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Drivers of Native Species Regeneration in the Process of Restoring a Dry Evergreen Forest from Exotic Tree Plantations in Northeastern Thailand

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Abstract: Establishment of exotic plantations is one of the most effective ways to induce natural regeneration for the restoration of degraded lands, as it has the potential to improve soil properties and creates favorable microclimates. This study aims to determine the effects of stand structure and composition as well as environmental factors under the canopies of three exotic plantations in northeastern Thailand on the regeneration of native species. For each plantation, we conducted three 10 m × 150 m transect lines with fifteen 10 m × 10 m subplots along a forest remnant gradient. The canonical correspondence analysis (CCA) was used to identify the environmental factors responsible for the differences in natural regeneration among these stands. Three exotic plantations had different stand structure in terms of number of tree species, basal area, and tree density but similar dominant native tree species. Across all stands, 74 native tree species, 60 genera, and 30 families were observed. Some physical and chemical properties in the topsoil were significantly different between species but similar among stands within a species. On the other hand, differences in environmental factors such as RLI were significant among species and stands within a species. The CCA ordination identified that the soil particles, soil pH, and light intensity were key factors influencing the native species composition, which could be categorized into three groups: drought-tolerant pioneer species; light-demanding pioneer species; and shade-tolerant climax species. However, most of the climax species were incapable of regenerating and maturing along the forest edge gradient to plantation stands. To accelerate the restoration process by converting these old exotic plantations to a dry evergreen forest, further research is required to determine the appropriate canopy management and/or dominant climax species for planting beneath their canopies.

Keywords: natural regeneration; soil properties; microclimate; exotic tree plantation; forest restoration; *Eucalyptus*; *Acacia*

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1. Introduction

Deforestation and forest degradation pose the greatest threat to the world's forests, primarily as a result of conversion to non-forest uses such as agricultural lands and illegal logging, as well as overexploitation caused by population growth. These have had a negative effect on natural resources, ecological services, and climate change mitigation. Globally, approximately 178 million ha of forest cover have been lost between 1990 and 2020 [1], resulting in the loss of biodiversity, natural resources, and ecosystem services [2]. The world's total forest area is 4.06 billion ha, of which 93 and 7% are composed of natural and planted forests. As a means of restoring forests and expanding forest coverage, 290 million ha are covered by forest plantations and other planted forests [1]. Although native tree species have been used for these purposes, 44 percent of global forest plantations consisted of introduced (exotic) species [1]. Extensive exotic tree plantations have been established for commercial plantation and forest restoration on degraded land in the tropics [2,3], primarily in Asia and South America, respectively [1].

Forest plantations not only provide economic and social benefits but also improve biological productivity and natural succession, as well as soil physical and chemical properties on degraded tropical forest lands such as in Puerto Rico [3], China [4], India [5], and Brazil [6]. Despite the benefits of planting mixed stands of native tree species, establishment of plantations of native species has been difficult due to insufficient knowledge of their biology, ecology, and silviculture, whereas establishment of exotic forest plantations of *Eucalyptus*, *Cupressus*, *Acacia*, *Pinus*, and *Casuarina* has increased due to their fast growth rates, multipurpose wood utilization, and readily available information on propagation techniques and silvicultural practices [7]. Commonly, nitrogen-fixing trees were planted in degraded areas to improve the soil, while fast-growing trees, such as *Eucalyptus* spp., *Acacia* spp., *Leucaena leucocephala*, and *Casuarina equisetifolia*, were planted in poor soil conditions due to their rapid growth and high wood production [2,8].

In addition to the production of wood as an economic resource, exotic tree plantations may have additional benefits, such as improving microclimatic conditions, protecting soil erosion, stabilizing soil development, and thereby enhancing soil nutrient status and increasing soil organic matter through the enhancement of litter and humus production and supporting water catchment values [7]. Similar to native plantations, old exotic plantations such as rubber trees, *Acacia* spp., *Eucalyptus* spp., and *Pinus* spp. have complex structure and community and their understory microclimate [4,7], soil properties [4,7,9,10], and understory vegetation [7,9,11] have been improved. The long-term potential of exotic plantations for fostering the regeneration of native species under their canopy and accelerating natural succession has been reported in different geographic areas, such as South Africa [7], Brazil [7], Australia [7], Puerto Rico [7,12], Congo [13], Ethiopia [7,14], and New Zealand [15], and the great influence of exotic tree species has been addressed. By comparing native woody species under their canopies, broad-leaved species, including *Eucalyptus*, appear to be more favorable nurse trees than conifers (e.g., *Pinus patula*, *Cupressus lusitanica*) due to greater light intensity and faster litter decomposition of the former [7,16]. In addition, plantation species and stand structure and age affect understory soil properties [3,13,17] and microclimate [15], leading to the difference in establishment of native tree species in plantation understories.

Environmental factors and vegetation structure and composition within an ecosystem are generally correlated. Forest community is influenced by soil properties including soil drainage [18], sand:clay [18], C:N [18], soil texture [19,20], soil pH [19,20], total N [19], available P [19,21], soil moisture [19,21], organic matter [20,21]. These factors are key drivers to species distribution, diversity, and abundance. Light is one significant factor in plant communities, influencing vegetation and colonization of woody species [22,23]. Pioneer trees favor high light intensity for growth and colonization, and difference in crown structure may affect light conditions and air temperature under plantation. These environmental factors varied according to crown characteristics of plantation species [22]. In addition, the distance of a forest remnant to a plantation also influenced species diversity and density of native tree species [24], such that forest structure and community varied along forest edge–interior to forest edge–exterior areas [23].

Sakaerat Biosphere Reserve, designated in 1976, is Thailand's first UNESCO Biosphere Reserve, with the dry evergreen forests serving as the most extensive and representative ecosystem, and the dry dipterocarp serving as the unique ecosystem. Part of the forest was encroached upon by local people and converted to farmland, such as cassava crop (*Manihot esculenta* (L.) Crantz), beginning in the 1960s. After a few decades, the soils became infertile, causing the area to be abandoned and covered by exotic tall grasses such as *Imperata cylindrical* and *Saccharum spontaneum*. Along with assistance from the Japan International Cooperation Agency (JICA), the Royal Forest Department (RFD) launched a forest restoration program in 1982 to restore approximately 2300 ha of degraded forest in the buffer zone of the Sakaerat Biosphere Reserve by 1994. Exotic fast-growing trees such as *Eucalyptus* and *Acacia* species were planted to assist light and nutrient competition with weeds and improve soil properties and microclimate under plantations [25]. These exotic tree plantations could enhance the establishment of native species and stimulate natural regeneration process for the restoration program. The role of exotic plantation as promoter of high density and variety of native species for natural regeneration has been reported in various tropical regions [7,12–15], but very few studies have been conducted in Thailand [26–28]. To address this knowledge deficit, our study aimed to determine the influence of environmental factors in different exotic tree plantations on natural regeneration of native species in the Sakaerat Biosphere Reserve's buffer zone. We hypothesized that different exotic tree plantations have distinct canopy structures and ecological and physiological characteristics that contribute to soil properties and understory microclimates suitable for natural regeneration of a particular species or group of species. Therefore, we determined the vegetation structure, species composition, and environmental factors of three exotic species plantations, including *Eucalyptus camaldulensis* (EC), *Acacia auriculiformis* (AA), and *Acacia mangium* (AM) plantations, and evaluated natural regeneration of native species along a gradient from forest remnants to the plantation stands.

2. Materials and Methods

2.1. Study Site

This study was carried out at the RFD's Sakaerat Silvicultural Research Station (14 °29′60′′ N, 101 °54′19′′ E, 420 m above mean sea level), located in the buffer zone of the Sakaerat Biosphere Reserve, Nakhon Ratchasima province, northeastern Thailand, about 300 km from Bangkok (Figure 1). This region has a tropical monsoon climate, with a wet season from May to October and a dry season from November to April. From 2006 to 2016, the annual average temperature was 25.6 °C, and the annual average precipitation was 1395 mm. The prevailing forest at the study site was dry evergreen forest, dominated by *Shorea henryana*, and had a high number of species [29]. The site had been converted to cropland starting in the 1960s and later deteriorated and was abandoned. The RFD launched a forest restoration program in 1982 with the assistance of the JICA by establishing three exotic tree plantations on degraded land totaling 2300 ha: *Eucalyptus camaldulensis* (EC, an endemic species to Australia), *Acacia auriculiformis* (AA, an endemic species to Australia, Indonesia, and Papua New Guinea), and *A. mangium* (AM, an endemic species to Australia) plantations [25].

In this study, the three exotic species plantations and respective forest remnants adjacent to plantations were chosen to determine natural regeneration of native tree species along forest edge–exterior gradients in the tree exotic plantations in 2016. Three transect lines of 10 m × 150 m were laid out in each selected plantation based on distance from the forest remnant (Forest, −50 m to 0 m) through forest edge–interior or forest–plantation edge (Edge, 0 m to 50 m) and forest edge–exterior or plantation stand (Plantation, 50 m to 100 m) [30], resulting in a total of nine stands: EC_Forest, EC_Edge, EC_Plantation, AA_Forest, AA_Edge, AA_Plantation, AM_Forest, AM_Edge, AM_Plantation (Figure 2). Each transect line was divided into 10 m × 10 m subplot, for a total of 15 subplots, and all trees with diameter at breath height (DBH) greater than 1 cm were tagged, measured for DBH and height, and identified. Identified specimens was then approved by the Forest Herbarium, Department of National Parks, Wildlife and Plants Conservation. In addition, native tree species were categorized as climax or pioneer species based on the previous study on structural characteristics of the dry evergreen forest at the Sakaerat Biosphere Reserve [31].

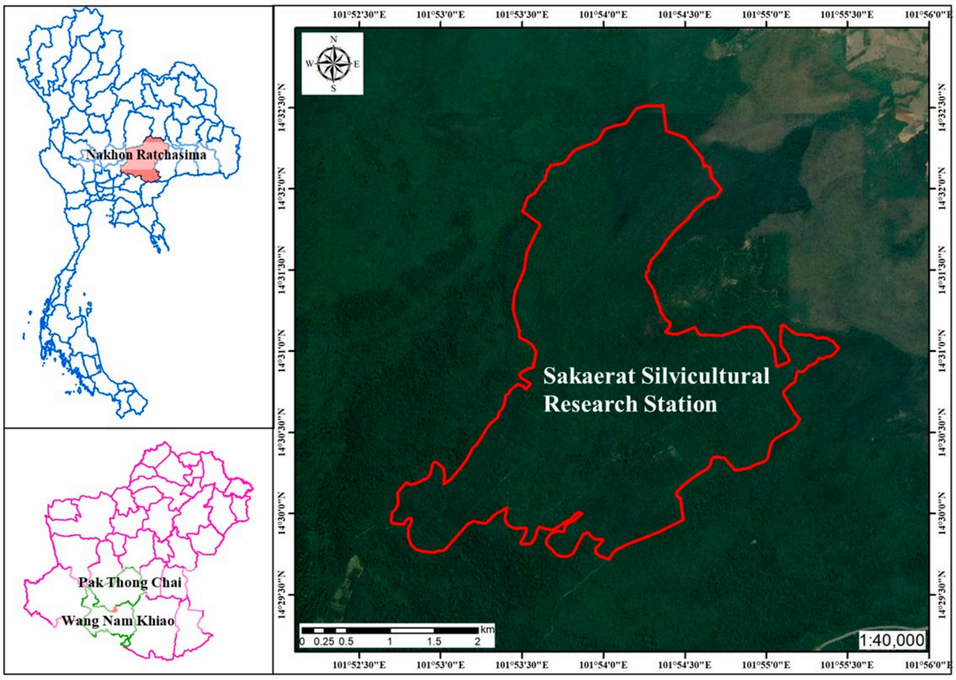

Figure 1. A map of the study site at the Sakaerat Silvicultural Research Station, northeastern Thailand (14 °29′60′′ N, 101 °54′19′′ E).

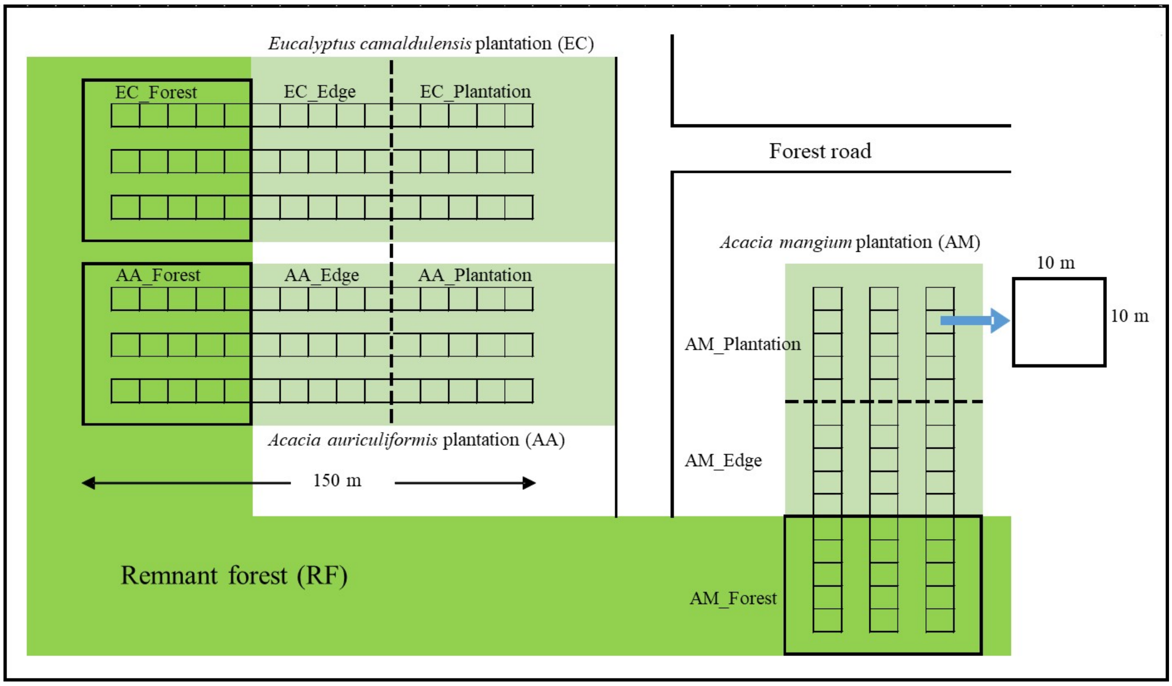

Figure 2. The layout of three transect lines of 10 m × 150 m set up along the forest remnant (Forest, −50 m to 0 m) through forest–plantation edge (Edge, 0 m to 50 m) and plantation stand (Plantation, 50 m to 100 m) in three exotic plantations: *Eucalyptus camaldulensis* (EC), *Acacia auriculiformis* (AA), and *A. mangium* (AM).

2.2. Environmental Factors

To examine the effects of exotic tree species on environmental changes, relative light intensity (RLI), air temperature (Temp), and relative humidity (RH) were investigated over a two-month period: February to December 2016. RLI was measured using the hemispherical photography technique. A Nikon DSLR camera with a fish-eye lens covering a 180-degree field of view was set up, and one photograph was taken from 1.2 m above the ground in the center of each 10 × 10-m subplot. RLI of each image was then indirectly calculated based on hemispherical models using the Hemi View software (Delta-T Devices) [32]. Temperature and RH were also measured where the photograph was taken with the Kestrel 3000 Pocket Weather Meter (Nielsen-Kellerman Company, Boothwyn, PA, USA).

In each stand, 15 soil samples (one sample from each 10 m × 10 m subplot) were taken from two depths (0–10 cm and 10–30 cm) using split-tube samplers to study physical and chemical properties of the soil. Bulk density was analyzed by the core method. Soil texture was analyzed by the hydrometer method. Soil pH was examined by the pH meter with a 1:1 soil to water ratio. Total nitrogen (N) was analyzed with the Dumas method [33] by a CHNS analyzer (PerkinElmer model 2400 Series II CHNS/O Elemental Analyzer). Organic matter (OM) was analyzed with Walkley and Black's rapid titration method [34]. Available phosphorus (P) was extracted by Bray II [35] and was analyzed by using the spectrometer. Exchangeable potassium (K), calcium (Ca), and magnesium (Mg) were extracted with ammonium acetate (NH4OAc) 1 N pH 7.0 and analyzed using an atomic absorption spectrometer [36].

2.3. Data Analysis

Species diversity based on the Shannon–Wiener index was analyzed [37]. The forest structure was described in terms of woody plant density, basal area, and DBH distribution. All tree species with a DBH > 4.5 cm in each stand were defined the dominant species according to the importance value index (IVI), which was calculated as the sum of three indices: relative dominance, relative density, and relative frequency [38].

The differences in stand structures and composition, including number of tree species, tree density, basal area, and tree diversity, and annual means of environmental factors, including RLI, Temp, RH, and soil properties (soil particles, soil bulk density, soil pH, total N, available P, OM, exchangeable of K, Ca and Mg), were analyzed through an analysis of variance (ANOVA). The data sets were analyzed by exotic tree plantations with a split plot along forest remnants to plantations. A post hoc test was also performed by Duncan's New Multiple Range Test to compare significant differences ($p < 0.05$) between means.

An ordination analysis based on canonical correspondence analysis (CCA) was used to determine the primary drivers of natural regeneration in exotic tree plantations [39]. For each plantation, the data were divided into three zones along the distance from the forest remnant: Forest, Edge, and Plantation, with three replicates for each zone, resulting in nine subplots. The first matrix was then divided into subplot × species matrices with the cells filled with the abundance values of each species (IVI). The second matrix of environmental factors was also setup into subplot × environmental factor matrices with the values of the following 14 environmental factors: sand, silt, clay particles, soil bulk density, soil pH, total N, available P, OM, exchangeable K, Ca, and Mg, RLI, Temp, and RH. The significant correlation between the matrix was determined, and only the environmental factors significantly related to tree species were retained. In the preliminary CCA, eight poorly correlated factors were removed; the remaining six factors were used in the final CCA including particles of sand, silt, clay, OM, soil pH, and RLI. The statistical analyses were performed using PC-OR version 5.10 software [40].

3. Results

3.1. Stand Structure and Species Composition

Three exotic plantations had different stand structure in terms of number of tree species, basal area, and tree density but similar dominant native tree species. Woody plants of 74 tree species, 60 genera, and 30 families were found in all three study areas: EC, AA. and AM stands. The top five dominant native species based on their IVI (%) in EC, AA, and AM stands were mostly similar, including *Alchornea rugosa* (23%–26%), *Clausena guillauminii* (20%–47%), *Nephelium hypoleucum* (12%–23%), *Ixora cibdela* (15%–20%), and *Antidesma acidum* (12%–35%) (Table A1). Nevertheless, planted tree species including EC, AA, and AM had the most dominance in the respective Edge and Plantation stands, which had highest IVI ranged from 88.31%–111.35%. The number of species and basal area were significantly different ($p < 0.05$) among three plantations and among stands along remnants to plantations, while significant differences in tree density were observed only among plantation stands (Table 1). Along the Forest to Plantation stands, the number of species tended to decrease while the basal area increased. Based on the Shannon–Wiener index, moderate plant diversity was discovered, ranging from 2.23 to 2.92. The forest remnant adjacent to all plantations exhibited a high species diversity and tree density, with a decreasing trend as distance from the forest edge increased. Lower similarity index was also observed in Plantation stands compared to the Edge stands. In contrast, the basal area in the remnant forest was approximately one-third of that in the plantation due to the greater basal area of exotic species observed in the Edge and Plantation stands (Figure 3).

Table 1. Structure and diversity in nine stands of three exotic plantations. EC: *Eucalyptus camaldulensis*, AA: *Acacia auriculiformis*, AM: *A. mangium*. Significant differences: ^{ns} $p \geq 0.05$; * $p < 0.05$, ** $p < 0.01$. Different superscript letters in the same column indicate significant difference at $p < 0.05$.

Stand	Number of Species	Basal Area (m^2/ha)	Tree Density (stem/ha)	Shannon–Wiener Index	Sorensen Similarity Index
EC_Forest	27.00 ± 1.73^{bcde}	15.04 ± 3.81^{c}	3406.67 ± 81.92^{cd}	2.69 ± 0.03^{abc}	100.00^{a}
EC_Edge	21.33 ± 0.33^{de}	35.81 ± 3.20^{a}	3220.00 ± 264.58^{cd}	2.53 ± 0.06^{bcd}	64.26 ± 1.24^{cd}
EC_Plantation	20.00 ± 3.79^{e}	29.55 ± 4.04^{ab}	2500.00 ± 726.91^{d}	2.35 ± 0.19^{cd}	58.28 ± 4.79^{d}
AA_Forest	28.67 ± 1.45^{abcd}	9.48 ± 1.73^{c}	4013.33 ± 544.10^{bc}	2.84 ± 0.13^{ab}	100.00^{a}
AA_Edge	24.33 ± 1.86^{cde}	26.78 ± 6.20^{ab}	4480.00 ± 242.49^{abc}	2.55 ± 0.10^{bcd}	67.55 ± 0.45^{bc}
AA_Plantation	22.33 ± 2.33^{de}	29.23 ± 1.48^{ab}	3786.67 ± 363.75^{bcd}	2.23 ± 0.08^{d}	68.10 ± 3.84^{bc}
AM_Forest	35.33 ± 1.20^{a}	9.38 ± 0.40^{c}	5566.67 ± 335.13^{a}	2.92 ± 0.03^{a}	100.00^{a}
AM_Edge	34.00 ± 2.08^{ab}	25.92 ± 2.92^{ab}	5113.33 ± 81.10^{ab}	2.87 ± 0.09^{ab}	73.66 ± 3.02^{b}
AM_Plantation	32.00 ± 4.16^{abc}	19.78 ± 3.50^{bc}	4406.67 ± 666.57^{abc}	2.86 ± 0.18^{ab}	65.97 ± 0.68^{c}
F-value (Species)	19.37 **	15.80 **	16.28 *	4.54^{ns}	1.03^{ns}
F-value (Stand within species)	3.73 *	27.29 **	2.60^{ns}	10.88 **	1.79^{ns}
F-value (Species * Stand)	2.23^{ns}	0.84^{ns}	0.36^{ns}	2.38^{ns}	0.99^{ns}

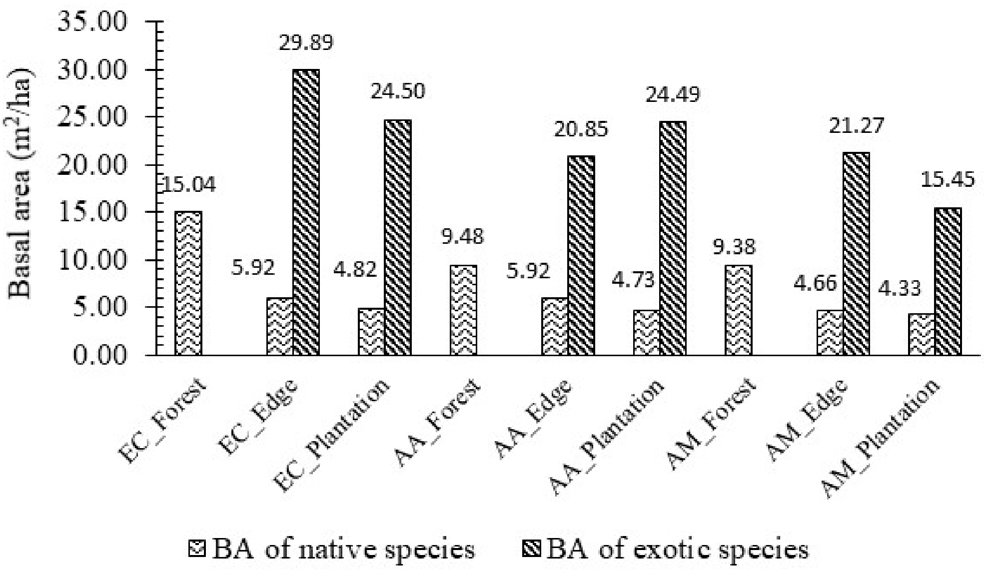

Figure 3. Basal area of native and exotic species in nine stands of three exotic plantations. EC: *Eucalyptus camaldulensis*, AA: *Acacia auriculiformis*, AM: *A. mangium*.

Tree regeneration for native species based on DBH class distribution in all plantations exhibited L-shaped negative exponential growth (Figure 4). In all stands, the frequency of small trees was higher, while the frequency of large trees decreased with increasing stem diameter. In the DBH class of 1–4.5 cm, the AM_Forest contained the greatest number of trees (654 stems/ha) compared to the EC_Edge and EC_Plantation, which contained 111–119 stems/ha. Plantation stands, on the other hand, had more trees in the 17.5–20.5 and >20.5 cm DBH size classes than forest remnant, which was consistent with their basal area. Furthermore, the basal area of AM stands was lower than that of AA and EC stands (Figure 4), most likely due to the standing dead and felled trees of *A. mangium*. In addition, the distribution of dominant native species along the edge gradient varied depending on plantation species.

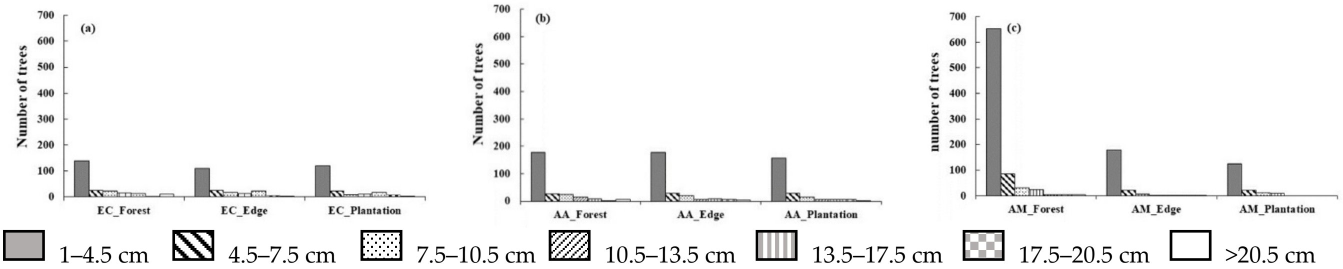

Figure 4. Diameter class distribution in nine stands of three exotic plantations. (**a**) *Eucalyptus camaldulensis* (EC), (**b**) *Acacia auriculiformis* (AA), and (**c**) *A. mangium* (AM) stands.

Pioneer species such as *Gonocaryum lobbianum*, *Microcos tomentosa*, and *Wrightia arborea* were more commonly found in EC and AA stands than in AM stands (Figure 5). For climax species, *Shorea henryana* was more prominent in EC and AM stands, whereas *Nephelium hypoleucum* Kurz was the dominant and widespread species in all studied stands. In addition, *S. henryana* was more prevalent in forest remnants and diminished as distance from forest remnant increased. Interestingly, the frequency of a climax species like *Walsura trichostemon*, was observed only in AM_Forest and AM_Edge, decreased with the distance along the Forest to Plantation stands (Figure 6).

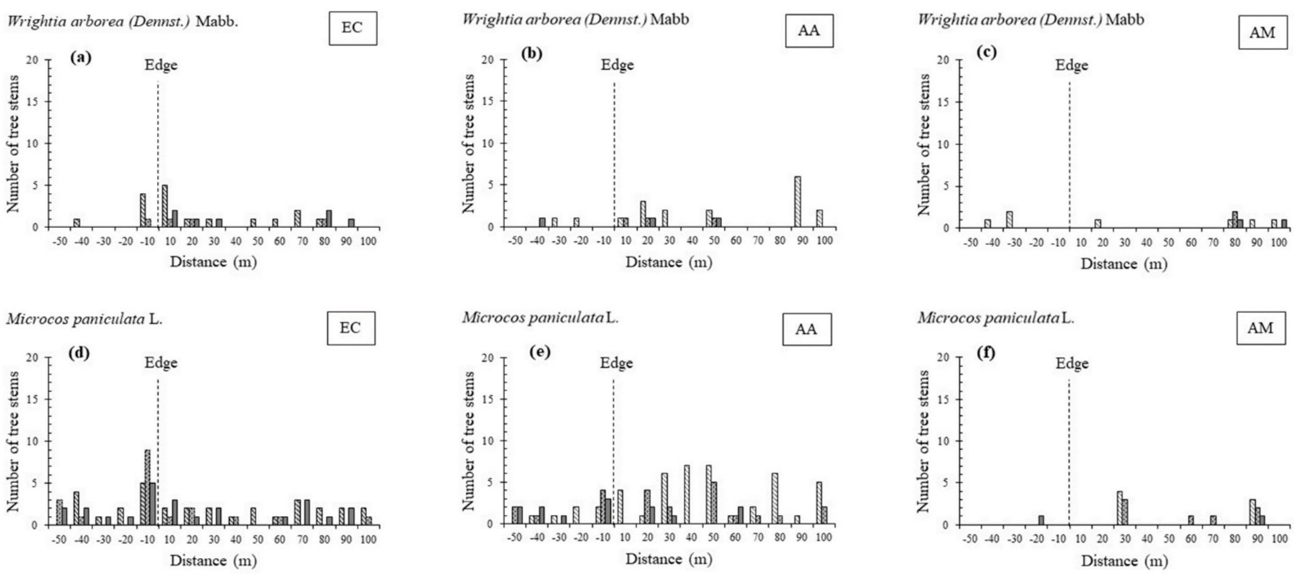

Figure 5. *Cont.*

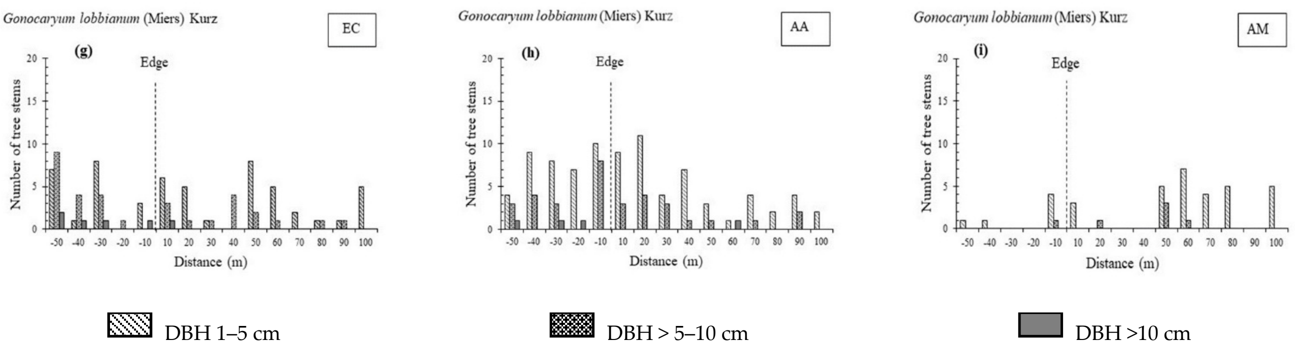

Figure 5. Diameter class distribution of some pioneer tree species along the forest remnants to plantation stands of three exotic plantations. (**a**–**c**) *Wrightia arborea* in *Eucalyptus camaldulensis* (EC), *Acacia auriculiformis* (AA), and *A. mangium* stands, (**d**–**f**) *Microcos tomentosa* in EC, AA and AM stands, (**g**–**i**) *Gonocaryum lobbianum* in EC, AA and AM stands.

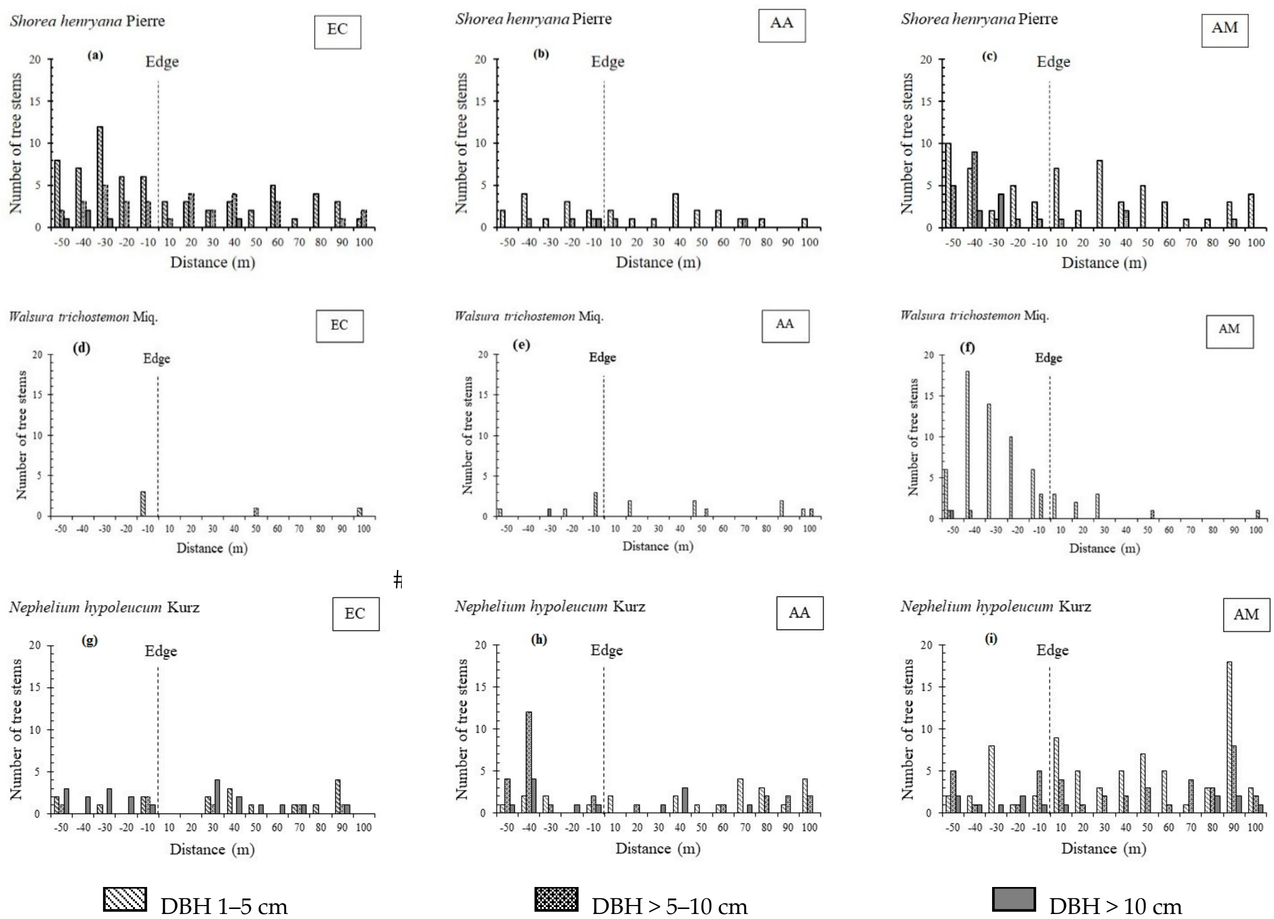

Figure 6. Diameter class distribution of some climax tree species along the forest remnants plantation stands of three exotic plantations. (**a**–**c**) *Shorea henryana* in *Eucalyptus camaldulensis* (EC), *Acacia auriculiformis* (AA), and *A. mangium* stands, (**d**–**f**) *Walsura trichostemon* in EC, AA and AM stands, (**g**–**i**) *Nephelium hypoleucum* in EC, AA and AM stands.

3.2. Soil Properties in Exotic Plantation Stands

Soil physical and chemical properties of the topsoil and subsoil all three exotic plantations seemed similar. Because EC stands were adjacent to AA stands (Figure 2), the topsoil and subsoil of all AA and EC stands was sandy clay loam, except for the topsoil of EC_Forest, which was sandy loam. While the soil texture of both the topsoil and subsoil at the AM stands was clay loam. Soil particles, namely sand, silt, and clay, in the topsoil and subsoil were significantly different between exotic plantations ($p < 0.05$) but not among stands within plantation ($p \geq 0.05$). All EC and AA stands had higher sand particle percentages (54.40%–63.40%), while all AM stands had greater clay particle (28.27%–33.43%). On the other hand, neither difference in bulk density of the topsoil and subsoil between exotic plantations nor between stands within plantation was statistically significant ($p < 0.05$) (Table 2).

Table 2. Soil physical properties in nine stands along the forest remnants to plantation stands of three exotic plantations. EC: *Eucalyptus camaldulensis*, AA: *Acacia auriculiformis*, AM: *A. mangium*. Significant differences: *ns* $p \geq 0.05$; * $p < 0.05$, ** $p < 0.01$. Different superscript letters in the same column indicate significant difference at $p < 0.05$.

Stand	Soil Texture	Soil Particle (%)			Bulk Density (g m^{-3})
		Sand	Silt	Clay	
Topsoil (Soil depth 0–10 cm)					
EC_Forest	Sandy loam	61.07 ^{a}	19.67 ^{b}	19.27 ^{e}	2.33
EC_Edge	Sand clay loam	59.73 ^{a}	16.33 ^{b}	23.93 ^{cde}	2.15
EC_Plantation	Sand clay loam	56.57 ^{a}	18.00 ^{b}	25.43 ^{bc}	2.27
AA_Forest	Sandy clay loam	54.40 ^{a}	20.33 ^{b}	25.27 ^{bc}	2.34
AA_Edge	Sandy clay loam	60.40 ^{a}	16.33 ^{b}	23.27 ^{cde}	2.39
AA_Plantation	Sandy clay loam	63.40 ^{a}	15.50 ^{b}	21.10 ^{de}	2.40
AM_Forest	Clay loam	42.40 ^{b}	29.33 ^{a}	28.27 ^{bc}	2.34
AM_Edge	Clay loam	39.73 ^{b}	30.67 ^{a}	29.60 ^{ab}	2.36
AM_Plantation	Clay loam	35.90 ^{b}	30.67 ^{a}	33.43 ^{a}	2.35
F-value (Species)		373.14 **	39.72 **	25.19 **	4.04 ^{ns}
F-value (Stand within species)		0.27 ^{ns}	0.37 ^{ns}	1.67 ^{ns}	0.36 ^{ns}
F-value (Species * Stand)		1.27 ^{ns}	0.47 ^{ns}	4.24 *	0.54 ^{ns}
Subsoil (Soil depth 10–30 cm)					
EC_Forest	Sandy clay loam	55.73 ^{a}	18.00 ^{c}	19.27 ^{e}	2.43
EC_Edge	Sandy clay loam	59.40 ^{a}	15.00 ^{c}	23.93 ^{cde}	2.26
EC_Plantation	Sandy clay loam	54.07 ^{a}	16.83 ^{c}	25.43 ^{bcd}	2.32
AA_Forest	Sandy clay loam	51.07 ^{a}	16.67 ^{c}	25.27 ^{bcd}	2.31
AA_Edge	Sandy clay loam	55.73 ^{a}	17.67 ^{c}	23.27 ^{cde}	2.35
AA_Plantation	Sandy clay loam	58.07 ^{a}	18.50 ^{c}	21.10 ^{de}	2.41
AM_Forest	Clay loam	42.07 ^{b}	24.67 ^{b}	28.27 ^{bc}	2.40
AM_Edge	Clay loam	35.73 ^{bc}	28.00 ^{ab}	29.60 ^{ab}	2.31
AM_Plantation	Clay loam	31.57 ^{c}	30.67 ^{a}	33.43 ^{a}	2.26
F-value (Species)		59.38 **	73.90 **	22.44 **	3.51 ^{ns}
F-value (Stand within species)		2.42 ^{ns}	0.82 ^{ns}	0.35 ^{ns}	0.13 ^{ns}
F-value (Species * Stand)		0.98 ^{ns}	1.23 ^{ns}	1.51 ^{ns}	2.20 ^{ns}

Soils of all studied stands were extremely acidic, with a pH range of 3.6 to 4.1, but significant differences only between exotic plantations ($p < 0.05$) were observed in the subsoil (Table 3). In the topsoil, only differences in exchangeable Mg and OM between exotic plantations were significant ($p < 0.05$), whereas in the subsoil, all soil chemical properties except total N were significant ($p < 0.05$). In both topsoil and subsoil, the AM_Edge and AM_Plantation stands had higher exchangeable Mg, whereas all AA and AM stands, apart from AM_Forest, had approximately twice as much OM as all EC stands (Table 3).

Table 3. Soil chemical properties in nine stands along the forest remnants to plantation stands of three exotic plantations. EC: *Eucalyptus camaldulensis*, AA: *Acacia auriculiformis*, AM: *A. mangium*. Significant differences: *ns* $p \geq 0.05$; * $p < 0.05$, ** $p < 0.01$. Different superscript letters in the same column indicate significant difference at $p < 0.05$.

Stand	pH	Exchangeable (mg kg^{-1})			Available P (mg kg^{-1})	Total N (%)	OM (%)
		K	Ca	Mg			
Topsoil (Soil depth 0–10 cm)							
EC_Forest	4.1	63.47 ^{ab}	165.34	73.94 ^{ab}	12.18	0.16	3.29 ^{c}
EC_Edge	3.9	58.54 ^{b}	111.68	46.51 ^{ab}	11.63	0.13	3.14 ^{c}
EC_Plantation	3.8	71.27 ^{ab}	134.10	47.22 ^{ab}	13.70	0.14	3.94 ^{c}
AA_Forest	3.8	70.31 ^{ab}	94.03	46.91 ^{ab}	10.76	0.16	8.45 ^{ab}
AA_Edge	3.7	50.11 ^{b}	63.51	22.83 ^{b}	13.96	0.14	8.97 ^{a}
AA_Plantation	3.7	55.05 ^{b}	47.65	19.77 ^{b}	10.00	0.13	8.07 ^{ab}
AM_Forest	4.1	56.28 ^{b}	214.91	44.91 ^{ab}	10.58	0.17	3.70 ^{c}
AM_Edge	3.6	99.61 ^{ab}	131.53	80.41 ^{a}	10.07	0.15	8.81 ^{a}
AM_Plantation	3.8	109.5 ^{a}	167.24	95.22 ^{a}	11.07	0.17	6.41 ^{b}
F-value (Species)	3.59 ^{ns}	2.29 ^{ns}	3.90 ^{ns}	10.37 *	0.41 ^{ns}	1.82 ^{ns}	28.32 **
F-value (Stand within species)	1.55 ^{ns}	0.25 ^{ns}	0.59 ^{ns}	0.06 ^{ns}	0.97 ^{ns}	2.50 ^{ns}	5.15 *
F-value (Species * Stand)	0.14 ^{ns}	1.39 ^{ns}	0.95 ^{ns}	0.91 ^{ns}	0.71 ^{ns}	0.68 ^{ns}	3.77 *
Subsoil (Soil depth 10–30 cm)							
EC_Forest	3.9 ^{bcd}	28.45 ^{b}	41.63 ^{b}	28.16 ^{b}	9.64 ^{ab}	0.09	2.15 ^{b}
EC_Edge	3.8 ^{bcd}	30.72 ^{b}	17.57 ^{b}	10.85 ^{b}	9.05 ^{abc}	0.09	1.84 ^{b}
EC_Plantation	3.8 ^{bcd}	40.92 ^{ab}	22.88 ^{b}	18.17 ^{b}	10.65 ^{a}	0.09	1.81 ^{b}
AA_Forest	3.7 ^{d}	31.77 ^{b}	20.79 ^{b}	12.73 ^{b}	6.69 ^{bc}	0.10	7.25 ^{a}
AA_Edge	3.7 ^{d}	37.04 ^{ab}	29.59 ^{b}	13.41 ^{b}	6.85 ^{bc}	0.12	7.33 ^{a}
AA_Plantation	3.8 ^{cd}	29.77 ^{b}	15.82 ^{b}	7.76 ^{b}	7.67 ^{abc}	0.10	6.82 ^{a}
AM_Forest	4.1 ^{a}	34.78 ^{b}	58.04 ^{b}	71.49 ^{a}	5.78 ^{c}	0.10	1.49 ^{b}
AM_Edge	4.0 ^{a}	72.40 ^{a}	116.68 ^{a}	90.68 ^{a}	5.86 ^{c}	0.10	6.77 ^{a}
AM_Plantation	3.9 ^{abc}	72.58 ^{a}	68.26 ^{b}	74.71 ^{a}	6.83 ^{bc}	0.13	5.60 ^{a}
F-value (Species)	4.41 *	8.60 *	14.73 **	21.56 **	3.82 *	2.20 ^{ns}	40.11 **
F-value (Stand within species)	0.30 ^{ns}	0.24 ^{ns}	0.76 ^{ns}	0.63 ^{ns}	0.21 ^{ns}	0.10 ^{ns}	0.77 ^{ns}
F-value (Species * Stand)	0.94 ^{ns}	0.98 ^{ns}	0.71 ^{ns}	0.44 ^{ns}	0.26 ^{ns}	1.36 ^{ns}	0.31 ^{ns}

3.3. Environmental Factors in Exotic Plantation Stands

In all studied stands, annual variations in environmental factors such as relative humidity (RH), air temperature (Temp), and relative light intensity (RLI) were observed, with the annual mean ranging between 63.86%–68.69%, 26.80–28.72 °C, and 14.64%–21.98%, respectively. The mean annual Temp in AM stands was significantly lower than in AA and EC stands, and the differences between exotic species, but stands within species, were statistically significant. In contrast, no significant differences were observed between exotic plantations or between stands within exotic plantations due to relatively small area. Annual mean RLI varied significantly between plantations and stands within exotic plantations. The annual mean RLI under plantation stands tended to be higher compared to those under the edge and forest remnants. Particularly, the AM_Plantation stand had the highest RLI and the AA_Forest and EC_Forest had the lowest RLI (Figure 7).

3.4. Relationship between Environmental Factors and Native Tree Distribution

The CCA findings revealed a strong relationship between tree species and environmental factors including sand, silt, and clay particles, OM, soil pH, and RLI (Table 4). CCA axis 1 and 2 had tree species to environmental factors of 0.298 and 0.142, respectively. The CCA analysis could be divided into three groups based on the correlation of species composition to environmental factors in all studied plots, and the graphical presentation is shown in Figure 8. For Group 1, which included EC_Edge, EC_Plantation, AA_Edge, and AA_Plantation, the sand particle played a significant role in promoting the establishment of native tree species. The species composition of this group was *Microcos tomentosa*, *Gonocaryum lobbianum*, *Wrightia arborea*, and *Ixora cibdela*. Clay and silt particles and RLI had a significant impact on the establishment of native species such as *Mangifera caloneura*, *Mallotus philippensis*, *Baccaurea ramiflora*, *Alchornea rugosa*, *Garcinia speciosa*, *Croton persimilis*, and *Suregada multiflorum* in Group 2, which can be found only in the AM_Edge and AM_Plantation stands. All forest remnants including AM_Forest, AA_Forest, and EC_Forest were classified as Group 3, and all native species observed in this group, including *Shorea henryana*, *Hydnocarpus ilicifolia*, *Memecylon cyaneum*, *Garcinia speciosa*, *Cinnamomum iners*, and *Dialium cochinchinense*, were strongly influenced by soil pH. The findings indicate the impact of different exotic plantations on understory environmental factors, thereby affecting the establishment of native species.

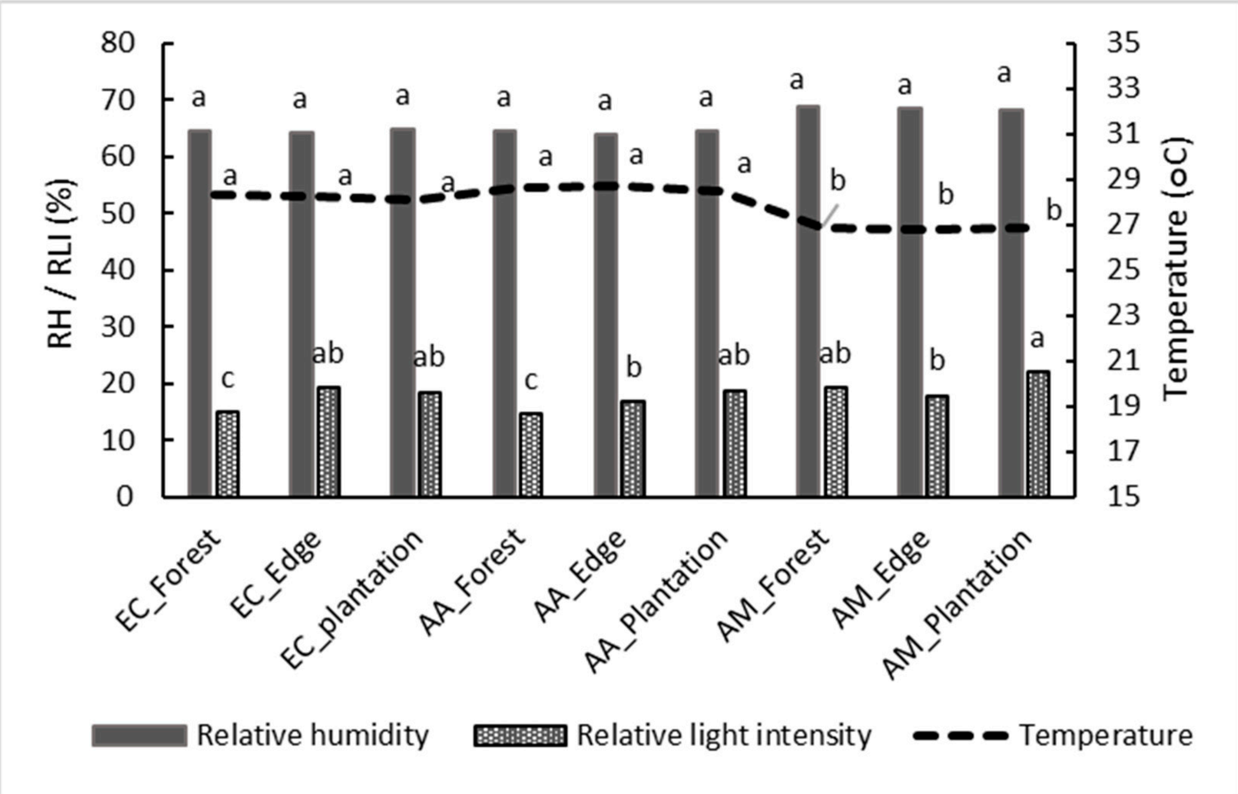

Figure 7. Annual means of relative humidity (RH), air temperature (Temp), and relative light intensity (RLI) in nine stands along the forest remnants to plantation stands of three exotic plantations. EC: *Eucalyptus camaldulensis*, AA: *Acacia auriculiformis*, AM: *A. mangium*. Different superscript letters of each each parameter indicate significant difference at $p < 0.05$.

Table 4. Results of the canonical correspondence analysis (CCA) of the relationship between tree species and the environmental factors.

CCA Results	Axis 1	Axis 2	Axis 3
Eigenvalues	0.298	0.142	0.084
Variance in species data % of variance explained	41.40	19.70	11.70
Cumulative % explained	41.40	61.10	72.80
Pearson correlation (species–environment)	0.984	0.998	0.944

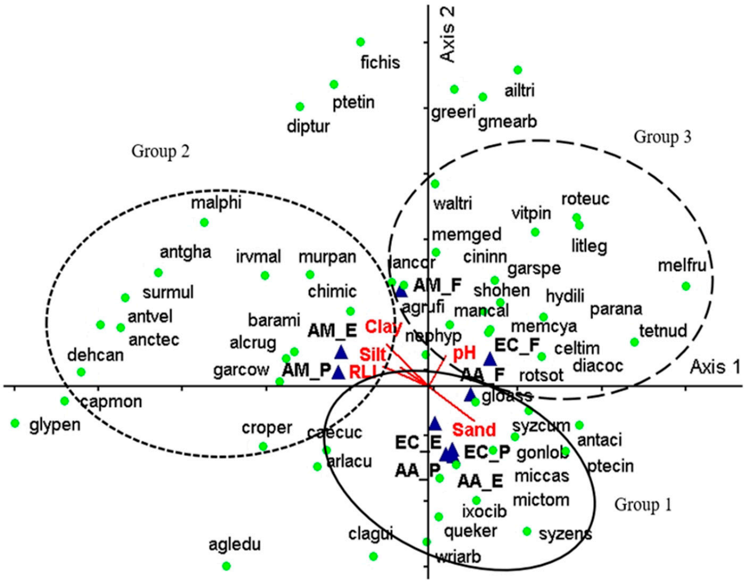

Figure 8. The CCA ordination diagram representing the relationship between the distribution of native tree species and the environmental factors: sand, silt, and clay particles, soil pH, and relative light intensity (RLI) along the forest remnants to plantation stands of three exotic plantations. EC: *Eucalyptus camaldulensis*, AA: *Acacia auriculiformis*, AM: *A. mangium*. A filled triangle (▲) represents each stand, and a green circle (●) indicate the distribution of species against Axis 1 and Axis 2.

4. Discussion

4.1. Stand Structure and Composition Influencing Understory Vegetation and Environments

Exotic fast-growing tree plantations, such as *E. camaldulensis*, *A. auriculiformis,* and *A. mangium*, had distinct canopy structures, ecological and physiological characteristics, and tree functional traits, all of which influence microclimate conditions, nutrient cycling, and species diversity within an ecosystem [22,24,41]. In this study, *A. auriculiformis* and *A. mangium* are nitrogen-fixing species with nitrogen-rich nutrients in their plant litter [42]. Because of their ability to improve soil in degraded land through litter decomposition, they have been widely used in afforestation and restoration. Plantations that fix nitrogen are an efficient way to improve soil by increasing soil nutrients and organic matter [17,43]. *E. camaldulensis*, on the other hand, was a non-nitrogen-fixing tree that was widely used in commercial plantations. However, because of its great survival rate, growth performance, and adaptability to extreme site conditions with a mean annual increment of aboveground biomass of 11.11 Mg/ha/year [44], *E. camaldulensis* was often planted on degraded land.

Some of the most important environmental factors facilitating natural regeneration include soil physical and chemical properties, particularly the availability of soil nutrients and organic matter, that influence the structure and diversity of forest plant communities [45]. Establishment of exotic plantations may alter the nutrient cycle either directly, by modifying the quality and quantity of litter entering the soils below, or indirectly, by altering the soil physical and chemical properties beneath their canopy. In this study, all exotic plantation stands, including the nearby forest remnants, had similar soil physical and chemical properties. The bulk density of the topsoil and subsoil did not differ between exotic plantations. Although a majority of the subsoil chemical properties varied among exotic plantations, most of chemical properties of the topsoil including pH, total N, available P, exchangeable Ca, and exchangeable K were comparable. Moreover, the soil nutrients of Forest, Edge, and Plantation stands within an exotic plantation were also similar. The study area was planted with cassava for a few decades in the past, resulting in degraded land and poor soil conditions. The findings indicated that these old plantations of exotic, fast-growing trees could improve physical and chemical properties of degraded soils, particularly increasing soil nutrients in the topsoil in a manner similar to a nearby forest remnant. In southern Thailand, the soil structure and bulk density of an old *Acacia* plantation on an abandoned mining area have been restored, and some physical properties of soil were comparable to those of nearby primary and secondary forests [43]. High litter production as well as high N and P concentration of the *Acacia* plantation could contribute to accumulation of organic matter, thereby promoting soil formation and soil aggregates [10,46]. This accumulation also increased nitrogen mineralization and changed soil properties; these have important roles for plant growth and species composition during the succession process. Furthermore, depending on tree species, *Acacia* and *Eucalyptus* spp. plantations in southern Thailand played a significant role in enhancing soil structure and the availability of essential nutrients [47].

The plantations of fast-growing trees had high aboveground biomass and litter production and the decomposition of litter by soil microorganisms released nutrients to forest floor [3,47]. Plant litters are also significant sources of OM and nutrients in ecosystems, especially nitrogen [3]. Plantations of species with certain functional traits, specifically ability of biological N fixation, generally promote soil fertility [43], enhance natural regeneration beneath their canopy [41], and influence development of forest community and diversity [48]. In our study, higher OM was found in the Edge and Plantation stands of nitrogen-fixing tree species like AM and AA, compared to EC, underlining their importance for soil improvement, because OM has a positive relationship with soil properties such as soil nutrients, water holding capacity, and bulk density [39]. Greater N nutrient return to the forest floor from nitrogen-fixing tree plantations was pronounced and widely reported e.g., [41,47,49].

However, the number of species and amount of tree diversity were not different between AA and EC stands. The results indicated that, despite being a non-nitrogen-fixing tree, *E. camaldulensis* can introduce native species into plantations and improve the heterogeneity of forest structure, as previously reported in various sites in Thailand. Similar to an old *E. camaldulensis* plantation in northeastern Thailand, species composition of the EC_Edge and EC_Plantation stands were more than 50% identical to the forest remnant [28]. Furthermore, seedlings of native species of a dry evergreen forest performed well under a 20-year-old *E. camaldulensis* plantation, with high survival and growth rates [44]. High biodiversity and density of regenerating native woody plants under the canopy of exotic tree plantations, including *Eucalyptus* spp., have also been reported in various tropical regions, implying that plantation stands can promote a high density and variety of species for natural regeneration [7]. Nevertheless, growing concern regarding adverse effects of *Eucalyptus* plantations on ecosystems in terms of higher competitive strength for water, nutrients, and light than indigenous plants has been addressed [50]. Our results indicated that soil physical and chemical properties of EC stands were not different from those of adjacent AA stands. The findings suggest that exotic fast-growing trees, either N-fixing species like *Acacia* or non-N-fixing species like *Eucalyptus*, could be planted on degraded lands to improve forest structure and increase soil properties, thereby facilitating forest restoration processes by reducing the time it takes to transition from degraded to climax forest.

When soil nutrients are uniform, the diversity of understory species in various stand structures and densities is frequently comparable [45]. Even though there were differences in tree density between exotic plantations and species diversity between Forest, Edge, and Plantation stands of each exotic plantation, dominant native species in all EC, AA, and AM edge and plantation stands were relatively similar. Many of these species were pioneer trees, including *Vitex pinnata*, *Gonocaryum lobbianum, Wrightia arborea*, *Microcos tomentosa*, *Croton cascarilloides*, and *Mallotus philippensis*. In addition, some pioneer species such as *G. lobbianum*, *M. tomentosa*, *and W. arborea* were more abundant in EC and AA stands compared to AM stands (Figure 5), most likely due to similar soil texture of EC and AA stands. Due to the availability of their seeds or fruits to dispersers, such as small seed sizes and seeds dispersed by birds and wind, pioneer species were well-distributed in the restoration of disturbed forests [51]. Pioneer species had regenerated and become well-established in disturbed areas, as observed in dry evergreen forest in northeastern Thailand [29]. In addition, the climax species, which are often shade-tolerant trees, were discovered not only on remnant forest but also in forest edges and plantations. These species, such as *S. henryana* and *W. trichostemon*, were frequently observed in forest remnants and diminished as distance from remnant forest increased. The former was more prevalent in EC and AM stands, whereas the latter was typically found only in AM stands, indicating that the structure and species compositions of the overstory play a role in the natural regeneration of these species.

4.2. Environmental Factors Driving Natural Regeneration of Native Tree Species

In ecosystems, the distributions of species and environmental factors are strongly correlated. The environmental factors, particularly soil properties [18,20,21,48,52], light intensity, and other microclimates [22,23] affected establishment, survival rate, growth, species composition, density, and diversity of plant species [21–23,53]. Our study site was divided into three exotic plantations (EC, AA, and AM) and three stands in each plantation along the remnant forest to plantation, resulting in a total of nine stands: EC_Forest, EC_Edge, EC_Plantation, AA_Forest, AA_Edge, AA_Plantation, AM_Forest, AM_Edge, AM_Plantation (Figure 2). The CCA results indicate the relationships between environmental factors and species composition, which can be categorized into three groups of plantation stands with respective abundant native species (Figure 6). Tree composition and development of forest community were highly correlated with soil physical properties [21,48]. Soil texture could be a limiting factor for species composition and distribution in various ecosystems. The first species group was observed in forest edge and plantation stands of EC and AA plantations and the most abundant native species in this grouping were pioneer species such as *M. tomentosa*, *G. lobbianum*, and *W. arborea*. The sand particle had a close relationship with these species. Soils with higher sand particles have lower water storage capacity, thereby causing plants to compete more for soil moisture during the dry season. As a result, sand particles become one of the limiting factors for survival and establishment of native seedling and saplings during drought conditions [52,54]. In our study, low density and number of species were observed in the EC and AA Edge and Plantation stands where the soil texture was sandy clay loam, containing a large proportion of sand particles. Soil moisture content was also a key factor for establishment of seedling and sapling observed in the dry evergreen forest in northeastern Thailand [41]. The pioneer species abundant in the EC and AA Edge and Plantation stands could have a high amplitude of drought tolerance consistent with that reported in the restoration of a degraded evergreen forest by teak (*Tectona grandis*) plantations in central Thailand [27].

Clay and silt particles influenced the abundance of native trees in AM Edge and Plantation stands, the second native species group (Figure 6). The clay loam soil observed in these stands contained higher clay and silt particles compared to the sandy clay loam observed in the first group. Similarly, clay content was among the most important factors explaining the distribution of the three ecological species groups in the lowland-mountain forests in northern Iran [20]. In addition, *A. mangium* planted on clay site, compared with that planted on sandy site, had lower biomass and litter production but provided more favorable conditions for natural regeneration [47]. Our study indicated that soil particles, including sand, silt, and clay, were significant factors influencing natural regeneration in all three exotic species in the edge and plantation stands, thereby contributing to development of forest community and succession of restored tropical forests [19].

In addition to soil texture, light is one of the most important factors influencing understory vegetation [22]. The RLI was higher in AM plantation stands compared to EC and AA plantation stands. This could have contributed to their higher mortality, with greater number of standing dead and felled trees, as well as their smaller basal area. As a result, large gaps developed in this area, leading to a greater light availability for seedling and sapling development under plantations. This may be a favorable environmental condition that promotes the natural succession of native species. This study showed the significance of light for tree composition in these AM plantation stands. It also found that understory RLI was positively correlated with the abundance of native species, such as *Mallotus philippensis*, *Baccaurea ramiflora*, *Alchornea rugosa*, *Garcinia speciosa*, *Croton persimilis*, and *Suregada multiflorum*, suggesting that these pioneer species were light-demanding [55]. Natural regeneration of tree species under plantation canopies was more abundant in low-density stands not only due to favorable light intensity, but also due to favorable moisture content for the understory and soil physical and chemical properties [45]. The appropriate gap sizes created by thinning of old plantation stands may be considered for enhancing suitable light conditions and encouraging the growth and regeneration of native species beneath the canopy. Also, [56] discovered that thinning improved forest structure and increased species diversity and abundance of tree species. The thinning is, therefore, necessary to enhance the growth of native species in tropical forests [25,57].

Soil particles, organic matter, and understory light intensity were driving factors in the Edge and Plantation stands, depending on exotic species that influenced soil properties and understory microclimate conditions. On the other hand, the natural regeneration in all forest remnants (EC_Forest, AA_Forest, and AM_Forest) was restricted by soil pH and most of the abundant native species were climax species including *Shorea henryana*, *Memecylon cyaneum*, *Vitex pinnata*, *Aglaia rufinervis*, and *Dialium cochinchinense*. Soil pH was among the most important factors explaining the distribution of forest communities in lowland-mountain forests [19] and other tropical forests [21]. Soil pH of plantations and secondary forest was relatively low compared to primary forest [54], indicating that soil pH was the most important factor determining the forest community of these shade-tolerant native species.

4.3. Natural Regeneration along Forest Remnants to Plantations

Tree diversity and density were higher in sampling plots close to natural forest and decreased along the edge–interior gradients as observed in deciduous forest in northern Thailand [23] and tropical rainforest in Vietnam [24]. Similarly, in our study, we observed a greater diversity and density of native species in forest remnants adjacent to all exotic plantations, and this diversity and density decreased with increasing distance along forest edges through plantation stands. The abundance and diversity of native plants in forest fragments also declined along a broad gradient from secondary forest to agroforestry to exotic plantations to croplands to pasture because natural forest is a significant seed source for natural regeneration [58,59]. The regenerated native species in the *A. mangium*, *A. auriculiformis*, and *E. camaldulensis* plantations in Vietnam were found within 50 m from natural forest and decreased gradually to the distance up to 400 m. The rate of decline varied among tree plantations, with *A. auriculiformis* plantation experiencing the most rapid decline [24]. Likewise, our study also showed differences in the decline between the three exotic plantations, with AM stands exhibiting the greatest diversity and EC stands exhibiting the most rapid decline. In our study, however, the number of regenerated native species to distances up to 100 m was greater than that reported in Vietnam [24]. Furthermore, the variations in the natural regeneration of the tree plantations contributed to seed dispersals in the form of dispersal syndromes, fruit or seed size, and availability of fruits for frugivores, which in turn could be affected by initial species composition, planting density, and site conditions [60]. Large seeds of primary forest were most dispersed by animal and weight gravity, while seeds of pioneer trees were dispersed by wind, birds, and bats [60,61]. *Litsea cubeba*, *Schima wallichii*, and *Ficus fulva* pioneer trees with small seeds were also found in exotic plantations up to 400 m from a natural forest [24]. Similarly, *N. hypoleucum*, a shade-tolerant species, was abundant in all three exotic plantations up to 100 m from adjacent forest remnants because of its frugivore-attractive fruits. However, certain pioneer species such as *G. lobbianum*, M. tomentosa, and *W. arborea* were only found along EC and AA Plantation stands, and their presence was also influenced by the quantity of sand particles.

Furthermore, based on the diameter class distribution pattern of native species, the L-shaped or reversed J-shaped curve observed in all exotic plantation stands is an indicator of a steady and expanding population. It has more trees in the smaller classes, indicating continuous recruitment in a sustainable manner for natural succession [62]. Similar good natural succession was also found in forest edges, but tree composition and forest community were different between forest edges [23,53]. Except for the AM_Forest, however, the diameter class distribution pattern of native species along forest edge gradient was also similar. The AM_Forest contained approximately three times more small-sized trees than forest edge and plantation stands, probably attributable to its lower basal area. Although the most abundant native species in this forest remnant were shade-tolerant, the stand structure and composition could enhance the light intensity in the understory, thereby facilitating the establishment of a few climax species, such as *W. trichostmon* and *Hydnocarpus ilicifolia*. Nevertheless, these species were incapable of growing to mature stage in these conditions or regenerating along the forest edge gradient to plantation stands. In conclusion, the success or failure of natural succession of some climax species in our study was primarily attributed to key factors associated with seedling and sapling colonization, including stand structure-related factors, soil properties, and other environmental factors, that matched the edge and plantation environment [23].

5. Conclusions

The findings support the hypothesis that we have proposed that, despite having similar dominant native tree species, three exotic plantations had distinct stand structures in terms of the number of tree species, basal area, and tree density, influencing soil physical and chemical properties and understory microclimates. These factors individually or in combination induced natural regeneration of native woody species in various ways, depending on plantation stands and distances along forest remnants to plantations. Our study suggests that the soil texture (sand, silt, and clay particles), soil pH, and RLI were primary factors influencing the native species composition in EC, AA, and AM plantation, edge, and forest-remnant stands in a forest restoration project in northeastern Thailand. Using these environmental factors, the abundance of native tree species could be divided into three groups. First, drought-tolerant pioneer species occurred in EC and AA plantation and edge stands in response to sand particles. Second, light-demanding pioneer species were abundant only in AM plantation and edge stands and were correlated with clay and silt particles and understory light availability. Third, shade-tolerant climax species were widespread only in forest remnants and were restricted to soil pH. Our results also indicated that diversity and density of native species were greater in forest remnants adjacent to all exotic plantations, and this diversity and density decreased with increasing distance along forest edges from plantation stands. Separate from environmental factors, further research is needed to determine how the availability of seed sources and seed dispersal syndromes affect the success or failure of natural succession of some climax species.

In conclusion, these exotic tree plantations enhanced soil properties and created favorable microclimates for the emergence of native species, thereby stimulating the natural regeneration process for the restoration program. However, most of the climax species were unable to regenerate in these conditions, possibly due to environmental and recruitment limitations, such as seed limitation. To develop these stands into forests dominated by native tree species and accelerate the ecosystem restoration process, additional research is required to determine the optimal canopy management and/or planting of dominant climax species beneath these old exotic plantations to facilitate their capacity for regenerating and maturing.

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Appendix A

Table A1. List of top five tree species in nine stands along the forest remnants to plantation stands of three exotic plantations based the importance value index (IVI). EC: *Eucalyptus camaldulensis*, AA: *Acacia auriculiformis*, AM: *A. mangium*, RD: relative density, RF: relative frequency, RDo: relative dominance.

Stand	Tree Species	RDo	RF	RD	IVI
EC_Forest	*Lithocarpus elegans* (Blume) Hatus. ex Soepadmo.	30.08	5.29	3.52	38.90
	Antidesma acidum Retz.	5.56	7.41	21.72	34.69
	Shorea henryana Pierre	7.74	7.41	12.13	27.28
	Nephelium hypoleucum Kurz.	11.44	4.76	3.72	19.92
	Gonocaryum lobbianum (Miers) Kurz.	5.90	5.82	7.83	19.54
EC_Edge	*Eucalyptus camaldulensis* Dehnh.	83.45	9.26	18.63	111.35
	Clausena guillauminii Tanaka.	0.82	7.41	12.22	20.44
	Microdesmis caseariifolia Planch. ex Hook.	0.30	8.02	8.49	16.82
	Antidesma acidum Retz.	0.66	8.02	7.25	15.93
	Ixora cibdela Craib	0.15	6.17	8.28	14.60
EC_Plantation	*Eucalyptus camaldulensis* Dehnh.	83.69	10.42	16.80	110.90
	Clausena guillauminii Tanaka.	1.45	9.72	22.67	33.84
	Ixora cibdela Craib	0.11	9.03	10.13	19.27
	Microcos tomentosa Sm.	4.23	7.64	2.67	14.54
	Gonocaryum lobbianum (Miers) Kurz	0.43	7.64	4,53	12.60
AA_Forest	*Gonocaryum lobbianum* (Miers) Kurz.	9.93	5.80	10.59	26.32
	Nephelium hypoleucum Kurz.	12.95	4.46	5.38	22.79
	Antidesma acidum Retz.	6.23	6.70	9.41	22.34
	Microcos tomentosa Sm.	12.24	5.36	3.53	21.12
	Microdesmis caseariifolia Planch. ex Hook.	1.94	6.70	10.76	19.39
AA_Edge	*Acacia auriculiformis* A. Cunn. ex Benth.	76.99	6.38	5.51	88.88
	Clausena guillauminii Tanaka.	4.29	7.45	23.81	35.54
	Ixora cibdela Craib	0.39	7.98	11.76	20.13
	Antidesma acidum Retz.	1.58	6.91	8.78	17.28
	Microcos tomentosa Sm.	3.17	6.91	5.80	15.89
AA_Plantation	*Acacia auriculiformis* A. Cunn. ex Benth.	83.82	9.74	8.63	102.18
	Clausena guillauminii Tanaka.	4.96	9.74	32.57	47.27
	Hopea odorata Roxb.	1.69	9.74	13.38	24.82
	Microdesmis caseariifolia Planch. ex Hook.	0.59	7.14	4.75	12.48
	Antidesma acidum Retz.	0.47	7.14	4.58	12.19
AM_Forest	*Alchornea rugosa* Muell. Arg.	1.77	5.93	15.88	23.59
	Shorea henryana Pierre	11.60	5.53	6.02	23.15
	Dipterocarpus turbinatus C. F. Gaertn.	9.64	5.14	7.34	22.12
	Pterocymbium tinctorium (Blanco) Merr.	4.88	5.53	10.35	20.76
	Nephelium hypoleucum Kurz	10.35	4.74	4.21	19.31
AM_Edge	*Acacia mangium* Willd.	81.86	4.72	5.04	91.61
	Alchornea rugosa Muell. Arg.	0.60	5.91	18.48	24.99
	Clausena guillauminii Tanaka.	2.34	5.91	8.91	17.16
	Dipterocarpus turbinatus C. F. Gaertn.	1.59	3.15	8.01	12.75
	Nephelium hypoleucum Kurz	2.28	4.33	5.43	12.04
AM_Plantation	*Acacia mangium* Willd.	78.14	6.09	4.08	88.31
	Alchornea rugosa Muell. Arg.	0.79	5.65	19.97	26.1
	Nephelium hypoleucum Kurz.	4.66	4.72	8.02	17.46
	Clausena guillauminii Tanaka	1.64	5.65	7.41	14.71
	Mallotus philippensis Mull. Arg.	2.85	3.48	4.69	11.01

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