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ORIGINAL ARTICLE

Spatial patterns of *Cephalostachyum pergracile* Munro in a mixed deciduous forest in Myanmar

Toshihiro Yamada[1]*, Chihiro Oshige[2], Miyabi Nakabayashi[1*], Toshinori Okuda[1], Aung Zaw Moe[3] and Ei Ei Swe Hlaing[3]

[1] Graduate School of Integrated Sciences for Life, Hiroshima University, 1–7–1 Kagamiyama, Higashi-Hiroshima, 739–8521, Japan.
[2] Graduate School of Integrated Arts and Science, Hiroshima University, 1–7–1 Kagamiyama, Higashi-Hiroshima, 739–8521, Japan.
[3] Myanmar Forest Research Institute, Forest Department, Yezin, Nay Pyi Taw, 05282, Myanmar.
* Corresponding author: yamada07@hiroshima-u.ac.jp and nmiyabi@hiroshima-u.ac.jp

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ABSTRACT Bamboo species are common in Myanmar forests. They are monocarpic and some (but not all) conspecific bamboo clumps in a forest flower concurrently. The timing of flowering usually differs among bamboo species. Therefore, when flowering occurs in a forest, some spaces within a forest are expected to be occupied by conspecific and/or heterospecific nonflowering clumps of bamboo species. This may lead to the competition for space between seedlings and nonflowering clumps. Two species of bamboo, *Cephalostachyum pergracile* Munro and *Bambusa polymorpha* Munro were distributed in a commercial mixed-deciduous plantation forest in Myanmar. In 1997, some clumps of *C. pergracile* flowered but *B. polymorpha* did not. We analyzed the spatial relationships between *C. pergracile* seedlings generated in 1997 flowering and large conspecific and heterospecific bamboo clumps that must not have flowered in that flowering event. The present spatial analysis showed that bamboo seedlings were exclusively distributed in relation to conspecific large clumps and large clumps of counterpart species. Given that bamboo species are early successional and shade intolerant, these pre-empted spaces occupied by nonflowering clumps are assumed to be unsuitable for regeneration of the cohort that will be generated by the flowering event. In this manner, the occupation of spaces by nonflowering clumps during a flowering event will limit the space available for regeneration. Therefore, it was concluded that pre-emption by nonflowering clumps likely plays an important role in shaping the distribution of the two bamboo species in the forest.

Key words: flowering interval, flowering cycle, monocarpic, regeneration, spatial relationship

INTRODUCTION

Bamboo is distributed over a broad geographic area worldwide (FAO 2010). In Myanmar, bamboo occupies 27.85 million ha of forest, which comprise approximately 84 % of the total forested area in the country (FAO 2015). Bamboo plays an important role in ecosystem services, such as prevention of landslides and soil erosion, improvement of soil fertility, water conservation, carbon sequestration, and the provision of food and construction materials (Ben-zhi et al. 2005, ITTO 2007, Kharlyngdoh et al. 2021, Lobovikov et al. 2012, Rao et al. 1998, Scurlock et al. 2000, Yuen et al. 2017). However, bamboo may negatively affect forest ecosystems, for example, by causing erosion of tree biodiversity and delay of tree regeneration (Larpkern et al. 2011). Despite the large impacts of bamboo on forest ecosystems, limited information is available on the ecological characteristics, such as regeneration and the flowering ecology, of bamboo species.

Two bamboo species, *Cephalostachyum pergracile* Munro and *Bambusa polymorpha* Munro, grow in mixed deciduous forest near Ottarathiri Township, Naypyitaw Union Territory, Myanmar. Both are subcanopy species that, at maturity, attain a height of more than 15 m and culm diameter of 6 cm (Yamada et al. 2023b). As described in

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"Materials and Methods" section in detail, many clumps of both bamboo species were found in this forest.

Bamboos show monocarpy which is a historical life trait in which plants sexually reproduce only once and then die. Bamboos are long-lived monocarpic monocotyledonous, which remains sterile for many years before suddenly flowering and dying (Yamada et al. 2023a). For example, *Phyllostachys bambusoides* and *Phyllostachys nigra* var. *henonis* in Japan have a flowering interval of 120 years (Ikematsu and Shimamura 2021, Isagi 2010, Kobayashi et al. 2022). *Melocanna baccifera* (Roxburgh) Kurz ex Skeels in Myanmar flowered every 48 years (Shibata 2010).

Our target species, *B. polymorpha* and *C. pergracile* are also monocarpic with a long flowering interval. *Bambusa polymorpha* flowers once every about 60 years (ranged from 54 to 80 years) (Zheng et al. 2020), but the flowering interval is unknown for *C. pergracile*. The flowering years usually differ between the species. The most recent flowering event for *C. pergracile* at the present study site was in 1997 and, at that time, *B. polymorpha* did not bloom (Nyan 1998).

Another interesting characteristic of bamboo flowering is conspecific synchronization (Isagi 2010, Suyama et al. 2010). Suyama et al. (2010) proposed some terminology of bamboo flowering. They defined "synchronous flowering" as synchronization of flowering among conspecific clumps. Both *B. polymorpha* and *C. pergracile* shows synchronous flowering within a region (Devi et al. 2014, Marod et al. 2005, McClure 1993, Suyama et al. 2010) and some, but not all, conspecific bamboo clumps flower concurrently at a given site. Tanaka et al. (2010) noted that approximately 90 % of *C. pergracile* clumps at a study site in Thailand flowered simultaneously and the remaining 10 % did not flower. In India, approximately 30 % of clumps of *C. pergracile* participated in synchronous flowering in the period from 2013 to 2018, suggesting that remaining about 70 % of clumps did not flower (Kharlyngdoh et al. 2021). These findings strongly suggest that, when synchronous flowering of bamboo occurs in a forest, some niche spaces will be occupied by clumps of nonflowering conspecific and heterospecific bamboos.

Spatial distribution patterns of a bamboo species provide us with important ecological insights of the bamboo species. In a forest, the spatial distribution of bamboos may be influenced by biotic factors. For example, the spatial distribution of a tree is often affected by the spatial distribution of other trees in a forest (Masaki et al. 1992, Yamada and Suzuki 1997). Shade-intolerant short-stature trees are usually clumped in canopy gaps and avoid large trees because they cannot survive in dense shade. Consequently, such species may not distribute with large trees. In Myanmar forests, bamboos are subcanopy or understory species and are fast-growing, early successional species (Gadgil and Prasad 1984, Lessard and Chouinard 1980, Rao and Ramakrishnan 1987, Söderström and Calderon 1979). Hence, bamboos seedlings are expected to be spatially separated from large trees, nonflowering conspecific and heterospecific bamboo clumps to avoid the shade created by them.

In the present study, we analyzed the spatial distributions of *C. pergracile* and *B. polymorpha* in a mixed deciduous forest in Myanmar to understand their ecological characteristics. Here, we aimed to address the following three questions: (1) are bamboo seedlings exclusively distributed in relation to conspecific large clumps? (2) are bamboo seedlings exclusively distributed relative to large clumps of the heterospecific bamboo? and (3) are bamboo seedlings exclusively distributed relative to large trees? By answering these questions, we tried to discuss their regeneration ecology in a mixed deciduous forest in Myanmar.

MATERIALS AND METHODS

This study was conducted in a commercial mixed-deciduous plantation forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar, in February and September in 2016. The climate and vegetation at the study site have been described previously (Yamada et al. 2023b).

Three bamboo species occur in the studied forest, namely, *C. pergracile*, *B. polymorpha*, and *Dinochloa macllelandii* Gamble. All three species are deciduous and shed their leaves in the dry season. These species are pachymorphic (McClure 1993), and lack leptomorphic rhizomes (long length relative to width, long internodes, and indeterminate growth), resulting in dense aggregations of culms. As a result, each clump could be spatially separated from other clumps as an apparent clump. *Cephalostachyum pergracile* and *B. polymorpha* are important forest resources for residents in Myanmar, who utilize the species for construction materials and as raw materials for everyday necessities, such as mats, hats, baskets, and food (ITTO 2007, Rao et al. 1998).

We established an 80 m × 110 m (0.88 ha) plot in a commercial plantation of *Tectona grandis* L.f., *Pterocarpus macrocarpus* Kurz, *Markhamia stipulata* (Wall.) Seem., *Xylia xylocarpa* (Roxb.) Taub., and *Millettia tetraptera* Kurz trees planted once in 1978 by the Myanmar Government. Prior to plantation establishment, the site was cut and

burned. Bamboo might have been able to survive these treatments because the species are tolerant of fire and other disturbances (Kachina et al. 2017, Tanaka et al. 2010). In this forest, naturally regenerated trees, which emerged after plantation establishment, were also recorded. Hence, all trees growing in the study plot originated during or after the establishment of the plantation. The height of the forest canopy was approximately 25 m. The largest diameter at breast height (DBH) of individual trees observed in the forest was approximately 50 cm. The forest floor is burnt annually by local residents in the dry season to manage the forest understory. Given that bamboo exhibit a certain degree of fire tolerance (Kachina et al. 2017, Tanaka et al. 2010), the bamboo species in the study plot are expected to survive the fire treatment.

The topography of the plot was heterogenous, comprising steep and gentle slopes as well as gentle ridges (Yamada et al. 2023b). Given that the target species, *C. pergracile* and *B. polymorpha*, were concentrated on gentle slopes and ridges, we delimited an 80 m × 80 m gently sloping area within the plot that excluded steeply sloping areas. *Dinochloa macllelandii* was concentrated on steep slopes (Yamada et al. 2023b) ; as a result, only 10 clumps of this species were situated in the 80 m × 80 m portion of the plot. Owing to the small sample size, we excluded this species from the present analysis.

A bamboo seedling produces several annual culms less than 2 cm in diameter that are replaced each year. Eventually, perennial culms more than 2 cm in diameter are produced. In this study, a bamboo seedling was defined as a clump with no culms more than 2 cm in diameter. The present study plot was divided into 256 quadrats, each 5 m × 5 m in size. The number of seedlings of *C. pergracile* and *B. polymorpha* in each quadrat was counted. Only seven *B. polymorpha* seedlings were recorded in total. This small sample size precluded examination of the spatial patterns of seedlings of this species, and thus *B. polymorpha* seedlings were excluded from the spatial analysis.

We mapped all clumps of *C. pergracile* and *B. polymorpha* with a perennial culm broader than 2 cm in diameter and identified the species. We measured the perimeter of the polygon enclosing the culms of a clump at breast height (Yamada et al. 2023b). The polygon was approximated to a circle with the same circumference length. The diameter of the circle was termed the "clump diameter". Large (mature) clumps may cast shade on seedlings and thereby prevent seedlings from invading the niche space occupied by a large (mature) clump. Therefore, we focused only on the distribution of large (mature) clumps for the spatial distribution analysis. We assumed that clumps greater than 50 cm in clump diameter were large and mature (Yamada et al. 2023b) . Such clumps usually included a culm that attained the maximum attainable height of the species. Size distributions of clump diameters for both species are shown in (Yamada et al. 2023b).

All tree stems with DBH ≥ 20 cm were tagged, mapped, identified to species, and the DBH was measured.

ANALYSIS

The spatial patterns of the two bamboo species were analyzed using Morisita's I δ method (Morisita 1959). Because we were interested in whether bamboo seedlings were exclusively distributed relative to large bamboo clumps due to the exclusion of the seedling by shade by large clumps, the quadrat sizes smaller than 5 m × 5 m were used; the crown projection area of large clumps were usually less than this quadrat sizes. A value of I δ = 1.0 indicates that the spatial distribution of a focal species is random. A value of I δ > 1.0 indicates an aggregated (clumped) distribution and a value of I δ < 1.0 indicates a uniform distribution. Whether the observed distribution differed significantly from the Poisson model of random distribution was tested using the *F*-test (Morisita 1959). The spatial relationship between a pair of species was analyzed using Iwao's ω method (Iwao 1977). The quadrat size for the ω analysis was 5 m × 5 m, too. The value of ω ranges from the maximum of +1.0 for complete overlap to a minimum of − 1.0 for complete exclusion. A value of ω = 0 indicates that the spatial distributions of the two species are independent from each other, and ω values > 0.0 and < 0.0 indicate positive (attraction) and negative (repulsion) spatial relationships, respectively.

Spatial relationships were examined for the following comparisons: *C. pergracile* seedlings and *C. pergracile* large clumps, *C. pergracile* seedlings and *B. polymorpha* large clumps, *C. pergracile* seedlings and large trees, *C. pergracile* large clumps and *B. polymorpha* large clumps, *C. pergracile* large clumps and large trees, and *B. polymorpha* large clumps and trees.

RESULTS

In the study plot, we recorded 2391, 173, and 49 clumps for *C. pergracile* seedlings, *C. pergracile* large clumps, and *B. polymorpha* large clumps, respectively, and

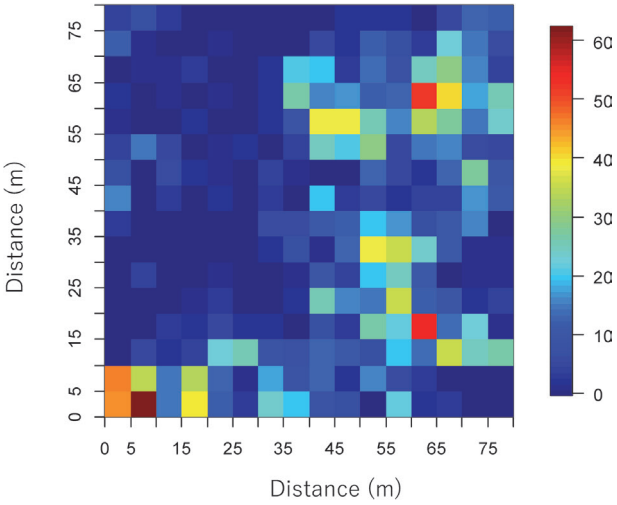


Fig. 1. Density of *Cephalostachyum pergracile* seedlings within an 80 m × 80 m plot in a mixed deciduous forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar. Seedling density was recorded in 256 quadrats each of 5 m × 5 m ($n = 2391$).

74 large trees. Fig. 1 shows the distribution of *C. pergracile* seedlings, and Fig. 2 shows the distributions of *C. pergracile* large clumps, *B. polymorpha* large clumps, and large trees in the plot. The results of the I δ analysis were indicative of a significant aggregated distribution for *C. pergracile* seedlings, *C. pergracile* large clumps, and *B. polymorpha* large clumps (Table 1).

Spatial analysis examined by calculating Iwao's ω revealed a negative relationship for the pairing of *C. pergracile* seedlings and *C. pergracile* large clumps (Table 2), implying that *C. pergracile* seedlings avoided *C. pergracile* large clumps. *Cephalostachyum pergracile* seedlings had a negative spatial relationship with *B. polymorpha* large clumps, but a weak positive spatial relationship with large trees. The pairing of *C. pergracile* large clumps and *B. polymorpha* large clumps showed a strong negative spatial relationship, indicating that large clumps of each species were exclusively distributed relative to each other. *Cephalostachyum pergracile* large clumps and *B. polymorpha* large clumps had a weak and strong negative spatial relationship, respectively, with large trees (Table 2).

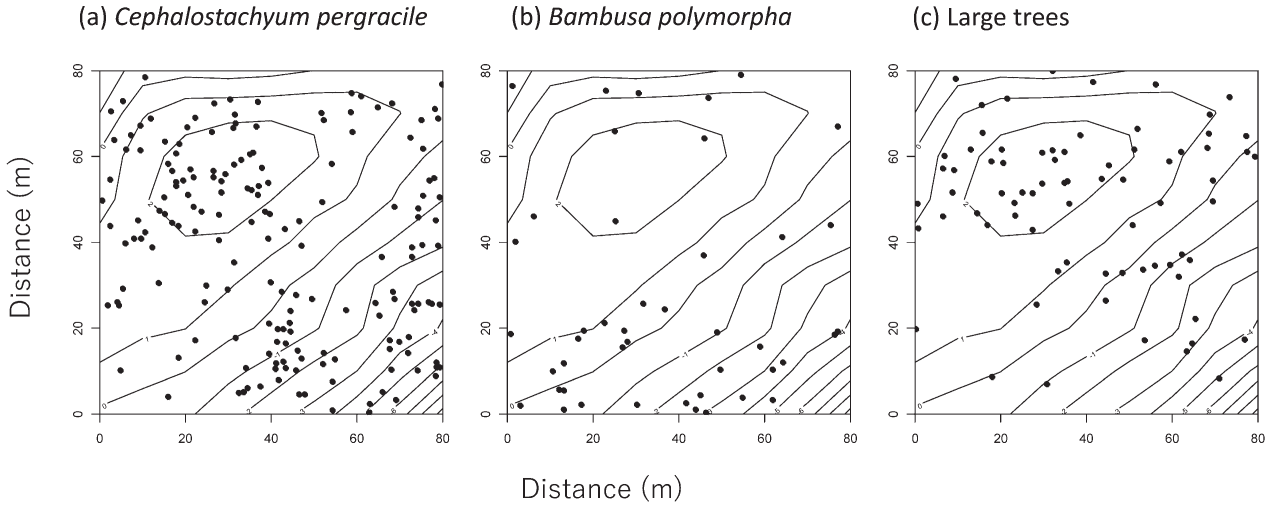


Fig. 2. Spatial distributions of *Cephalostachyum pergracile* clumps (A; $n = 173$), *Bambusa polymorpha* clumps (B; $n = 49$), and large trees (C; DBH ≥20, $n = 74$) in an 80 m × 80 m plot in a mixed deciduous forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar. The contour interval is 1.0 m in altitude.

Table 1. Spatial patterns (represented by I δ values) among bamboo species and large trees in a mixed deciduous forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar.

C. pergracile seedlings	*C. pergracile* large clumps	*B. polymorpha* large clumps	large trees+
2.451***	1.510***	3.130***	1.194

The quadrat size was 5 m × 5 m (25 m^2).
+ Trees with DBH ≥20 cm.
*** $P < 0.001$

Table 2. Spatial relationships (represented by ω values) between pairings of bamboo species and large trees in a mixed deciduous forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar.

	C. pergracile large clumps	*B. polymorpha* large clumps	large trees
C. pergracile seedlings	**−0.209**	**−0.158**	0.091
C. pergracile large clumps		**−0.327**	**−0.100**
B. polymorpha large clumps			**−0.450**

The quadrat size was 5 m × 5 m (25 m^2). A negative spatial relationship ($\omega < 0.0$) is indicated by values highlighted in bold.

DISCUSSION

The three questions addressed, namely, (1) are *C. pergracile* seedlings exclusively distributed relative to conspecific mature clumps? (2) are *C. pergracile* seedlings exclusively distributed in relation to mature clumps of heterospecific species? and (3) are bamboo seedlings exclusively distributed relative to large trees? were all affirmatively answered by the present data.

Yamada et al. (2023b) and this study showed that the large clumps of the two species exhibit an exclusive distribution with respect to each other. From this fact with the findings that seedlings of *C. pergracile* were distributed away from large clumps of conspecific and heterospecific bamboos and large trees, an idea about the limitation of niche space for bamboo regenerations can be deduced as follows.

These bamboos are subcanopy, fast-growing, and early-successional species (Gadgil and Prasad 1984, Lessard and Chouinard 1980, Rao and Ramakrishnan 1987, Söderström and Calderon 1979). Therefore, seedlings of the bamboo species may not be able to establish in sites that are already occupied either by conspecific or heterospecific bamboo clumps due to shade that is created by the large trees.

Not all conspecific clumps flower in a synchronous flowering (Kharlyngdoh et al. 2021, Tanaka et al. 2010). Consequently, when synchronous flowering of bamboo occurs in a forest, some niche spaces will be occupied by clumps of nonflowering conspecific and heterospecific bamboos. These niche spaces must be unsuitable for regeneration of the cohort generated by the focal flowering event.

In this manner, pre-emption by nonflowering conspecific and heterospecific bamboos should limit the niche spaces available for regeneration of the flowering bamboo species. Given that bamboo clumps occupy niche space in a forest at the time of flowering of a bamboo species, seedlings generated by the flowering event cannot establish in the pre-empted sites and can only exploit the remaining available niche spaces. In addition, seedlings may regenerate only in canopy gaps remaining by chance or in brightly lit sites that become available after the death of flowering culms. An exclusive spatial relationship between seedlings and conspecific and heterospecific bamboos clumps that was observed in this study supports this idea.

We propose this constraint of niche space for regeneration as "pre-empted space hypothesis" (Fig. 3). Occupation of niche spaces by nonflowering clumps limits the spaces available for regeneration. Therefore, pre-emption by nonflowering clumps disables a flowering species to deprive a nonflowering, counterpart species of niche spaces to occupy. However, either species can enhance the opportunity for conspecific individuals to regenerate in niche spaces that are presently occupied, because pre-emption does not allow seedlings of the counterpart species to enter the niche space that heterospecific flowering clumps presently occupy. In this manner, both species may be able to occupy the same niche spaces for multiple generations.

In the plot, *C. pergracile* were more abundant than *B. polymorpha*. The pre-empted space hypothesis may explain the difference in abundance between the two bamboo species. Once a species occupies a niche space in the forest by any reasons or by chance, this occupied niche space may be taken over for multiple generations. This may be true for the counterpart species, too. This suggests that if an abundance difference between the species is once created it will be maintained for multiple generations.

A shuffling of niche spaces available for regeneration might occur if both species flower simultaneously. However, this may seldom arise in a mixed deciduous forest in Myanmar given that *C. pergracile* and *B. polymorpha* may have different flowering cycles. Such an event might occur once in several centuries.

The pre-empted space hypothesis expects the competition for niche spaces between seedlings generated by the focal flowering event and nonflowering conspecific and heterospecific bamboos and. If all clumps in a forest flower in a synchronous flowering, this competition between the generations will never happen; niche space will be taken

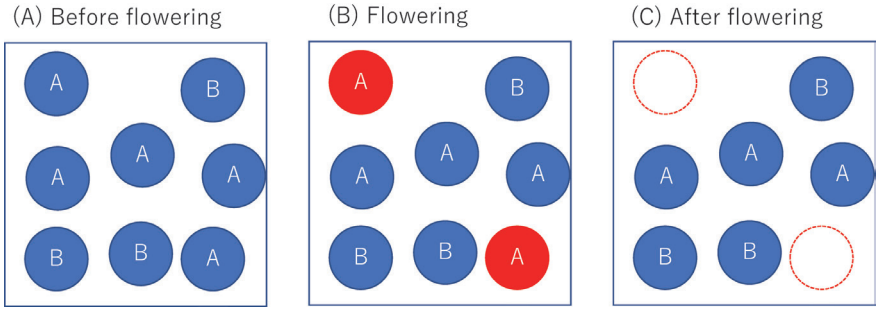


Fig. 3. Schematic diagram showing pre-empted space hypothesis. (A) Before flowering, a forest stand has 8 bamboo clumps which consists of 5 clumps of species A and 3 clumps of species B (shown by blue circles). (B) At flowering, only two clumps of species A (shown by red circles) bloom. In other words, remining 3 clumps of species A and 3 clumps of species B do not bloom (shown by blue circles). (C) The regeneration of flowering clumps of species A by seeds after flowering is considered. Seeds that are fallen under non-flowering clumps of species A and B may have a difficulty to be established due to a heavy shade by bamboo clumps (= pre-empted spaces represented by blue circles). Because a flowering clump dies after flowering, an empty space that has once been occupied by the flowering clumps will appear after flowering (indicated by red dotted lines). Then, regeneration of flowering clumps of species A via seeds may be limited to areas originally occupied by the parent clumps (red dotted lines) or areas which are not occupied by any clumps of bamboo (other white spaces). In addition, because they are pachymorphic bamboos that do not develop leptomorphic rhizomes, it is not realistic that non-flowering clumps will extend underground stems and will take over the space occupied by flowering individuals after flowering. In conclusion, a flowering clump may have a large chance to regenerate in a space where the flowering clump occupied (red circles), while it must have a little chance to regenerate in a space pre-empted by non-flowering clumps (blue circles). This idea (limitation of the space for the regeneration by seeds) is the preemption hypothesis. If this is true, the distribution of bamboo in a forest must be constrained not only by the physical site conditions that suit to the bamboo species, but also by biological conditions that a space has not been occupied by any bamboos.

over from the parent generation to the next generation. Therefore, the premise of the pre-empted space hypothesis is that some clumps do not flower in a synchronous flowering.

Cephalostachyum pergracile most recently flowered at the present study site in 1997. The question remains of whether the *C. pergracile* seedlings at the study site represent the cohort of the 1997 flowering event. If this is the case, the seedlings were 19 years old when we conducted the fieldwork, but all were shorter than several meters in height. *Cephalostachyum pergracile* is tolerant of fire disturbance and can survive repeated fires in a mixed deciduous forest in Thailand (Kachina et al. 2017). However, fire disturbance results in the production of thin culms (Kachina et al. 2017). Janzen (1976) suggested that a seedling of *Dendrocalamus strictus* shorter than 1 m in Orissa, India, may be 15−20 years old and that repeated die-back caused by severe annual fires had a dwarfing effect. These observations imply that the *C. pergracile* seedlings at the present study site may indeed be the 19-year-old cohort established after the 1997 flowering event because the study site also experiences annual fires.

Janzen (1976) noted that dwarfed clumps of *C. pergracile* caused by annually repeated forest fires flowered in 1867 in Myanmar. The culms remained short for many years, as a result of the repeated fires, until they flowered. If annual fire at the present study site persists into the future and *C. pergracile* culms remain short until the counterpart bamboo flowers, the seedlings of *B. polymorpha* may have a greater chance of entering the niche space occupied by *C. pergracile* seedlings. This is because the effects of pre-emption may be negated by dwarfing and may result in a change in spatial patterns of bamboo species in the forest.

Apparently, forest fires give a large impact on bamboo ecologies. We need to examine the spatial distribution patterns of the two bamboo species in a forest without forest fires to check if the spatial patterns that were observed in this study can be found there.

We have provided strong circumstantial evidence for the validity of the pre-empted space hypothesis to explain bamboo spatial patterns in this study. However, the flowering event of C. pergracile in 1997 in the forest was not described in detail and important information like the intensity of flowering was missing. Plus, we acknowledge that the pre-empted space hypothesis is only a possible hypothesis to explain the distribution patterns of bamboos in the forest. A direct test of the hypothesis is required by examining the distribution of seedlings established following the next flowering event in combination with long-term monitoring of the seedlings.

Bamboo species are distributed in extensive areas of forest, especially in Asia (FAO 2010). Tropical bamboo species commonly exhibit similar ecological characteristics; they are monocarpic with a flowering cycle of many years, pachymorphic, early successional, and shade intolerant.

Given these common features of bamboo, the pre-empted space hypothesis may be applicable to many bamboo species. Therefore, further tests of the pre-empted space hypothesis using bamboo species not included in the present study are required.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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