Effect of Forest fire on the regeneration of a bamboo species (*Cephalostachyum pergracile* Munro) at a mixed deciduous forest in Mae Klong Watershed Research Station, Thailand

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ABSTRACT   To understand the effect of forest fire on the regeneration of *Cephalostachyum pergracile* Munro bamboo, we compared the culm dynamics in the early regeneration stage for 3 years between a site protected from natural fires since 1995 and a site that had been burnt almost annually in a mixed deciduous forest in Thailand. Although the repeated fires distinctly decreased the number and basal area of culms per clump and the proportion of surviving culms throughout the study period, this bamboo species basically represents an adaptation to fire disturbance. A greater number of thin culms and many small branches produced by the fire-disturbed bamboos may have maximized photosynthesis with minimum allocation of photosynthate after they lose their aboveground parts. Further, the ratio of surviving clumps was higher at the unprotected site than at the protected site where self-thinning among clumps occurred. In contrast to these dynamic responses of bamboos against the fire disturbances, the number of individual clumps and their sizes remained smaller at the unprotected site than at the protected site. These results indicate that the intensity and frequency of fires primarily determine the dynamics of the bamboo population, having potential to alter the forest succession to either less or more bamboo dominating forest community. Further studies are required to elucidate the role of fire on the interaction between bamboo and tree species, specifically at the middle and matured stages of bamboo life history and along a gradient of fire regimes for better understanding assembly of the MDF community.

Key words: bamboo regeneration, forest fire, mixed deciduous forest

INTRODUCTION

Bamboos are widely distributed in temperate to tropical areas and form an important component of plant communities in tropical and temperate forests, especially in Asia (McClure 1966, Dransfield and Widjaja 1995). Bamboo is a fast-growing plant (Lessard and Chouinard 1980) and often colonizes environments disturbed by human activities, wind (Gagnon et al. 2007), flood (Guilherme et al. 2004), or fire (Gagnon and Platt 2008, Franklin et al. 2009, Gagnon 2009, Zaczek et al. 2010). Once a disturbed forest becomes dominated by bamboo, the dense and closed bamboo canopy limits light penetration to the forest floor (Montti et al. 2011), suppressing germination, regeneration, recruitment, and survival of tree seedlings and saplings in many regions (Nakashizuka 1988, Marod et al. 1999, Griscom and Ashton 2003, Budke et al. 2010, Montti et al. 2011). For example, a high density of the dwarf bamboo *Sasa kurilensis* prevents the establishment of beech (*Fagus crenata*) seedlings on the forest floor (Nakashizuka 1988). Bamboo plants have a long lifespan and often exhibit semelparity. Within semelparous species, all individuals at a site die simultaneously after gregarious flowering (Janzen 1976). Following this event, tree regeneration often improves (Capellesso et al. 2016). Thus, the regeneration and dynamics of bamboo can critically influence forest community structure and dynamics (Nakashizuka 1988, Marod et al. 1999).

Fire is one of the main disturbances that affect forest dynamics (Mooney et al. 1995, Zedler 2007), and its frequency and severity control the distribution of forest types (Webb et al. 2011, Chen et al. 2014, Torres and
The component species within a forest community respond differently to fire. Fire generally does not critically damage fire-tolerant species or large trees, but severely harms the regeneration and survival of seedlings or small saplings of woody species (Prasad 1985, Marod et al. 2002). Continuous fire disturbance could therefore encourage the formation of a relatively homogeneous stand by removing fire-intolerant species (Platt and Connell 2003). On the other hand, some plants require fire to regenerate or are adapted to survive fire (Smith 1962). For example, repeated fire may have favored the expansion of some pine species (Agee 1998, Christopoulou et al. 2014, Han et al. 2015). The stem buds of clonal plants are sometimes stimulated to resprout by fire (Bond and Wilgen 1996, Zedler 2007). Therefore, organisms such as bamboos that are capable of rapid clonal growth should have an advantage in post-fire environments because they can quickly monopolize the resulting open space and its resources (Gagnon and Platt 2008). At the same time, however, bamboo is easily destroyed by fire (Giri and Shrestha 2000, Murray et al. 2013). Thus, repeated forest fires could positively or negatively affect clump regeneration, culm production, and development in forest communities, depending on their intensity and frequency.

In mixed deciduous forest (MDF) in western and northern Thailand, some bamboo species (i.e., Bambusa tulda, Cephalostachyum pergracile, Gigantochloa albociliata, and Gigantochloa haskariiana) dominate the middle- to sub-canopy layers of natural forests composed of diverse species assemblages of small trees and shrubs when the forests are disturbed by fires (Rundel and Boonprakob 2009). All bamboo species in the MDF are semelparous. Their dominance often limits tree regeneration and long-term forest succession (Marod et al. 2002). Marod et al. (1999) found that tree regeneration was promoted after the simultaneous flowering and subsequent death of a bamboo species in the MDF, since this event reduces shading for tree seedlings. Therefore, the frequency of gregarious bamboo death and the recovery of bamboo afterward are important factors for forest dynamics in the MDF.

The MDF and dry dipterocarp forests in Thailand experience frequent forest fires that typically burn only the surface of the forest floor (Marod and Kutintara 2009). During the dry season, fires are accidentally or intentionally caused by human activities, and are naturally spread out due to dry condition in those forests (FAO 1998). This disturbance regime should create a different forest regeneration pattern from that of tropical rain forests (Marod et al. 1999, Webb et al. 2011). In the MDF, the intensity and frequency of fire affect the forest dynamics both directly and indirectly, through changes in bamboo dynamics. Many researchers have studied the interaction between forest fire and bamboo (Prasad 1985, Zedler 2007, Franklin et al. 2009, Smith and Nelson 2010). Forest fires not only destroy the aboveground biomass of large bamboo individuals (Prasad 1985), but also reduce their cover, height, and culm diameter just after germination (Zaczek et al. 2010). However, how forest fire affects the demographic aspects of semelparous bamboo during their early regeneration after simultaneous death is still poorly understood because of the long lifespan of bamboo species (Taylor and Qin 1993, Taylor et al. 1996, Franklin et al. 2009). More information on the interactions between forest fire and bamboo and their influence on tree species dynamics is required to understand the dynamics of the MDF (Marod et al. 1999).

Here, we investigated the effect of forest fire on bamboo recovery during early regeneration stage after simultaneous death of flowering bamboo clumps. We measured the production of newly recruited culms and branches that emerge from the nodes at ground level, and the survival of bamboo culms and clumps (individual genets) in a regenerated cohort of the species Cephalostachyum pergracile Munro at burned (unprotected) and unburned (protected) sites in a MDF in Thailand, where the species showed gregarious flowering and death in 2001 (Marod et al. 2005). By investigating such responses of bamboo individuals to fire disturbance in early stage of regeneration, we aim to understand the adaptation of C. pergracile to fires and how its clump recovery is affected by fires. We predicted that the repeated fires delay the recovery of C. pergracile after its dieback by reducing production of new culms per clump at the unprotected site where is burned repeatedly compared to the protected site. This study should shed light for the interaction between bamboo and tree regeneration and the role of bamboo in forest dynamics under repeated-disturbed condition.

**MATERIALS AND METHODS**

**Study area**

The field study was conducted at the Mae Klong Watershed Research Station in Sri Nakarin National Park, Thong Pha Phum District, Kanchanaburi Province, Thailand (14° 30’ N to 14° 45’ N, 98° 45’ E to 99° E). The catchment covers approximately 108.9 km², and elevations range from
100 to 900 m a.s.l. Annual rainfall exceeds 1600 mm, and rainfall is concentrated from late April to October. The mean monthly temperature is about 27.5 °C, with a maximum of 39.1 °C in April and a minimum of 14.6 °C in December (Marod et al. 1999). The dominant forest type is MDF. The dominant tree species are Pterocarpus macrocarpus, Xyloxylocarpus var. kerrii, A. xylocarpa, Lagerstroemia calyculata, Terminalia superba, and V. peduncularis. Four bamboo species are common in the middle canopy layer: Gigantochloa albociliata, Gigantochloa hasskarliana, Cephalostachyum pergracile, and Bambusa tulda. During the dry season, fires often occur in this forest. They usually burn only the understory plants, although they also burn the trees in some rare cases (Rundel and Boonprakob 1995, Marod et al. 1999). Since the national park was established in 1980, logging has ceased, although the current fire history suggests that the forests have been affected by fires for a long time. In 1995, a fire-protected area (approximately 8 ha) was established at the Research Station, and has been protected by 10 m-width firebreaks since then.

Study species

We focused on C. pergracile, one of the most dominant and widespread bamboos in MDF of Thailand and Myanmar. Its rhizome type is sympodial. Clumps generally take 12 to 15 years after germination to produce full-sized culms 2.5 to 7.5 cm in diameter with a mature height of 7 to 30 m (Dransfield and Widjaja 1995). In Myanmar, this species reaches between 10 and 20 m in height in unburned forests and between 1 and 3 m in regularly burned forest (Janzen 1976). In our study area, it reaches 10 to 30 m (D. Marod, personal observation). During 1993 to 2001, mature stands in the study area had a mean of 8.2 ± 1.3 (mean ± SD) culms per clump and a mean basal area of 172.8 ± 49.0 cm² per clump (D. Marod, unpublished data; Appendix 1). In 2001, the C. pergracile population in the forests in the study area flowered and died, and then a new population started to regenerate from seeds that germinated in 2002. This kind of occasional event provides a large amount of vacant space in which not only tree species but also the bamboos themselves can regenerate (Nakashizuka 1988). However, the regeneration dynamics of the species, especially bamboos, that colonize the vacant space after the bamboo’s simultaneous death were unclear.

Study sites and field data

In 2008, 6 years after germination, seedlings had reached an average height of 0.5 to 3 m in the forests in the study area. We established two study sites: one at the center of the fire-protected area (ca. 600 m a.s.l.) to avoid an edge effect, the other at an unprotected area (ca. 700 m a.s.l.) where fire freely spreads out under no control. The sites were ca. 3 km apart, and their annual rainfall and mean monthly temperatures were similar. The mean tree density, number of tree species, and tree basal area were calculated based on data of all trees with a diameter ≥ 4.5 cm at breast height (1.3 m above the ground) collected in 2004 from 100 quadrats (each 10 m × 10 m) in a 1-ha plot at each site (D. Marod, unpublished data). At the protected site, the results were 2.5 ± 1.6 trees, 1.8 ± 1.4 species, and 0.06 ± 0.08 (m²) per 100 m² (Appendix 2), where 50 tree species were found in total. The forest was dominated by P. macrocarpus, Schleicheria oleosa, X. xylocarpa, Dillenia grandifolia, and V. peduncularis. At the unprotected site, the values were 3.3 ± 2.4 trees, 2.1 ± 1.9 species, and 0.16 ± 0.31 (m²) per 100 m², where 61 tree species were found in total. The forest there was dominated by Lagerstroemia tomentosa, Polyalthia viridis, Dipterocarpus turbinatus, Gmelina arborea, and L. calyculata. The number of trees species and the tree density were not significantly different between the sites (t = 0.937, P = 0.349 and t = 1.708, P = 0.08, respectively), but the tree basal area (t = 3.058, P < 0.01) was significantly higher at the unprotected site. At the unprotected site, fire occurred in April 2008 and April 2010 during the study period. The intensity of fire was more severe in 2010 (because there was no fire in 2009) than in 2008 (following a fire in 2007) (P. Kachina, personal observation).

We established 20 plots (each 1.5 m × 1.5 m) at 5-m intervals to form a 5 × 4 grid at both sites. In each plot, we tagged all individuals (clumps) of C. pergracile with numbered metal tags (n = 260 in total at the protected site, n = 127 in total at the unprotected site). We also tagged every stem (culm) and measured its diameter at ground level, or at 1.3 m above ground if it was taller than 2 m. After fire burned the aboveground parts of culms, the clumps that survived produced many small branches directly from the nodes at ground level. These branches were also tagged and measured. We calculated the sum of the basal area of culms and branches for a given clump and used this as the indicator of clump size.

We repeated the censuses at both sites in April 2008 (late in the dry season, before the fire), June 2008 (middle of the rainy season, after the fire, unprotected site only),
September 2009 (late in the rainy season), June 2010 (middle of the rainy season, after the fire), and May 2011 (early in the rainy season). At each census, we defined living culms as those with a green stem, even if it was broken or had no leaves. We classified clumps that had at least one living culm or branch in the middle of the rainy season as living. Since the emergence of culms and branches after a fire was sometimes delayed by a year, we could not confirm the death of a clump until the middle of the next year’s rainy season. If there were no culms or branches produced by 2 years, we judged the clump to be dead.

**Data analysis**

All statistical analyses were performed using R software v. 3.3.1 (R Core Team 2016). We focused on responses of bamboo individuals to fire events. To investigate the effects of site (fire-protected or unprotected), time (April 2008, June 2008, September 2009, June 2010, May 2011), and their interaction on the number of culms per clump, we used a generalized linear mixed-effects model (glmer in lme4 package). To investigate their effects on the basal area of culms (+ branches) and newly recruited culms (+ branches) per clump, we used a linear mixed-effects model (lmer in lme4 package). To investigate their effects on the numbers of living and dead clumps and of living and dead culms per clump, we used glmer. We calculated the survival of clumps and culms at both sites from April 2008 before the fire to September 2009, from September 2009 to June 2010, and from June 2010 to May 2011. We included plot and clump ID as random factors in all models. To test the significance of each explanatory variable, we performed a type-II likelihood-ratio test using the Anova function in car package. When the interaction term was significant, we conducted multiple comparisons to identify significant differences between the means of the parameters among times at each site using the general linear hypothesis (glht) tool of the multcomp package.

We assessed the size distribution of clumps (total culm basal area per clump) that did or did not produce one or more culms in the next year, between April 2008 and September 2009, between September 2009 and June 2010, and between June 2010 and May 2011. All clump size values were log-transformed. To examine whether the observed differences in the size distribution between the protected and unprotected sites could be caused by difference in the number of clumps, we conducted a randomization test. In this test, we sampled same number of clumps from each site in each year with allowing replacement and calculated range of clump size. For the number of clumps, we used number of clumps in the unprotected site of the year. We repeated this procedure 1000 times. After getting 1000 values of range for both sites, we conducted t-test to see the difference between them.

We calculated the relative growth rate (RGR) of each clump in each interval as:

\[
RGR = \frac{(\ln M_t - \ln M_i)}{(t_2 - t_1)}
\]

where \(M_i\) is clump size at time \(t_i\) and \(M_t\) is clump size at time \(t_2\). Then we investigated the relationships between \(M_i\) and RGR at \(t_2\) using a lmer with consideration of differences in the sites. To test the effect of initial clump size, fire disturbance, and their interaction on RGR, we conducted a type-II likelihood ratio test using the Anova function of the car package. All clump size values were log-transformed.

**RESULTS**

Effects of fire on the number of culms and branches per clump

At the protected site, the mean number of culms per clump (2.5 ± 0.5 over the study period; Fig. 1a) was relatively lower than the mean of the mature stand at our study area before the simultaneous death (8.2 ± 1.3; App. 2a). On the other hand, the mean culm basal area per clump (6.9 ± 3.8 over the study period; Fig. 1c) was much smaller than the mean of the mature stand at our study area before the simultaneous death (172.8 ± 49.0 cm²; App. 2b).

The number of culms per clump was significantly affected by site, time, and their interaction (site: \(\chi^2 = 12.4, \, df = 1, \, P < 0.001\); time: \(\chi^2 = 14.9, \, df = 4, \, P < 0.01\); interaction: \(\chi^2 = 90.0, \, df = 3, \, P < 0.001\) (Fig. 1a). It was generally lower at the unprotected site than at the protected site. At the protected site, it was significantly higher in May 2011 (last census) than in April 2008 (first census). At the unprotected site, on the other hand, it was lower just after the fires (in June 2008 and June 2010) than in the other three censuses (although not significantly in June 2008; Fig. 1a).

The number of branches per clump was significantly affected by site, time, and their interaction (site: \(\chi^2 = 701.3, \, df = 1, \, P < 0.001\); time: \(\chi^2 = 1557.9, \, df = 4, \, P < 0.001\); interaction: \(\chi^2 = 187.0, \, df = 3, \, P < 0.001\) (Fig. 1b). It was generally higher at the unprotected site than at the
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The culm basal area per clump was significantly affected by time and by its interaction with site (time: \( \chi^2 = 41.8, \text{df} = 4, P < 0.001 \); interaction: \( \chi^2 = 23.2, \text{df} = 3, P < 0.001 \)), but not by site (Fig. 1c). At the protected site, it increased significantly throughout the study period. At the unprotected site, on the other hand, it was stable throughout the study period, with no significant difference among times. Even when the basal area of all branches was included, the results were similar, except that the culm + branch basal area per clump was significantly higher in May 2011 (last census) than in April 2008 (first census) at the unprotected site (Fig. 1c, d).

Effects of fire on bamboo death and survival

The ratio of surviving culms to total culms per clump for each interval (April 2008 – September 2009, September 2009 – June 2010, and June 2010 – June 2011) was significantly affected by site, time, and their interaction (site: \( \chi^2 = 72.3, \text{df} = 1, P < 0.001 \); time: \( \chi^2 = 147.4, \text{df} = 2, P < 0.001 \); interaction: \( \chi^2 = 28.9, \text{df} = 2, P < 0.001 \) (Fig. 2a). It was generally lower at the unprotected site. Many clumps lost all their culms to fire, but new culms appeared several months later and gradually multiplied until the next fire.

The ratio of live clumps at each census to the previous total was significantly affected by site and time in each interval (site: \( \chi^2 = 47.5, \text{df} = 1, P < 0.001 \); time: \( \chi^2 = 150.0, \text{df} = 2, P < 0.001 \) (Fig. 2b). It was higher at the unprotected site. At both sites, it was significantly lower in 2008 than in 2009 or 2010. At the protected site, it was particularly low in 2008 possibly because of the severe competition among dense and small-sized clumps in relatively younger regeneration stage.

Effects of fire on bamboo recruitment and growth rate

The number of newly recruited culms per clump was significantly affected by site, time, and their interaction (site: \( \chi^2 = 8.7, \text{df} = 1, P < 0.01 \); time: \( \chi^2 = 287.2, \text{df} = 3, P < 0.001 \); interaction: \( \chi^2 = 61.3, \text{df} = 2, P < 0.001 \) (Fig. 3a). At the unprotected site, it fluctuated throughout the study period, being significantly lower in June 2008 and June 2010, just after the fires, than at the other two census times. At the protected site, it was also significantly lower in June 2010 than in September 2009 and in May 2011, although it was relatively stable throughout the period.

The number of newly recruited branches per clump was significantly affected by site, time, and their interaction...
(site: $\chi^2 = 241.7$, df = 1, $P < 0.001$; time: $\chi^2 = 307.2$, df = 3, $P < 0.001$; interaction: $\chi^2 = 371.2$, df = 2, $P < 0.001$) (Fig. 3b). At the unprotected site, it fluctuated greatly throughout the study period, being significantly higher in June 2008 and June 2010, just after the fires, than at the other two census times. At the protected site, it was significantly higher in June 2011 than in September 2009, although it was relatively stable and low throughout the study period.

The basal area of the newly recruited culms per clump was significantly affected by time ($\chi^2 = 38.7$, df = 3, $P < 0.001$), but not by site or the interaction (Fig. 3c). At the unprotected site, it was significantly lower in June 2008 and June 2010 than in September 2009 and May 2011. At the protected site, it was significantly lower in June 2010 than in September 2009 and May 2011.

The basal area of newly recruited culms and branches per clump was significantly affected by time ($\chi^2 = 24.2$, df = 3, $P < 0.001$), but not by site or the interaction (Fig. 3d). At the protected site, it was significantly lower in June 2010 than in September 2009 and May 2011. At the unprotected site, on the other hand, it was stable throughout the study period, with no significant differences among census times.
The clump size distributions were wider at the protected site than at the unprotected site at all census times (Fig. 4). At the protected site, small to large clumps occurred, and clumps of all sizes produced new culms in the next year (Fig. 4a–c). At the unprotected site, on the other hand, only middle-sized clumps occurred, all sizes of which produced new culms following 2008 and 2010 (Fig. 4d, f), although not following 2009 (Fig. 4e), because the census was conducted just after the fire in June 2010. We also found that the range of clump size derived from the randomization test was significantly different between the protected site and the unprotected site throughout the study period in 2008 ($t = -243.4, P<0.001$, Fig. 4a, d), in 2009 ($t = -129.8, P<0.001$, Fig. 4b, e) and in 2010 ($t = -140.1$, Fig. 4c)
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produce more thinner and shorter culms after fire disturbance when the bamboo receive enough light compared to the bamboo was under closed canopy in North America, even though the rhizome type of this species was different from ours (Gagnon et al. 2007, Gagnon and Platt 2008).

The clumps disturbed by fire also produced many small branches from the nodes at ground level, since fire triggers the growth of surviving buds (Franklin et al. 2009). Although these branches contributed little to the total basal area, they may increase photosynthesis by producing many leaves with minimal allocation of resources immediately after the fire, when the bamboo does not have any surviving aboveground parts (Kleinhenz and Midmore 2001). These characteristics seem to be adaptations that allow rapid recovery after a fire by allocating stored reserves to photosynthetic parts, as is seen during resprouting of many woody species, including shrubs (Shibata et al. 2016). Since our study site has a clear dry season, fire is a frequent disturbance (typically, at least once every few years), so the production of small branches should be an effective strategy for bamboos in this area. Additional research will be required to determine the extent of the adaptation and how it differs among species.

DISCUSSION

Adaptation of C. pergracile to fires

Cephalostachyum pergracile showed some adaptation to fire disturbance, even the repeated fires clearly delayed the recovery of C. pergracile after its dieback in MDF at Sri Nakarin National Park, Thailand. Despite high mortality of culms, that of clumps was low even at the unprotected site. This can be because their rhizomes in soils are protected from fire and store photosynthate to produce new culms (Prasad 1985). The culms recruited at the unprotected site were thinner than those at the protected site, being suggested by that the number of newly recruited culms per clump was higher at the unprotected site, but the basal area of recruited culms was comparable between the sites. Since the production cost of thick culms is higher, the strategy to produce many thin culms has the advantage of producing many leaves. In addition, the light condition at understory was higher at the unprotected site than at the protected site because fires open the canopy. Therefore, the thinner and shorter culms at the unprotected site would be enough to receive light without intensive competition for light, while the thicker and taller culms would be required to overcome the competition at the protected site. Gagnon and his colleague also found that a bamboo species, Arundinaria gigantean, produce more thinner and shorter culms after fire disturbance.

Survival and self-thinning

Even though the culm survival is also affected by natural process of clump growth, fires obviously decreased culm survival in this study. The observed fluctuation in the survival ratio of culms at the unprotected site likely reflected the changing intensity of fire disturbance year by year. On the contrary, the cause of the fluctuation of culm survival at the protected site is attributable to a fragile nature of newly recruited culms which, particularly in early stage of regeneration, are easily broken or die during clump growth until the productivity becomes stable (Kleinhenz and Midmore 2001). On the other hand, the ratio of surviving clumps was generally higher at the unprotected site than at the protected site. This may due to higher intensity of self-thinning at the protected site because of severe competition for light or nutrients among individuals in even-aged stands (Yoda et al. 1963). Makita (1992) divided the early regeneration process of Sasa kurilensis after mass flowering into three phases: establishment (0–1 year after germination), density-stable (1–3 years after germination), and thinning (>3 years after germination). During the density-stable phase, mortality is low. Although the species characteristics of S. kurilensis are different from
our species, the bamboo canopy at the protected site was already closed and it seems to have reached the thinning phase, in which some clumps die owing to competition. However, at the unprotected site, fire seems to have enhanced clump survival by reducing competition and by keeping surviving culms and clumps small. Thus, fires at the early regeneration stage could prevent the formation of a closed canopy, which could maintain relatively high light levels at the forest floor.

**Clump growth and fires**

All the clumps at our study sites should have same age because they germinated simultaneously in 2002. However, the clump size distributions differed, being narrower at the unprotected site. This suggests that the small-sized clumps can easily die due to fires. This is probably because small-sized clumps are more susceptible to frequent fires. In contrast, even though large-sized clumps may be less susceptible to fire, the larger culms represent a greater investment in aboveground tissue, leaving lower belowground reserves to produce new culms after a fire. On the other hand, the RGR of middle-sized clumps was generally larger at the unprotected site than at the protected site, probably because the higher density of culms at the protected site causes strong competition for light among the culms, while the middle-sized clumps at the unprotected site can receive more light. Further, in the year without fire between 2010 to 2011, the RGR of clumps at the unprotected site showed the positive relationship with the clump size. This suggested that larger clumps took the advantage of one sided competition suppressing smaller clumps, when they were released from fire. On the other hand, at the protected site, the RGR at the largest clump size ranged around zero through the study period. Therefore, clumps at this size class barely showed net growth and were just replacing short life-span culms.

**The significance of fire on tree community**

The repeated fires can delay the dominance of *C. pergracile* by slowing the development of large culms at their early stage of regeneration. This bamboo species is monocarpic and dies simultaneously after flowering. This life history, i.e. simultaneous death after flowering, gives trees a chance to regenerate (Nakashizuka 1988), but quickly regenerating bamboos may be the strong competitor of the regenerating trees (Marod et al. 2005). Repeated fires may prevent the bamboo to recover from the depletion of the nutrients and photosynthates stored in the belowground part by destroying the new flush of branches. Delay of bamboo recovery may favor the tree regeneration. When we compare the forest structure at the two sites, the tree density was marginally and tree basal area was significantly higher at the unprotected site than at the protected site, respectively (D. Marod, unpublished data). Thus, the fire could inhibit bamboo domination and prefer recoveries of fire-resistant tree species that possibly account for the tree rich structure at the unprotected site.

Bamboos showed a strong persistence at the unprotected site, even though the clump size remained smaller than at the protected site. A relatively low fire frequency or low intensity fire could allow bamboos to grow with thin culms after producing many branches. However, bamboos reconciled more trees to establish at the unprotected site. Therefore, bamboos would be replaced or suppressed by more fire-resistant trees if the intensity and frequency of fire exceeded the resistant capacity of bamboo against fire, and also might be replaced or suppressed by late successional tree species in a complete absence of fire disturbances. Thus, the timing, frequency and intensity of fire disturbances determine the growth and establishment of bamboos and consequently determine the structure of the MDF community. Further studies are required to elucidate the roles of fire on the interaction between bamboos and tree species and to better understand the assembly of MDF community, specifically at the middle and matured stages of bamboo populations and along a gradient of fire regimes.

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Appendix. 1. Mean of (a) number of culms and (b) culm basal area per clump of *Cephalostachyum pergracile* from 1993 to 2001 (flowering year) in a 0.2-ha plot in an unprotected area at the Mae Klong Watershed Research Station.

Appendix. 2. Mean of (a) number of species, (b) number of individuals, and (c) total basal area per hectare at protected and unprotected sites. Significant differences between the two sites is indicated by: \( P<0.1, * P<0.05, ** P<0.01, *** P<0.001 \).