Tropical Natural History 17(2): 94–110, October 2017

Factors Affecting Size Distribution and Sapling Occurrence of Podocarpaceae at Khao Yai National Park, Thailand

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Received: 23 December 2016; Accepted: 7 September 2017

ABSTRACT.– The objective of this study was to examine factors affecting the occurrence of saplings (height 0.15-1.35 m) of Podocarpaceae at Khao Khiew (Khiew Mountain) in Khao Yai National Park, Thailand. Four species of Podocarpaceae were studied: *Podocarpus neriifolius*, *Nageia wallichiana*, *Dacrycarpus imbricatus*, and *Dacrydium elatum*. The total area encompassed 20 hectares, with 70 systematically placed plots and 15 subjectively placed plots. We expected that sapling occurrence is influenced by a combination of factors, including soil nutrients, canopy cover, local slope, and disturbance. We therefore tested a series of candidate models for each species. Akaike's Information Criterion (AIC_c) was used to compare the weight of evidence for each model. We found the highest support for models varied among species. The combination of soil available phosphorus (P) with soil depth had most support in explaining the occurrence of *P. neriifolius* saplings, while for *N. wallichiana* the depth of the soil showed the most support. *D. imbricatus* sapling occurrence was best supported by the pH model. A positive relationship was found between soil nitrogen (N), local slope, soil depth and sapling occurrence for all species surveyed. *P. neriifolius* and *D. imbricatus* sapling occurrence declined with increasing soil P, but increased for *N. wallichiana*. This research provides basic information useful for the conservation and management of Podocarpaceae, a little studied family in Southeast Asia.

KEY WORDS: ***Podocarpus*, *Nageia*, *Dacrycarpus*, *Dacrydium*, generalized linear mixed models (GLMM), Akaike's Information Criterion**

INTRODUCTION

Podocarpaceae are a family of 17 genera and 122-165 species of conifers (Order Pinales, Division Pinophyta), consisting of evergreen trees or shrubs with scale, clawed, or flattened needlelike or broader leaves, usually with a single, undivided midvein (multiple veins in *Nageia*). This family is distributed mainly in the Southern Hemisphere, but infrequently in the tropics. *Podocarpus* is by far the largest genus (82 species) with the next largest genus being *Dacrydium* (21 species) (Eckenwalder, 2009). The family is represented in Thailand by seven species from four genera, *Dacrycarpus*, *Dacrydium*, *Nageia*, and *Podocarpus* (Phengklai, 1975; Eckenwalder, 2009).

Regeneration, or the production of new generations, of conifer trees requires the success of each step in the life cycle, including pollination, seed dispersal, seed germination and seedling and sapling survival. Seed germination and seedling establishment are the most vulnerable

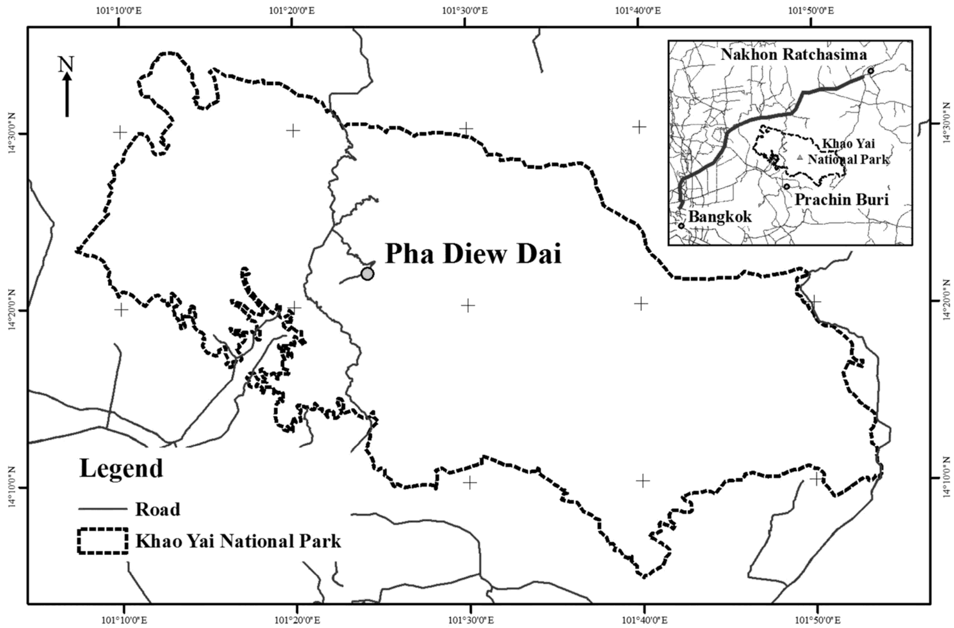

FIGURE 1. Khao Khiew at Khao Yai National Park. The dot shows site at Pha Diew Dai (Guide To Thailand, 2016).

phases in plant life cycles (Solbrig, 1980), and information about them is especially important in understanding the distribution of rare plants. Seeds must be distributed to appropriate areas to allow sprouting of seedlings. The emerging seedlings must survive and grow to saplings and then to mature trees (Corlett, 2009). Carswell et al. (2007) investigated the factors related to the occurrence of seedlings of Podocarpaceae in New Zealand. They concluded that the best supported model to predict the occurrence of seedlings of two podocarp species included all of the following factors: soil nutrients, canopy composition, land form index, and disturbance type. A positive relationship was found between soil nitrogen (N) and seedling occurrence of all species studied. For two additional podocarp species the most important factor was the combination of soil nitrogen (N) and phosphorus (P) levels. The seedlings of podocarp species were found on soils with low soil P but high soil N concentrations; the authors concluded that soil nutrient status should be taken into account during forest management (Carswell et al., 2007). In other studies in New Zealand, variation in mature conifer-angiosperm forest composition was linked to soil nutrients, with greater podocarp dominance at lower concentrations of total P and higher total N concentrations, whereas soils of higher P concentrations are more likely to give rise to increased angiosperm dominance (Richardson et al., 2004; Coomes et al., 2005). As there have been few similar studies on tropical podocarps, we supposed that similar factors may apply to tropical members of Podocarpaceae.

Although seven species of Podocarpaceae occur in Thailand (Phengklai, 1975), they are usually present at very low densities, making ecological studies difficult. However, near the summit of Khao Khiew mountain at Khao Yai National Park, in central Thailand, 4 species occur in abundance and are among the dominant species in that area and thus amenable for study. The objective of this study is to investigate the factors affecting the size distribution and sapling (height 0.15-1.35 m) occurrence of these four species of Podocarpaceae at Khao Yai National Park, Thailand. As for other species of Podocarpaceae, it is hypothesized that the quality of soil and other environmental factors play an important role in the distribution of these species. This research can provide basic information useful for the conservation and management of Podocarpaceae in this area.

MATERIALS AND METHODS

Study site

This study was carried out at Pha Diew Dai or Diew Dai Cliff and the adjacent ridge located on Khao Khiew in Khao Yai National Park, central Thailand (101°22' E and 14°26'N, 1,129 m in altitude), in Nakhon Nayok province (Fig. 1 and 2).

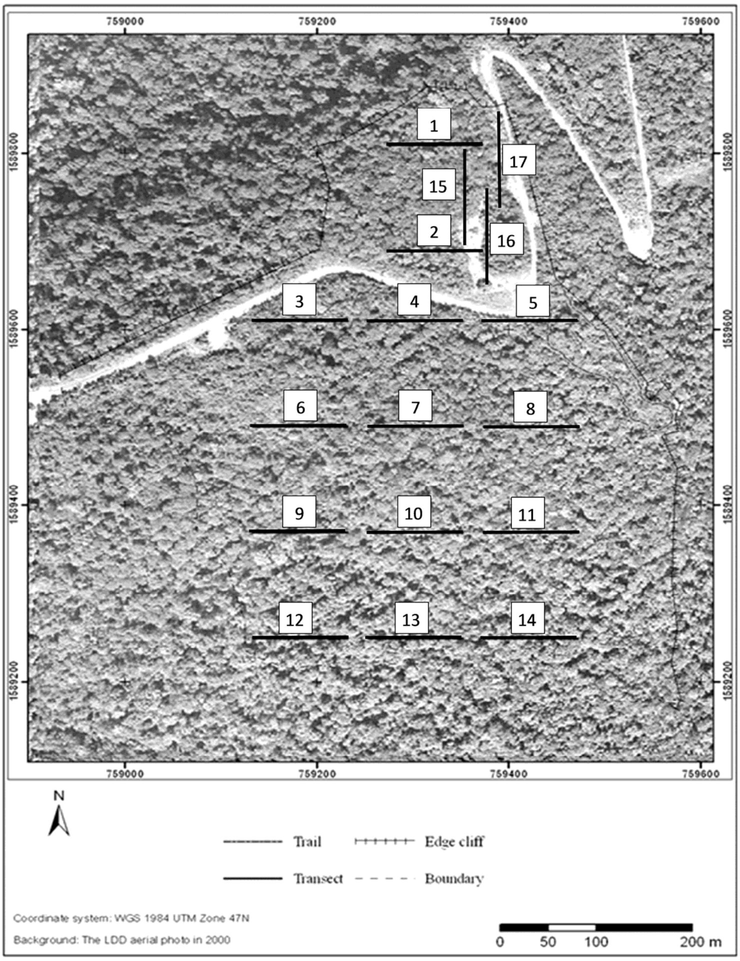

FIGURE 2. Geographical study site showing arrangement of intercepts and 14 systematically arranged transects (1 – 14), plus 3 subjectively arranged transects (15 – 17) on Khao Khiew.

TABLE 1. Summary of study species at Khao Khiew in Khao Yai National Park

Species	Common name	Where found in Khao Khiew
Dacrydium elatum	Son Samphan Pee, Son hang Krarok, Chuang Pha	The adjacent ridge and Pha Diew Dai mixed angiosperm conifer evergreen closed canopy forest
Dacrycarpus imbricatus	Makhampom Dong	Pha Diew Dai mixed angiosperm conifer evergreen closed canopy forest
Nageia wallichiana	Khun Mai	Pha Diew Dai mixed angiosperm conifer evergreen closed canopy forest
Podocarpus neriifolius	Phaya Mai	Pha Diew Dai and the adjacent ridge mixed angiosperm conifer evergreen forest; young trees in open area with shallow, sandy soil

Khao Khiew reaches an altitude of around 1,351 meters above sea level, has average relative humidity of 89.85 percent and an average temperature of 21.8°C, and had 4,444.75 mm annual rainfall in 2010. The rock type at Pha Diew Dai is sedimentary and classified as part of the Phra Wihan Formation, Korat Group, from the Early Cretaceous period (Racey et al. 1994; Suwanpatra 2006). The vegetation is tropical lower montane seasonal evergreen forest. Dipterocarpaceae are not present at all, but conifers are found, namely *Podocarpus neriifolius* D. Don (Pha ya mai), *Nageia wallichiana* (C. Presl) Kuntze (Khun mai), *Dacrycarpus imbricatus* (Blume) de Laub. (Makhampom dong), and *Dacrydium elatum* (Roxb.) Wall. ex Hook. (Son samphan pee). Other trees include *Syzygium gratum* (Wight) S.M. Mitra (Samet daeng) (Myrtaceae), *Quercus brandisiana* Kurz (Ko ta kwai) and *Quercus kerrii* Craib (Ko ta moo noi) (Fagaceae), *Cinnamomun iners* Reinw. ex Blume (Aob chei) (Lauraceae), *Schima wallichii* Korth. (Ta lo) (Theaceae), *Anneslea fragrans* Wall. (Saraphi pa) (Pentaphylacaceae), *Cedrela toona* Roxb. (Yom haom) (Meliaceae), and *Pandanus* sp. (Pandanaceae). The ground flora includes herbaceous plants, ferns and the terrestrial orchid *Spathoglottis eburnea* Gagnep. In addition, several types of moss occur along streams (Foundation for Khao Yai National Park Protection, 2010; P.J. Grote, unpublished data).

Study species

The study species were the four species of Podocarpaceae found at Khao Khiew, including Pha Diew Dai, at Khao Yai National Park: *Dacrydium elatum, Dacrycarpus imbricatus, Nageia wallichiana* and *Podocarpus neriifolius* (Table 1).

Size-frequency distributions

Size-frequency distributions were determined for trees of Podocarpaceae within a 10 meter radius surrounding the center of seventy systematically arranged plots (details in the next section). All the trees of Podocarpaceae were mapped (location, altitude, slope), and the height and diameter at breast height (dbh, at 1.3 m) was measured for each tree. The size-frequency distribution graphs were made according to Enright (1995).

Sapling occurrence

Saplings (0.15 to 1.35 m in height) were surveyed to indicate regeneration at the study site of Khao Khiew at Khao Yai National Park. The study site included Pha Diew Dai and the adjacent ridge within an area of 400 by 500 m. The size of the site is limited by cliffs. Transects were selected for sampling in the site. Fourteen transects were arranged systematically in the site in a grid of 120 m x 80 m rectangles. Part of the study site consists of steep cliffs and was excluded. Transect lengths were 100 m oriented parallel to each other and beginning on each intersect. Sapling plots of 2 m radius were positioned at 25 m intervals along each transect. Additionally, three more transects were measured with the positions placed subjectively to maximize the number of sapling in the plots. Five sapling plots were positioned subjectively along each of these transects (modified from Carswell et al., 2007).

In each sapling plot, saplings (≥ 0.15 m and ≤ 1.35 m in height) of *Dacrydium elatum*, *Dacrycarpus imbricatus*, *Nageia wallichiana*, and *Podocarpus neriifolius* were counted. The definition of seedlings used by Carswell et al. (2007) was: plants ≥ 0.15m and < 1.35m in height. However, in the present study plants of this size range are referred to as saplings. Densities of saplings of the four study species were calculated from the data. Environmental parameters that are considered to possibly influence sapling occurrence were measured.

1. Percentage of total canopy cover

Percentage of total canopy cover above 1.35 m in height was measured along a 4 m line (north to south) in each plot.

2. Local slope

For each of the seedling plots, the mesoscale landform was subjectively identified as a ridge, gully, or slope (McNab 1993). For local slope, 8 slope measurements were made on the soil surface from the center to the edge of each 2 m radius plot. Measurements were made to the north and then in a series of rotations of 45°. The highest of the 8 slopes was used to identify the slope of each plot.

3. Soil sampling and analysis

In each plot, soil depth was measured using a rod penetrometer. Soil samples of 500 g were collected at a depth of 0-30 cm and were placed in plastic bags for later analysis. The soil samples were dried indoors under laboratory conditions for 24 hours. The soils were crushed using a pestle and mortar and filtered with a 2 mm sieve, rejecting roots and stones to give the fine earth fraction. For pH measurement, ten grams of soil were dispensed to water (1:1). The soil was stirred and the slurry allowed to settle; then the pH was monitored using a pH meter (Mettler-Toledo MP220, Schwerzenbach, Switzerland). Carbon, hydrogen, and nitrogen were analyzed with a Leco CHN-628 analyzer. Easily extractable phosphorus was measured using inductively coupled plasma (ICP) spectroscopic methods. Soils were dried at 35 ºC and ground to pass through a 2.0 mm screen. Two grams of dried, ground soil was extracted with 20 ml of M3 extracting solution (0.2M CH_3COOH, 0.25M NH_4NO_3, 0.015M NH_4F, 0.013M HNO_3, and 0.001M EDTA) for 5 minutes at 200 reciprocations per minute on an end-to-end Eberbach shaker. The mixture was filtered using P4 filter paper (Fisher Scientific, Pittsburgh, PA). The same filtrate was analyzed spectroscopically (ICP-P) using a Spectra CirOs Inductively Coupled Argon Plasma Spectrometer (Spectra CirOs, ICAP, Fitchburg, MA) for M3P at 178.2 nm (Pittman et al., 2005) .

Soil particle size was measured using the hydrometer method. Briefly, pre-treatment for soil high in organic matter was carried out using hydrogen peroxide (30%). Fifty grams of soil (dry weight equivalent) was placed into a soil dispersing cup. The weight was recorded to at least 0.1 g. The cup was filled with deionized water to within two inches of the top, and 5 ml of 1N sodium hexametaphosphate were added. The cup was then attached to a mixer and mixed for 5 minutes. The suspension was transferred to a sedimentation cylinder, deionized water was added to the cylinder to the 1,000-ml mark, and the suspension was mixed with a plunger. The hydrometer was carefully placed into the suspension and read at 40 seconds. After removing the plunger, timing began. The temperature (°C) was recorded. The suspension was allowed to sit and the hydrometer was read again at 2 hours, followed by a temperature reading. A blank cylinder was prepared with water and sodium hexametaphosphate (Anderson and Ingram, 1993). The percent of sand, clay, and silt was calculated.

Soil was classified as 1) clay loam, 2) clay, 3) silt clay loam, 4) silt loam, or 5) loam according to the percentages of sand, silt, and clay, based on the 12 categories recognized by the United States Department of Agriculture (Soil Survey Division Staff, 1993).

4. Presence of Syzygium gratum

Syzygium gratum is a dominant angiosperm tree species at Pha Diew Dai but absent from the ridge. This species was observed to commonly occur along a stream, so it was hypothesized that there may be a correlation between presence of this species and podocarp species frequently inhabiting streamsides. For each sapling plot, the distance to the nearest *Syzygium gratum* tree was measured. A tree less than or equal to 10 meters distant was classified as present, and trees more than 10 meters were classified as absent.

5. Disturbance

Each sapling plot was placed in one of three categories of disturbance: 1.) undisturbed (ten percent or less of the plot area disturbed), 2.) natural disturbance (greater than 10 percent disturbance, such as by tree fall), 3.) human-caused disturbance (greater than 10 percent disturbance, such as road construction).

Data analysis

A Chi-square contingency test was used to determine possible spatial correlations between pairs of saplings of the four podocarp species. For example, *Nageia wallichiana* and *Podocarpus neriifolius* appear to occur together at the study site. In addition, a series of models with various combinations of predictor variables were proposed, using generalized linear mixed models (GLMM) with a binomial distribution, using maximum likelihood. The R version 3.1.2 statistical package was used (Venables and Smith, 2010; Mathiopoulos, 2011). For each species of podocarp, the majority of plots lacked saplings, so the models used presence/absence data (binomial data). Data from systematic plots were used, but individual analyses were made for each species (Carswell et al., 2007).

Based on the literature (Ogden and Stewart, 1995; Coomes et al., 2005; Carswell et al., 2007; Adie and Lawes, 2009) and preliminary surveys, we expected sapling occurrence to be influenced by a combination of factors, including soil nutrients, canopy cover, landform index, and disturbance. We therefore tested a series of candidate models for each species (Table 2). Akaike's Information Criterion (AIC_c) was used to compare the weight of evidence for each model, using R version 3.1.2 (Carswell et al., 2007). We also analyzed the probability of sapling occurrence in relation to various parameters. Sapling occurrence of each group, average values with SEM (Structural Equations Modeling

TABLE 2. Candidate models for describing relationships between sapling occurrence and environmental factors in a conifer-angiosperm forest on Khao Khiew at Khao Yai National Park.

Model terms	Justification
Soil N+P	The balance between N and P may be an important predictor of regeneration success of conifers (Carswell et al., 2007; Coomes et al., 2005)
Percent canopy cover	Some podocarp species regenerate after catastrophic disturbances that reduce canopy cover, and podocarp species are thought to exhibit a range of shade tolerances (Adie and Lawes, 2009; Carswell et al., 2007)
Soil particle size	Important factor related to sapling occurrence
Soil available phosphorus	Important factor related to sapling occurrence
Soil carbon	Important factor related to sapling occurrence
Soil nitrogen	Important factor related to sapling occurrence
Soil hydrogen	Important factor related to sapling occurrence
Soil pH	Important factor related to sapling occurrence
Soil depth	Important factor related to sapling occurrence
Presence of *Syzygium gratum*	A dominant angiosperm tree species at Pha Diew Dai but absent from the ridge. This species is found in wetter soil.
Local slope	Adult podocarp trees show a tendency of growing on mid-slope to ridge positions (Carswell et al., 2007; Ogden and Stewart, 1995).
Full model	Podocarp sapling distributions are influenced by all the above variables.
Null model	Podocarp sapling distributions are random with regard to the above variables.

or regression analysis) were analyzed using ANOVA with the sites as blocks (Adie and Lawes, 2009). A probability value < 0.05 of Tukey's HSD (honest significant difference) Post Hoc Test denoted the presence of a statistical difference.

Curves were fitted using binomial regression. Additionally, correlations between the environmental variables were analyzed using Pearson's correlations for continuous predictor variables (Carswell et al., 2007).

RESULTS

Size-frequency distributions

Geographical maps were used to show the slope of each of the 14 systematically placed transect lines. The overall mesoscale landform of the forest was slope. However, transect line 6 was both slope and gully.

A survey was made of all the trees of Podocarpaceae within a 10 meter radius of the center of seventy systematically arranged plots. The trees were placed in categories based on dbh: 0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-50 cm, and 50-60 cm. The results can be summarized as follows: for *Podocarpus neriifolius*, all size classes were present, but small trees, 0-10 cm dbh, were the most numerous with 9 out of 22 trees (40.9%) (Fig. 3A). For *Nageia wallichiana*, trees of all size classes were present, but with smaller trees, 0-10 cm dbh (11 out of 35, 31.4%) and 10-20 cm dbh (8 out of 35, 22.9%) being the most numerous (Fig. 3B). For *Dacrycarpus imbricatus*, all size classes of trees were present except for 40-50 cm dbh. Trees with dbh of 0-10 cm (8 out of 27, 29.6%) and 20-30 cm (8 out of 27, 29.6%) were most numerous (Fig. 3C). Finally, for *Dacrydium elatum*, the majority of the trees, 11 out of 18 (61.1%), were small (0-10 cm dbh). The remaining 7 trees

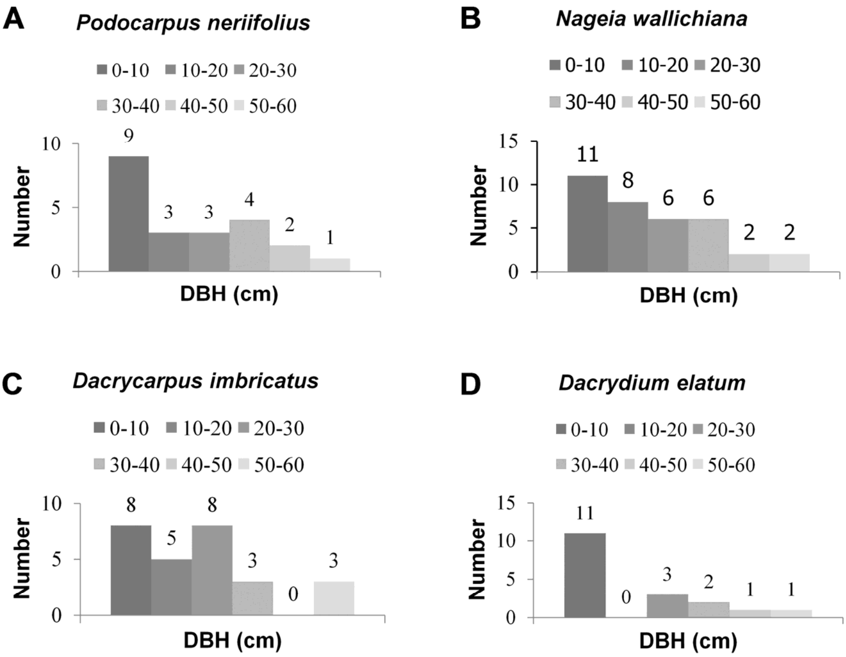

FIGURE 3. The diameter at breast height (dbh) of podocarp trees found on Khao Khiew. 3A. *Podocarpus neriifolius*. 3B. *Nageia wallichiana*. 3C. *Dacrycarpus imbricatus*. 3D. *Dacrydium elatum*.

ranged from 20 to 60 cm dbh with no medium sized trees of 10-20 cm (Fig. 3D).

Sapling occurrence of Podocarpaceae species

Sapling densities

The total number of *Podocarpus neriifolius* saplings present on systematically located plots was the highest for the Podocarpaceae species (Table 3), followed by *Nageia wallichiana*, *Dacrycarpus imbricatus*, and *Dacrydium elatum*, respectively. However, frequency (presence on number of plots) of *P. neriifolius* was comparable to *Nageia wallichiana*. In addition, *P. neriifolius* presented the highest in subjectively located plots, followed by *D. elatum* and *N. wallichiana*, but *D. imbricatus* was not found. These results suggest that *P. neriifolius* was most successful in the dispersal and early survival of podocarp saplings.

Spatial correlations among sapling species

Two out of 6 pairwise comparisons were positive and significant. *P. neriifolius* and *N. wallichiana* showed positive correlations with *D. imbricatus* indicating that the distribution of these saplings was clustered and that regeneration conditions for these species were frequently similar (Table 4).

Candidate models predicting sapling occurrence

A series of models were tested to predict sapling occurrence in the 70 systematically placed plots. Each model used one or more of the following predictor variables: percent canopy cover, soil particle size, concentrations of soil nutrients, available P, N, C, and H, soil pH, soil depth, presence of *Syzygium gratum,* and local slope. Disturbance was not included as only 2 plots showed human disturbance.

TABLE 3. Mean densities (stems/ha) ± standard error of saplings (≥0.15 m and 1.35 m) of four podocarp species at Khao Khiew in Khao Yai National Park, Thailand.

Species	Saplings		
	Density (stems/ha)	% Frequency (plots on grid)	% Frequency (subjective samples)
Podocarpus neriifolius	465.89±67.37[a]	28.57	73.33
Nageia wallichiana	386.35±41.41[ab]	28.57	13.33
Dacrycarpus imbricatus	306.35±54.09[ab]	15.71	0.00
Dacrydium elatum	22.75±0.64[b]	1.42	46.66

- Also given are the frequencies of plots on the grid in which saplings occurred (70 plots). The frequencies of plots in which saplings occurred in subjectively placed transects are also given (15 plots). P<0.05.

For *P. neriifolius*, there was more support for a model that combined available phosphorus with soil depth than for any of the other components combined or alone (Table 5). Local slope received the best support of the single factor models for *P. neriifolius*. For *N. wallichiana*, soil depth alone received the best support for predicting its occurrence. This was the only model with more support than the null model. However, several other models with one or a combination of predictor variables showed substantial support ($\Delta i \leq 2$), namely, presence of *Syzygium gratum*, soil C, soil N, soil depth + soil C, soil depth + soil N, soil pH, soil available P, local slope, and soil depth + soil pH. The model with the best support for *D. imbricatus* was pH. The presence of *Syzygium gratum* also showed stronger support than the null model. Local slope + soil pH, soil depth + soil H, and soil depth + soil pH, and soil H showed substantial support ($\Delta i \leq 2$). However, the full model showed lowest support for these 3 podocarp species. In addition, *D. elatum* was found in only one plot from 70 plots, so the sample size was too small for AIC_c analysis.

The probability of seedling occurrence in relation to environmental factors was evaluated (Fig. 4-6 and Table 6). *P. neriifolius* had a negative relationship between sapling occurrence and available soil P. On the other hand, *N. wallichiana* and *D. imbricatus* showed a positive relationship (Fig. 4A). Support for the nutrient influence on all species was derived from a strong positive relationship between

TABLE 4. Spatial correlations among sapling species at Khao Khiew in Khao Yai National Park, Thailand.

	Podocarpus neriifolius	*Nageia wallichiana*	*Dacrycarpus imbricatus*
Nageia wallichiana	Negative correlation $\chi^2 = 0.252$ $P = 0.615$		
Dacrycarpus imbricatus	Positive correlation $\chi^2 = 8.953$ $P = 0.003$	Positive correlation $\chi^2 = 7.670$ $P = 0.006$	
Dacrydium elatum	Negative correlation $\chi^2 = 0.004$ $P = 0.949$	Negative correlation $\chi^2 = 3.084$ $P = 0.079$	Negative correlation $\chi^2 = 1.452$ $P = 0.228$

- These were assessed using Chi-square contingency tables and the direction of the correlation is given along with the Chi-square statistic and probability (P) value. P<0.05 was considered as position correlation.

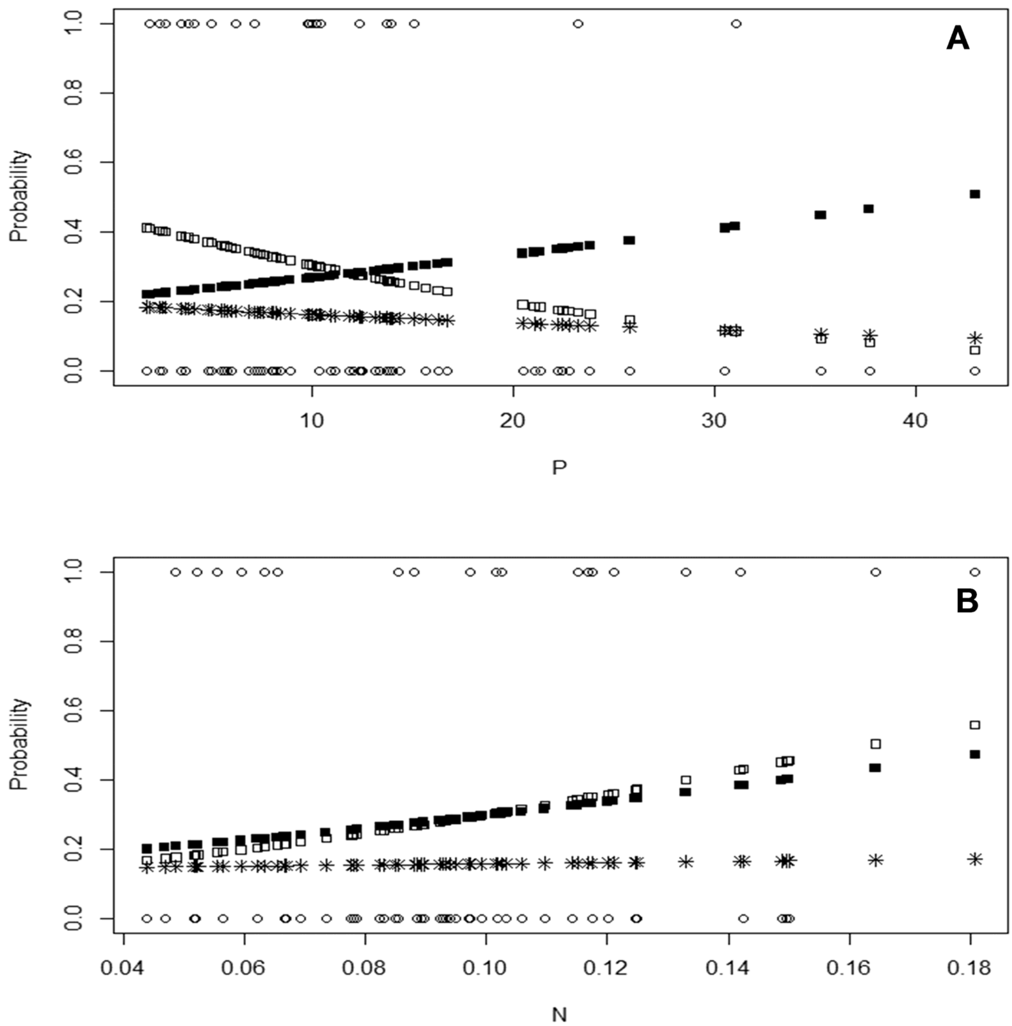

FIGURE 4. The probability of seedling occurrence in relation to soil available P (A) and N (B) fitted to three conifer species at Khao Khiew in Khao Yai National Park, Thailand. Curves were fitted using binomial regression. (□) *P. neriifolius*; (■) *N. wallichiana*; and (✳) *D. imbricatus*.

sapling occurrence and soil N (Fig. 4B), except for *D.imbricatus*. For *P. neriifolius* and *D. imbricatus*, their sapling occurrence increased with increasing soil pH (Fig. 5A), whereas for *N. wallichiana* occurrence increased with lower pH levels. In addition, occurrences of *N. wallichiana* and *D. imbricatus* increased with increasing canopy cover (Fig. 5B), while occurrence decreased for *P. neriifolius*. All species occurrences increased with increasing local slope (Fig. 6A). We assumed that canopy was related to local slope. At higher slope and open canopy, we can find *P. neriifolius* species. Although the model relating sapling occurrence to local slope and canopy received less support than other models, it still received greater support than the null

TABLE 5. Comparison of candidate models predicting the occurrence of saplings of three species at Khao Khiew in Khao Yai National Park, Thailand.

Model	*Podocarpus neriifolious*	*Nageia wallichiana*	*Dacrycarpus imbricatus*
Depth+P	**0.00**	2.08	4.91
N+Depth+P+H	**0.21**	5.95	7.24
Depth+H	**0.76**	**1.90**	4.02
Local slope+H	**0.82**	3.76	3.77
N+Depth+P	**1.02**	3.48	7.30
Local slope	**1.19**	**1.62**	2.23
Local slope+N	**1.59**	2.56	4.55
Depth+H+pH	**1.83**	3.91	3.01
H	**1.99**	2.14	**1.88**
Local slope+C	**2.00**	2.40	4.55
Local slope+P	2.03	2.29	4.54
N+Local slope+P	2.33	3.31	6.93
N+Local slope+pH	2.71	4.58	3.38
Canopy+H	2.92	4.20	4.12
Local slope+H+pH	2.95	5.26	3.21
Local slope+pH	3.15	2.99	**1.44**
P+N	3.17	2.19	5.11
P	3.39	**1.59**	2.83
C	3.81	**0.60**	2.89
N	3.92	**0.89**	2.88
Syzygium gratum	4.02	**0.34**	**0.44**
Depth	4.02	**0.00**	2.77
Null model	4.09	**0.26**	**0.67**
Depth+C	4.66	**1.19**	5.09
Depth+N	4.77	**1.49**	5.08
Depth+pH	5.22	**1.92**	**1.71**
pH	6.01	**1.52**	**0.00**
Full model	15.19	24.40	22.22

- Values shown are Δi, the difference in AICc between the best model (model with smallest value of AICc) and the *i*th model. The best model has a Δi value of 0.
- All models with $\Delta i \leq 2$ have substantial support (sensu Burnham and Anderson, 2002) and are shown in bold. AICc = Akaike's Information Criterion. N = 70 for all species.

model (Table 5). Saplings of *P. neriifolius* and *N. wallichiana* occurred more frequently in deep soil areas (Fig. 6B).

Pearson's correlations between continuous predictor variables at Khao Khiew in Khao Yai National Park, Thailand were calculated (Table 7). Soil C was positively correlated with soil H and N, while it showed negative correlation with soil pH. It was uncorrelated with local slope, canopy cover, soil depth and soil P. Canopy was uncorrelated with depth, soil H, local slope, soil N, soil P, and soil pH. Soil depth showed positive correlation with soil P and negative correlation with soil pH. Soil P was correlated negatively with soil H and local slope. In addition, soil H had a positive correlation with local slope and soil N. Some of the predictor variables in the candidate models are correlated (Table 7).

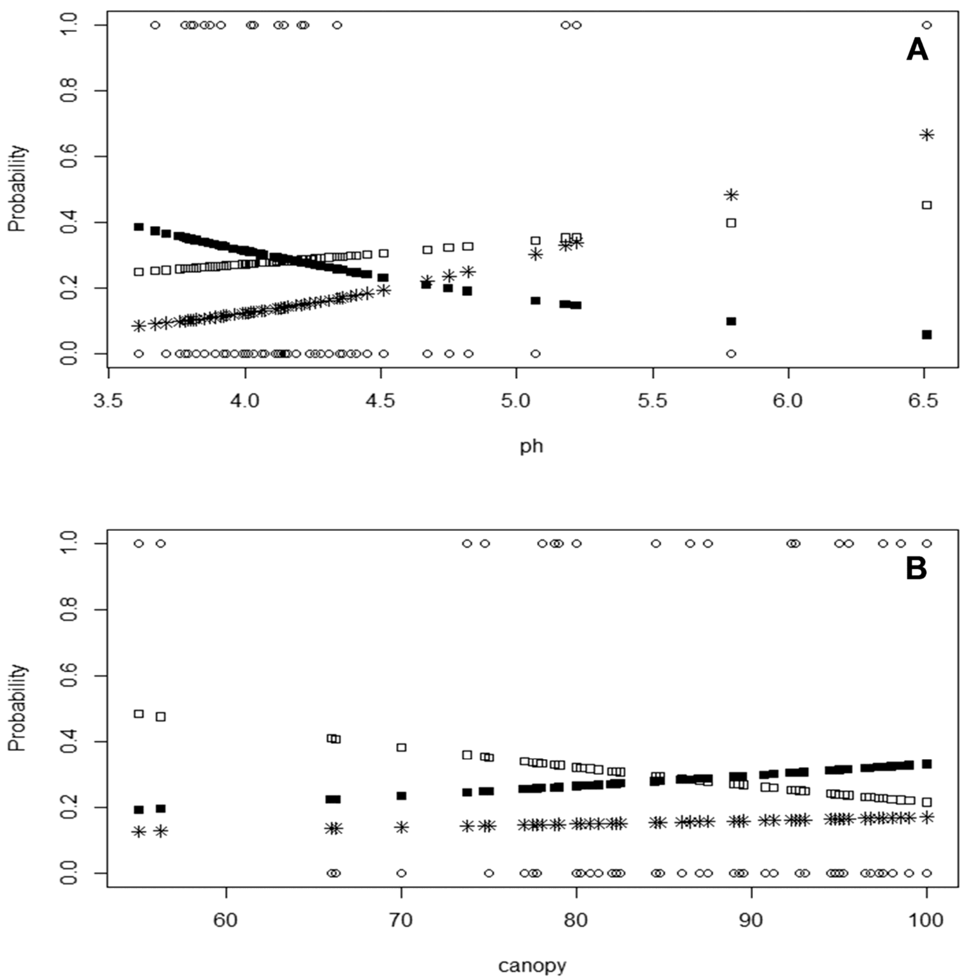

FIGURE 5. The probability of seedling occurrence in relation to soil pH (A) and canopy (B) fitted to three conifer species at Khao Khiew in Khao Yai National Park, Thailand. Curves were fitted using binomial regression. (□) *P. neriifolius*; (■) *N. wallichiana*; and (✳) *D. imbricatus*.

DISCUSSION AND CONCLUSIONS

Four species of Podocarpaceae at Khao Khiew in Khao Yai National Park were used in this study: *D. imbricatus*, *P. neriifolius*, *N. wallichiana*, and *D. elatum*. The results of size-frequency distribution of these 4 species indicates that regeneration is successful for all 4 species in the study site; all species have trees ranging from 0-10 to 50-60 cm dbh size categories. However, trees of *D. elatum* are predominantly in the smallest category, with only 7 out of 18 (38.9%) larger than 10 cm in dbh.

The density of *P. neriifolius* saplings in the study area was the highest, and the lowest was that of *D. elatum*. From subjective samples, saplings of *D. elatum* were increased, but only in the top ridge and

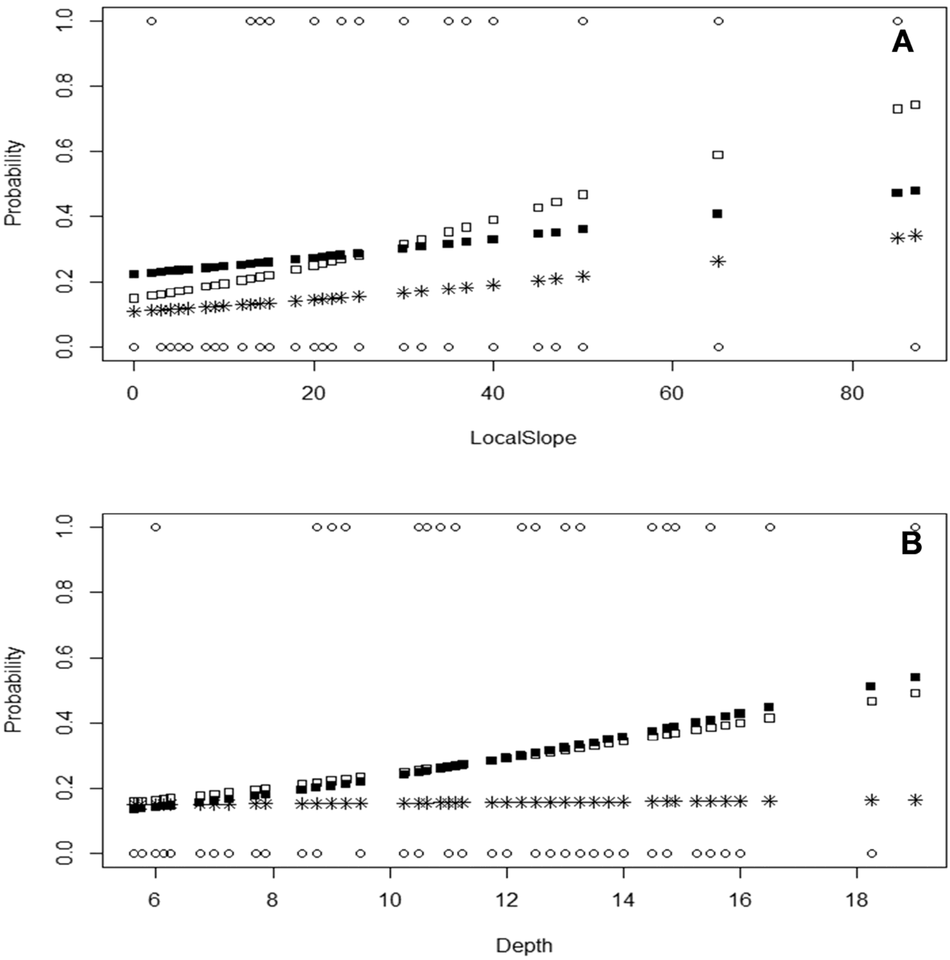

FIGURE 6. The probability of seedling occurrence in relation to local slope (A) and soil depth (B) fitted to three conifer species at Khao Khiew in Khao Yai National Park, Thailand. Curves were fitted using binomial regression. (□) *P. neriifolius*; (■) *N. wallichiana*; and (✳) *D. imbricatus*.

cliff in areas with much light (canopy 0%), suggesting that the saplings of *D. elatum* prefer the light more than under the canopy. This may be due to the seeds of this species needing light to germinate more than the other three species. On the other hand, saplings of the other three species usually grow under the canopy.

Candidate models were developed for predicting the influence of environmental factors on saplings regeneration. We found that the most support for models of each species was different and variable. The best model for saplings of *P. neriifolius* was a combination of soil depth and soil P; the occurrence of this species was higher in plots with deeper soil but lower levels of available phosphorus. There was also substantial support ($\Delta i \leq 2$, according to Burnham and Anderson, 2002) for various combinations of soil depth, N, P, H, local slope, and pH; most of the models

TABLE 6. Comparison of average slope values of the probability of three conifer species sapling occurrence in relation to continuous predictor variables at Khao Khiew in Khao Yai National Park, Thailand**.**

Species	**Slope value**					
	P	**N**	**pH**	**Canopy**	**Local slope**	**Depth**
P. neriifolius	- 0.0098	+2.3529	+0.0945	-0.0048	+0.0068	+0.0016
N. wallichiana	+0.0056	+1.4117	-0.0409	+0.0011	+0.0034	+0.0170
D. imbricatus	-0.0024	0.0000	+0.9449	+0.0001	+ 0.0023	-0.0000

comprised soil depth or local slope plus one or more additional factors. For saplings of *N. wallichiana*, the soil depth model showed the most support for prediction of sapling occurrence and was the only model with greater support than the null model. However, other models with one or a combination of factors showed substantial support. The only models for the occurrence of *D. imbricatus* that were better than the null model were soil pH and the presence of *S. gratum*. Association with *S. gratum* showed a high level of support for both *N. wallichiana* and *D. imbricatus*. Trees of the angiosperm *S. gratum* are commonly found along the sea shore near mangrove forest in areas with poor soil. In Pha Diew Dai, this species is found in areas with shallow, often flooded soil, especially near the stream. This species, as well as the two podocarp species, may similarly survive in areas with poor, often wet soil. Larger trees of both *D. imbricatus* and *S. gratum* were found to occur close to a stream near Pha Diew Dai cliff. For all three podocarp species, the model with the least support was the full model. Reasons may be that several of the factors were highly correlated and the sample size of podocarps was rather limited. This result differs from that of two species of podocarps in New Zealand for which the full model of factors showed the highest support, but agrees with *Prumnopitys taxifolia* (D. Don) de Laub. for which the full model showed the least support (Carswell et al., 2007). Saplings of *P. neriifolius* were more likely to occur in soils with higher N and lower P, in agreement with other species of podocarps, including *P. ferruginea* (Carswell et al., 2005, 2007). However, *N. wallichiana* saplings were more common in soils with higher N and P; *D. imbricatus* saplings appeared to be little effected by the soil nutrient levels. The saplings in this study also differed in their relationship with soil pH, with *P. neriifolius*

TABLE 7. Pearson's correlations between continuous predictor variables at Khao Khiew in Khao Yai National Park, Thailand.

	pH	Canopy cover (%)	Depth	P	C	H	N
Canopy cover (%)	0.024						
Depth	**-0.316**	0.188					
P	**-0.355**	0.134	**0.398**				
C	**-0.329**	0.079	0.189	0.048			
H	0.078	0.088	-0.139	**-0.280**	**0.795**		
N	**-0.327**	0.040	0.211	-0.016	**0.933**	**0.733**	
Local slope	-0.008	0.031	0.024	**-0.276**	0.187	**0.250**	0.108

- *N* = 70, degrees of freedom = 68, critical r for 0.05 level of significance = 0.250 (Carswell et al., 2007). All of the correlations in bold are significant.

and *D. imbricatus* saplings occurring more often in plots with a higher pH soil value, whereas *N. wallichiana* seemed to prefer soil with lower pH. *Podocarpus neriifolius* saplings appeared to fare better in open canopies, whereas *N. wallichiana* and *D. imbricatus* were slightly more common with greater canopy cover. Seedlings of these 3 species were found to be shade tolerant in a study in Vietnam (Nguyen and Thomas, 2004). For all three species, sapling occurrence increased with higher local slope. Saplings of *P. neriifolius* and *N. wallichiana* were more likely found in deeper soils, but soil depth appeared unimportant for *D. imbricatus*. Soil carbon was positively correlated with nitrogen and hydrogen indicating that the three factors were correlated. Soil C was positively correlated with soil H and N, while it showed negative correlation with soil pH. In addition, soil H had a positive correlation with local slope and soil N. Given that podocarp seedlings were found on soils with low soil P, but high soil N concentrations, soil nutrient status should be taken into account during management.

The Pearson's correlation between continuous values of slope and P was negative, indicating a lower level of soil P in higher slopes. Burns and Leathwick (1996) studied a conifer-angiosperm forest in New Zealand and found that the podocarps occurred on ridges where P concentration was lower. Therefore, our study is consistent with this previous study. Saplings of podocarp species had a preference for ridges rather than gullies (Carswell et al., 2007). Coomes et al. (2005) reported that seedlings and adult podocarps (particularly *P. ferruginea* and *D. cupressinum*) occur in low P environments and/or near ridges.

In addition, Bergin and Kimberley (2014) found that the regeneration of *P. totara* D.Don was most prevalent on steeper slopes of lower fertility with typically sparse vegetation cover. The study of Wilf (2012) revealed that *Dacrycapus puertae* grew on the margins of an ancient, montane, caldera-lake system, where it occupied ridges with rapidly weathering volcanic soils. Nguyen and Thomas (2004) found that all the species of Podocarpaceae in Vietnam, which include the four species in the present study, regenerate in the shade, under the forest canopy. This differs from species of Pinaceae, including *Pinus merkusii* Jungh. & de Vriese and *P. kesiya* Royle ex Gordon found in Thailand, which regenerate in open areas.

There have been few studies of conifers in Thailand, other than *Pinus*. However, conifers are important species in their ecosystems as well as economically. Furthermore, it is important to know the potential for regeneration of conifers in the face of natural threats, such as severe storms and seedling-attacking fungi, and human caused threats, including deforestation and climate change (Carswell et al., 2007).

Sapling occurrence was influenced by a combination of factors, including soil nutrients, canopy cover, and local slope. In general these podocarps were present on steeper slopes with lower soil phosphorus and higher nitrogen with typically sparse canopy cover. This study has provided fundamental information on sapling occurrence and survival of trees of Podocarpaceae in Thailand, which can be used as a guideline for preparing the seedlings for reforestation and to use as a database for conservation, monitoring and management in the future.

ACKNOWLEDGEMENTS

This work was financially supported by Suranaree University of Technology, Nakhon Ratchasima, Thailand. We wish to thank Kunchit Srinopawan, and staff from Khao Yai National Park. We are grateful to Colin T. Strine, Phillip Serrano, Inés Silva and staff from Sakaerat Environmental Research Station for their help on data analysis. We also would like to thank Chaiwat Kongmanklang and Komson Taisup for their help on soil analysis and Fengchun Yang for suggestions and help. An anonymous reviewer provided helpful comments. Finally, the first author would like to thank important people in her life including her family, Wichet Chaijumroen, and friends who encouraged her throughout the course of this study.

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