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FIRE AND THE REPRODUCTIVE OUTPUT OF THE DECIDUOUS TREE *SINDORA SIAMENSIS* IN THAILAND

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ABSTRACT

Fire is an anthropogenic phenomenon of increasing frequency in deciduous dipterocarp forests in Thailand. The impact of fire on the reproductive biology of *Sindora siamensis*, a common legume canopy tree in the deciduous forests in Thailand, was investigated. Pod and seed production, seed abortion, and seed predation were recorded from trees at two forest sites: one burnt 6 months previously and the other 4 years previously. The number of developing pods per infructescence was similar on trees across sites, although seed abortion was significantly higher at the burnt site. Aborted pods contained fewer seeds than pods remaining on the tree. We suggest that selective abortion of seed and pods is due to limiting soil nutrient conditions. These conditions may be a direct result of the fire but may also occur indirectly by competition with early successional grasses. There is, however, little evidence to suggest that increasing fire frequency has an important impact on the overall reproductive output of *S. siamensis*, which, due to its nitrogen fixing ability, may be buffered from some indirect effects of fire.

INTRODUCTION

Fire is an indigenous ecological factor in many tropical forests (recently reviewed by WHELAN, 1995) though there is some controversy over whether this is true for the deciduous dipterocarp forests (DDF) of Thailand. However, it is clear that in the past 50 years there has been a significant increase in extent and frequency of fire throughout large parts of the tropics beyond that which can be attributed to natural causes (WHELAN, 1995). In Thailand this increase is human-induced, the primary causes being path clearing and field burning (KANJANAVANIT, 1992). The increasing frequency of fires is of concern to the continued preservation of tropical forest reserves, some of the finest examples of which are found in Thailand.

Fire affects the reproductive ecology of trees both directly, by destroying dispersed seeds and young saplings, and indirectly, by disrupting pollination, seed predation and nutrient cycling resulting in reduced reproductive output and gene flow and, ultimately, loss of genetic and species diversity. At present the impact of disturbance on pollination and seed production is poorly understood. This study assessed the impact of fire on plant reproduction in a DDF, by comparing pod and seed production of a common legume tree, *Sindora siamensis*, from recently burnt and unburnt forest.

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METHODS

Sindora siamensis Teysm. ex Miq. var. *siamensis* (Leguminosae, Caesalpinioideae) is an abundant, obligately outcrossing, bee-pollinated, canopy tree (Ghazoul & Liston, unpublished) typical of DDFs in Thailand. Some individuals achieve a height of 25 m, but most are between 12 and 16 m tall. At Sakaerat *S. siamensis* is the only DDF tree to flower during the early wet season (May–July). Dependence on pollinators, ease of access, and unique flowering period make this a convenient species to study.

Study Site

The research was conducted between 1 June and 16 July 1995 in DDF at Sakaerat Environmental Research Station (SERS), Nakhon Ratchasima Province, in northeastern Thailand. Within the reserve, deciduous forest covers 1222 ha. The northern and eastern boundaries of the forest are adjacent to farmland, while the southern and western edges are bounded by evergreen forest. There is a single canopy layer at 10–15 m height with some emergents reaching 20–25 m. Canopy trees are predominantly dipterocarps and legumes typical of such a forest type.

In January 1995, fire spread through much of the deciduous forest but left large areas undamaged. The precise area affected is unknown, but we estimate about 200 ha of forest had been burnt. Thus the deciduous forest at Sakaerat could be divided into two categories: forest that was last burnt in February 1991 (which for the purpose of this study is called the "undisturbed" site; see Fig. 1); and forest that was recently burnt in January 1995 (disturbed forest, see Fig. 2). These study areas were adjacent to each other and no major environmental difference between them was apparent. The entire area of DDF had been affected by fire in February 1991 (unpublished records from SERS).

Pod and Seed Production

Seed production is the definitive measure of tree reproductive output. Fire may limit reproductive success by acting on the survival of germinating seeds and also saplings, but this study considers only the impact of fire on pod and seed production.

It was not possible to accurately record the entire seed crop of any single tree. Instead, seeds per pod and pods per infructescence were recorded for a sample of pods and infructescences from each tree. Reproductive output for these is presented as the average number of healthy seeds per infructescence.

Pods per infructescence were recorded for a random sample of at least 40 infructescences per tree on more than 30 trees in each site. Pods developed on erect infructescences (Fig. 3) at the top of the canopy and were thus easily counted. Trees were placed in one of three categories (A = 10–100 infructescences; B = 100–1000; C = >1000) according to the total number of infructescences, determined by visual estimates.

Pods were dissected to gauge the number of aborted, damaged and healthy seeds, and the presence of seed or pod predators. Aborted seeds were small, shrivelled and browned (Fig. 4), and easily distinguished from the much larger white healthy developing seeds (Fig. 5). Pods were collected randomly from the whole canopy of 21 trees at each site,

Figure 1. "Undisturbed" forest at Sakaerat Environmental Research Station in July 1995. This area was last burnt in January 1991.

Figure 2. "Disturbed" forest at Sakaerat Environmental Research Station in July 1995. This area was last burnt in January 1995.

Figure 3. Developing pod of *Sindora siamensis* on the tree.

Figure 4. Aborted seeds of *Sindora siamensis* in a pod.

Figure 5. Developing seeds of *Sindora siamensis* in a pod.

using rope climbing techniques and a 3 m pruning pole. Distances to nearest neighbouring conspecific trees were recorded for all trees from which pods were collected. Aborted pods were collected from the ground and were similarly dissected.

Soil samples, from both disturbed and undisturbed sites, were air dried before being sent to the Soil Sciences Division of the Department of Agriculture (Bangkok) for analysis. Soil was analysed for pH, organic content and available nitrogen, potassium and phosphorous.

Parametric statistics (t–tests and ANOVA) were used to analyse data where appropriate. Percentage data were arcsine-transformed prior to analysis.

RESULTS

Fire in the disturbed site destroyed the undergrowth, leaf litter and many saplings. Six months after the fire, and during the main study period, grasses (*Chrysopogon orientalis* (Desv.) A. Camus, and *Imperata cylindrica* (L.) P. Beauv. var. *major* (Nees) C.E. Hubb. ex Hubb. & Vaugh) had grown to a height of about 1 m. The resulting understorey layer lacked the complexity of the multi-layered understorey of unburnt forest (see Fig. 1 and 2). There was no appreciable litter layer in the burnt area. In contrast, the unburnt site had accumulated 4 years of leaf litter amounting to a depth of 3–4 cm. There was no evidence that the large trees had been directly damaged by fire.

Pods per Infructescence

The number of infructescences in the canopy of *S. siamensis* (divided into three categories of 10–100, 100–1,000 and > 1,000) did not correlate with mean infructescence pod load (ANOVA: $F = 1.34$; $P = 0.273$; d.f. = 46) enabling comparison of this variable between sites using trees of varying size.

Infructescences had between 0–8 pods (see Fig. 3 and 6), but most had only one or two (Fig. 6). Frequency distributions of pods per infructescence were similar between sites (Fig. 6), as were the overall mean values (Table 1).

Seeds per Pod and Seed Abortion

The number of developing seeds in a single pod varied from 0 to 6 with a mean value of 1.55±0.06 (N = 1,485), and no difference was detected across sites in the total number of seeds per pod (Table 1). Aborted seeds were more frequent in pods at the disturbed site (Table 1). Abscised pods collected from the ground had very high frequencies of aborted seeds; much greater than for pods collected from the tree (Table 1) and significantly fewer seeds per pod than pods on trees (Table 1).

Insect Damage To Seeds and Pods

Pre–dispersal predation of *S. siamensis* seeds was inflicted by a single species of scolytid beetle. This species was not specific to *S. siamensis* seeds, as individuals were also found in abundance tunnelling through the seed aril of another legume tree, *Afzelia xylocarpa* (Kurz) (Leguminosae, Caesalpinioideae). Only eight beetles were found in

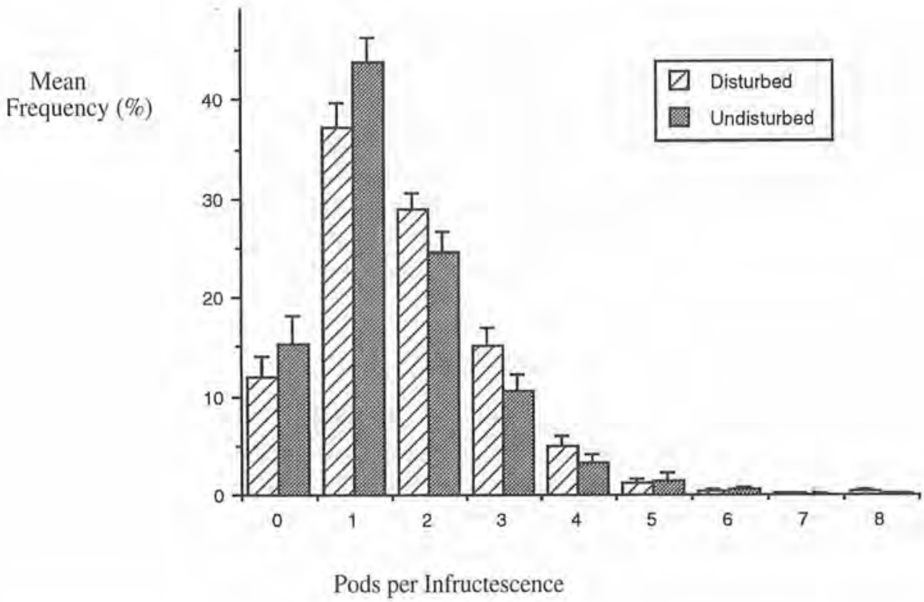

Figure 6. Number of pods per infructescence of *Sindora siamensis*. The disturbed and undisturbed site frequency distributions are statistically similar (t–test on log-transformed values of variance/mean for each tree: $t = 1.06$; $P = 0.29$; d.f. = 44).

Table 1. Reproductive output and seed loss of *Sindora siamensis* at burnt and unburnt sites.

	Pods per infructescence	Seed per pod	Aborted seed (%)	Damaged pods (%)	Reproductive output (viable seeds/infruct.)
Undisturbed (U)	1.5±0.1	1.5±0.1	7.5±1.6	2.7±1.0	2.0±0.2
Disturbed (D)	1.7±0.1	1.4±0.1	12.4±1.7	3.6±1.1	2.0±0.3
Ground (G)	-	1.2±0.1	85.9±7.5	1.9±1.0	-
P-values U–D[1]	n.s.	n.s.	0.05	0.05	n.s.
P-values T–G[2]		0.01	0.001	n.s.	

[1] Comparison between pods collected from trees at disturbed and undisturbed sites

[2] Comparison between pods collected from trees at both sites with pods collected from ground at both sites

three seeds (one from disturbed site trees and two from undisturbed trees) out of a total of 1,487 seeds examined (= 0.2% seeds infested). Pod infestation by insects was also low at 3% and no difference in proportion of pods attacked was apparent between the disturbed site, undisturbed site or abscised pods.

Pod consumers, which were more abundant than seed predators, caused no direct damage to the seeds. In some cases the seeds were apparently healthy (i.e. not discoloured or visibly damaged), but had become misshapen due to the the secretion of resin by the plant, induced by insect larvae tunnelling through the pod wall. Rearing of insect larvae was largely unsuccessful due to rapid dessication of collected unripe pods, though two Lepidoptera (Gelechiidae) and an unidentified hymenopteran parasitoid did successfully emerge.

Squirrels accounted for the loss of some seeds. It was not possible to quantify the amount of damage caused as pods attacked by squirrels were removed from the tree and discarded. Such pods clearly contained large and well developed seeds, the loss of which would be energetically more expensive to the tree than damage due to scolytid beetles which attacked seeds at an earlier stage of development. While it is not possible to determine which predator is of greater importance in reducing seed production, observations suggest that both squirrels and beetles account for a small proportion of seed death, but considerably less than that due to seed abortion.

Reproductive Output

Reproductive output at disturbed and undisturbed sites is calculated using the data presented in the preceeding sections. After accounting for initial pod set, seed set, and seed damage by abortion and insects, there is no overall difference in reproductive output between the disturbed and undisturbed sites (Table 1).

The distance to the nearest conspecific did not correlate with reproductive output. The greatest distance recorded between nearest conspecific neighbours was 18.3 m and well within the flight range of even the smallest bees. Reproductive isolation of *S. siamensis* trees can therefore be ruled out as a factor controlling seed and pod production in this study.

Soil Nutrient Content

Organic content, and available nitrogen, phosphorous and potassium were, relative to other soil types, low at both sites. However, all of these constituents showed significant differences between the two sites, though not in the same direction (Table 2). The unburnt site had a lower organic content and lower potassium, though the opposite was true for phosphorous. Soil depth was significantly greater at the undisturbed site ($P < 0.001$).

DISCUSSION

Pod abortion was the only factor that appeared to be different between trees in unburnt and burnt forest. This cannot be attributed to insect seed predation, as no difference was detected in infestation of pods between sites or of pods collected from the ground. Indeed,

Table 2. Soil nutrient content of burnt and unburnt deciduous dipterocarp forest at Sakaerat. Probability values are obtained from a two sample t–test (N = 8 for each site).

Site	Unburnt	Burnt	Significance
Organic content (%)	1.75±0.25	2.56±0.21	0.028
Phosphorous (ppm)	4.62±0.96	1.13±0.13	0.0087
Potassium (ppm)	48.6±6.3	139.9±14.0	0.0002
pH	4.93±0.08	4.86±0.06	n.s.
Profile depth (cm)	50.6±4.6	26.2±3.5	0.001

insect seed predation was very low compared to loss of seeds by abortion. *S. siamensis* shows few traits that indicate adaptive strategies responding to pre-dispersal seed predation by beetles. The pod walls are not thick and woody, although they become so at maturity, and the testa is thin. Pods are not apparently toxic and were readily consumed by squirrels. Mechanical damage induces the production of resin which may hinder the ability of seed predators to infest the pods, though insect larvae found in the pod wall were free from resin.

Pod abortion appears to be selective in that aborted pods containing single seeds are over–represented compared with pods on trees. This fact suggests that nutrient availability may be the cause of seed and pod abortion, as it is energetically more economical to spread the production costs of the remaining pods over greater seed numbers. Nutrient availability has been shown to limit both flower and seed production in other woody plants (LAMONT & BARRETT, 1988; STOCK ET AL., 1989) and resource availability might limit pod production by causing some proportion of young pods to be aborted (STEPHENSON, 1981).

The soils of both sites at Sakaerat are indeed poor in organic nitrogen (N) content, and particularly phosphorous (P). Potassium (K) falls within or exceeds the range of 20–100 ppm reported to be adequate for good growth of most trees (PRITCHETT & FISHER, 1987) and is therefore assumed not to be limiting *S. siamensis* pod production. Low N may not be a critical limiting factor for leguminous trees such as *S. siamensis* which fix atmospheric N (MCKEY, 1994). However, phosphorous is essential for growth and reproduction, and was, at both sites, less than the minimum 12–20 ppm required for good growth (LANDON, 1991). Acute phosphorous deficiency of burnt site soils very likely explains the observed high seed abortion there.

Herbaceous plants and other ground cover are often very efficient in their uptake of most of the available nutrients concentrated in the upper soil after fire (COUTINHO, 1982; ABRAMS ET AL., 1986). During the six months from the fire event to *S. siamensis* pod production, grasses grew from below ground level to a height exceeding one metre. Competition for nutrients with these grasses may exacerbate the effects of nutrient deficiency for pod production by *S. siamensis*. Indeed, low soil P levels might be an indirect affect of fire acting through these grasses.

The study sites, which were identical in all other environmental respects, differed only in the affects of the recent fire. During a fire event nutrients might be lost directly to the atmosphere (HOLT & COVENTRY, 1990). Furthermore, loss of surface vegetation frequently results in erosion of surface soil (BELILLAS & RODA, 1993), particularly in areas subject to heavy rainfall. Fire has had an important role in facilitating soil erosion at Sakaerat (AKSORNKOAE, 1971) and soils of the undisturbed site were deeper (Table 2). More nutrients will therefore be available to trees growing on the deeper soils of the unburnt site, than on the shallow soils of the disturbed site. It seems unlikely that the large differences in soil depth can be attributed solely to fire-related erosion, but due to the lack of any obvious topographical differences between sites we are unable to suggest alternative explanations.

Tree species composition in forest subject to repeated fires may change over time as a function of the reproductive capacity of each species. While fire had little impact on overall seed production of *S. siamensis* at Sakaerat, the reproductive output of other tree species may be affected. Emmigration of seeds from nearby unaffected areas may offset reduced seed production of individuals in burnt forest, though dispersal efficiency will mediate this.

Changes in forest tree composition will have associated impacts on many other forest plant and animal species, particularly those that are closely associated with the tree species most seriously affected. Such events might not be easy to detect as the decline of a tree population will occur gradually over many years. However, by monitoring seed production and seedling establishment of trees at undisturbed and disturbed areas it may be possible to predict which species are most vulnerable to disturbance and to take action to prevent forest decline and associated loss of biodiversity.

Aside from seed abortion, there is little evidence in this study to indicate that fire has much indirect affect on overall reproductive output of *S. siamensis*. An unavoidable weakness of this study is clearly the absence of data from a site which has only been subjected to fire at natural frequencies, a situation which is not found at Sakaerat. Despite this weakness, fire has been shown to indirectly affect seed abortion by acting through changes in soil nutrients. While this paper deals solely with the process of pod and seed production, further studies are underway on the impact of fire on the pollinator communities that maintain gene flow. We expect that such information will, in the long term, contribute to the successful conservation of plant genetic resources and to the maintenance of community stability in the face of increasing disturbance pressure.

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