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Effects of Past Burning Frequency on Woody Plant Structure and Composition in Dry Dipterocarp Forest

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ABSTRACT

Anthropogenic burning in dry dipterocarp forests has become a common phenomenon throughout Thailand. Too frequent fires may affect plant species composition, soil properties and processes, and nutrient dynamics, thereby impacting upon ecosystem productivity and sustainability. Conversely, complete fire exclusion, may result in changes to ecosystem components, and an increased risk of high-intensity wildfire. This study aimed to investigate the effects of different burning histories (7, 2, 1 or 0 fires in the past 10 years) and prescribed fire on sites with different past burning regimes on woody plant structure and composition in a dry dipterocarp forest at Huai Kha Khaeng Wildlife Sanctuary, Thailand. Each burning history comprised of three 30m×30m plots for the measurement of overstorey vegetation. Four 4m×4m subplots were set up within the plot to assess saplings and seedlings. These investigations were measured both pre-burn and one-year post-burn. The study revealed that the structure of stands that had been frequently burned in the past differed from that of the less frequently burned stands. Moreover, the species composition of the small-sized overstorey vegetation in the frequently burned stands also differed significantly from that of the other stands. The species composition of the unburned site differed from that of the other burning regimes only modestly. Frequent burning also resulted in a reduction of the sprouting capacity of seedlings and saplings, inhibited regeneration and, consequently, resulted in a disproportionate representation of individuals of certain tree species at the various stages of development. Therefore, fire-free intervals of at least 6-7 years should be introduced to facilitate the successful recruitment of young trees.

Keywords: Burning frequency, Dry dipterocarp forest, Huai Kha Khaeng Wildlife Sanctuary, Prescribed fire, Woody plant

INTRODUCTION

In many parts of the world, fire maintains the existence of forest ecosystems (Pyne 2001). However, the response of vegetation to fire is highly variable. Crown fires can kill mature trees and initiate a recovery process that may take several decades or even centuries to complete. In grassland communities, recovery from fire may be so rapid that the effects may disappear within a matter of months. Fire behaviour, fire duration, the pattern of fuel consumption, and the amount of subsurface heating all influence injury and mortality of plants, and tree population subsequent recovery (Miller 2000). Plant species vary greatly in terms of their fire resistance and recovery mechanisms, namely, their sprouting capacity, life history, timing of reproduction and recruitment, evolution of fire-survival traits such as a thick bark, and flammability (Bond and Wilgen 1996).

Dry dipterocarp forest (DDF) is a fire-dependent ecosystem (Sabhasri *et al*. 1968, Kutintara 1975, Mueller-Dombois and Goldammer 1990). The DDFs have a long history of fire disturbance, derived from both natural and anthropogenic sources. Fires are lit annually for various reasons, such as, for gathering non-timber forest products (NTFPs) and to facilitate hunting (Akaakara 2000). Burning usually occurs between January and April when the annual available surface fuel, i.e., leaf litter is greatest, due to the earlier leaf fall by the deciduous species found in these forests (Figure 1). The desiccation of grasses also provides additional dry fuels. Some DDFs in protected areas by contrast have long been unburned, as a result of fire prevention activities.

From an ecological perspective, the reduction in fire frequency may cause structural changes to DDF stands, including increased tree density, canopy cover, succession towards more fire-sensitive and shade tolerant overstorey species. However, too frequent burns may result in a considerable loss of nutrients and plant species, resulting in ecosystem degradation (Sukwong and Dhamanityakul 1977). Therefore, an appropriate burning frequency is crucial for the maintenance of ecosystem functions in DDF. In recent decades, the effects of fire on the vegetation of DDF in Thailand have been investigated by a number of researchers (Sukwong and Dhamanityakul 1977, Sunyaarch 1989, Kanjanavanit 1992, Wachrinrat 2000, Samran and Tongtan 2002, Himmapan 2004). However, the afore-mentioned studies were only concerned with single fire events. The effect of burning frequency, which is crucial for plant species persistence, composition and structure, is poorly understood and needs to be assessed to gain a better understanding of the role of fire, especially burning frequency, on vegetation dynamics in this fire-dependent ecosystem.

This paper presents the woody plant structure and compositions associated with the different past burning regimes in DDF at Huai Kha Khaeng Wildlife Sanctuary (HKK), Thailand. Also, this paper attempts to determine the effects of prescribed fires on the woody plant structure and composition of stands with different burning frequency histories. Specifically, the hypotheses tested were that, with increasing burning frequencies, the rates of establishment of woody plants decline and mortality increases, and that frequent burning reduces the species richness and diversity of woody plant species in DDF.

Figure 1 The dry dipterocarp forest in rainy season and dry season.

MATERIALS AND METHODS

Study area

The study was conducted in the HKK, located approximately 350 km northwest of Bangkok in Thailand. The study site was located in DDF, in the northeast region of the sanctuary (Figure 2). The region has a tropical monsoonal climate with dry season extending from November to April, and a wet season from May to October. The average annual rainfall is 1348 mm year-1. The mean daily temperature varies from 23.2˚C in December to 30.9˚C in April. The mean relative humidity is 89.1%, which varies from 79% in April to 93% in September (Forest Fire Research Center 2006). The elevation of the study area ranges from 300-400 m a.s.l. The DDF is dominated by deciduous tree species belonging to the Dipterocarpaceae, such as, *Shorea obtusa*, *S. siamensis*, *Dipterocarpus tuberculatus*, and to the Leguminosae, such as *Xylia kerrii* and *Sindora siamensis*. The understorey consists mainly of a grass layer dominated by *Heteropogon contortus* and *Imperata cylindrica* as well as other shrubs, herbs, and saplings and seedlings of overstorey tree species (Forest Research Center 1997).

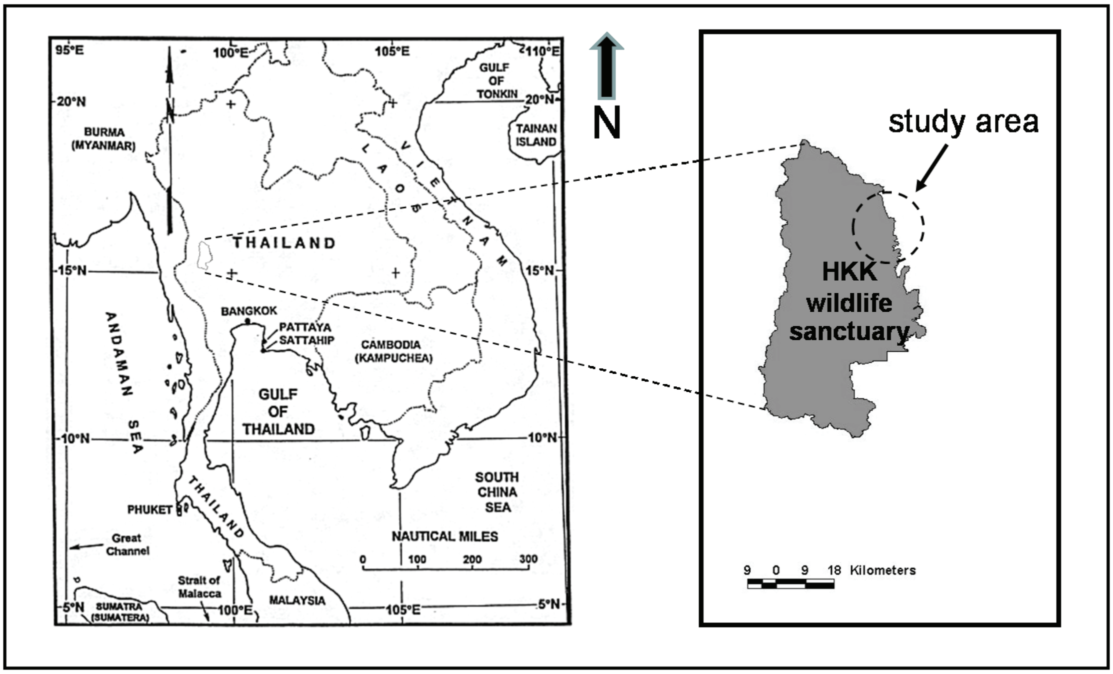

Figure 2 Location of the experimental study area in dry dipterocarp forest, Huai Kha Khaeng Wildlife Sanctuary, Thailand..

Fire history reconstruction

The past burning history was reconstructed for the study area by mapping burned areas using fire reports from the National Parks, Wildlife and Plant Conservation Department, and a series of satellite images spanning a 10-yr period from 1995 to 2004. As a result, 4 different burning histories were identified. These included fire frequencies of 7, 2, 1 and 0 fires over the past 10 years, which are subsequently referred to as frequent (FB), infrequent (IB), rare (RB) and unburned (CB), respectively. The times since the last fire in relation to these burning regimes were 1, 3, 7, and 10 years, for FB, IB, RB, and CB, respectively.

For experimental purposes, three replicate plots were established for each burning regime (treatment). It was not possible to replicate patches of the same fire frequency and time since last fire in the landscape, so that treatments were not interspersed in space. Therefore, the plots represent pseudo-replications (Hurlbert 1984) of the same fire event and history. Within each treatment, plots were approximately 300-500m apart. Within the mapped areas of different fire frequencies, all plots were selected to represent the same geologic parent material, soil unit, and forest type. They were also located at similar elevation and topography.

Burning protocol

Three experimental plots 50m×50m were set up in each treatment. These plots contained an inner plot of 30m×30m for detailed monitoring, and a 10-m wide buffer strip that permitted measurements to be made across the entire inner plot without edge effects. Fire lines were established around the margins of each 50m×50m plot. With the exception of the unburned area (CB), experimental burning was carried out in the nine plots during the period from 28th December 2004 to 9th January 2005. Three-strip burning techniques (each strip approximately 16 m wide) were applied for the experimental burning. The experimental burns were low-intensity surface fires, with flame lengths of about 1.5 m. The rate of fire spread ranged from 1.3-2.6 m min^{-1}, whereas the frontal fire line intensity was generally less than 500 kW m^{-1} (Table 1) (Wanthongchai *et al.* 2008).

Table 1 Quantitative fire behaviour characteristics observed for the experimental fires at sites of different fire frequency plots; frequently burned site (FB), infrequently burned (IB), and rarely burned (RB).

Fire characteristics	Fire frequency plots [1]		
	RB	**IB**	**FB**
Rate of spread ($m\ min^{-1}$)	1.3 [a] (0.2)	2.6 [b] (0.3)	2.7 [b] (1.0)
Flame length (m)	1.27 [a] (0.11)	1.53 [a] (0.09)	1.51 [a] (0.22)
Fireline intensity ($kW\ m^{-1}$)	291 [a] (43)	467 [a] (62)	361 [a] (150)

Remarks: [1]Different letters (a, b) indicate significant differences (ANOVA, $P<0.05$, followed by Duncan's multiple range test) in the fire characteristics between the fire frequency plots. Standard errors are given in parentheses. Flame length and fire line intensity were calculated using Byram's formula (1959).

Sampling procedure

The inner 30m×30m plot was further divided into four 15m×15m sections. The overstorey vegetation, consisting of trees with diameter at breast height (dbh) at least 4.5 cm, was monitored across the whole section. One 4m×4 m subplot was set up in the middle of each section to assess saplings (woody plants at least 1.3 m tall, but dbh less than 4.5 cm), and seedlings (woody plant less than 1.3 m tall). All woody plant species and life forms were identified according to Smitinand (2001).

Prior to burning, each tree was marked with a numbered aluminium tag, and the dbh was measured. The overstory crown area was determined by projecting the crown perimeter to the ground on 2 perpendicular axes, by measuring the crown radii along these axes and calculating the crown area using the equation to determine the area of an ellipse. Tree mortality was assessed in the year after the burning experiment. The mean overstorey canopy cover and the leaf area index were estimated using a hemispherical photography technique by mounting a fisheye lens (8 mm Nikon lens, Japan) on a digital camera (Nikon Coolpix 4500, Japan). The photograph position was located in the middle of each of the 15m×15m sections. Sapling and seedling were identified to the species level. The diameter at ground level (d_0), density, number of stems per individual, height and coverage were recorded both pre-burn and one year post-burn for these understory woody plants. The sapling and seedling coverage was calculated from crown projection areas.

Data analysis

1. Vegetation structure

Tree mortality was examined one year after the fire. The crown projection area, cover, basal area and stem density were compared between the burning regimes, and for pre-burn and post-burn. An estimated crown cover and leaf area index (LAI) of the overstorey was analysed using the Hemiview software (Hemiview 2.1, Delta-T Devices Ltd., Burwell, Cambridge, UK).

The relative abundance of trees was calculated from stand basal area. The importance value index (IVI) was also evaluated. The IVI integrates three important phyto-sociological measures, namely, density, frequency and basal area of species abundance. Logistic regression procedures were employed to evaluate the probability of tree mortality for some important tree species as functions of fire frequency and tree dbh, using JMP IN software, version 4.0.4 (SAS Institute Inc 2001). A log-likelihood statistic was used to test the null hypothesis that fire frequency and tree dbh did not affect the probability of tree mortality. Wald statistics were used to test the statistical significance of individual linear predictors. Predictor variables were considered significant if $P<0.05$.

2. Vegetation composition

The Shannon-Wiener index (H') was applied to express the effects of different past burning regimes, as well as the effects of prescribed fire, on woody plant diversity. This was done using the Species Diversity & Richness software, version 2.64 (Seaby and Henderson 2006). The Shannon-Wiener index was calculated as follows: $H' = -\sum pi \ln p_i$, where H' is the Shannon-Wiener index, p_i is the proportion of species i in the community and ln is natural logarithm.

To incorporate species composition into the analysis, the multi-response permutation procedure (MRPP) was introduced to compare the past burning regimes, as well as the effects of burning (before and after burns). The MRPP is a non-parametric procedure to test the hypothesis that there is no difference between samples in the overstory composition. Sørensen (Bray-Curtis) distances, which are less prone to exaggerating the influence of outliers (McCune and Mefford 1999), were used to determine the dissimilarity of species composition of the past burning regimes. The chance-corrected within-group agreement (A) describes within-group homogeneity, compared to random expectation. When all items within a group are identical, then A=1, the highest possible value for A. If heterogeneity within groups equals chance expectation, then A=0. If there is less agreement within groups than might be expected by chance, then A<0. In community ecology, values for A are commonly below 0.1, and A>0.3 is considered relatively high (McCune and Mefford 1999). Pair-wise comparisons were utilised whenever significant differences in species composition ($A\geq0.3$) were found. To determine the species that mark the differences between burning regimes, both prior to and after the burning experiment, an indicator species analysis (Monte Carlo test) was conducted. Both the MRPP and indicator species analysis were carried out using the PC-ORD software, version 4 (McCune and Mefford 1999).

3. Statistical analysis

The data were processed and analysed using SPSS® 13.0 for Windows (SPSS Inc.

2005). All of variables were first tested for homogeneity of variance (Levene's test) and normal distribution (Kolmogorov-Smirnov), to meet the requirements of ANOVA. Where these requirements were not met, the data were transformed using either common logarithm or square root forms. Statistically significant differences between past burning regimes ($P<0.05$) were further analysed using Duncan's multiple range test. If the afore-mentioned transformations of the data were not sufficient to meet the requirements of ANOVA, an analogous non-parametric statistical test (Kruskal-Wallis test) was applied, followed by a Mann-Whitney U-test. A paired-sample *t-test* was used to ascertain the effect of burning on vegetation structure parameters within each burning regime.

RESULTS AND DISCUSSION

Effects of different past burning regimes on woody plant structure

Tree density, basal area, canopy area and LAI increased with the length of fire-free interval (Table 2 and Figure 3), pointing to the influence of the past burning regime. However, the average tree dbh did not differ significantly between the burning regimes. The crown cover was more than 70% on the CB site, compared to only approximately 40% on the FB site. On the unburned (CB) and the less frequently burned (IB, RB) sites, the IVI showed that *S. obtusa* was the most important overstorey species (basal area 27-30%), followed by *S. siamensis* (basal area 14-28%). On the frequently burned (FB) sites, *S. siamensis* was the most important species (basal area more than 50%) (Table 3).

Prior to the burning experiment, the stocking density of saplings and seedlings differed significantly between the past burning regimes. The seedling and sapling density was significantly lower on the FB sites than on the less frequently burned sites (Tables 4 and 5). The d_0, and the corresponding basal area, also increased with a decreasing fire frequency, from 0.6 m^2 ha^{-1} on the FB site to 3.3, 4.0, and 4.3 m^2 ha^{-1} on the IB, CB and RB sites, respectively. The majority of the sapling d_0 values, both prior to and after burning, were between 20-40 mm, whereas the seedling d_0 values were concentrated between 0-5 mm (Figure 4), both prior to and after burning.

The tree dbh distributions (Figure 4) showed that a high proportion of the trees present belonged to the smallest diameter class (4.5-10 cm). The number of individuals decreased with an increase in dbh, irrespective of the past burning regime. The number of trees in the smallest diameter class was significantly lowest only on the FB site ($P<0.05$).

Table 2 Overstorey tree characteristics of each burning regime; unburned (CB), frequently burned (FB), infrequently burned (IB) and rarely burned (RB). Standard errors are given in parentheses.

	Burning regime[1]				*P*- value
	FB	**IB**	**RB**	**CB**	
Tree density (indiv. ha^{-1})	667^{a} (54.7)	1344^{b} (129.0)	1311^{b} (108.2)	1558^{b} (113.0)	0.000
dbh (cm)	14.0 (1.5)	11.1 (0.6)	11.4 (0.5)	11.6 (0.5)	0.092
Basal area (m^2 ha^{-1})	12.9^{a} (2.1)	17.2^{ab} (1.4)	19.4^{b} (1.4)	23.6^{c} (1.7)	0.000
Crown area (m^2 ha^{-1})	8221.7^{a} (1827.0)	9984.4^{ab} (783.8)	12590.1^{b} (965.2)	16505.8^{c} (1289.5)	0.000

Remarks: [1]Different letters (a, b, c) indicate significant differences (ANOVA, $P<0.05$, followed by Duncan's multiple range test or Kruskal-Wallis test followed by Mann-Whitney U-test) in the tree structure parameters associated with each of the past burning regimes.

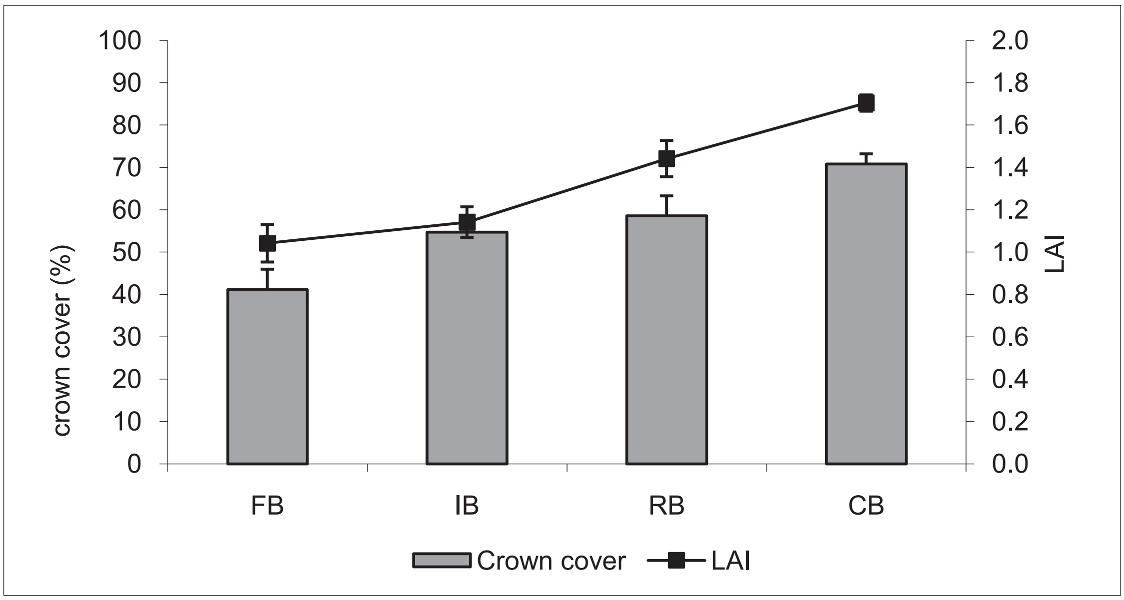

Figure 3 Overstorey crown cover and leaf area indices (mean ± SE) at the sites of the different past burning regimes; unburned (CB), frequently burned (FB), infrequently burned (IB) and rarely burned (RB).

Table 3 Relative density (RD), relative dominance (RDo), relative frequency (RF) and importance value index (IVI) of 5 important trees species on the frequently burned site (FB), infrequently burned (IB), rarely burned (RB), and unburned (CB) in the dry dipterocarp forest, Huai Kha Khaeng Wildlife Sanctuary.

Burning regime	No.	Species	RD (%)	RDo (%)	RF (%)	IVI
FB	1	*Shorea siamensis* Miq.	43.65	54.99	15.00	113.64
	2	*Gardinia obtusifolia* Roxb.	7.18	1.85	11.25	20.28
	3	*Sindora siamensis* Teijsm.ex.Miq.	5.52	5.81	6.25	17.59
	4	*Antidesma ghasembilla* Gaertn.	7.18	2.38	7.50	17.06
	5	*Xylia xylocarpa* Taub.	4.97	2.88	8.75	16.60
IB	1	*Shorea obtusa* Wall.	26.72	27.31	10.08	64.11
	2	*Shorea siamensis* Miq.	13.50	21.75	8.40	43.65
	3	*Aporosa ficifolia* Baill.	14.60	9.23	9.24	33.08
	4	*Dipterocarpus tuberculatus* Roxb.	6.34	15.08	3.36	24.78
	5	*Buchanania latifolia* Roxb.	6.06	5.03	6.72	17.82
RB	1	*Shorea obtusa* Wall.	27.12	28.41	9.02	64.55
	2	*Shorea siamensis* Miq.	15.25	13.98	6.02	35.25
	3	*Dipterocarpus tuberculatus* Roxb.	5.93	11.64	3.76	21.33
	4	*Aporosa ficifolia* Baill.	5.37	5.52	6.02	16.90
	5	*Dalbergia cultrata* Grah. Ex Benth.	3.39	3.90	4.51	11.80
CB	1	*Shorea obtusa* Wall.	31.73	32.90	7.73	72.36
	2	*Shorea siamensis* Miq.	16.58	28.27	7.73	52.57
	3	*Xylia xylocarpa* Taub.	6.24	4.01	5.80	16.04
	4	*Canarium subulatum* Guill.	3.03	6.70	5.31	15.04
	5	*Buchanania latifolia* Roxb.	3.03	3.91	4.35	11.29

Table 4 Characteristics of sapling populations in plots of different past burning regimes (unburned (CB), frequently burned (FB), infrequently burned (IB) and rarely burned (RB)), before and after experimental burning. Standard errors are given in parentheses.

	Burning regime[1]							
	FB		IB		RB		CB	
	Before	After	Before	After	Before	After	Before	After
Density	573^{Aa}	833^{Aa}	2969^{Ab}	1927^{Aa}	3385^{Ab}	1875^{Ba}	4570^{Ab}	3906^{Ab}
(indiv. ha^{-1})	(210)	(247)	(746)	(740)	(862)	(576)	(705)	(796)
D_0	25.1^{Aa}	25.5^{Aa}	35.1^{Ab}	37.0^{Aa}	38.2^{Ab}	32.1^{Aa}	31.3^{Aab}	34.1^{Aa}
(mm)	(2.6)	(2.0)	(2.1)	(5.3)	(3.7)	(3.3)	(1.6)	(2.0)
Ht	1.6^{Aa}	1.7^{Aa}	2.2^{Aab}	2.3^{Aa}	3.1^{Ac}	3.0^{Aa}	2.6^{Abc}	2.4^{Aa}
(m)	(0.2)	(0.1)	(0.2)	(0.3)	(0.3)	(0.4)	(0.2)	(0.2)
Basal area	0.6^{Aa}	0.7^{Aa}	3.3^{Ab}	1.9^{Aa}	4.3^{Ab}	2.2^{Ba}	4.0^{Ab}	4.0^{Bb}
(m^2 ha^{-1})	(0.3)	(0.3)	(0.9)	(0.4)	(0.9)	(0.7)	(0.6)	(0.9)
Cover	4.3^{Aa}	7.2^{Aa}	20.2^{Aab}	11.6^{Aa}	45.1^{Abc}	22.3^{Aa}	61.4^{Ac}	63.3^{Ab}
(%)	(1.6)	(2.2)	(4.6)	(3.5)	(13.5)	(7.8)	(16.0)	(26.9)

Remark: [1] Identical lower case letters indicate no significant difference between treatments within a sampling period (ANOVA, *P<0.05,* followed by Duncan's multiple range test or Kruskal-Wallis test followed by Mann-Whitney U-test). Identical capital letters indicate no significant difference between treatments of each burning regime either before burning or 1 year after burning (paired *t*-test, *P*<0.05).

Table 5 Characteristics of seedling populations in plots of different past burning regimes (unburned (CB), frequently burned (FB), infrequently burned (IB) and rarely burned (RB)), before and after burning. Standard errors are given in parentheses.

	Burning regime[1]							
	FB		IB		RB		CB	
	Before	After	Before	After	Before	After	Before	After
Density	13438^{Aa}	16823^{Ba}	22917^{Abc}	26771^{Bb}	17292^{Aab}	28698^{Bb}	28711^{Ac}	40365^{Bc}
(indiv. ha^{-1})	(1622)	(1755)	(2308)	(2651)	(2662)	(4110)	(2561)	(3662)
Density	40208^{Ab}	41667^{Aa}	31042^{Aab}	53750^{Ba}	20521^{Aa}	49583^{Ba}	40273^{Ab}	61354^{Ba}
(stems ha^{-1})	(6305)	(5404)	(2978)	(5510)	(2520)	(6365)	(3875)	(6122)
Ht	0.44^{Aa}	0.40^{Aa}	0.36^{Aa}	0.33^{Aa}	0.40^{Aa}	0.35^{Aa}	0.41^{Aa}	0.31^{Ba}
(m)	(0.03)	(0.02)	(0.03)	(0.03)	(0.03)	(0.02)	(0.02)	(0.02)
Cover	18.2^{Abc}	24.1^{Aa}	12.5^{Aab}	31.3^{Ba}	8.5^{Aa}	32.3^{Ba}	21.7^{Ac}	37.4^{Ba}
(%)	(2.5)	(4.5)	(2.0)	(4.3)	(2.3)	(4.4)	(3.2)	(4.2)

Remark: [1] Identical lower case letters indicate no significant difference between treatments within a sampling period (ANOVA, *P<0.05,* followed by Duncan's multiple range test or Kruskal-Wallis test followed by Mann-Whitney U-test). Identical capital letters indicate no significant difference between treatments of each burning regime either before burning or 1 year after burning (paired *t*-test, *P*<0.05).

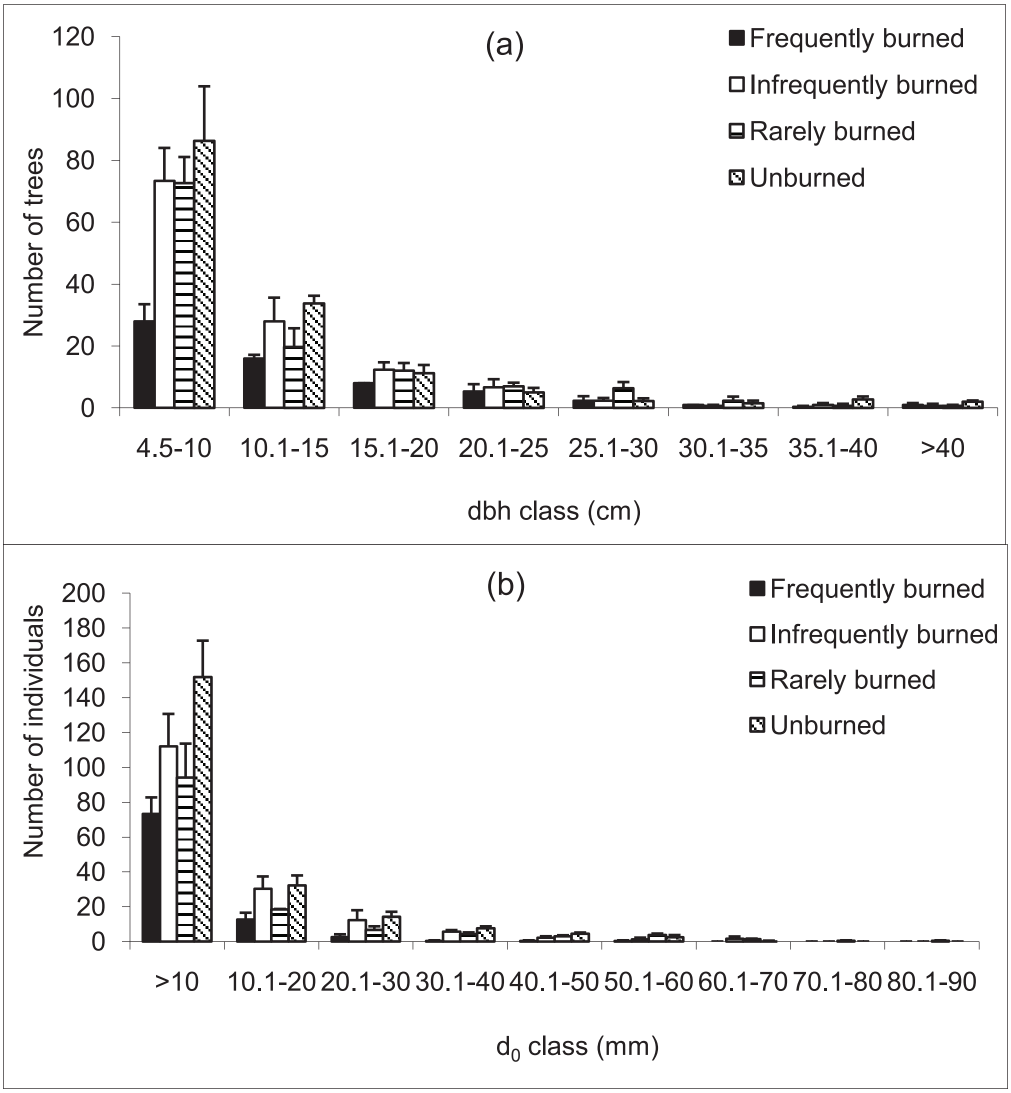

Figure 4 Diameter distribution (mean ± SE) of the tree (a) and diameter at ground level (d0) of young trees (seedlings and saplings) (b) in the different past burning regimes.

Effects of different past burning regimes on woody plant composition

A total of 54 overstorey species was found in this study (Table 6), but only 25 species were found on the FB site, with the number of species increasing to 33, 43 and 51 species at the IB, RB and CB sites, respectively. The *H′* value, however, did not differ significantly between the past burning regimes. The MRPP revealed that the overstorey species composition did differ between the past burning regimes (A=0.32, P<0.005). Further, pair-wise comparisons revealed that the species composition of the IB, RB and CB sites broadly overlapped (A<0.1, P>0.05), whereas the species composition of the FB site differed significantly from the others (A>0.3, P<0.05) (Table 7). An indicator species analysis revealed that there were certain species associated with specific burning regimes (observed IV>40, P<0.05).

For example, *S. obtusa, Canarium subulatum, Xylia xylocarpa* and *Aposula villosa* were most abundant on the CB site. By contrast, the overstorey species found at all burning regimes (observed IV<40, P>0.05) were *S. siamensis, Pterocarpus macrocarpus, Grewia eriocarpa, Terminalia alata, Dillenia spp*. and *Lannea coromandelica* (Table 8).

A total of 37 different species was recorded as saplings prior to burning. Only 7 of these were found on the FB site, while the number of species present as saplings on the IB, RB and CB sites was 15, 16 and 16 species, respectively. Likewise, of the total number of 66 species present amongst the seedlings prior to burning, 30 were recorded on the FB site, whereas 37, 39, and 42 species were found on the IB, RB and CB sites, respectively. The pre-burn H' of the saplings was lowest on the FB site (0.6) and highest on the RB site (1.9) (P<0.05). However, in the year following the burn, H' of the understory woody plants did not differ significantly between the burning regimes.

Table 6 Tree species observed on the sites of the different past burning regimes; frequently burned (FB), infrequently burned (IB), rarely burned (RB) and unburned (CB) in the dry dipterocarp forest, Huai Kha Khaeng Wildlife Sanctuary.

No.	Species	Family	FB	IB	RB	CB
1	*Anthocephalus chinensis* Rich.ex Walp.	Rubiaceae	✓	✓	✓	✓
2	*Antidesma ghasembilla* Gaertn.	Euphorbiaceae	✓	✓	✓	✓
3	*Aporosa ficifolia* Baill.	Euphorbiaceae	✓	✓	✓	✓
4	*Aporosa villosa* Baill.	Euphorbiaceae		✓	✓	✓
5	*Bauhinia* spp.	Caesalpiniaceae			✓	✓
6	*Berrya mollis* Wall. ex. Kurz	Tiliaceae	✓		✓	✓
7	*Bombax valentonii* Hochr.	Bombacaceae				✓
8	*Bridelia retusa* (L.) A.Juss.	Euphorbiaceae	✓	✓	✓	✓
9	*Buchanania latifolia* Roxb.	Anacardiaceae		✓	✓	✓
10	*Canarium subulatum* Guill.	Berseraceae	✓	✓	✓	✓
11	*Careya sphaerica* Roxb.	Barringtoniaceae	✓	✓	✓	✓
12	*Catunaregam tomentosa* (Blume ex DC.) Tirveng.	Rubiaceae			✓	✓
13	*Cratoxylum cochinchinense* (Lour.) Blume	Guttiferae				✓
14	*Cratoxylum formosum* subsp. Pruniflorum	Guttiferae			✓	✓
15	*Croton oblongifolious* Roxb.	Euphorbiaceae			✓	✓
16	*Dalbergia cultrata* Grah. Ex Benth.	Papilionaceae	✓	✓	✓	✓
17	*Dalbergia oliveri* Gamble	Papilionaceae		✓		✓
18	*Dillenia spp.*	Dilleniaceae		✓	✓	✓
19	*Diospyros ehretioides* Wall. ex. G.Don	Ebenaceae		✓		✓
20	*Diospyros ferrea* (Willd.) Bakh.	Ebenaceae	✓	✓	✓	✓
21	*Dipterocarpus obtusifolious* Teijsm. Ex. Miq.	Dipterocarpaceae			✓	✓
22	*Dipterocarpus tuberculatus* Roxb.	Dipterocarpaceae		✓	✓	✓
23	*Ellipanthus tomentosus* Kurz	Connaraceae		✓	✓	

Table 6 (Cont.)

No.	Species	Family	FB	IB	RB	CB
24	*Erythrophleum succirubrum* Ganep.	Caesalpiniaceae	✓	✓	✓	✓
25	*Flacourtia indica* (Burm.f.) Merr.	Flacourtiaceae		✓	✓	✓
26	*Garcinia spp.*	Guttiferae			✓	
27	*Gardinia obtusifolia* Roxb.	Rubiaceae	✓	✓	✓	✓
28	*Grewia eriocarpa* Juss.	Tiliaceae	✓	✓	✓	✓
29	*Haldina cordifolia* (Roxb.) Ridsdale	Rubiaceae	✓		✓	✓
30	*Heterophragma sulfureum* Kurz	Bignoniaceae	✓	✓	✓	✓
31	*Hymenodictyon excelcum* Wall.	Rubiaceae	✓			✓
32	*Lannea coromandelica* Merr.	Anacardiaceae	✓	✓	✓	✓
33	*Mammea harmandii* Kosterm.	Guttiferae		✓	✓	✓
34	*Melanorrhoea usitata* Wall.	Anacardiaceae		✓		✓
35	*Millettia leucantha* Kurz	Papilionaceae				✓
36	*Morinda coreia* Ham.	Rubiaceae			✓	✓
37	*Ochna integerrima* Merr.	Ochnaceae		✓		✓
38	*Pavetta tomentosa* Roxb. ex. Sm.	Rubiaceae				✓
39	*Phyllanthus embrica* Linn.	Euphorbiaceae				✓
40	*Pterocarpus macrocarpus* Kurz	Papilionaceae	✓	✓	✓	✓
41	*Schleichera oleosa* (Lour.) Oken	Sapindaceae		✓	✓	✓
42	*Shorea obtusa* Wall.	Dipterocarpaceae	✓	✓	✓	✓
43	*Shorea roxburghii* G. Don	Dipterocarpaceae			✓	
44	*Shorea siamensis* Miq.	Dipterocarpaceae	✓	✓	✓	✓
45	*Sindora siamensis* Teijsm.ex.Miq.	Caesalpiniaceae	✓	✓	✓	✓
46	*Spondias pinnata* (L.f.) Kurz	Anacardiaceae			✓	✓
47	*Strychnos nux-vomica* L.	Strychnaceae	✓	✓	✓	✓
48	*Terminalia alata* Heyne ex Roth	Combretaceae	✓	✓	✓	✓
49	*Terminalia bellerica* Roxb.	Combretaceae				✓
50	*Terminalia chebula* Retz.	Combretaceae	✓		✓	✓
51	*Terminalia corticosa* Pierre ex Laness.	Combretaceae	✓	✓	✓	✓
52	*Vitex glabrata* R. Br.	Verbenaceae			✓	✓
53	*Vitex limonifolia* Wall.	Verbenaceae		✓	✓	✓
54	*Xylia xylocarpa* Taub.	Mimosaceae	✓		✓	✓

Table 7 Summary statistics for the multi-response permutation procedure (Sørensen distances) of the overstorey species compositions associated with the different past burning regimes; unburned (CB), frequently burned (FB), infrequently burned (IB) and rarely burned (RB). The results provide a comparison between all burning regimes, as well as multiple pairwise comparisons of the Sørensen distances.

Sørensen distance	δ under null hypothesis				T	P-value	A
	Observed δ	Expected δ	Variance	Skewness			
Overall comparison	0.341	0.500	0.0020	-0.73	-3.55	0.003	0.318
Multiple comparisons							
FB vs IB	0.310	0.500	0.0051	-1.74	-2.67	0.024	0.381
FB vs RB	0.333	0.500	0.0033	-2.33	-2.90	0.022	0.333
FB vs CB	0.281	0.500	0.0039	-1.83	-3.49	0.010	0.439
IB vs RB	0.532	0.500	0.0010	-0.39	1.03	0.850	-0.063
IB vs CB	0.491	0.500	0.0014	-0.87	-0.23	0.357	0.017
RB vs CB	0.481	0.500	0.0009	-0.17	-0.64	0.255	0.037

Table 8 The Monte Carlo test of significance of observed maximum indicator values (*IV*) for certain selected overstorey species (most common species and the species more abundant under specific burning regimes), based on 1000 randomisations. The means and standard deviations of the *IV* from the randomisations are given along with *P*-values for the hypothesis that there were no differences the between past burning regimes.

Burning Regime	Species[1]	Observed indicator value (*IV*)	IV from randomised groups		
			Mean	Std. dev.	P-value
FB	*Antidesma ghasembilla* *	65.8	40.9	14.18	0.048
RB	*Dipterocarpus tuberculatus* *	65.8	36.8	11.86	0.022
CB	*Xylia xylocarpa**	65.2	35.6	12.48	0.037
CB	*Canarium subulatum* *	65.2	32.9	14.55	0.05
CB	*Aporosa villosa* *	65.2	38.5	12.95	0.02
RB	*Erythrophleum succirubrum* *	61.4	37.1	10.14	0.019
CB	*Shorea obtusa* *	40.4	34.2	4.35	0.048
	Terminalia corticosa **	31.5	48	18.25	0.775
	Shorea siamensis **	31.4	31.7	2.26	0.537
	Grewia eriocarpa **	31.3	35	17.96	0.576
	Lannea coromandelica **	26.5	39.3	13.21	0.863
	Morinda coreia **	23.8	35.3	10.76	0.875
	Flacourtia indica **	21.4	31.6	15.95	0.85
	Pterocarpus macrocarpus **	21.4	36.6	15.1	0.844
	Terminalia chebula **	19.6	34.2	17.28	0.828
	Dillenia spp. **	19.6	34.2	17.28	0.828
	Terminalia alata **	16.7	31.9	15.43	0.851
	Strychnos nux-vomica **	16.7	35.5	15.94	0.908

Remarks: [1] *Species specifically associated with a particular past burning regime ($P<0.05$)
**Species generally observed under all past burning regimes ($P>0.05$)

Effects of prescribed burning on woody plant mortality

It was not clear whether prescribed burning caused tree mortality in DDF. Most of the dead trees were in the lower dbh classes, irrespective of the burning regime. Most of the dead trees were either *S. obtusa, S. siamensis* or *A. ficifolia*. The relative tree mortality was 4, 5, 14 and 5% on the FB, IB, RB and CB sites, respectively, though it was not significant between past burning regimes. The logistic regression analysis revealed that although the probability of tree mortality increased with decreasing dbh (P<0.01), this only explained tree mortality to a very small degree (r^2=0.03). There was no relationship between the probability of tree mortality and the past burning regime (P=0.22). The probability of tree mortality was further investigated for selected species, namely, *S. obtusa, S. siamensis* and *A. ficifolia*. Whereas in the case of *S. siamensis* the probability of tree mortality was related to dbh (P<0.05), this was not so for *S. obtusa* and *A. ficifolia*. However, tree dbh was again not sufficient to explain the mortality of *S. siamensis* (r^2=0.13).

Burning caused a significant decrease in sapling density and basal area only on the RB site (P<0.01). However, the sapling cover across all site types was not found to have been significantly altered after the fire. By contrast, one year after the fire the seedling density had increased significantly on all sites in comparison to the pre-burn levels, both in terms of the number of individuals (new seedling emergence) and the number of freshly sprouted shoots. On the FB site, for example, the seedling density increased from approximately 13000 individuals ha^{-1} to approximately 17000 individuals ha^{-1} (Table 5). The seedling coverage on the less frequently burned and unburned sites also increased significantly after the fire. The ratio of the number of newly sprouted shoots, or suckers, to the number of individual seedlings was even more interesting. The capacity for the vegetative propagation of seedlings (as indicated by ratio of suckers to individuals) increased on the less frequently burned sites after the burning experiment (Figure 5). On the FB site, by contrast, the number of suckers decreased after the fire.

Figure 5 The seedling ratio (the number of suckers to the number of individuals) before burning and one year after the burning experiment (mean ± SE) associated with the different past burning regimes; unburned (CB), frequently burned (FB), infrequently burned (IB) and rarely burned (RB).

Effects of past burning regime on woody plant structure

The results revealed that the overstorey structure was clearly lower on the frequently burned site than that on the less frequently burned sites. The overstorey species composition of the FB site also differed significantly from that of the others (IB, RB and CB). The species diversity (*H'*), on the other hand, exhibited no differences between the past burning regimes. The differences in the stocking densities between the sites of the different past burning regimes were mainly due to variations in the number of small trees, supported by the well known fact that small trees are more readily killed by fire than the large ones. This implies that the establishment and the growth of young trees into the higher diameter classes (i.e., progressing from sapling to tree stage) is a more continuous process during the longer fire-free intervals on less frequently burned sites. Watson and Wardell-Johnson (2004) reported that, although species richness did not differ significantly with either the time since fire or the fire frequency, both of these factors affected community structure and composition in open forest and woodland vegetation in Girraween National Park, South-East Queensland, Australia.

The densities of saplings and seedlings were lower on the FB site than on the less frequently burned sites, an observation similar to that of Peterson and Reich (2001). This also corresponded with the findings of Wachrinrat (2000), who reported numbers as low as 203 saplings ha^{-1} and 3140 seedlings ha^{-1} in DDF where fire protection activities were not conducted. By contrast, in DDF where fire management was implemented, the author recorded as many as 1292 saplings ha^{-1} and 9110 seedlings ha^{-1}. The lower sapling and seedling densities on the FB site might have been due to the fact that fire occurred almost every year, limiting the regeneration and subsequent development of seedlings to saplings to a very short fire-free period (Sukwong 1982). The development of fire resistance is closely linked to height and diameter growth. The growth rates of seedlings and saplings in DDF-HKK were studied extensively by Himmapan (2004), who calculated the average diameter growth of all species to be 1.1 cm yr^{-1} for saplings and 1.2 cm yr^{-1} for seedlings, with height growth of 65 cm yr^{-1} for saplings and 38 cm yr^{-1} for seedlings. Based on the height growth calculated by Himmapan (2004) and the flame height observed in this study (about 1.2-1.5 m), the seedlings may require a fire-free interval of about 5-6 years before their crowns lift above the average flame heights so they can develop into saplings.

The seedling coverage was significantly higher on the FB site than on the IB and RB sites. This can be attributed to the fact that more than 53% of the seedlings and 80% of the saplings on the FB site had more than one main stem. The corresponding values on the IB site were only 18% and 20%, respectively, and 10% and 7% on the RB site.

Absence of woody plant species as a result of different burning regime

A disparity in the proportions of *S. siamensis* and *S. obtusa* trees, two of the most dominant species in DDF, in the different stages of development, was observed. The number of saplings of these dominant species increased with the length of the fire-free interval (Figure 6). This suggests that these two species may require a fire-free interval of between 4 to 7 years for seedlings to reach the sapling stage, as was the case on the RB site. This inference is reinforced by the findings of a study by Sukwong (1982), who reported that S. obtusa seedlings required a fire-free interval of at least 7 years to attain a size that enables them to withstand fire damage. A shorter fire-free interval, as observed on the FB site, is not sufficiently long for the development of these species. Even though dominant on all sites, the disproportionate representation of these species amongst the various stages of development on the FB site may impact negatively upon their long-term development in the landscape.

The species composition of the overstorey on the frequently burned sites differed significantly from that of the others (IB, RB and CB). This difference was caused by the absence of certain species from the FB site. For example, *Diospyros ehretioides, Vitex limonifolia, Aporosa villosa, Schleichera oleosa* and *Buchanania latifolia* were not observed on the FB site, yet they were present on the other three, resulting in the differing species compositions. The absence of some species on the FB site raised the question of comparability between past burning regimes. Himmapan (2004) stated that the average diameter increment across all species in the DDF-HKK was about 0.4 cm yr^{-1}. Therefore, overstorey trees with dbh over 15 cm can be considered old trees, and have probably been alive for at least 40 years.

The analysis of the species composition using MRPP revealed that the overstorey old tree (dbh > 15 cm) species composition broadly overlapped between the past burning regimes (A=0.14, P=0.051). This suggests that differences in the species composition of the various past burning regimes was due to differences in the number of young mature trees (dbh < 15 cm). Moreover, this also reveals that the species composition of sites was similar historically, and was, therefore, comparable. The differences in the young mature tree composition, therefore, may have been influenced by the frequency of burning. Consequently, it is unlikely that the loss of the afore-mentioned species was brought about by site differences. However, the absence of these species was generally observed in DDFs throughout Thailand (Sunyaarch 1989, Sahunalu and Dhanmanonda 1995, Wachrinrat 2000, Samran and Tongtan 2002, Himmapan 2004). These species have fire adaptive traits, such as, a thick bark and the ability to sprout (Kaitpraneet 1987, Rundel and Boonpragob 1995), and may be considered fire-tolerant species. It is possible, however, that they cannot withstand frequent burning, such as on the FB site, because the regeneration process is too severely impeded. These species may also be less light-demanding, and possibly found the conditions under the relatively open canopy on the FB site unsuitable. The lesser degrees of canopy openness on the other sites (IB, RB, and CB), on the other hand, may have served to favour less light-demanding species. However, these less frequently burned sites were still bright enough that light-demanding species could occur.

S. siamensis appears to have been an important overstorey species in the frequently burned sites, as this species was also reported to be the most dominant tree by Himmapan (2004), who studied frequently burned forest sites in the HKK. *Gardinia obtusifolia, Sindora siamensis* and *Antidesma ghasembilla* were also dominant on the FB site. On less frequently burned sites, however, *S. obtusa* was the most abundant species, with *S. siamensis, A. ficifolia* and *D. tuberculatus* also dominant on the IB and RB sites. These species have adaptation traits such as thick barks, and re-sprouting capacity following damage to the stem. In addition, the fruits of *Shorea spp.* and Dipterocarpus spp. are dispersed by wind after the peak of the fire season, and germinate at the beginning of the wet season (Sukwong *et al.* 1975).

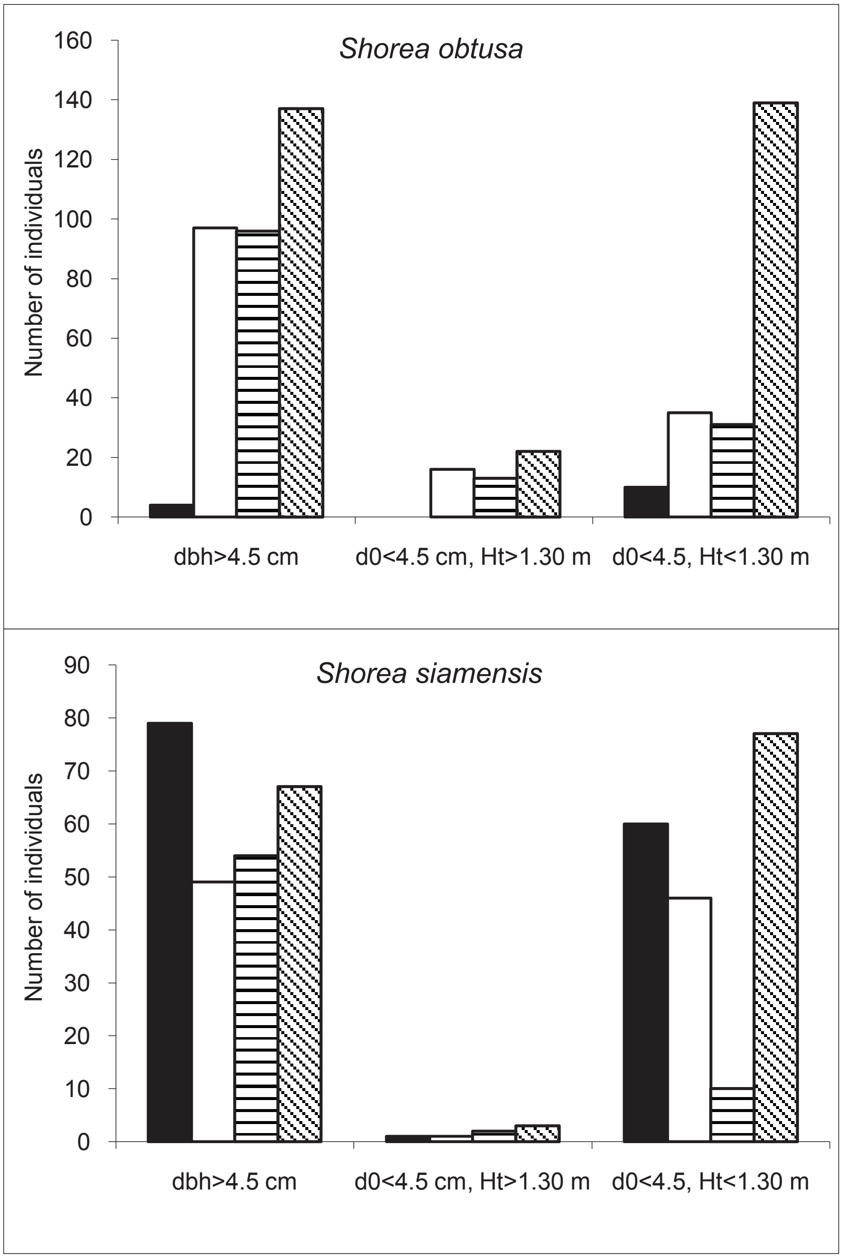

Figure 6 Diameter distributions of selected tree species in the different burning regimes.
■ Frequently burned, □ Infrequently burned, ▤ Rarely burned, ▧ Unburned.

Effects of prescribed burning on woody plant

There was no evidence to show that prescribed burning caused tree mortality in DDF. Indeed, the tree mortality rate observed on the unburned (CB) site was similar to that on the burned areas. The low incidence of fire-related mortality can be attributed to thick bark, which reduces heat effects on the cambium; the low-intensity surface fires (approximately 290-470 kW m^{-1}) and low flame length never reached the tree crowns (flame length was only 1.2-1.5 m). Whelan (1995) suggested that mortality after fire is not always an indication that the fire has had a significant impact on the community as the dead trees may have been sick, weakened, old or injured, and may have been destined to die even without the fire. It is possible that the mortality that set in after the low-intensity surface fires was confined to suppressed trees, which develop fire resistance characteristics much more slowly than vigorous trees of the same age and species. Exceptional drought conditions in the year 2004 may also have influenced tree mortality, particularly that of small trees. Total rainfall in the year 2004 was only 996.4 mm, compared to 1332.9 mm and 1453.7 mm in the years 2003 and 2005, respectively (Forest Fire Research Center 2006). However, the mortality of small trees as a result of frequent burning suggests that if this trend continues, future stand development and, consequently, the productivity of these species, could be jeopardised because of the reduction of the regenerative capacity of the forest (Guinto *et al.* 1999).

It appeared that burning resulted in an increase in the number of saplings on the FB site, whereas fire likely reduced the number of saplings at the other sites. This may be attributed to the fact that the stems of seedlings may not be seriously affected by fire and that they continue to grow, or that where the stem is damaged a new shoot can sprout rapidly and reach the sapling stage (>1.3 m height) in the following year. Except for the RB site, the fact that there was great variation in the sapling density at the subplot level after the fire, characterised by both increases and decreases, meant that a statistical analysis (paired *t-test*) revealed no significant differences to the pre-burn situation. Increases in the seedling density may be attributed to the improved seedbed conditions after fire. Fire stimulates seed germination, and improves nutrient availability. This result corresponds with the findings of Sunyaarch (1989) and Himmapan (2004). A reduction in re-sprouting capacity in the frequently burned site (Figure 5) may be attributed to better root system development and nutrient storage in the roots on the less frequently burned sites. Even though most woody plants in DDF can sprout after the above-ground part of the plant has been either killed or damaged by fire (Sukwong *et al.* 1975, Kaitpraneet 1987, Stott *et al.* 1990, Rundel and Boonpragob 1995), the capacity to sprout declines when burning is too frequent, as the nutrient and starch reserves stored in the root system cannot be replenished. By contrast, the longer fire-free interval at the less frequently burned sites allowed for a recovery of the sprouting capacity. Therefore, frequent burning may jeopardise long-term tree population dynamics and, hence, the productivity of DDF.

CONCLUSION

This study revealed that the structure of stands that had been frequently burned in the past differed from that of the less frequently burned stands. Moreover, the species composition of the small-sized overstorey vegetation in the frequently burned stands also differed significantly from that of the other stands. The species composition of the unburned site differed from that of the other burning regimes only modestly. Frequent burning also resulted in a reduction of the sprouting capacity of seedlings and saplings, inhibited regeneration and, consequently, resulted in a disproportionate representation of individuals of certain tree species at the various stages of development. Therefore, fire-free intervals of at least 6-7 years should be introduced to facilitate the successful recruitment of young trees.

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