborhood competition by thinning is more influential than TI in DBH growth and which is consistent with the mention by Krishnapillay (2000).

Secondly, the significant positive effect of DBH_{2014} on G_{DBH} (Table 3) indicates that initial size advantages of individual trees tend to be maintained during the subsequent growing period in even-aged plantations. Our data confirm that it is rare for small trees to surpass larger trees, which is consistent with the results of previous studies (Seiwa and Kikuzawa 1987; Stephenson et al. 2014) and has implications for the development of criteria for selecting trees for removal during thinning operations. Among trees with similar qualitative characteristics, smaller trees should be selected for removal to ensure that the larger, retained trees will subsequently maximize stand volume increases. We consider DBH_{2014} and BA_T , which were used as explanatory variables in Model B, to be independent because of their low correlation coefficient ($r^2 = 0.06$).

In previous studies, the effects of thinning on diameter growth in teak trees were reported both at the stand level (Kollert and Kleine 2017; Quintero-Méndez and Jerez-Rico 2019) and the individual level (Ugalde Arias and Monteuis 2013; Sadono 2014; Budiadi and Ishii 2017). Although *Thinning* was included as an explanatory variable in Model D (final model with BA_L), the AIC value of the model was larger than that of Model B (final model with BA_T) with the lowest AIC value (Table 3). Our results demonstrate that variables representing competitive status at the individual level, such as DBH and BA_T , are more appropriate for predicting future diameter growth of individual trees than is thinning history. *Thinning* by definition reduces BA_T ; therefore, the operation indirectly increases the diameter growth of remaining trees.

Conclusion

The initial diameter and height of teak trees 10 years after planting, but before thinning, was slightly affected by TI. After thinning, diameter growth was significantly affected by two factors: neighborhood competition and initial tree diameter. Neighborhood competition, as evaluated based on the sum of the basal area of all trees surrounding the focal tree, was a more appropriate index for predicting diameter growth than was the sum of the basal area of trees with a diameter larger than that of the focal tree. Our results indicate that individual-based competition among trees in even-aged teak plantations is size-symmetric, or two-sided, thus demonstrating the effectiveness of removing inferior trees by thinning. An outcome of our study is a basis for an individual-based model of teak stand dynamics which is quite beneficial to provide silvicultural guidelines of teak grown in smallholder plantations in Thailand. Although it is difficult to yield some profit from logs out of the removed inferior trees at an early stage of stand growth, the thinning operation is essential to raise the value of remaining trees and to realize future benefit at the final harvest.

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Disclosure statement

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Author contributions

T. Vacharangkura and W. Himmapan conceived the experiment, planned and established the experimental site. W. Himmapan conducted field surveys in 2014. W. Himmapan and G. Hitsuma conducted measurements of the position and relative elevation of stem bases in 2016, as well as field surveys in 2019. T. Yagihashi performed TI and BA calculations. T. Yagihashi, K. Miyamoto, and G. Hitsuma conducted growth analyses. G. Hitsuma wrote the first draft, and all authors reviewed the results and contributed to the final manuscript.

Geolocation information

The study site was located 20 km to the east of the provincial capital of Uttaradit in northern Thailand (17° 41' N, 100° 17' E).

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