

Spatially heterogeneous natural regeneration of tall evergreen dipterocarps, a target of selective logging

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ការកាប់បំផ្លាញ និងការសឹករិចរិលព្រៃឈើនៅប្រទេសកម្ពុជាកំពុងត្រូវបានដោះស្រាយ ប៉ុន្តែនៅតែជាបញ្ហាប្រឈម។ ព័ត៌មានលំអិតអំពីដើមឈើមិនទាន់ពេញវ័យនៃប្រភេទដែលបានកាប់ និងមានសារៈប្រយោជន៍ចំពោះការលើកកម្ពស់ការដំណុះឡើងវិញនូវប្រភេទរុក្ខជាតិ និងការស្តារព្រៃឈើឡើងវិញ។ យើងបានផ្តោតលើពពួកឈើទាលមានកម្ពស់ខ្ពស់ចំនួនពីរប្រភេទគឺ *Anisoptera costata* (ផ្កៀក) និង *Dipterocarpus costatus* (ឈើទាល បង្កូយ) ដោយបានធ្វើជំរឿនដើម្បីកំណត់របាយទំហំរបស់ពួកវានៅភាគកណ្តាលនៃប្រទេសកម្ពុជា។ សមមាត្រទាប (ប្រភេទ *A. costata* ៣៩.៣% និងប្រភេទ *D. costatus* ៤៣.១%) នៃដើមឈើមានអង្កត់ផ្ចិតតូចបំផុត (៥ - ១០ សង់ទីម៉ែត្រ) បានបង្ហាញពីដំណុះឡើងវិញមិនគ្រប់គ្រាន់នៃប្រភេទដើមឈើទាំងពីរ ទោះបីជាគេឃើញវត្តមានរបស់ដើមឈើមេក៏ដោយ។ លក្ខខណ្ឌសំណើមនៅទីតាំងសិក្សារបស់យើង ត្រង់កន្លែងមានដើមឈើមិនទាន់ពេញវ័យគឺដុះច្រើនលើសលុបបញ្ជាក់ថាដើមឈើតូចៗលូតលាស់លើដីសើមច្រើនជាងដើមឈើពេញវ័យ។ លទ្ធផលនៃការសិក្សារបស់យើងបង្ហាញពីភាពចាំបាច់នៃការកំណត់អត្តសញ្ញាណព្រៃឈើ រួមទាំងទីតាំងសមរម្យសម្រាប់ជ្រើសរើសដើមឈើដើម្បីប្រឈមនឹងបម្រែបម្រួលអាកាសធាតុ។

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Abstract

Deforestation and forest degradation in Cambodia are being addressed, but remain challenging. Detailed ground-based insights on juvenile trees of logged species will be useful for efforts to promote species regeneration and forest restoration. We focused on two species of tall dipterocarps, *Anisoptera costata* (*phdiek*) and *Dipterocarpus costatus* (*chhoeuteal bankouy*), undertook a tree census to determine their size distributions in central Cambodia. The small proportion (39.3% & 43.1% for *A. costata* & *D. costatus*, respectively) of individuals in the smallest diameter class (5–10 cm) suggested inadequate regeneration of both species, despite the presence of mother trees. The moist site conditions of our study site, where juvenile trees are exceptionally abundant, imply that small trees thrive on wetter soils than mature individuals. Our findings demonstrate the need to identify forests including suitable sites for tree recruitment in the face of continuing climate change.

Keywords *Anisoptera costata*, conservation, *Dipterocarpus costatus*, forest regeneration, seedling, topography.

Introduction

Despite efforts to limit deforestation and forest degradation in Cambodia (MoE *et al.*, 2020), large-diameter trees of Dipterocarpaceae species such as *Dipterocarpus costatus* C.F.Gaertn. (*Chhoeuteal Bankouy* in Khmer) and *Anisoptera costata* Korth. (*Phdiek*) have been extensively felled in lowland dry evergreen forests in Kampong Thom Province (Ito *et al.*, 2010). Various initiatives have been considered to strengthen forest conservation in Cambodia, including proposals for systematic conservation plans (Strange *et al.*, 2007), accumulated findings based on seed supply demand for plantations (Norn & Sobon, 2014) and identifying framework tree species (Sobon *et al.*, 2017). Although forest structure information for each forest-type has been obtained from ground-based studies in-country (Kimphat *et al.*, 2000, 2002; Kao & Iida, 2006; Ouk, 2006; Pin *et al.*, 2013; Toyama *et al.*, 2015; Chheng *et al.*, 2016; Ito *et al.*, 2017, 2022), understanding of forest dynamics in Cambodia is far from complete. To the best of our knowledge, there is no information on whether or not lowland dry evergreen forests undergoing exhaustive selective logging are stocked with sufficient numbers of young trees to allow them to recover from forest degradation. In other words, it has yet to be determined whether forest resources can recover from the anthropogenic disturbance of exhaustive selective logging without human assistance. In this study, we analysed the results of a tree census undertaken before selective logging at the site was intensified to determine the size distribution of two dipterocarp species in the study area.

Methods

Our study was conducted in lowland dry evergreen forests in Kampong Thom Province in central Cambodia. The forests typically develop on gently undulating,

sandy alluvial plains with deep soils (Ito *et al.*, 2021). The study site features a sandy soil, Haplic Acrisol (Alumic, Profondic) within the World Reference Base system (Toriyama *et al.*, 2007, 2008). Mean annual precipitation in the study area is 1,625.8 mm (Kabeya *et al.*, 2021). The monthly average temperature ranges from 24°C to 29°C, with a mean of 27°C (Chann *et al.*, 2011). The seasonal tropical climate is governed by monsoons and described in detail elsewhere (Ito *et al.*, 2021; Kabeya *et al.*, 2021).

We used data from past tree censuses undertaken in 15 plots established within a rectangular area measuring 6 km east-west and 13 km north-south (centered on 12.72° N, 105.47° E). The location of the plots is shown in a digital surface model in Fig. 1 and almost all plots were located on the gentle hill tops of undulating terrain within the catchment area of the Chinit River. The plots measured 30 × 40 m ($n=13$), 30 × 80 m ($n=1$, plot no. 05) and 200 × 200 m ($n=1$, plot no. 09) (Table 1). Plot no. 05 was the most well-preserved forest plot in the area and was first surveyed in 2003.

We employ data from plot measurements undertaken in 2011. To estimate the reduction in biomass accumulation associated with forest degradation, 13 plots (30 × 40 m) were established to include forests with a similar species composition to plot no. 05, but with different degrees of human-induced degradation. Plot no. 09 was established as a reference forest plot for a meteorological observation tower. In accordance with observation protocols for forest hydrology, the tower was located in a transitional section between lower and higher ground in the centre of the plot. As our objective was to investigate relationships between hydrological data and forest structure, the plot spanned 100 m in all cardinal directions from the tower (i.e., 200 m × 200 m in total), which is generally considered to be the range of influence for hydrological data. In each plot, we divided the plot area

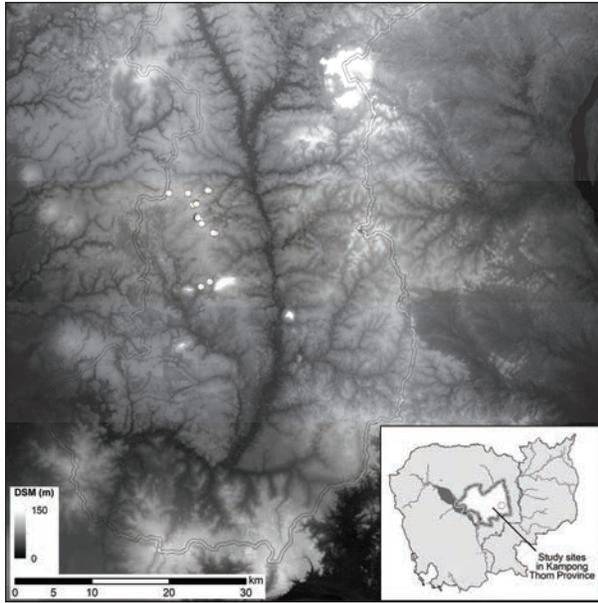


Fig. 1 Digital surface model of the study sites (white circles) in Kampong Thom Province, Cambodia. The background gradient is the digital surface model provided by JAXA (ALOS World 3D–30m). Double lines indicate the catchment area of the Chinit River.

into sub-quadrants measuring 10 × 10 m and the girth of all standing woody stems with a diameter at breast height (DBH, defined as 1.3 m above ground) ≥ 5 cm was measured to the nearest 1 mm. For trees with buttress roots at a height of 1.3 m, the measurement was made just above their protrusions. Species were categorized as *D. costatus*, *A. costata*, or others.

As the plots were located in lowland dry evergreen forests, they were dominated by evergreen tree species, with a predominance of *Vatica odorata* (Griff.) Symington (Dipterocarpaceae) (*Chromas*), *Diospyros venosa* Wall. ex A.DC. (Ebenaceae) (*Angkot Khmao*), *D. undulata* Well. ex G. Don. var. *cratericalyx* (Craib) Bakh. (Ebenaceae) (*Chhoeu Phleung*), *Melodorum fruticosum* Lour. (Annonaceae) (*Romdoul*), *Sindora siamensis* Teysm. ex Miq. (Fabaceae) (*KoKoh*), *Syzygium* spp. and *Memecylon* spp. Plot no. 09 was located in a transitional zone between lower and higher ground, the former being a swamp dominated by *Myristica iners* Blume (Myristicaceae), which has aerial roots and is thus able to grow in water-logged sites (Theilade et al., 2011). Stand structure parameters derived from the tree census are provided in Table 1.

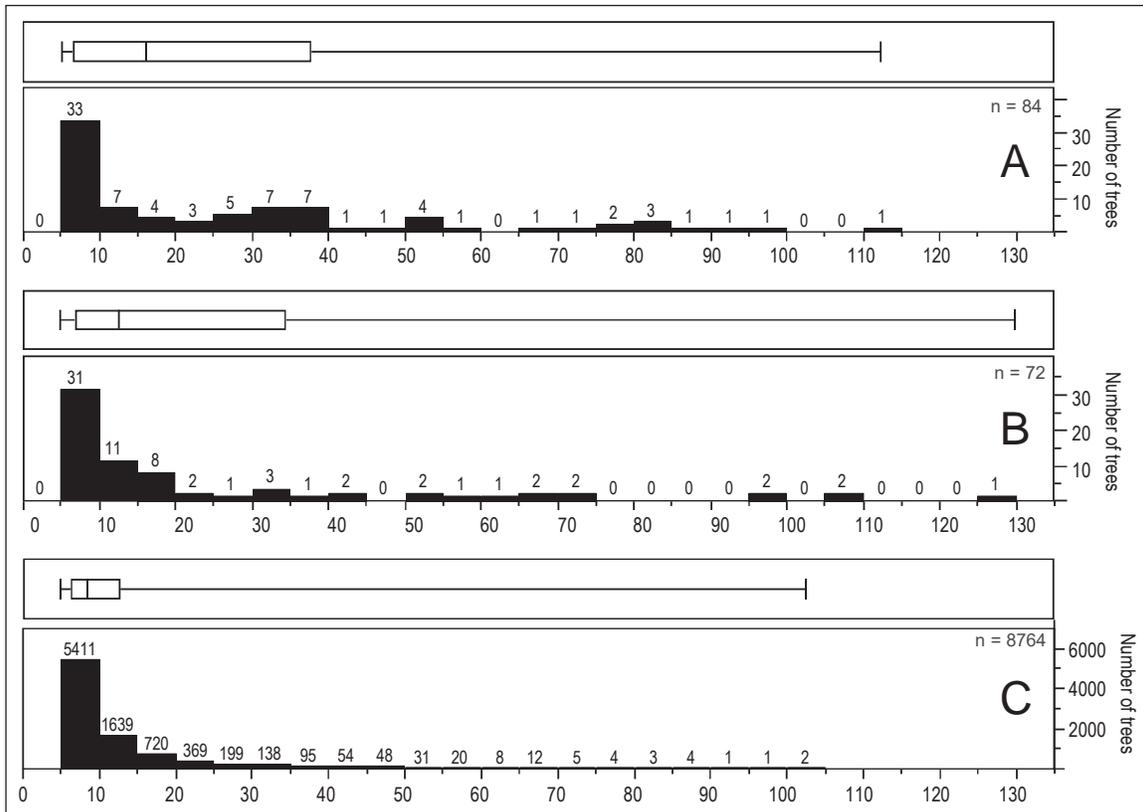


Fig. 2 Size (DBH, cm) distribution of A) *Anisoptera costata*, B) *Dipterocarpus costatus*, C) other species.

Table 1 Stand structure parameters for plots in study area. Values for basal area, stem density and maximum stem diameter are given as average (\pm SD) (range) for all species in each 10 \times 10 m sub-quadrant within each plot.

No.	Location ¹	Alt (m) ²	Size (m)	Census Year	Basal Area (m ² /100 m ⁻²)	Stem Density (stems /100 m ⁻²)	Maximum Stem Diameter (cm)
1	548292, 1412088	91–93 (102–106)	30 \times 40	2010	0.26 \pm 0.10 (0.10–0.48)	19.5 \pm 5.9 (8–29)	27.1 \pm 9.2 (17.4–49.1)
2	550755, 1412086	100 (101–105)	30 \times 40	2010	0.31 \pm 0.28 (0.08–1.07)	12.1 \pm 2.3 (8–17)	39.2 \pm 24.7 (14.6–109.1)
3	553334, 1412455	81 (95–97)	30 \times 40	2010	0.29 \pm 0.15 (0.13–0.61)	16.4 \pm 4.7 (8–24)	32.2 \pm 16.7 (15.4–77.6)
4	553506, 1412400	81 (95–97)	30 \times 40	2010	0.29 \pm 0.06 (0.18–0.39)	18.8 \pm 3.9 (13–25)	32.9 \pm 6.7 (23.1–45.4)
5	551425, 1410577	101 (113–121)	30 \times 80	2011	0.42 \pm 0.35 (0.11–1.48)	18.2 \pm 5.1 (8–26)	44.2 \pm 32.3 (15.7–129.8)
6	551791, 1410814	102 (115–120)	30 \times 40	2010	0.38 \pm 0.32 (0.07–1.26)	13.6 \pm 3.1 (9–19)	42.0 \pm 23.1 (13.2–99.9)
7	551868, 1410718	101 (107–116)	30 \times 40	2010	0.29 \pm 0.24 (0.03–0.91)	13.5 \pm 6.2 (4–22)	37.1 \pm 21.6 (10.6–87.9)
8	551871, 1410671	101 (111–116)	30 \times 40	2010	0.34 \pm 0.20 (0.09–0.73)	17.8 \pm 4.9 (10–25)	37.4 \pm 16.5 (17.9–71.5)
9	551851, 1408841	85–90 (89–105)	200 \times 200	2015 (2017, 2020) ³	0.28 \pm 0.21 (0.01–1.08)	14.8 \pm 5.5 (3–33)	36.0 \pm 19.0 (7.5–112.3)
10	552294, 1408635	91 (105–108)	30 \times 40	2010	0.39 \pm 0.27 (0.11–0.91)	15.0 \pm 3.4 (10–22)	43.1 \pm 18.3 (23.5–80.8)
11	552537, 1408086	91 (107–111)	30 \times 40	2010	0.32 \pm 0.18 (0.09–0.58)	17.2 \pm 4.2 (10–22)	40.6 \pm 20.9 (17.2–79.9)
12	554068, 1406888	86 (97–101)	30 \times 40	2010	0.24 \pm 0.17 (0.07–0.61)	13.0 \pm 2.9 (9–18)	32.0 \pm 15.7 (14.1–59.1)
13	554288, 1406844	84–85 (87–94)	30 \times 40	2010	0.27 \pm 0.13 (0.08–0.50)	20.3 \pm 5.7 (13–29)	42.0 \pm 23.1 (13.2–99.9)
14	553592, 1400648	74 (88–94)	30 \times 40	2010	0.23 \pm 0.10 (0.08–0.40)	12.2 \pm 3.9 (8–19)	34.6 \pm 8.3 (18.8–50.4)
15	552453, 1400014	70–71 (77–79)	30 \times 40	2010	0.15 \pm 0.07 (0.05–0.27)	25.6 \pm 8.8 (11–36)	16.1 \pm 6.2 (9.8–33.4)

¹ Southwest corner of the plot (WGS 1984, UTM Zone 48N). ² DTM (DSM). Altitude based on digital terrain model (DTM) with 50 m resolution and digital surface model (DSM) of ALOS World 3D–30m, ver. 3.1 with approximately 30 m resolution (https://www.eorc.jaxa.jp/ALOS/en/dataset/aw3d_e.htm). ³ For plot no. 09, juvenile tree data from tree censuses in 2017 and 2020 are also shown in Fig. 6, but are not included in the size distributions given in Figs 2 & 3.

Results

The size (DBH) distribution of the two dipterocarp species (*A. costata*, *D. costatus*) and other species was examined using the combined data from all plots (Fig. 2). When all tree species were combined, the size distribution was L-shaped, with a significant proportion (61.4% of 8,920 trees) belonging to the smallest diameter class (5–10 cm). A rather small proportion of individuals in the smallest

diameter class (5–10 cm) were found for two dipterocarp species, namely 39.3% of 84 trees for *A. costata* and 43.1% of 72 trees for *D. costatus* (Fig. 2a, 2b). Moreover, comparison of plot-by-plot size distributions for the two dipterocarp species revealed that L-shaped size distribution was only found in plot no. 09 (Fig. 3). The total population density of the two dipterocarp species in plot no. 09 was relatively low (9.3–10.0 tree ha⁻¹). Nonetheless, a considerable proportion of the smallest-diameter individuals of

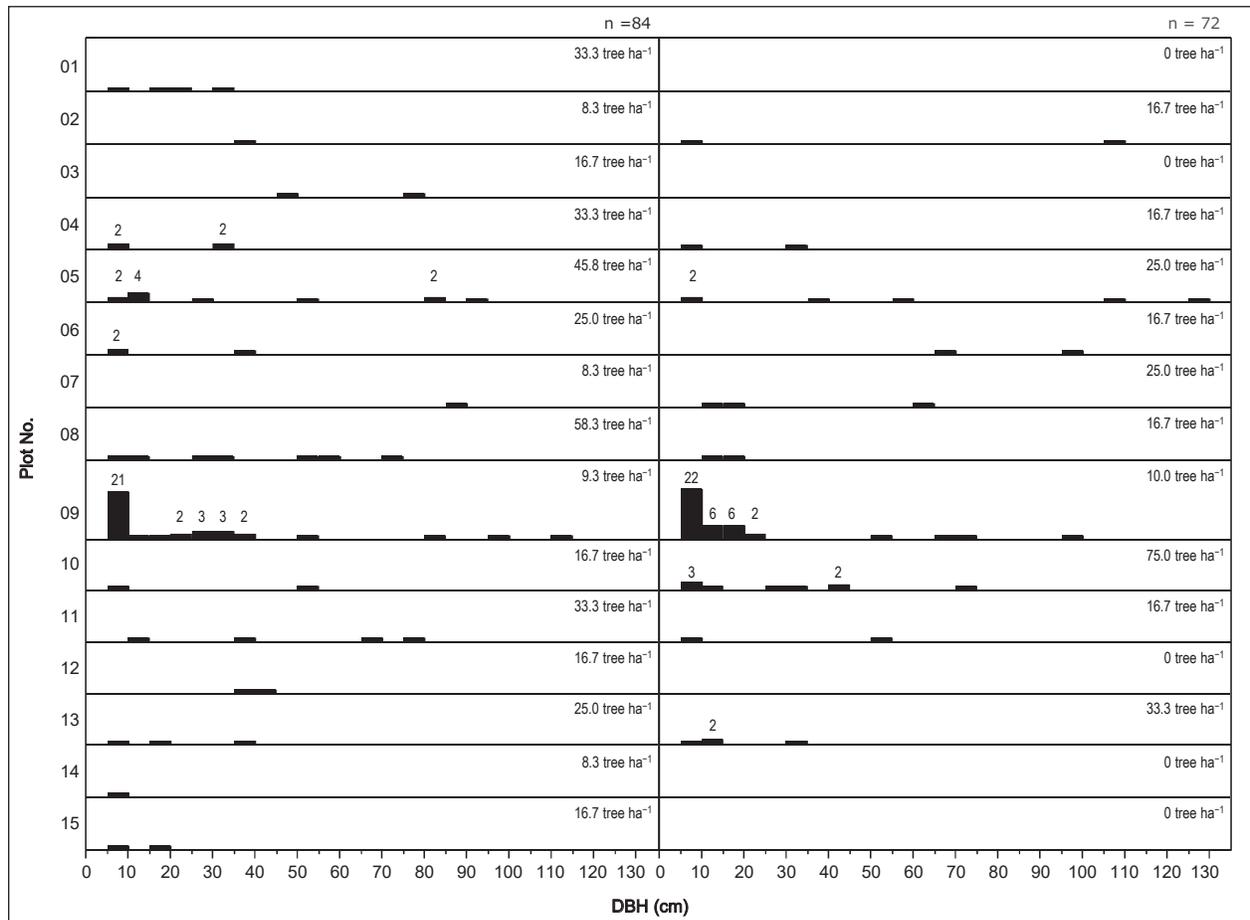


Fig. 3 Size (DBH) distribution of *Anisoptera costata* (left) and *Dipterocarpus costatus* (right) by plot. Figures above the columns indicate the number of individuals. Columns without a number indicate one individual per class and tree densities (trees ha⁻¹) for each plot are included in the figure.

these species occurred in plot no. 09 (56.8% of 37 trees for *A. costata* and 55.0% of 40 trees for *D. costatus*), whereas the proportion in our remaining 14 plots was about half of this (25.5% of 47 trees for *A. costata* and 28.1% of 32 trees for *D. costatus*).

Our survey plots spanned a narrow elevation range, between 70 and 102 m (Table 1). Almost all of the plots were located on gentle hill tops in undulating terrain (Fig. 4a), with the exception of plot no. 09 (tower plot, Fig. 4b). A previous field survey (Ohnuki *et al.*, 2022) showed that the ground surface of the plot no. 09 was higher in the northeast and lower in the southwest (Fig. 5). In other words, the plot no. 09 was located in a transitional section between higher ground (hilltops) and lower ground and contained areas of water accumulation. Soil thickness became shallower from northeast to southwest across the topographic conversion area (Fig. 5a). Soil thickness is directly related to the moisture content of the

soil surface layer during the dry season (Fig. 5b; Ohnuki *et al.*, 2022).

Examination of the spatial distribution of the two tall dipterocarps in plot no. 09 showed that both species were absent from the swampland in the central area where *M. iners*, a large tree, predominated (Fig. 6). The area where the aerial roots were distributed was swampy and had water on the surface even during the dry season (Fig. 6, field observation). The distribution of *M. iners* reflected the distribution of soil moisture conditions determined in this plot (Fig. 5b; Ohnuki *et al.*, 2022). Analysis of the spatial distribution of the two dipterocarps species by diameter class showed that large-diameter trees (DBH > 50 cm) occurred in the northeastern portion of the plot and thus at a topographically higher location (Fig. 6). Medium-diameter trees (DBH 20–40 cm) were also present in the northeastern portion of the plot as well as the southwestern portion (for *A. costata*), but were absent

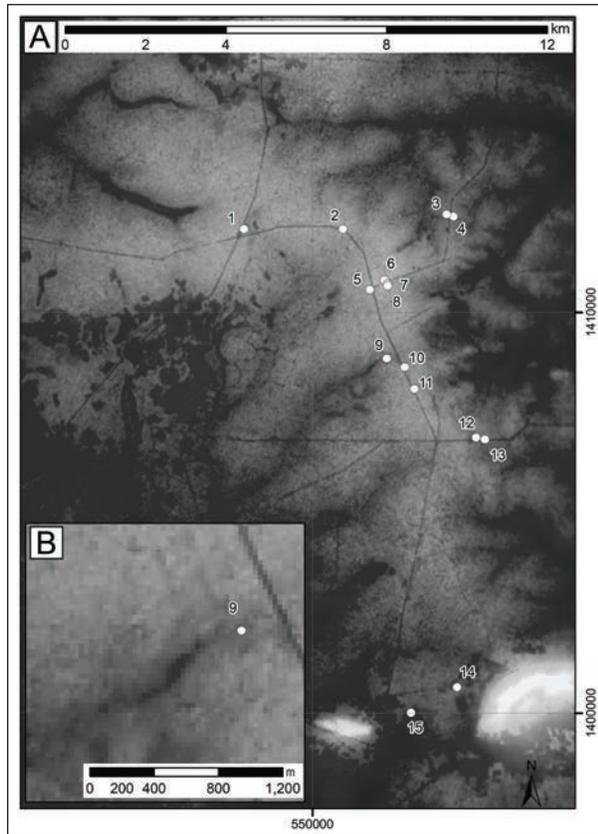


Fig. 4 Microtopography in A) study area, B) plot no. 09. White circles indicate southwest corner of the 15 survey plots. Background gradient is a digital elevation model (50 m resolution) overlapped by the digital surface model provided by JAXA (ALOS World 3D-30m), in which white indicates higher terrain.

from the swampy area. Among the small-diameter trees, those with a DBH of 10–20 cm occurred in the marginal area of the swampy forest, but mostly in the northeastern upland area. The smallest individuals (DBH 5–10 cm) grew closer to the swamp than larger individuals. In particular, *A. costata* occurred at higher density in the southwest portion (Fig. 6a).

Discussion

Despite the presence of mother trees, regeneration in the 14 plots other than plot no. 09 seemed inadequate (Fig. 3). Selective logging has led to a sharp decline both in the number of flowering plants and in the population density of the two tall dipterocarp species in the lowland dry evergreen forests of Kampong Thom Province (Ito *et al.*, 2023). Reduction in population density has a serious impact on genetic diversity and pollination effi-

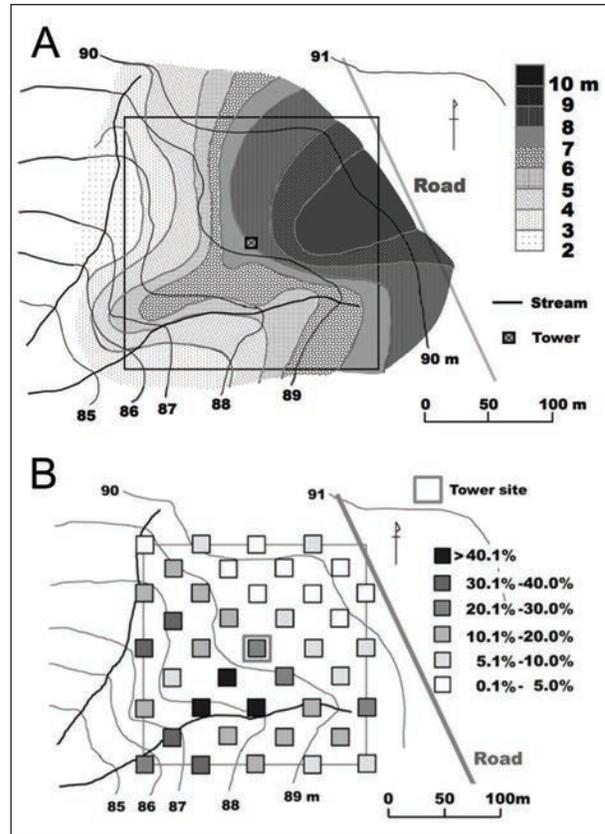


Fig. 5 A) Soil thickness and B) soil water content during the late dry season in plot no. 09. Redrawn from Ohnuki *et al.* (2022).

cacy (Ghazoul *et al.*, 1998; Tani *et al.*, 2009, 2012; Duc *et al.*, 2016). It is therefore unlikely that useful dipterocarp timber will be available again in the lowland dry evergreen forests. However, in the process from reproduction to the establishment and survival of juvenile and immature trees, the most limiting stage for regeneration remains to be identified. This information is critical for implementation of proactive measures to ensure sustainable forest use.

The spatial distribution of the two dipterocarps species in plot no. 09 differed by diameter class (Fig. 6). This trend differs from the pattern for *Shorea curtisii* (Dipterocarpaceae) seedlings in hill dipterocarp forest in Peninsular Malaysia, where suitable microtopography for seedling establishment was the same as those for mother trees, both being abundant on ridges (Yagihashi *et al.*, 2010). Seeds and seedlings most susceptible to pathogen attack and mortality are those closest to the mother tree (Gilbert, 2002), which may explain the discrepancy in the distribution of large vs. small dipterocarp individuals in our plot no. 09. Furthermore, there may have been

a change in soil moisture conditions since the time when the current large-diameter trees first established.

A comparison of the site conditions of plot no. 09, which was exceptionally abundant in juvenile trees of the two dipterocarps, with those of the other plots may provide insights for effective forest management. Plot no. 09 was located in the transitional zone between lowland dry evergreen forest (in the northeast) and wet evergreen forest (in the southwest). The density of trees in plot 09 (9.3–10.0 tree ha⁻¹; Fig. 3) was only slightly higher than the threshold density of 9 trees/ha at which the fertility of *S. siamensis* (Dipterocarpaceae) rapidly declines (Ghazoul *et al.*, 1998). However, the calculation which provided the relatively low value for tree density in plot no. 09 included the swamp area which was characterized by *M. iners*. The spatial distribution of the two dipterocarps overlapped little with that of *M. iners* and the swamp area is probably unsuitable for dipterocarp growth (Fig. 6). Conversely, small dipterocarps tended to be more abundant than larger individuals in the vicinity of the swamp, where the soil moisture content was high even during the dry season (Fig. 5). These observations suggest that small trees may thrive better than mature individuals in areas with a higher soil moisture content. This hypothesis is consistent with the lower density of small trees in the other 14 plots, which were located in the higher portions of our study area.

We also need to consider the origin of the seed supply for small trees in the southwestern portion of plot no. 09. There are three possible seed sources: large trees in the northeast, small- to medium-sized trees in the southwest and large trees that existed in the southwest until recently. The distance from a large tree (>50 cm DBH) in the northeast to the group of small trees in the southwest was approximately 130–150 m (Fig. 6). While Dipterocarpaceae species are characterized by winged seeds, their dispersal distance is usually less than 30 m (Tamari & Jacalne, 1984; Ghazoul, 2016) because they rely on wind-assisted gyration. Estimation of the seed dispersal distances of other Dipterocarpaceae species using genetic analysis has shown that the majority of these occur within 50 m of the mother tree and that dispersal beyond 100 m is both species-limited and under-represented (Takeuchi *et al.*, 2004). Water dispersal could have compensated for the limited distance achieved by wind dispersal. Seeds could have been dispersed by flood waters after water stagnated in swamp areas and then established in the southwest. Water dispersal of Dipterocarpaceae seeds has been observed in *D. oblongifolius* (Ridley, 1905) and the dispersal distance of seeds may be extended via animals; in *A. costata*, there appears to be dispersal by

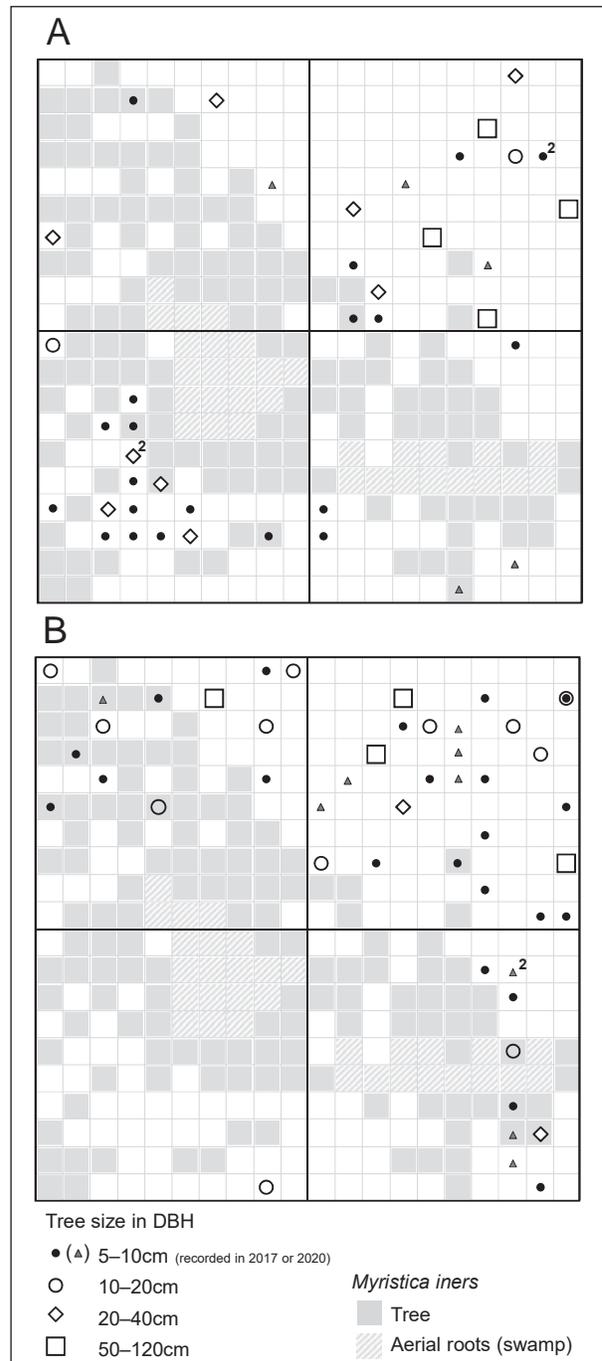


Fig. 6 Spatial distribution of A) *Anisoptera costata* and B) *Dipterocarpus costatus* in plot no. 09. Symbols indicate tree size (DBH) of both species. Data are based on tree census in 2015, although data for smallest individuals (DBH 5–10 cm) recorded during tree censuses in 2017 and 2020 are also shown. All symbols represent one individual, apart from the annotated symbol where two individuals were present. Gray and gray-shaded cells indicate the location of *Myristica iners* and the swampy areas where aerial roots of *M. iners* were present, respectively.

birds, squirrels and bats (Nguyen *et al.*, 2021). Regarding the second possibility (i.e., small- to medium-sized trees in the southwest), we have no information on the fruiting initiation size for *A. costata* or *D. costatus*, although DBH values of 20–30 cm accounted for 90% of tree reproduction for other Dipterocarpaceae species in Cambodia (Ito *et al.*, 2016). Therefore, it is possible that medium-sized individuals (DBH 20–40 cm) around the young trees in the southwestern part of the plot produced seeds. Leaves and flowers of *A. costata* were collected using litter traps in the northeastern portion of the plot, but only small amounts of leaves were trapped in the southwestern portion (Ito, unpubl. data). In the case of *D. costatus*, flower bud scales and seeds were collected in the northeastern portion of the plot, but only leaf bud scales were trapped in the southwestern portion (Ito, unpubl. data). Although not fully investigated, fruiting has yet to be confirmed in the southwestern population. Regarding the third possibility (i.e., large trees that existed in the southwest until recently), our field surveys did not find any large-diameter stumps or naturally dead trees in the southwestern 1-ha area. However, because dead stumps of large-diameter trees tend to be covered by termite mounds (Ito & Tith, 2023), the possibility that large-diameter trees were once present cannot be completely ruled out. As discussed below, it is necessary to clarify the actual condition of seed dispersal for forest management that encompasses both mother trees and suitable areas for the growth of juvenile trees.

Despite a seasonal tropical climate, whereby little rain falls for half the year (Kabeya *et al.*, 2021), plants in lowland dry evergreen forests in Cambodia have access to abundant groundwater (Araki *et al.*, 2008; Ohnuki *et al.*, 2008b; Toriyama *et al.*, 2011) via their deep root systems (Tanaka *et al.*, 2004; Ohnuki *et al.*, 2008a), which facilitates year-round foliage retention. Dry-season water availability is determined by the vertical distance to the groundwater table. The relative position of trees in undulating terrain is closely related to water availability during the dry season (Ohnuki *et al.*, 2022) and being dependent on soil moisture at shallower depths, juvenile trees are more vulnerable to drought than larger trees. Climate-driven changes in drought in Southeast Asia may alter tree recruitment rates (Nguyen *et al.*, 2019). Our study suggests a shift in suitable recruitment sites, or at least those related to moisture availability, to areas lower than those which allowed the establishment of presently large trees. While registration of new forest reserves to protect mother trees is clearly important, our findings demonstrate the need to identify forests including suitable sites for tree recruitment in the face of continuing climate change.

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