

BARK THICKNESS AND THE INFLUENCE OF FOREST FIRE ON TREE POPULATION STRUCTURES IN A SEASONAL EVERGREEN TROPICAL FOREST

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ABSTRACT

The forests of continental Southeast Asia occur in a mosaic pattern of evergreen and deciduous forest types. Fire is an integral part of these seasonal forests, but is widely perceived as being detrimental to the evergreen forest. Previous research has suggested that increased fire activity due to human encroachment and changing regional climate patterns will favor regeneration of the fire-adapted deciduous forest species at the expense of the fire-sensitive evergreen forest species. We tested this hypothesis by comparing bark thickness, a proxy measure of fire susceptibility, with the regeneration status of 10 seasonal evergreen forest tree species from a large forest dynamics plot at the Huai Kha Khaeng Wildlife Sanctuary in western Thailand that has experienced at least three fires in the past decade. Among the study species, bark thickness (at a reference size of 5 cm DBH) ranged from 1.8 to 6.4 mm. We found no correlation between fire susceptibility and the regeneration status of the study species. *Baccaurea ramiflora*, the species with the most abundant regeneration on the study plot (69% of all stems were < 5 cm DBH), had the second-thinnest bark in the study. In contrast, *Hopea odorata*, the species with the thickest bark, had almost no recruitment in the plot (5% of all stems were < 5 cm DBH). These results suggest that occurrence of the low-intensity forest fires is not limiting the ability of seasonal evergreen forest species to recruit and that their recruitment may instead be controlled by a suite of other factors.

Keywords: *Baccaurea ramiflora*, forest regeneration, *Hopea odorata*, Huai Kha Khaeng Wildlife Sanctuary, resprouting, surface fires

INTRODUCTION

In the seasonal tropics of Southeast Asia, evergreen and deciduous forest types occur together in mosaic patterns across large landscapes. The location of each forest type within a given landscape has been attributed to edaphic factors and disturbance regimes (WHITMORE, 1984; RUNDEL & BOONPRAGOP, 1995). Fire is an important type of disturbance in these seasonal tropical forests (STOTT, 1988). Each year during the dry season, mean monthly temperatures exceed 25°C and mean monthly rainfall is < 50 mm for several months. This

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creates a pronounced drying effect on the vegetation and the likelihood of fire occurrence increases dramatically during the 3–6 months of the dry season. Xeric sites experience more intense levels of drought and evaporative demand, suffer greater dieback and seasonal drying, and are more prone to fires. The vegetation on such sites is typically deciduous and fire-adapted. In contrast, at mesic and hydric sites greater availability of soil water may buffer against seasonal drought, leading to less drought-induced drying and dieback in the above-ground vegetation and decreased risk of fires. The plant species on these sites are predominantly evergreen and are assumed to lack specific adaptive traits associated with fire-prone environments (RABINOWITZ, 1990).

Fire has been an historical element of the continental Southeast Asian landscape for at least 10,000 years (STOTT, 1988). In recent decades, human encroachment and forest fragmentation have increased throughout most of the region (e.g., FOX *ET AL.*, 1995). Because fire is widely used by local populations to clear forest, prepare fields, increase forage for livestock, and improve hunting conditions, it is widely believed that these factors have led to shorter fire return intervals in the seasonal forests of Southeast Asia in recent decades relative to historical levels (STOTT, 1986, 1988; RABINOWITZ, 1990). While long-term data on historical fire frequencies are scant, there is considerable concern that the evergreen forest types may be significantly threatened by an increase in fire frequency. Historically, evergreen forest types may have been resistant to fire under normal environmental conditions. Nonetheless, extreme drying conditions in which low rainfall and drought persist for extended periods may generate fuel conditions that enable fires to burn in the evergreen forest. These conditions are often associated with extremely strong El Niño-Southern Oscillation (ENSO) events that occur every few decades (SANFORD *ET AL.*, 1985; BARLOW & PERES, 2004). Given the long return intervals between such extreme fire conditions, many of the evergreen forest tree species are assumed to lack adaptations to fire and to be highly susceptible to fire-induced mortality. A relatively abrupt increase in the fire frequency could restrict or eliminate recruitment of species that lack adaptations to fire by repeatedly killing the regeneration, and facilitate the invasion of evergreen forests by plant species better adapted to fire. Over the long term an increase in the fire frequency is expected to lead to the exclusion of evergreen forest types by deciduous, fire-adapted forest types (STOTT, 1988).

Despite these concerns, no studies have explicitly examined the influence of fire in structuring tree species' populations in seasonal evergreen forests. In this paper we test whether fire susceptibility was correlated with population structure among a group of common evergreen forest tree species. We used bark thickness, a common proxy measure of susceptibility to fire damage (GILL & ASHTON, 1968; HENGST & DAWSON, 1994; PINARD & HUFFMAN, 1999), to quantify the relative sensitivity of each tree species to fire. Because fire-induced mortality in trees is strongly size-dependent (PERES, 1999; PINARD *ET AL.*, 1999; HAUGASSEN *ET AL.*, 2003), often the most profound effect of fire on tree populations is to eliminate new recruitment. Using data from a large-scale forest dynamics plot, we developed two measures to assess the regeneration status of each tree species. Given the known occurrence of three fires that burned through the study plot in the past decade, we hypothesized that if forest fires were having a deleterious effect on the evergreen forest, then the regeneration status of the study species would be positively correlated with bark thickness.

METHODS

Study Site

The research was conducted in Huai Kha Khaeng Wildlife Sanctuary (HKK). HKK is located at 15° 40' N latitude and 99° 10' E longitude in Uthai Thani Province, west-central Thailand, about 300 km northwest of Bangkok and 60 km east of the Burmese border. The climate is monsoonal and can be divided into three seasons: the rainy season (May–October), the cool season (November–January), and the hot or dry season (February–April). Mean annual rainfall at the Kapook Kapiang Ranger Station (4 km from the study site) is 1476 mm (± 113 mm; 1983–1993). Mean July temperature is 27°C; mean January temperature is 19°C. Soil moisture content in the seasonal dry evergreen forest ranges from 9 to 13% (% dry weight of soil) during the rainy season and 2–7% during the dry season (BAKER, 1997).

Forest Dynamics Plot

A 50-ha Forest Dynamics Plot (FDP) was initiated in the north central portion of HKK in 1991 as part of a collaborative research initiative between the Royal Forest Department of Thailand and the Center for Tropical Forest Science (CTFS) of the Smithsonian Institution. The plot is a 50-ha rectangle 1 km long (north-south axis) and 0.5 km wide (east-west). To foster cross-site comparisons and meta-analyses, each tree was measured, mapped to plot coordinates, and identified following a standard protocol established for the FDPs of the CTFS network (CONDIT, 1997). The enumeration was completed in 1994 and included all free-standing woody plants ≥ 1 cm DBH. The initial census included 80,436 stems from 250 species, 164 genera, and 62 families (BUNYAVEJCHEWIN *ET AL.*, 2001). The stand of seasonal dry evergreen forest included in the 50-ha plot is notable for the high number of rare species and the dominance in basal area and frequency of a relatively small number of species (BUNYAVEJCHEWIN *ET AL.*, 2002). Taxonomy and nomenclature follow BUNYAVEJCHEWIN *ET AL.* (2004).

Bark Thickness

Measures of bark thickness and DBH were obtained from 11 species spanning the full range of tree sizes and life history patterns in the seasonal dry evergreen forest at HKK. We used the 50-ha plot database to randomly select individuals of the 11 species from across the range of size classes on the study plot. Bark samples were obtained from ~20 individuals per species using a standard tree corer. Two bark samples from each tree were taken at a height of 25 cm above the ground on opposite sides of the bole. Bark thickness for each sample was measured in the field to the nearest 0.1 mm using dial calipers and averaged to provide a mean bark thickness value for each tree. Nonlinear regressions of DBH vs. bark thickness were developed for each species. Several regression forms were compared. The power, or allometric, relationship ($Y = \alpha X^\beta$) consistently provided the best fit across species. To provide a relative comparison of fire susceptibility among species, the bark thickness for a 5-cm DBH tree of each species was estimated using a species-specific regression model.

Tree Population Structures

The population structures of the study species were described quantitatively using two approaches. First, the ratio of juvenile trees to adults was calculated from the 50-ha plot diameter distributions. Juvenile trees were defined as those trees that were < 5 cm DBH; adults were trees \geq 5 cm DBH. While this is a somewhat arbitrary threshold and the distinction between juveniles and adults will differ from species to species based on growth rates and longevity, our interest was in identifying the new recruits (*i.e.*, seedlings and saplings) and the 5-cm threshold provides a reasonable estimate given the range of study species we examined. Hereafter, the ratio of trees < 5 cm DBH to the entire population is referred to as the regeneration ratio, R . Second, a Weibull probability density function was fit to each diameter distribution using a maximum likelihood algorithm (COHEN, 1965; BAILEY & DELL, 1968). The shape parameter of the Weibull distribution, c , was used as a measure of the population structure. When $c < 1$, the function is a steeply descending, monotonic function; when $c = 1$ it is a negative exponential distribution. The function is unimodal for values of $c > 1$, positively skewed from $1 < c < 3.6$, approximately normal at $c = 3.6$, and negatively skewed when $c > 3.6$. As such, tree species with low values of c have populations dominated by small individuals, whereas tree species with high values of c have populations dominated by larger individuals.

The relationship between bark thickness and each measure of regeneration status was assessed by regression analyses. All analyses were performed using the statistical software package, Statistica (version 5.1, Statsoft, Tulsa, USA).

RESULTS

Sampled bark thickness ranged from 1 mm thick in a *Baccaurea ramiflora* sapling to 30 mm thick in an emergent *Dipterocarpus alatus*. Species-specific relationships between bark thickness and DBH were well-described by power functions (Table 1, Fig. 1). The estimated bark thickness for trees at 5 cm DBH based on the fitted power functions ranged from 1.8 mm in *Baccaurea ramiflora* to 6.4 mm in *Polyalthia viridis* (Fig. 2). All three of the dipterocarp species included in the study were among the species with the thickest bark. *Hopea odorata*, the dominant canopy species in the 50-ha plot (BUNYAVEJCHEWIN ET AL. 2001), had the third thickest bark among the 11 study species based on the fitted power function (5.6 mm in an individual of 5 cm DBH).

The study species showed considerable variation in their regeneration status based on the two metrics we used (Table 2). Values of R ranged from 0.71 for *Tetrameles nudiflora* to 0.05 for *Hopea odorata*. Four species (*Baccaurea ramiflora*, *Neolitsea obtusifolia*, *Polyalthia viridis*, and *Persea* sp.) had almost identical R values (0.20–0.22). The shape parameters of the Weibull probability distributions fit to the size-class data for each study species showed a similar pattern. *Tetrameles nudiflora* (0.66) had the lowest c value and *Hopea odorata* (4.09) had the highest.

The relationship between predicted bark thickness of a 5-cm-DBH tree and the regeneration status of the population was not significant for either the regeneration ratio, R ($r^2 = 0.056$, $F = 0.57$, $P = 0.461$) or the Weibull shape parameter, c ($r^2 = 0.029$, $F = 0.27$, $P = 0.617$) (Fig. 3). The two pioneer species, *Macaranga siamensis* and

Table 1. Summary of non-linear regression analyses of bark thickness vs. DBH for 11 study species from the seasonal dry evergreen forest at HKK. All regressions are based on the power function, $Y = \alpha X^\beta$, where Y is bark thickness and X is DBH. Bark thickness for a tree of 5 cm DBH was predicted using the fitted power function.

Species	α	β	R^2	Bark thickness (mm) at 5 cm DBH
<i>Baccaurea ramiflora</i> Lour.	1.2333	0.2472	0.230	1.8
<i>Macaranga siamensis</i> S. J. Davies	0.6943	0.7549	0.800	2.3
<i>Saccopetalum lineatum</i> Craib	1.1501	0.5363	0.616	2.7
<i>Persea</i> sp.	0.8309	0.7892	0.889	3.0
<i>Garcinia speciosa</i> Wall.	2.1434	0.3831	0.621	4.0
<i>Tetrameles nudiflora</i> R. Br.	2.1138	0.4337	0.823	4.2
<i>Neolitsea obtusifolia</i> Merrill	2.1003	0.4542	0.499	4.4
<i>Dipterocarpus alatus</i> Roxb. ex G. Don.	1.5467	0.6536	0.840	4.4
<i>Hopea odorata</i> Roxb.	2.8120	0.4315	0.872	5.6
<i>Vatica odorata</i> (Griff.) Sym.	2.2378	0.4770	0.600	5.8
<i>Polyalthia viridis</i> Craib	2.4935	0.5809	0.961	6.4

Table 2. Summary of regeneration status metrics for the 11 study species from the seasonal dry evergreen forest at HKK. Species are arranged in order of increasing bark thickness for a 5 cm DBH stem. The regeneration ration, R , is the ratio of trees < 5 cm DBH to the total population for each species. The Weibull distribution parameter, c , describes the shape of the Weibull function fitted to the diameter distribution (see Methods for details).

Species	R	c
<i>Macaranga siamensis</i>	0.69	0.92
<i>Baccaurea ramiflora</i>	0.20	1.63
<i>Saccopetalum lineatum</i>	0.20	1.05
<i>Persea</i> sp.	0.09	2.91
<i>Garcinia speciosa</i>	0.39	1.00
<i>Tetrameles nudiflora</i>	0.71	0.66
<i>Neolitsea obtusifolia</i>	0.22	1.16
<i>Dipterocarpus alatus</i>	0.14	1.01
<i>Hopea odorata</i>	0.05	4.09
<i>Vatica cinerea</i>	0.41	0.89
<i>Polyalthia viridis</i>	0.22	1.47

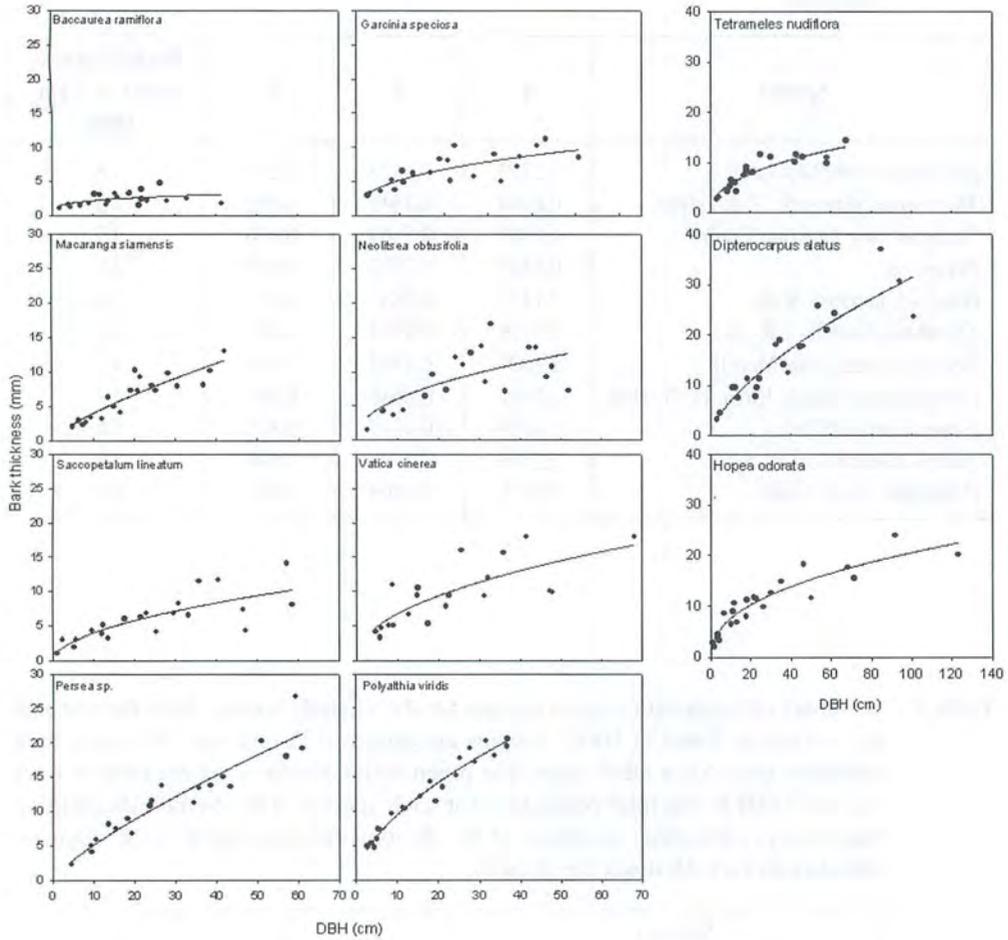


Figure 1. The relationship between bark thickness (mm) and diameter at breast height (DBH; cm) for 11 sympatric tree species from seasonal evergreen forest at the Huai Kha Khaeng Wildlife Sanctuary in western Thailand. The lines in each panel are the best-fit allometric model for each species. The species are arranged in order of increasing bark thickness (from top to bottom)

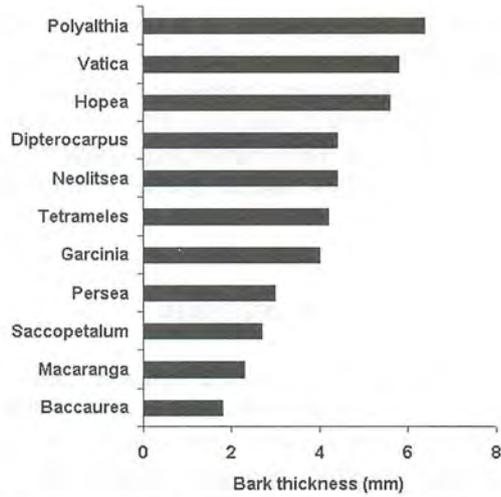


Figure 2. Bark thickness for an individual of 5 cm DBH for each tree species based on the species-specific allometric relationship between bark thickness and DBH (see Table 1).

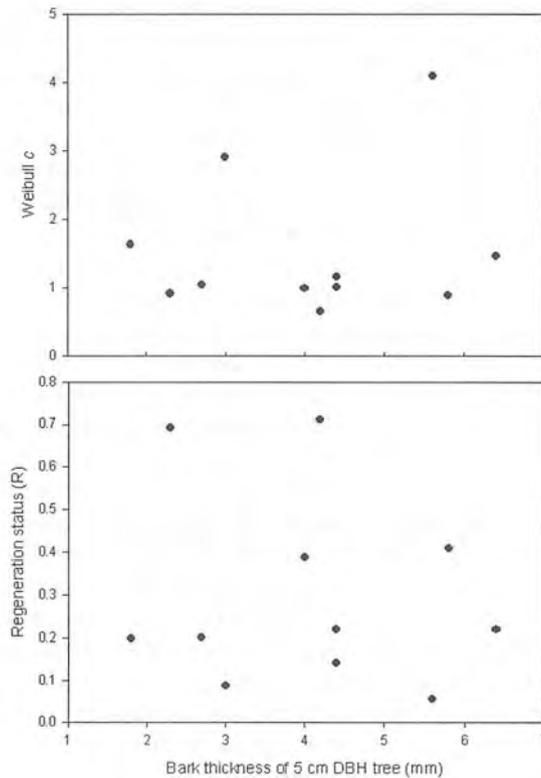


Figure 3. The relationship between bark thickness of a 5 cm DBH individual and two measures of reproductive status for each species (upper panel: Weibull shape parameter c ; lower panel, R , the ratio of trees < 5 cm DBH to the total population for each species).

Tetrameles nudiflora, had the highest values of R (both ~ 0.7 , indicating that 70% of all individuals were < 5 cm DBH), but had very different predicted bark thicknesses (1.2 mm vs. 4.3 mm). The four species (*Baccaurea ramiflora*, *Neolitsea obtusifolia*, *Saccopetalum lineatum*, and *Polyalthia viridis*) with R -values of ~ 0.2 exhibited a 3-fold range of predicted bark thickness for individuals 5 cm DBH that included both the species with the thinnest bark (1.8 mm in *Baccaurea ramiflora*) and the species with the thickest bark (6.4 mm in *Polyalthia viridis*).

DISCUSSION

In the past two decades, fires have been a common feature of the HKK landscape. Fires burned through some or all of the 50-ha plot in 1993, 1998, and 2005. While there are no data on historical fire frequencies in the area, anecdotal evidence suggests that fire frequency has increased (and fire return interval decreased) in recent decades for most sites at HKK. There is considerable concern that increased fire frequency will shift the composition of the seasonal evergreen forest toward a more deciduous forest formation dominated by species commonly associated with mixed deciduous or deciduous dipterocarp forest types. However, the data from this study do not support the hypothesis that the increased fire frequency of recent decades has led to recruitment failure of thin-barked, fire-sensitive tree species in the seasonal evergreen forest at HKK. It is true that many tree species in the seasonal evergreen forest at the 50-ha plot are not regenerating *in situ*. The most notable example is the dominant canopy species, *Hopea odorata*. *Hopea odorata* accounts for $> 10\%$ of the basal area on the 50-ha plot, but $< 0.5\%$ of the total number of individuals on the plot (BUNYAVEJCHEWIN *ET AL.*, 2001). The mean DBH of the *Hopea odorata* in the plot is 88 cm; however, only 18 of the 330 individuals are < 5 cm DBH. A common explanation for this pattern is that *Hopea odorata* is a fire-sensitive species and that its regeneration is killed by low-intensity surface fires (*e.g.*, STOTT, 1988; RABINOWITZ, 1990). However, when compared with other common tree species in the 50-ha plot, *Hopea odorata* has relatively thick bark. Indeed, *Hopea odorata* has much thicker bark than species such as *Baccaurea ramiflora* that have extremely abundant regeneration in < 5 cm DBH size class. This suggests that sensitivity to fire-induced mortality of juveniles, based on comparisons of relative bark thickness of individuals of 5 cm DBH, is not the primary factor controlling regeneration success in the seasonal evergreen forest.

One source of uncertainty arises from the fact that the 11 species that we examined represent a small fraction of the 250 species that occur in the 50-ha plot. It may be that these 11 species do not represent the range of species-specific responses and population structures within the seasonal evergreen forest. However, while it would be extremely useful to expand this study to include more species from the 50-ha plot, we believe that the species that we chose broadly represent the spectrum of life histories, population structures, and bark thicknesses that are found on the plot. In addition, the 11 species account for $\sim 23\%$ of the trees on the plot and $\sim 43\%$ of the plot basal area and should, therefore, be reasonable indicators of seasonal evergreen forest sensitivity to fire.

There are several potential explanations for the disparity between the bark thickness and population structure data. First, the observed regeneration failure of some species in the seasonal evergreen forest may be due to the long-term disturbance history and stand

development trajectory of the seasonal evergreen forest at HKK. In the early to mid-1800s an intense, large-scale disturbance occurred that severely impacted a contiguous patch of ~300 ha of forest in and around the location of the 50-ha plot (BAKER *ET AL.*, 2005). In the aftermath of that disturbance, a massive pulse of recruitment occurred. Many of the dominant canopy species in the forest today, such as *Hopea*, *Persea* sp., *Dipterocarpus alatus*, *Neolitsea obtusifolia*, and *Saccopetalum lineatum*, established at that time. In the subsequent 150 years small-scale disturbances of varying intensity created small- and medium-sized gaps in the seasonal evergreen forest allowing regeneration of gap-dependent species, such as *Macaranga siamensis* and *Tetrameles nudiflora*, and recruitment from the seedling bank of the more shade-tolerant species, such as *Saccopetalum lineatum* and *Garcinia speciosa*, that established in the wake of the earlier catastrophic disturbance.

Another possible explanation for the poor relationship between bark thickness and population structure is that some of the study species may be fire-sensitive but possess other adaptations that make them resilient to fire. In particular, some species may be able to resprout following loss of above-ground biomass from fire-induced heating of the cambium (i.e., top-kill). For example, *Baccaurea ramiflora*, which has very thin bark, may be sensitive to fire-induced mortality of the stem but be able to resprout vigorously soon after the fire. This would allow large numbers of small trees to persist in the population even under a regime of increasing fire frequency. Anecdotal evidence supports this possibility. In early 1998 fires burned through the entire 50-ha plot leading to widespread mortality of seedlings, saplings, and small trees. In the months that followed the fires we made note of which species showed evidence of resprouting. We found that all of the common species within the 50-ha plot showed the ability to resprout. The sole exception was *Macaranga siamensis*, for which we found widespread mortality but no evidence of resprouting. This raises a third possible explanation for the disparity in bark thickness and population structure patterns.

Macaranga siamensis and *Tetrameles nudiflora* had the highest ratios of juveniles to adults among the 11 study species, but *Macaranga siamensis* had the thinnest bark and *Tetrameles nudiflora* had an intermediate bark thickness. The inability of *Macaranga siamensis* to sprout means that its juveniles must regenerate *after* fires. Both *Macaranga siamensis* and *Tetrameles nudiflora* are extreme heliophiles that depend on forest gaps to regenerate. *Macaranga siamensis* has bird-dispersed seed that can persist in the soil seed bank for years, while *Tetrameles nudiflora* produces large crops of wind-dispersed seeds every year. The fires that have occurred at the 50-ha plot in the past decade are relatively low intensity and primarily kill seedlings and saplings. However, where local fire intensity is high due to accumulations of woody debris, large trees may also be killed indirectly when the fires weaken the base of the tree and make it more susceptible to being knocked over by the strong winds that often accompany the onset of the annual monsoon. The death of such large trees often leads to the formation of large gaps in the forest that pioneer species such as *Macaranga siamensis* and *Tetrameles nudiflora* rapidly colonize in great numbers. As a consequence the population structure of both species, when averaged over an area as large as the 50-ha plot, is dominated by small trees that occupy a shifting mosaic of recently disturbed areas.

CONCLUSION

Fire is an integral part of continental Southeast Asia's forest ecosystems. Where large, unfragmented landscapes occur, several forest types are often found together in mosaic fashion. Ecologists and conservationists have expressed concerns that increasing fire frequencies due to increasing fragmentation and anthropogenic ignition sources will lead to shifts in the relative abundance of these forest types. In particular, increasing fire frequency is expected to lead to the reduction or elimination of putatively fire-sensitive evergreen forests and expansion of fire-adapted mixed deciduous and deciduous dipterocarp forests. Our study of bark thickness and population structures in seasonal evergreen forest at HKK where several fires have occurred in the past decade provides little support for this hypothesis. Bark thickness, a proxy measure of fire sensitivity, was unrelated to population structure among the study species. There remains much to learn of the fire ecology of these forests and the contribution of disturbance, life histories, and environmental factors to determining the relative abundance of the different forest types across the landscapes of Southeast Asia. Empirical studies that examine the short- and long-term responses of the different forest types to fires are urgently needed to improve our understanding of the role of fire in these ecosystems.

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