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Research Article

Teak (*Tectona grandis* Linn. f) and Edaphic Factors Affecting the Regeneration of Woody Species and Their Functional Traits in Economic Forest Plantation, Northern Thailand

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Improved understanding of relationships among plant traits, stand characteristics, and soil properties can provide insights into the regenerating tree communities of commercial teak plantations. We investigated whether plant traits could be used to predict the natural regeneration of woody species in teak plantations with different soil and stand conditions. Data were collected in fifty 20 m × 20 m plots that were established in teak plantations of varying ages in northern Thailand. We analyzed differences in stand characteristics, soil properties, and community-level functional traits among sites. The RLQ analysis was performed to explore the associations among species abundances, plant traits, and a combined set of soil variables and stand characteristics. Our results showed that tree species with high leaf dry matter contents and high wood density dominated communities in an older teak plantation and were associated with high OM and N concentrations. Trees with larger leaves are increased in plantations that had experienced their first teak thinning, and were rich in organic matter. Species with high specific leaf areas increased in sites with high teak basal areas and which had experienced more intense thinning on fertile soils. Thick-leaved species had high importance values on sites with high densities of teak and infertile soils. Our results indicated that tree communities with similar conspecific traits were associated with specific soil and stand conditions in teak plantations. A knowledge of these regeneration dynamics may allow forest managers to encourage increased natural regeneration and enhanced diversity in commercial teak plantations.

1. Introduction

Forest plantations are intensively managed planted forests that are composed of one or more species at maturity. Plantations are characterized by controlled age structure and intertree spacing during the processes of afforestation or reforestation [1]. They provide goods and services that include timber, nontimber forest products, watershed protection, air purification, erosion control, biodiversity, aesthetic value, carbon sequestration, and climate control [2]. A large proportion of global wood products are sourced from plantation forests [3]. Industrial plantations are often established on degraded lands, which represent an opportunity for restoring forest landscapes and reducing threats to natural systems [4, 5]. However, commercial plantations are usually planted in monocultures that are expected to have lasting effects on forest structure, diversity, and functioning [6]. Therefore, promoting the natural regeneration of other native plants in plantations could enhance plant diversity and promote forest structures and functions that are closer to those of the natural forests [7–9].

Teak (*Tectona grandis* Linn f.) is an important plantation species that has gained worldwide prominence due to the durability and attractive appearance of its wood. Teak is one of the most valuable timber species in the tropics and is grown on over 2.25 million ha globally [10]. Teak is native to India, Myanmar, Thailand, and Laos and was translocated to parts of Africa and Central and South America during the past century [11]. In Thailand, teak grows in natural forests throughout the northern part of the country. The suitable natural habitats of them are most positively significant with elevation and soil variable [12, 13]. Teak is a dominant species in the mixed deciduous forest (MDF); however, it can be absent from the MDF [14, 15] and the other co-dominant species such as *Pterocarpus macrocarpus*, *Xylia xylocarpa*, *Afzelia xylocarpa*, and *Dalbergia oliveri*, and deciduous bamboos can be associated [16].

The Thai government has pursued a policy of intensive teak logging in these natural forests, resulting in the depletion of teak throughout the northern part of Thailand [17]. Currently, the Thai government is promoting the establishment of teak plantations to support the country's wood demand, foster watershed improvement, and restore degraded forest reserves [18]. The Forest Industry Organization (FIO) is the state enterprise that operates planted commercial plantations to produce timber, and it manages teak, eucalyptus, and para rubber across 245 plantation sites. Teak plantations occupy the largest proportion of this area and cover 79,680 ha, especially in northern Thailand. These plantations are managed using principles of sustainable commercial forest plantation management to promote both environmental and socioeconomic sustainability [19]. Therefore, there is an urgent need to promote the diversification of plant communities in FIO plantations to comply with Thailand's environmental sustainability policy.

Previous studies have suggested that promoting the natural regeneration of native species in teak plantations is a key step to increasing their plant diversity [20–22]. Soil properties and plantation characteristics are important factors that influence plant regeneration in teak plantations. Soil nutrient concentrations, organic matter, and other chemical and physical properties of soils in teak plantations tend to promote high soil fertility [23]. Teak plantations may increase soil fertility relative to the soil conditions that prevail in disturbed forests [24]. Relative soil fertility can influence woody species richness in teak plantations [25]. Plantation density, canopy cover, and age all affect plant regeneration in teak plantations. For example, densely planted teak plantations reduce colonization by other native plants because closed canopies effectively shade out and inhibit the natural regeneration of woody species [22, 26, 27].

Plant functional traits can potentially be used to develop predictive frameworks for the community assembly of natural regeneration in plantations [28–30]. Plant functional traits are morphological and physiological characteristics that affect plant performance by influencing survival, growth, and reproduction. Traits represent biological adaptations to local environments that determine ecological strategies for reproduction and resource capture [31, 32]. Recently, the relationships between plants and soils have been used to create trait-based frameworks for examining plant community establishment [33–35]. Thus, a better understanding of the relationships among plant traits, soil properties, and conditions in teak plantations should improve researchers' ability to predict the regeneration characteristics that are likely to be successful in these environments.

In this study, we investigated the natural regeneration of woody species in teak plantations, paying special attention to the associations between plant functional traits, soil variables, and plantation characteristics. Specifically, we addressed two questions. First, can the functional traits of woody species be used to predict the successful establishment of natural regeneration in teak plantations? Second, how do different soil conditions and teak plantation characteristics influence the plant functional traits that promote successful regeneration? The results of this study may contribute to the development of trait-based management frameworks and improve predictions of woody species regeneration in teak plantations.

2. Materials and Methods

2.1. Study Sites. This study was conducted in Khun Mae Khum Mee Plantation (18° 21′ 32″–18° 28′ 44″ N, 100° 24′ 49″–100° 30′ 60″ E). This forest covers 31.35 km^2 of Phrae province, northern Thailand (Figure 1). The site spans elevations of 350–700 meters above mean sea level (m asl). The mean annual rainfall is 1,281.6 mm, and the mean annual temperatures vary between 21.75°C and 31.83°C. The region experiences a tropical monsoon climate with two main seasons: a wet season (May–October) and a dry season (November–April). The dry season is subdivided into cool-dry (November–January) and hot-dry subseasons (February–April) [36].

The commercial teak plantation was established in Khun Mae Khum Mee by dividing the area into 17 planting plots. The first plantation plots were established in 1968. Successive episodes of logging and replanting resulted in 36 subplots with tree ages that vary from 1 to 40 years. All plantation plots were planted with teak at a spacing of 4 m × 4 m (625 trees per ha). Pruning and weeding were performed annually for the first five years using hand tools. The first thinning was performed after 15-year-old by cutting 50% of the stems, yielding a residual tree density of 312 trees per ha. A second 50% thinning took place at 25-year- old, resulting in a residual density of 156 trees per ha. The final harvest mostly took place after 30-year-old, but some plots were left until 40-year-old to produce large-dimension timber. Some old-growth forests that stand in the area are the secondary MDFs that remained in the area after government-sponsored logging. They cover approximately 20% of the plantation area and are currently protected [36].

2.2. Sampling Plot Selection and Tree Data Collection. We collected data from January to December 2020. Sampling was conducted in 10-, 20-, 30-, and 40-year-old plots and in old-growth forests. All sites had similar topographic and geographic settings (elevation 400–450 m asl and slope approximately 40–45%) (Table 1). Within each site, we established ten 20 m × 20 m (0.04 ha) plots for a total of 50 plots (2 ha). Diameter at breast height (DBH, cm) and height (m) of all mature trees ≥1.3 m tall and ≥4.5 cm DBH were measured in each 0.04 ha plot. All trees were identified to the species level by comparing collected specimens with identified specimens in

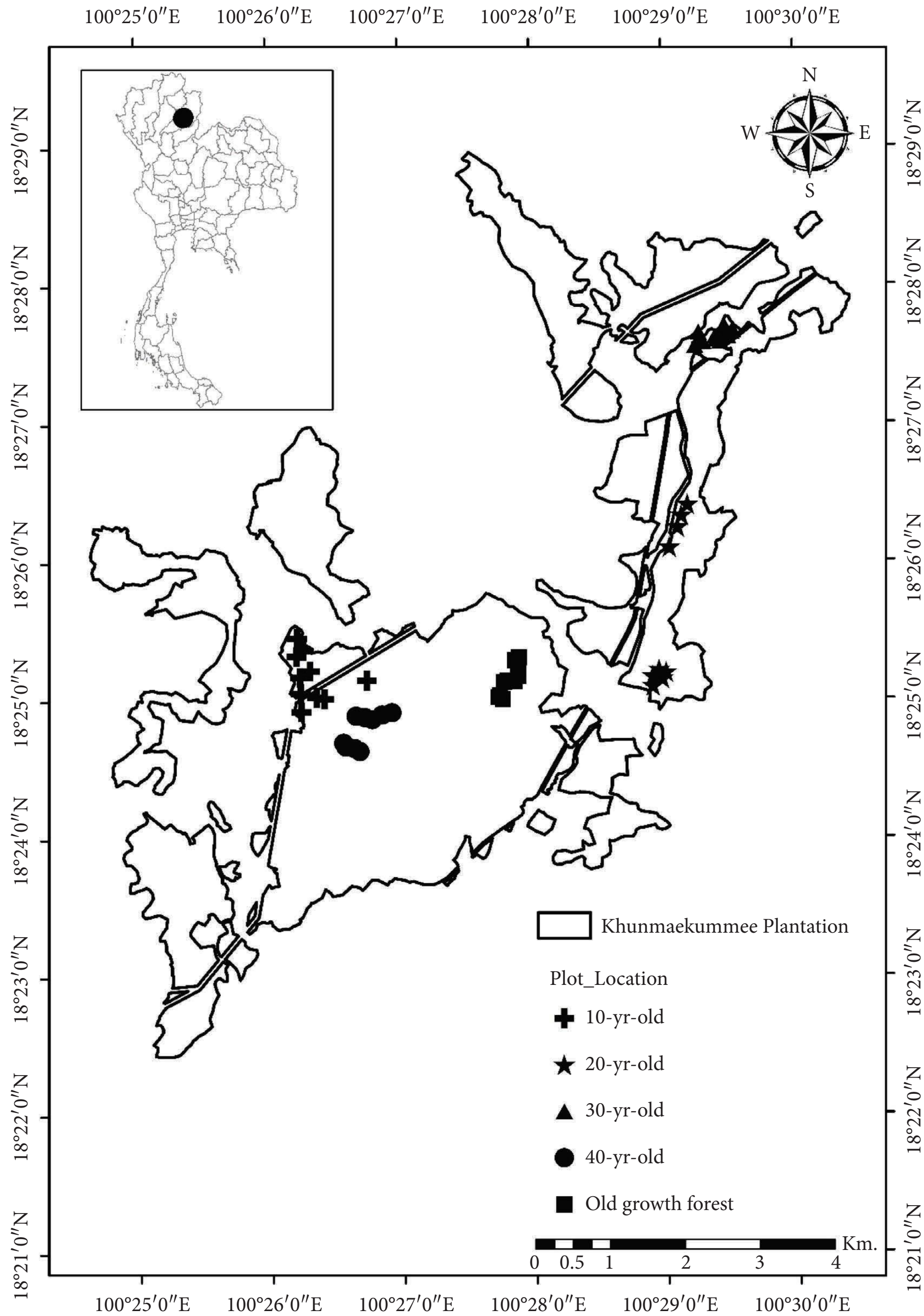

Figure 1: Location of sampling plots and the Khun Mae Khum Mee plantation in Phrae province, northern Thailand.

the Forest Herbarium (BKF), Department of National Parks, Wildlife and Plant Conservation. The nomenclature used in this study followed the system used by Pooma and Suddee [37].

2.3. Soil Measurements. In each 20 m × 20 m sampling plot, we sampled soil variables that included soil texture (percent sand, silt, and clay), pH, organic matter (OM, %), and soil nutrients, including N (%), P (mg kg^{-1}), K (mg kg^{-1}), Ca (mg kg^{-1}), and Mg (mg kg^{-1}). Soil samples were collected as 100 cm^3 soil cores extracted from the topsoil layer (0–15 cm) in October 2020. To calculate the mean value of soil properties in each 20 m × 20 m plot, five cores were taken from the center and each of the four corners of the 0.04 ha plots. These soil samples were used to analyze the soil texture, pH, OM, and available N, P, K, Ca, and Mg at the soil laboratory of the Faculty of Forestry, Kasetsart University.

2.4. Functional Trait Measurements. Five functional traits of mature trees were chosen for analysis: specific leaf area (SLA, cm^2 g^{-1}), leaf dry matter content (LDMC, mg g^{-1}), leaf area (LA, cm^2), leaf thickness (LT, mm), and wood density (WD, g cm^{-3}). These traits are associated with plant ecological strategies that are related to competitive ability,

Table 1: Description and silvicultural practice of sampling sites of teak plantation plots on 10-, 20-, 30-, and 40-year-old and old-growth forest sites in Khun Mae Khum Mee plantation, Phrae province.

Sampling sites	Site conditions	Silvicultural practice
10-year-old teak	(i) Elevation 400 m asl (ii) Slope 35% (iii) Site is a ridge area	(i) Spacing 4 m × 4 m (ii) Left after 5 years of annual weeding and pruning (iii) No thinning
20-year-old teak	(i) Elevation 400 m asl (ii) Slope 40% (iii) Site is a ridge area	(i) Spacing 4 m × 4 m (ii) Abandoned 5 years after first thinning by 50% at 15-year-old
30-year-old teak	(i) Elevation 450 m asl (ii) Slope 43% (iii) Site is a ridge area	(i) Spacing 4 m × 4 m (ii) Abandoned 5 years after second thinning by 50% at 25-year-old
40-year-old teak	(i) Elevation 450 m asl (ii) Slope 45% (iii) Site is a ridge area	(i) Spacing 4 m × 4 m (ii) Abandoned 15 years after second thinning by 50% at 25-year-old
Old-growth forest	(i) Elevation 450 m asl (ii) Slope 40% (iii) Site is a ridge area	(i) Abandoned 31 years after logging by the government to promote natural succession

growth potential, and physical resistance to damage [32]. Fifty-six species of mature trees represented by ≥3 individuals in all 50 plots were selected for the measurement of trait data (Table 2). In this study, teak trait data were not collected. The traits in question were measured in three individuals from each species and the mean values for each trait were calculated. In October 2020, we sampled 3–10 sun leaves from each individual to calculate the mean values of SLA, LDMC, LA, and LT. Fresh leaves were scanned using ImageJ software (https://rsbweb.nih.gov/ij/), and LA was calculated from these leaf images. Leaf mass was measured from fresh leaves, and leaf dry mass was measured after samples had been oven-dried at 60°C for 48 h. Specific leaf area was calculated as the ratio of fresh LA divided by oven-dried mass, and LDMC was calculated as the ratio of oven-dried to fresh leaf mass. We determined LT from the mean leaf blade thickness from five leaf samples, measured using a thickness gauge (China YH-1; Zhejiang, China). Wood samples for WD determination were collected at breast height (1.3 m) using 5 mm increment borers, after which they were oven-dried at 70°C for 48 h. Wood density was then calculated as the ratio of oven-dried to fresh wood volume.

2.5. Data Analyses. For each site, we calculated mean values of DBH, stem density (stem ha^{-1}), stem basal area (BA; m^2 ha^{-1}), and height. Similarly, mean values of all soil properties were calculated for each site. One-way analysis of variance (ANOVA, critical $p < 0.05$) was used to test for statistically significant differences among functional traits and soil variables. We used stem density, basal area, relative stem density, and relative basal area to perform species composition analysis. From these data, we calculated the importance value index (IVI) to identify the dominant species at each site. An IVI value is calculated as the sum of relative stem densities and relative basal areas for each site [38]. In addition, we calculated the Shannon–Wiener index as a measure of tree species diversity in each site [39].

To characterize trait dominance, the community-level weighted mean (CWM) of each trait was calculated at each site, as follows:

$$\mathrm{CWM} = \sum_{i=1}^{n} p_i \times \mathrm{tr}_i, \qquad (1)$$

where p_i and tr_i are the relative abundance and trait value of species i and n is the total number of species per plot. Values of CWM were calculated using the FD package [40] in the *R* statistical environment. One-way ANOVAs were used to characterize and quantify differences in mean CWMs for SLA, LDMC, LA, LT, and WD at each site.

We used RLQ analysis and the fourth corner method to explore the association of species composition, plant traits, and environmental variables. RLQ analysis uses multivariate ordination techniques to explore the intercorrelations of species abundance (matrix *L*), species traits (matrix *Q*), and environmental variables (matrix *R*) [41]. Matrix *R* comprised soil pH, the percentages of sand, silt, and clay, OM, N, P, K, Ca, and Mg, together with teak stem density (stem ha^{-1}, TD), teak basal area (m^2 ha^{-1}, TBA), time since thinning (Thin), and plantation age. A Monte Carlo permutation test was performed with 999 permutations to assess the statistical significance of each environmental variable using the vegan package for *R*. Fourth corner analysis represents the correlation between plant traits and environmental variables when assessed using species relative abundance [42]. To assess individual species trait-environment relationships, we used the fourth corner to jointly perform a permutation test on the combined model 2 (permutation values of sites) and model 4 (permuted values of species) outputs ($n = 49{,}999$ permutations). RLQ and fourth corner analyses used the *ade4* package [41] for *R*.

Table 2: Woody species, species codes, and numbers of stems present in the fifty 0.04 ha plots.

No.	Species	Code	Family	Number of stems
1	*Pterocarpus macrocarpus*	PTEMA	Fabaceae	238
2	*Dalbergia cultrata*	DALCU	Fabaceae	105
3	*Xylia xylocarpa*	XYLXY	Fabaceae	98
4	*Albizia odoratissima*	ALBOD	Fabaceae	55
5	*Schleichera oleosa*	SCHOL	Sapindaceae	36
6	*Terminalia mucronata*	TERMU	Combretaceae	25
7	*Aporosa nigricans*	APONI	Phyllanthaceae	23
8	*Artocarpus lacucha*	ARTLA	Moraceae	15
9	*Hubera cerasoides*	HUBCE	Annonaceae	14
10	*Anogeissus acuminata*	ANOAC	Combretaceae	13
11	*Holarrhena pubescens*	HOLPU	Apocynaceae	13
12	*Canarium subulatum*	CANSU	Burseraceae	12
13	*Dalbergia ovata*	DALOV	Fabaceae	12
14	*Millettia brandisiana*	MILBR	Fabaceae	12
15	*Erythrina subumbrans*	ERYSU	Fabaceae	11
16	*Mitragyna rotundifolia*	MITRO	Rubiaceae	11
17	*Lagerstroemia duperreana*	LAGDU	Lythraceae	10
18	*Vitex peduncularis*	VITPE	Lamiaceae	10
19	*Dalbergia nigrescens*	DALNI	Fabaceae	9
20	*Harrisonia perforata*	HARPE	Simaroubaceae	9
21	*Lagerstroemia calyculata*	LAGCA	Lythraceae	9
22	*Grewia eriocarpa*	GREER	Malvaceae	8
23	*Terminalia bellirica*	TERBE	Combretaceae	7
24	*Cratoxylum cochinchinense*	CRACO	Hypericaceae	6
25	*Dolichandrone serrulata*	DOLSE	Bignoniaceae	6
26	*Markhamia stipulata*	MARST	Bignoniaceae	6
27	*Phyllanthus emblica*	PHYEM	Phyllanthaceae	6
28	*Shorea obtusa*	SHOOB	Dipterocarpaceae	6
29	*Spondias pinnata*	SPOPI	Anacardiaceae	6
30	*Dalbergia cana*	DALCA	Fabaceae	5
31	*Diospyros castanea*	DIOCA	Ebenaceae	5
32	*Irvingia malayana*	IRVMA	Irvingiaceae	5
33	*Miliusa velutina*	MILVE	Annonaceae	5
34	*Fernandoa adenophylla*	FERAD	Bignoniaceae	4
35	*Phanera bracteata*	PHABR	Fabaceae	4
36	*Terminalia chebula*	TERCH	Combretaceae	4
37	*Walsura pinnata*	WALPI	Malvaceae	4
38	*Wrightia arborea*	WRIAR	Apocynaceae	4
39	*Bombax anceps*	BOMAN	Malvaceae	3
40	*Careya arborea*	CARAR	Lecythidaceae	3
41	*Cassia fistula*	CASFI	Fabaceae	3
42	*Chukrasia tabularis*	CHUTA	Meliaceae	3
43	*Dalbergia oliveri*	DALOL	Fabaceae	3
44	*Diospyros ehretioides*	DIOEH	Ebenaceae	3
45	*Litsea glutinosa*	LITGL	Lauraceae	3
46	*Shorea siamensis*	SHOSI	Dipterocarpaceae	3
47	*Terminalia nigrovenulosa*	TERNI	Combretaceae	3
48	*Cananga brandisiana*	CANBR	Annonaceae	3
49	*Lagerstroemia macrocarpa*	LAGMA	Lythraceae	3
50	*Antidesma ghaesembilla*	ANTGH	Phyllanthaceae	3
51	*Buchanania lanzan*	BUCLA	Anacardiaceae	3
52	*Dalbergia assamica*	DALAS	Fabaceae	3
53	*Dipterocarpus obtusifolius*	DIPOB	Dipterocarpaceae	3
54	*Lannea coromandelica*	LANCO	Anacardiaceae	3
55	*Strychnos nux-vomica*	STRNU	Loganiaceae	3
56	*Terminalia alata*	TERAL	Combretaceae	3

Teak data were excluded from the species and trait matrices in CWM and RLQ because teak stand variables formed part of the environmental matrix. The CWM and RLQ were analyzed in R software (version 4.2.2) [43].

3. Results

3.1. Teak Characteristics. Mean values of DBH, basal area, stem density, and height of the teak varied significantly among sites (Table 3). The largest DBH trees (mean = 24.91 cm) were found in 40-year-old teak sites, followed by those in sites that were 30, 20, and 10 years old ($p < 0.001$). Old-growth forest sites had the smallest teak stems. Basal area was also larger in 40-year-old teak sites (10.85 m^2 ha^{-1}), followed by the 20-, 10-, and 30-year-old sites and old-growth forest ($p < 0.001$). Similarly, the tallest teak grew in the 40-year-old sites (mean height = 23.85 m), followed by 20-, 30-, and 10-year-old sites and the old-growth forest ($p < 0.001$, Table 3). Maximum stem density occurred in the 10-year-old sites (478 stems ha^{-1}), followed by 20-, 40-, and 30-year-old sites and old-growth forest, respectively ($p < 0.001$). The dimensional traits of teak were at their smallest on old-growth forest sites because most teak on these sites were stump sprouts that grew after logging had occurred.

3.2. Soil Properties. Several soil properties differed among sites (Table 4). The percent sand was significantly greater in 10-year-old and old-growth forest sites ($p < 0.001$). Percent clay was higher in 40- and 20-year-old sites than elsewhere ($p < 0.001$). Forty-year-old sites had a greater pH and higher concentrations of OM, N, Ca, and Mg than other sites, but the concentration of soil K was highest in old-growth forests (all $p < 0.001$). Percent silt and P concentrations were similar across sites (Table 4).

3.3. Woody Species Composition. Ten-year-old teak sites had the highest stem densities but the lowest basal area values (Table 5), suggesting that these sites supported large numbers of small stems. Twenty-year-old sites had the lowest species richness (21 species), species diversity (Shannon–Wiener index = 1.56), and stem densities (mean = 570 stems ha^{-1}). By contrast, 30-year-old sites supported the most species (47 species) and had the highest Shannon–Wiener diversity index (2.75), a value similar to that in old-growth forest sites (2.72). The BA of 40-year-old sites was greater than those of other sites. Both the BA and stem density of this age class were similar to values recorded at old-growth forest sites (Table 5).

The five dominant species ranked according to IVI are shown in Table 6. Planted teak dominated plantation sites at all ages but ranked fifth among woody species in old-growth forest sites due to their production of small postlogging stump sprouts. *Pterocarpus macrocarpus* was the dominant species in old-growth forests and the second most dominant species in 10-, 30-, and 40-year-old sites. *Xylia xylocarpa* was also dominant in old-growth forest sites and in 10-, 20-, and 30-year-old sites. *Albizia odoratissima* was the third most dominant species in old-growth forest sites and in 20-year-old sites and was the fourth most dominant species in 40-year-old sites. *Dalbergia cultrata* was the fifth most dominant species in 10- and 20-year-old sites. Species whose IVI values were ranked in the top five in only one age class were *Aporosa nigricans*, *Dalbergia nigrescens*, *Terminalia mucronata*, *Schleichera oleosa*, *Vitex canescens*, and *Croton persimilis* (Table 6).

3.4. Functional Trait Dominance. At the community level, CWM values of LT, LA, SLA, LDMC, and WD varied significantly among sites (Table 7). CWM values of LT were significantly higher in 10- and 20-year-old sites than in others. Similarly, the CWM of LA was highest in 20-year-old sites followed by 10-year-old sites. The CWM values of SLA and WD were significantly larger in 40- and 30-year-old sites and old-growth forest sites than in other age classes. Old-growth forest sites also had a significantly higher CWM of LDMC than any of the plantation-age classes (Table 7).

3.5. Relationships among Species Abundance, Functional Traits, and Soil Variables. The RLQ analysis revealed significant relationships among dominant species, plant traits, and local environmental variables. Fourth corner analysis indicated that the soil variables combined with teak stand characteristics were significantly correlated with all of the tree traits when assessed using species relative abundance ($p < 0.001$ for model 2, $p < 0.05$ for model 4; fourth corner test). The RLQ eigenvalues were 1.124 and 0.074 for axes 1 and 2, respectively. These axes captured 93% of the covariance in species abundances (*L* matrix), trait values (*Q* matrix), and environmental variables (*R* matrix) (Figure 2). Species characterized by high LDMC, large leaves, and dense wood, such as *Fernandoa adenophylla* (FERAD), *Albizia odoratissima* (ALBOD), *Xylia xylocarpa* (XYLXY), *Cassia fistula* (CASFI), and *Schleichera oleosa* (SCHOL), colonized old growth stands. These species were associated with soils containing greater proportions of silt and clay, as well as higher organic matter (OM) and N contents. Species with high SLA, such as *Dalbergia oliveri* (DALOL), *Phanera bracteata* (PHABR), *Pterocarpus macrocarpus* (PTEMA), *Terminalia nigrovenulosa* (TERNI), and *Dalbergia nigrescens* (DALNI) were abundant in teak plantations with higher BA in which more time had elapsed since thinning. These species were also associated with higher pH, Mg, Ca, P, and K. Thicker leaved species such as *Artocarpus lacucha* (ARTLA), *Canarium subulatum* (CANSU), *Dolichandrone serrulata* (DOLSE), *Terminalia bellirica* (TERBE), and *Lagerstroemia macrocarpa* (LAGMA) were abundant in dense teak plantations and were also associated with higher percent sand and lower concentrations of soil nutrients (Figure 2).

4. Discussion

Our results indicated that the relative abundance and conspecific functional traits of regenerating tree communities change in response to soil conditions and the

Table 3: Teak diameter at breast height (DBH, cm), basal area (BA, m^2 ha^{-1}), stem density (D, stems ha^{-1}), and height (H, m) in teak plantations and old-growth forest sites in Khun Mae Khum Mee plantations.

Teak value	10-year-old	20-year-old	30-year-old	40-year-old	Old-growth forest	Sig.
DBH	12.44 ± 1.58^{c}	15.13 ± 2.19^{bc}	18.11 ± 5.89^{b}	24.91 ± 4.84^{a}	8.13 ± 6.68^{d}	***
BA	6.77 ± 2.66^{b}	7.23 ± 2.05^{b}	4.81 ± 2.25^{b}	10.85 ± 4.29^{a}	0.73 ± 0.82^{c}	***
D	477.50 ± 88.55^{a}	362.50 ± 87.60^{b}	175 ± 107.37^{c}	202.50 ± 58.27^{c}	67.50 ± 70.76^{d}	***
H	12.01 ± 1.43^{cd}	17.08 ± 2.77^{b}	14.91 ± 3.91^{bc}	23.85 ± 3.31^{a}	9.08 ± 7.37^{d}	***

Different lowercase letters within a row indicate significantly different means by Tukey's test (one-way ANOVA, $p < 0.05$; $n = 50$). Values are expressed as mean ± SD; *** $p < 0.001$.

Table 4: Mean ± standard deviation (SD) of soil variables including sand, silt, clay, organic matter (OM), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) contents.

Soil	10-year-old	20-year-old	30-year-old	40-year-old	Old-growth forest	Sig
Sand (%)	47.43 ± 19.11^{a}	29.63 ± 6.15^{bc}	42.53 ± 9.73^{ab}	27.73 ± 4.30^{c}	45.93 ± 6.19^{a}	***
Silt (%)	21.15 ± 5.84	24.95 ± 2.37	23.95 ± 7.25	23.15 ± 1.68	21.85 ± 1.47	NS
Clay (%)	31.42 ± 13.43^{b}	45.42 ± 5.87^{a}	33.52 ± 5.53^{b}	49.12 ± 4.07^{a}	32.22 ± 5.32^{b}	***
pH	5.89 ± 0.42^{b}	5.97 ± 0.28^{b}	5.78 ± 0.22^{b}	6.57 ± 0.23^{a}	5.89 ± 0.23^{b}	***
OM (%)	3.21 ± 1.19^{b}	4.97 ± 0.83^{a}	3.55 ± 0.72^{b}	6.02 ± 0.85^{a}	4.91 ± 1.44^{a}	***
N (%)	0.13 ± 0.04^{c}	0.23 ± 0.04^{b}	0.16 ± 0.03^{c}	0.29 ± 0.03^{a}	0.24 ± 0.05^{b}	***
P (mg kg^{-1})	4.33 ± 1.58	4.79 ± 1.50	4.48 ± 1.60	8.73 ± 8.90	3.54 ± 1.16	NS
K (mg kg^{-1})	80.57 ± 37.12^{b}	77.83 ± 13.33^{b}	117.01 ± 38.79^{ab}	101.82 ± 27.08^{ab}	144.39 ± 47.82^{a}	***
Ca (mg kg^{-1})	570.79 ± 393.55^{b}	867.96 ± 266.09^{b}	520.24 ± 165.98^{b}	1476.6 ± 498.46^{a}	642.86 ± 191.59^{b}	***
Mg (mg kg^{-1})	170.3 ± 80.82^{c}	289.16 ± 81.36^{b}	196.86 ± 70.11^{c}	473.28 ± 71.01^{a}	194.27 ± 41.95^{c}	***

Measurements in teak plantations and old-growth forest sites in Khun Mae Khum Mee plantation. Different lowercase letters within a row indicate significantly different means by Tukey's test (one-way ANOVA test, $p < 0.05$; $n = 50$). *** $p < 0.001$; NS = nonsignificant.

Table 5: Ecological characteristics of teak plantation and old-growth forest plots in Khun Mae Khum Mee plantation.

Ecological characteristics	10-year-old	20-year-old	30-year-old	40-year-old	Old-growth forest
Number of species	42	21	47	27	40
Genus	36	17	38	25	35
Family	21	8	21	12	19
H'	2.41	1.56	2.75	2.12	2.72
D (stem ha^{-1})	1008	570	883	683	698
BA (m^2 ha^{-1})	12.75	17.81	17.31	22.73	21.82

Table 6: The five dominant species in teak plantation and old-growth forest plots in Khun Mae Khum Mee plantation.

Forest type/ranking	Species	Stem density	Basal area	IVI
Teak plantation 10-year-old				
1	*Tectona grandis**	477.50	6.77	109.91
2	*Pterocarpus macrocarpus*	57.50	2.8	35.23
3	*Xylia xylocarpa*	27.5	0.59	12.04
4	*Aporosa nigricans*	42.5	0.23	9.76
5	*Dalbergia cultrata*	30	0.1	9.44
Teak plantation 20-year-old				
1	*Tectona grandis**	362.50	7.23	123.08
2	*Xylia xylocarpa*	50	3.69	44.6
3	*Albizia odoratissima*	25	1.83	24.07
4	*Dalbergia nigrescens*	10	1.96	18.44
5	*Dalbergia cultrata*	32.50	0.20	12.49
Teak plantation 30-year-old				
1	*Tectona grandis**	175	4.81	56.30
2	*Pterocarpus macrocarpus*	157.50	4.93	54.14
3	*Dalbergia cultrata*	175	2.89	45.20
4	*Xylia xylocarpa*	40	0.45	12.35
5	*Terminalia mucronata*	27.50	0.31	8.36

Table 6: Continued.

Forest type/ranking	Species	Stem density	Basal area	IVI
Teak plantation 40-year-old				
1	*Tectona grandis**	202.50	10.85	91.91
2	*Pterocarpus macrocarpus*	217.50	7.62	66.82
3	*Schleichera oleosa*	47.50	0.36	18.71
4	*Albizia odoratissima*	22.50	1.41	18.21
5	*Vitex canescens*	35	0.33	16.72
Old-growth forest				
1	*Pterocarpus macrocarpus*	152.50	7.03	64.10
2	*Xylia xylocarpa*	95	4.93	46.21
3	*Albizia odoratissima*	55	2.72	27.33
4	*Croton persimilis*	110	1.26	26.54
5	*Tectona grandis*$_{\text{(resprouting)}}$	67.50	0.73	20.04

Species are ranked based on the importance value index (IVI); basal area (m^2 ha^{-1}) and stem density (stems ha^{-1}) are also shown. Asterisks (*) indicate planted species.

Table 7: Mean ± standard deviation (SD) of the community weighted mean (CWM) of leaf area (LA), specific leaf area (SLA), leaf thickness (LT), leaf dry matter content (LDMC), and wood density (WD) in teak plantation and old-growth forest plots in Khun Mae Khum Mee plantation.

CWM	10-year-old	20-year-old	30-year-old	40-year-old	Old-growth forest	Sig
LT	0.31 ± 0.01^{a}	0.31 ± 0.02^{a}	0.26 ± 0.02^{b}	0.26 ± 0.02^{b}	0.27 ± 0.02^{b}	***
LA	538.22 ± 155.93^{ab}	618.39 ± 81.46^{a}	314.30 ± 90.67^{c}	444.69 ± 86.61^{bc}	317.47 ± 86.05^{c}	***
SLA	121.25 ± 10.78^{ab}	113.19 ± 4.87^{b}	133.36 ± 12.51^{a}	133.78 ± 8.17^{a}	132.49 ± 12.57^{a}	***
LDMC	397.32 ± 38.71^{b}	417.93 ± 30.67^{ab}	392.69 ± 19.10^{b}	414.10 ± 24.45^{ab}	440.89 ± 49.44^{a}	*
WD	0.64 ± 0.03^{b}	0.66 ± 0.02^{b}	0.71 ± 0.04^{a}	0.72 ± 0.03^{a}	0.74 ± 0.03^{a}	***

Different lowercase letters within a row indicate significantly different means by Tukey's test (one-way ANOVA $p < 0.05$; $n = 50$). * $p < 0.05$; *** $p < 0.001$.

characteristics of teak plantations, as conditioned by forest harvesting practices. The RLQ and fourth corner analysis indicated that relationships between plant functional traits and the environment (soil variables and teak stand characteristics) could be explained by woody species composition at these sites. We found that tree community composition is driven by the dominant tree species. Thus, the plant functional traits of dominant species are modulated by soil conditions combined with teak plantation characteristics, and this feedback appears beneficial in the context of teak plantations.

The woody species associated with higher values of LDMC, dense wood, and larger leaves were positively associated with older teak plantations and soils with higher percent clay and elevated OM and N. At the community level, the CWM of LDMC reached its highest value in the old-growth forests, while the CWM of WD was higher in 40-year-old teak sites and old-growth forests. These older sites were associated with higher concentrations of OM and N. Trees with high LDMC and denser wood are often slow-growing, late-successional species associated with climax communities of tropical forests [44–46]. High wood density is associated with low volumetric stem growth rates, resistance to damage, high rates of survival, and resistance to drought [47, 48]. LDMC is a proxy for mass investment in photosynthetic organs that is negatively correlated with plant growth. Species associated with high values of LDMC usually display slow growth rates, low nutrient concentrations, and low rates of leaf turnover [49–51]. These findings indicate that stand conditions in teak plantations abandoned ten years after the second thinning (i.e., 30-year-old plantations) can encourage colonization by late-successional species.

We also found that large-leaved trees tended to dominate 20-year-old teak plantations with high values of OM. Large-leaved species are associated with soil nutrient stresses and high disturbance rates [32]. Leaf area determines light-interception capacity and is well suited for high-throughput screening of plants because LA measurements can be performed nondestructively and economically [52, 53]. In 20-year-old teak plantations abandoned for five years after a 50% thinning, the large gap sizes left by harvesting encouraged colonization by large-leaved species. However, dominant trees characterized by large leaves, high LDMC, and dense wood did not readily establish in 20- and 40-year-old plantations or old-growth forest areas. These sites tended to have high levels of OM and soil N due to leaf litter accumulation and decomposition. Leaf litter decomposition and the consequent accumulations of OM and N are crucial components of ecosystem functioning in forest soils [54, 55]. Organic matter maintains soil structure, especially in fine-textured soil [56]. Nitrogen is one of the most essential elements for plant growth and development [57]. In our study, it appears that high OM and soil N concentrations promoted colonization and survival of late-successional or climax species in the 40-year-old plantation and old-growth forest.

Tree species with high SLA were positively associated with high TBA and greater time since thinning. These species were positively associated with higher pH values and

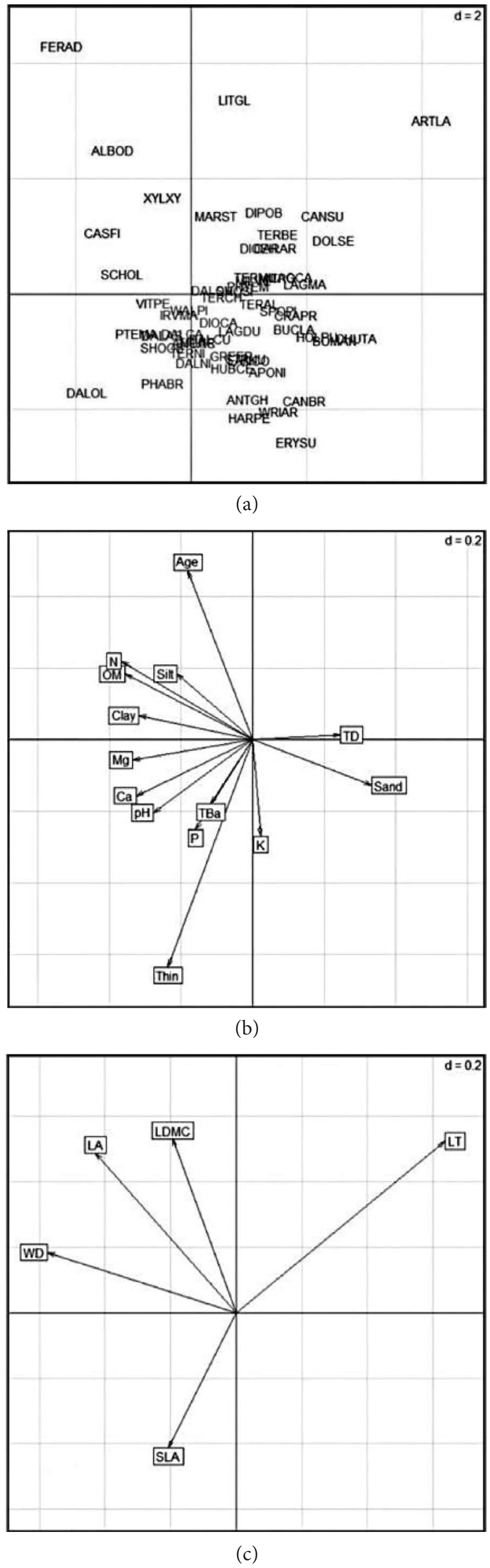

Figure 2: Results of RLQ analysis for axes 1 and 2 showing relationships among (a) dominant species, (b) soil variables and teak stand characteristics, and (c) plant traits. The value of *d* indicates grid size. Species codes are provided in Table 2. Abbreviations of soil variables and traits are provided in Tables 4 and 7, respectively.

high concentrations of Mg, Ca, P, and K. At the community level, species with high values of SLA were important components of 30- and 40-year-old plantations and old-growth forests. Specific leaf area is thought of as an acquisitive trait, which encourages a fast recovery of foliar investment and fast turnover of matter and energy. It is therefore linked to fast growth and high photosynthetic rates [58, 59]. Specific leaf area is a proxy for the leaf economic spectrum that plays an important role in determining plant productivity via high rates of photosynthesis and the accumulation of starch and sugars [60, 61]. Lohbeck et al. [45] reported that in dry tropical forests, SLA at the community level decreased with increasing BA during succession. This result contrasts with our finding that high-SLA species dominated the 40-year-old plantation, which had a high TBa. These results suggest that the larger size of teak in older plantations could have inhibited successional processes. These findings confirm that SLA is an important trait for predicting the outcomes of secondary succession in natural forests and plantations and may be used to predict successional patterns across different vegetation types [47].

High-SLA species were positively associated with greater time since thinning, suggesting that high-SLA species could become increasingly important in successional communities as abandoned plantations age. Dwyer and Mason [62] reported that thinning led to an overabundance of high-SLA species, akin to pioneer dominance during the early stages of rainforest succession. Thinning has been applied to ecological restoration and is thought to be particularly effective at accelerating plant community recovery in some forests that were dominated by a single species [62, 63]. The timing of thinning has a greater influence on plant regeneration than thinning intensity [64]. The greater time since the thinning of teak in 30- and 40-year-old teak plantations changed microenvironmental conditions by increasing light levels in open canopy gaps, which improves conditions for the regeneration of fast-growing species with high SLA.

High-SLA species that also had high IVI were associated with fertile soils in the 30- and 40-year-old sites and in the old-growth forest sites. This relationship indicated a plant response to soil nutrients that may reflect a nutrient-related trade-off between plant regeneration and SLA. This finding is supported by previous studies showing that plant communities dominated by high-SLA species are usually found in habitats with good soil nutrient supply and are characterized by rapid nutrient uptake [61, 62, 65]. Therefore, the timing of thinning treatments and fertile soil appear to have promoted the colonization and persistence of high-SLA species.

The CWM data showed that thick-leaved species achieved their greatest dominance in 10-year-old teak plantations with high densities of teak and sandy soils. Leaf thickness is a plant trait related to variations in sunlight and shade. Plant communities with thick-leaved species may also dominate dry, sunny habitats [32, 66]. The internal leaf structure of thick leaves may feature high stomatal densities and lower chlorophyll contents. Thick leaves are also expensive to construct and are associated with long leaf lifespans [66, 67]. Thick sun-grown leaves are associated with high water-use efficiency, where productivity is maintained without increased water use [68]. Leaf thickness is a conservative functional trait with a generally slow return on investment [58].

Although the 10-year-old sites showed high teak stem densities, these stems were short and had narrow canopies, allowing intense sunlight to reach the ground. These forest conditions may have favored the establishment of thick-leaved species. Lohbeck et al. [45] report that LT at the community level increases with dry forest succession in the tropics. Thick-leaved species were associated with sandy, nutrient-poor soils, which were also a feature of the 10-year-old sites. Sandy soils in the tropics are often infertile because of their high sand content, low water-holding capacity, low cation exchange capacity, and low plant-available nutrients [69]. Previous studies suggest that species with high LT are drought-tolerant in drought-prone and nutrient-poor soils, and thick leaves may enhance nutrient-use efficiency in these stressful environments [34, 35]. In accordance with these previous findings, thick-leaved species in our study preferentially colonized the intensely irradiated and nutrient-poor 10-year-old sites.

5. Conclusion

In this study, we investigated whether functional traits of woody species could be used to predict the composition of natural regeneration in teak plantations with different soil conditions and site characteristics (stem density, basal area, age, and time since thinning). We found that the 10-year-old teak plantation had the highest teak stem density but the smallest stems. This plantation was also established on sandy, nutrient-poor soils, and conditions that promoted the regeneration of woody species with thicker leaves. A 20-year-old teak plantation was highly disturbed after its first thinning at 15-year-old. This plantation was associated with high OM but lower nutrient concentrations, conditions that encouraged the regeneration of larger-leaved species. More time had elapsed since thinning in the 30- and 40-year-old plantations, and these sites were associated with fertile soils with high concentrations of Mg, Ca, P, and K. These conditions appear to have enhanced the regeneration of woody species with high SLA. The old-growth forest and 40-year-old teak plantation (both of which had experienced a longer period of abandonment) were associated with fertile soils, which appear to have promoted the regeneration of woody species with high LDMC and high WD. These results show that the impacts of teak plantation characteristics and soil conditions modify the balance of tree functional traits in regenerating communities of native tree species. Thus, future management interventions for enhancing tree diversity and abundance in teak plantations should consider the plant traits that are associated with a given combination of soil conditions and stand characteristics. By doing so, forest managers may successfully manage the biodiversity of regenerating trees in commercial plantations.

Data Availability

The data used to support the findings of the study are available from the corresponding author upon request.

Conflicts of Interest

All authors and the funding source of the Office of Agricultural Research and Extension, Maejo University, declare that they have no conflicts of interest regarding the publication of this paper.

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