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Understanding and assisting natural regeneration processes in degraded seasonal evergreen forests in northern Thailand

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Abstract

The Thai government has recently embarked upon a nation-wide project to restore degraded forests. One approach could be to assist natural regeneration (ANR) by counteracting particular limiting factors, such as insufficient dispersal of tree seeds into cleared areas, lack of beneficial shade or excessive competition from weeds. This paper describes part of a 2-year project in northern Thailand which analysed, stage by stage, the regeneration from seed of a range of tree species in an abandoned agricultural clearing to identify limiting factors and develop appropriate ANR techniques to overcome them. Fruit production, seed dispersal, seed germination and seedling survival were monitored in the field. Experiments on selected species were carried out in the field and nursery to determine the effects of high light and low moisture on seed germination and the effect of above-ground weed interference on seedling performance in the first year. Three species are compared here to demonstrate how systematic study of regeneration processes can be of use in devising strategies to accelerate tree regeneration in deforested areas. Despite high levels of production of *Beilschmiedia* sp. seeds, the low rate of seed dispersal limited seedling recruitment in the clearing. In addition, seed germination was sharply reduced by lack of rainfall and the seedlings were highly susceptible to scorching by direct sunlight. Raising seedlings in nurseries and planting them out in degraded areas under the shade of existing herbaceous vegetation may be a suitable method of accelerating the regeneration of this species. *Prunus cerasoides* seeds were produced abundantly in both years of the study but seedling recruitment in the clearing was limited mainly by insufficient dispersal of its seeds into the cleared area. Under experimental conditions seeds germinated and seedlings established readily, so direct seed sowing in degraded areas may be appropriate. Alternatively, natural seed dispersal could be encouraged by improving the habitat for birds. *Engelhardia spicata* seeds were widely dispersed by wind and its regeneration was limited at the germination and early establishment stages. Physical obstruction by thick stem and leaf litter appeared to be a limiting factor. This barrier could be overcome by cutting back weeds (particularly grasses and ferns) or by shading them out with nurse trees. © 1997 Elsevier Science B.V.

Keywords: Thailand; Seasonal tropical forest; Forest restoration; Assisted natural regeneration; Seed germination; Seedling establishment

1. Introduction

In northern Thailand, Royal Forest Department (RFD) policy is to encourage restoration of degraded

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native forests (Elliott et al., 1995). Traditional methods of intensive plantation forestry are employed, but now mixtures of native species are used instead of the previous practice of planting monocultures of pine, teak or eucalyptus. Tree seedlings are raised in nurseries, then planted out in degraded areas, usually in the centre of lines of about 1 m width cut through the vegetation (pers. obs.). Rates of establishment are high for some species (pers. obs.), but there are certain drawbacks to this method of forest restoration. For example, the cost is relatively high because an input of labour is required at every stage of the regeneration process, from collecting the seed or seedlings, to raising the seedlings in nurseries, preparing sites, planting seedlings and maintaining them afterwards. If the level of human input could be reduced, costs could correspondingly be lowered or the area of forest restored per annum increased. Furthermore, prescriptive tree planting takes no account of the natural regeneration potential of individual sites. A closer look may reveal that healthy regeneration of some species is already in progress and clearance of lines and intensive planting is superfluous or even counter productive.

An alternative approach to the restoration of native forest is to accelerate regeneration by assisting the natural processes of succession. This is already practised in the Philippines, where it is labelled 'assisted natural regeneration' or 'ANR' (Dalmacio, 1987; Jensen and Pfeifer, 1989). There, ANR methods include cutting or pressing the weeds around existing naturally established seedlings, protecting the area from fire and interplanting with desired species if necessary. ANR as explained here differs from 'natural regeneration' as defined by Fox (1976) which allows some human intervention but precludes tree planting.

The importance of basing tropical forest restoration on an understanding of ecological processes is often emphasised (e.g. Lugo, 1988; Janzen and Vazquez-Yanes, 1991). For the purposes of ANR, it is particularly important to know what specific factors limit the rate of regeneration of trees in deforested areas, so that minimum input strategies may be devised to overcome them. Several authors have focused on this, notably Fox (1976), Uhl (1987) and Nepstad et al. (1990). A systematic approach to such a study is firstly to determine the stage of the life-cycle where population size is limited and then to isolate the factors responsible (e.g. Alvarez-Buylla and Martinez-Ramos, 1992).

This paper describes part of a 2-year project in northern Thailand which used this method to study tree regeneration in abandoned agricultural clearings. Specific objectives were to identify the stages of the life-cycle where regeneration is blocked and the factors limiting regeneration at those stages for a range of tree species, and to develop ANR plans for each species.

2. Materials and methods

2.1. Study sites

The study was conducted on Doi (Mount) Pui in Doi Suthep-Pui National Park, Chiang Mai Province, northern Thailand, 18°50′N, 98°50′E. Study sites were located within the evergreen forest zone which occurs between about 950 m and the summit at 1685 m (Maxwell, 1988). All sites were on the eastern slopes of the park where the forest is still largely intact although degraded by long-term agriculture in some areas and subject to occasional fire. All work was carried out between elevations of 1450 and 1550 m above mean sea level (a.m.s.l.) where the average annual rainfall is 1819 mm (mean for period 1980 to 1988), falling mainly between May and November. Mean monthly temperatures range from 15.4°C in the cold dry season (December to January) to 22.6°C in the hot dry season (February to April). All meteorological data were recorded at the Kasetsart University Research Station, situated within the park about 3.5 km from the Doi Pui study site used in this study.

Phenology, seed dispersal and seedling survival were measured in an abandoned agricultural clearing and the forest surrounding it (further details below) at the Doi Pui study site. The clearing is approximately 0.9 ha at 1500 m a.m.s.l. It is roughly rectangular, about 160 m in length with a minimum width of about 50 m, slopes of up to 27° and a south-easterly aspect. The soil is a sandy loam with an organic matter content of 11% in the top 10 cm in the clearing centre (Hardwick, unpublished data). The clearing was completely cleared of trees about 35 years ago in order to grow maize and fruit trees and was abandoned 14 years ago (D. Nimnoo, RFD, pers. commun., 1996). After abandonment, both the clearing and surrounding forest were burnt occasionally, the last fire occurring in the dry season of 1993, a year before the start of the project (N. Chaleerat, RFD, pers. commun., 1996). The area was not burnt during the study. Dominant herbaceous species in the clearing are *Eupatorium adenophorum* Spreng. (Compositae) and *Pteridium aquilinum* (L.) Kuhn ssp. *aquilinum* var. *wightianum* (Ag.) Try. (Dennstaedtiaceae) with some *Imperata cylindrica* (L.) P. Beauv. var. *major* (Nees) C.E. Hubb. ex Hubb. & Vaugh. and a few patches of *Thysanolaena latifolia* (Roxb. ex Horn.) Honda (both Gramineae). A sparse scattering of small pioneer trees has established, mostly *Debregeasia longifolia* (Burm. f.) Wedd. (Urticaceae) and *Trema orientalis* (L.) Bl. (Ulmaceae). There are also a few isolated, abandoned fruit trees remaining from the period of agricultural use.

The forested land surrounding the clearing is steep in places, with slopes of up to 35°. The structure of the forest is heterogeneous, i.e. highly disturbed, open and grassy in some areas and less disturbed with a continuous canopy in other areas. Throughout, the canopy is dominated by evergreen trees such as *Castanopsis diversifolia* King ex Hk. f. (Fagaceae) and *Helicia nilagirica* Bedd. (Proteaceae), but also includes a few deciduous trees such as *Engelhardia spicata* Lechen. ex Bl. var. *spicata* (Juglandaceae). There is an abundance of the smaller multi-stemmed evergreen *Vernonia volkameriifolia* DC. var. *volkameriifolia* (Compositae).

The seedling establishment experiment was carried out at the Sunkoo study site, a deforested, south facing, 25° slope, which is more or less square and about 1 ha in area. It is situated approximately 1.5 km from the Doi Pui study site at 1450 m a.m.s.l. and is similar to the Doi Pui clearing in that the forest was first cleared at least 30 years ago and the area is still occasionally burnt, although not during the study. The agricultural history is unknown. Grass (mainly *Imperata cylindrica*) and ferns (*Pteridium aquilinum*) dominate the site and there are a few remaining isolated forest trees, such as *Castanopsis tribuloides* (Sm.) A. DC. (Fagaceae) and scattered small pioneer trees, such as *Litsea cubeba* (Lour.) Pers. (Lauraceae).

Germination experiments were carried out at the RFD nursery situated on a south facing slope, about 500 m from the Doi Pui study site at 1450 m a.m.s.l.

2.2. Species

The three species reported in this paper are *Beilschmiedia sp.* (Lauraceae), *Prunus cerasoides* D.Don (Rosaceae) and *Engelhardia spicata* Lechen. ex Bl. var. *spicata* (Juglandaceae); hereafter referred to as *Beilschmiedia*, *Prunus* and *Engelhardia*. *Beilschmiedia* is as yet unidentified, as flowering material could not be obtained. These species were selected for this paper for the reasons that although not dominant in the forest they are moderately abundant canopy species and therefore important components in the restoration of the forest, they demonstrate contrasting life histories and seed sizes (below), they provided sufficient data to enable analysis of the regeneration cycle on an individual species basis and they produced ripe fruit at least a month before the onset of the rainy season which permitted a comparison of germination responses to seasonal drought.

Beilschmiedia is an evergreen tree found in evergreen forest (i.e. forest dominated by evergreen species, Maxwell, 1988) and has large seeds about 3 cm long, probably dispersed by large animals or birds (Table 1). *Prunus* is a deciduous tree found in evergreen forest, especially where it is disturbed and has smaller, bird dispersed seeds about 1 cm in length. *Engelhardia* is also deciduous, found in several types of forest including evergreen, evergreen/pine, mixed deciduous/evergreen and in more open disturbed areas and has wind dispersed seeds with a diameter of about 0.5 cm. Although *Prunus* and *Engelhardia* are common in disturbed areas they are not in the group of pioneer species which first dominate newly abandoned clearings. This information is derived from personal observations and from Chiang Mai University's Herbarium Database (see Elliott et al., 1995). Voucher specimens of all three species are deposited at the Chiang Mai University Herbarium.

2.3. Field observations

Phenological observations were made at monthly intervals for 2 years, from June 1994 until May 1996, in forest around the clearing at the Doi Pui site. Twelve circular plots, 10 m in diameter, were

Table 1
Fruit characteristics of the three species described in the paper

Fruit characteristics	*Beilschmiedia*	*Prunus*	*Engelhardia*
Fruit type	Berry with thin fleshy pericarp	Drupe with succulent pulp	Three-winged nut
Number of seeds per fruit	1	1	1
Colour of fruit when ripe	Black	Red	Brown
Probable dispersal method	Large animal or bird	Bird	Wind
Fruit size (mm)[a]	33.6 (1.6) × 28.9 (3.5)	10.7 (0.7) × 8.7 (0.6)	42 (5.7) × 34 (7.1)
Seed size (mm)[a]	29.1 (1.4) × 24.4 (1.5)	9.7 (0.5) × 7.5 (0.2)	5.8 (0.5) × 5.1 (0.3)
Fresh seed mass (g)[a]	6.72 (1.33)	0.23 (0.02)	0.03 (0.01)
Fresh seed moisture content (%)[a]	26.9 (6.1)	22.8 (2.1)	25.0 (8.1)

[a]Values are mean and standard deviation, $n = 20$ (Pakkad, undated).

placed adjacent to the clearing's edge, spaced 20 m apart unless one happened to fall in a place with no trees, in which case it was moved forward until it lay entirely within an area with trees. This resulted in plots on all sides of the clearing. Twelve additional circular plots were arranged in the same way, deeper inside the forest between 10 m and 100 m from the edge and opposite an edge plot wherever possible. Forest edge plots contained a mean of 9.2 ± 1.0 trees ($n = 12$) (all values are mean ± SE unless otherwise stated); forest interior plots contained 6.1 ± 0.9 trees ($n = 12$). Ripe and unripe fruit abundance was scored for each mature tree using the crown density method (Elliott et al., 1994), derived from the system conceived by Koelmeyer (1959). A linear scale of 0–4 points was used, with 4, 3, 2 and 1 representing the maximum, three-quarters, half and one-quarter of the maximum density of fruit, respectively, and 0.5 representing a tiny amount of fruit, well below one-quarter of the maximum density.

The seed rain was measured monthly throughout the study in circular 1 m^2 seed traps made from plastic mosquito netting with a 1.7 mm mesh. Six traps were placed in each of three zones, i.e. clearing centre, clearing edge (the peripheral area of the clearing 10 m in width, adjacent to the forest) and forest (the area between 10 and 100 m distance from the clearing). The clearing centre and edge zones were each divided into six equal sized sub-sections and one trap was randomly placed in each. In the forest, traps were placed at least 20 m apart in areas with continuous canopy. The traps were supported about 50 cm above the ground on bamboo legs which were adjusted so that the traps were horizontal. Vegetation directly above the traps was undisturbed. No predation from the seed traps (as judged by the presence of fruit and seed remnants) was indicated for the three species described here.

Germination and establishment of the seed rain was monitored in 18 4 × 1 m permanent sample plots, each placed 2 m from a seed trap. All seedlings in the plots were censused in November 1994 at the end of the rainy season. Following the natural dispersal of ripe fruits of all three species at the end of the dry season in 1995, germination was measured throughout and after the rainy season in May, July, September and December 1995. All new seedlings were individually marked at each census and their survival was recorded in subsequent censuses and in May 1996 at the end of the following dry season. Seedling densities were standardised to a horizontal area by correcting for variation in slope angle in order to enable direct comparison with seed rain that was measured on the horizontal plane. In each plot, the percentage of exposed soil with no litter layer and the percentage canopy cover of trees at least 2 m in height were estimated.

2.4. Controlled experiments

A nursery experiment was carried out to test the limiting effect on germination of high light levels and low soil moisture, factors characteristic of deforested areas in the dry season. Seeds of all three species were collected and planted about a month before the end of the dry season in individual bags, 6 cm in diameter, containing forest top soil. The seeds were lightly pressed onto the surface of the soil. Bags were randomly assigned to one of three light treatments (full sunlight, partial shade and heavy shade, Table

Table 2
Percentage of full sunlight and maximum temperatures at a height of 10 cm in the RFD nursery and Doi Pui study site

Location	Treatment/habitat	Percentage of full sunlight[a]	Maximum temperature (°C) (hot season, 1995)
Nursery	Full sunlight	100	44
Nursery	Partial shade	7.8 ± 2.5	33.5
Nursery	Heavy shade	0.8 ± 0.2	34
Doi Pui study site	Clearing centre (below weed canopy)	5.9 ± 2.4	34
Doi Pui study site	Forest	1.1 ± 0.4	28

[a]Values are mean ± SE derived from repeated spot measurements taken with an LT-Data Bus hand-held digital light meter in sunny conditions between 1000 and 1400 h (nursery, $n = 5$; Doi Pui study site, $n = 15$).

2) and two watering treatments (low moisture and high moisture) combined in a factorial design.

Full sunlight was provided by an open area of the nursery, unshaded for about 4 h around midday (see Table 2 for light levels). Partial and heavy shade were provided by shade houses covered with loosely and tightly woven shade cloth, respectively. Neutral density shade cloth was used which changed the amount of PAR received, but did not affect the spectral composition of the light. Thus, any differences in germination between light treatments would probably result from the effect of exposure to sunlight on soil moisture and/or temperature and not from any difference in red to far red light ratios.

Seeds in the low moisture treatment, representing normal dry season drought, received only natural rainfall, which fell occasionally during the remainder of the dry season. Seeds in the high moisture treatment, representing regular rainfall, received supplementary watering between rain showers, the actual amount being adapted to each light treatment. In general those in full sunlight were watered twice a day, those under partial shade were watered once a day and those under heavy shade were watered once every 2 days.

Four replicate batches of 25 seeds (*Prunus*) and 15 seeds (*Beilschmiedia*) were planted in each light and watering treatment. *Engelhardia* was tested with two replicates of 50 seeds in each treatment. Germination was monitored at 2-weekly intervals until 4 months after planting, by which time all non-germinated seeds were found to be rotten. Germination percentages were arcsine transformed and the results were analysed separately for each species using two-way analysis of variance (ANOVA) with light and watering as factors. A priori comparisons between watering treatment for each species were made using a *t*-test, following the procedure of Sokal and Rohlf (1981).

A field experiment was used to investigate the effect of herbaceous vegetation on seedling survival in cleared areas. Cutting weeds at ground level is a standard technique used by Thai forest workers (pers. obs.). This temporarily removes above-ground interference and may reduce, but does not remove, root interference, especially when the dominant weed is *Imperata cylindrica* grass. The treatments did not affect soil moisture levels during the dry season; gravimetric analysis of soil water content down to a depth of 60 cm showed no significant difference between the two treatments (unpublished data). Therefore, this experiment primarily tested the effect of the weed canopy on tree seedling survival. Likely benefits are the protection of seedlings from heat damage due to direct sunlight and the reduction of transpiration due to a more humid micro-environment whereas likely detrimental effects are competition for sunlight and increased fungal disease due to increased humidity.

The experimental plot was on a deforested slope at the Sunkoo site. Twelve 1 m wide lines, 62 m long and 3 m apart were cut in the vegetation and seedlings were planted along them at 2 m intervals, together with seedlings of other species not described here. Each seedling in the row was paired with another of the same species, planted 50 cm into the uncut strip beside the row. Three pairs of seedlings of each species were randomly planted in each row, giving a total of 36 pairs, but as six randomly selected pairs were harvested for another study (not described here) final survival was assessed for 30 pairs of seedlings for each species. Planting was carried out at the beginning

Table 3
Phenological observations of mature trees

Species	Mean fruit score[a]		Period of ripe fruit on trees	Season of ripe fruit availability
	Year 1	Year 2		
Beilschmiedia	3	0	April–July (peak in June)	Late dry/early rainy
Prunus	4	4	March–June (peak in March)	Late dry/early rainy
Engelhardia	1.2	1.2	March–May (peak in April)	Late dry/early rainy

[a]Year 1 is June 1994 to May 1995 and year 2 is June 1995 to May 1996.

of September 1995, using approximately 3-month-old seedlings. Where possible, seedlings were taken from the partial shade-low moisture treatment in the nursery, but when insufficient numbers were available, these were supplemented with wildings of comparable age, carefully transplanted with root systems intact. To standardise root disturbance, nursery raised seedlings were also transplanted from bag to bag. All seedlings were 'hardened off' in the unshaded area of the nursery for 5 weeks prior to planting. Analysis of survival in the two treatments was carried out using a χ^2-test as in Sokal and Rohlf (1981).

3. Results

3.1. Beilschmiedia sp. (Lauraceae)

Beilschmiedia fruited prolifically in 1994/1995 but not at all in 1995/1996 (Table 3). Unripe fruit were present on the trees from the start of the study in June 1994 to April 1995 when they first began to ripen; ripe fruit had completely fallen by July 1995 and another crop was not produced during the study period.

The seed rain was sparse and uneven in the forest (a mean density of 1.2 seeds/m^2, with a frequency of two out of six traps) and absent from the clearing edge and centre (Table 4). The mean density of germinants in the forest was 93% of the mean density of seed rain, suggesting that seed viability was high and that the species was able to germinate in understorey shade. On average, 67% of forest germinants survived to the end of the first dry season. Only two germinants were recorded in the edge plots and none were recorded in the centre.

In the nursery experiment, seeds in the high moisture treatments began to germinate 5 weeks after planting (by which time the rainy season had commenced) and continued until 17 weeks after planting. Seeds receiving no extra watering scarcely germinated (Table 5). ANOVA of percentage germination showed significant differences between watering treatments ($F = 34.8$, df = 1,18, $P < 0.001$) and between shade treatments ($F = 7.6$, df = 2,18, $P < 0.01$) and a significant interaction between the two ($F = 4.4$, df = 2,18, $P < 0.05$). The highest percentage germination occurred under partial shade with high moisture (35 ± 6%); germination in partial shade with low moisture was significantly less (2 ± 2%, $n = 15$). A similar trend was observed under heavy shade (Table 5). In full sunlight, germination was very low (5 ± 5% or less, $n = 15$) irrespective of moisture treatment.

In the planting experiment, seedling survival was higher than 90% in both treatments for the first 4 months until the end of the cold dry season (Table 6). During the following 4 months of the dry season, survival in the weeds cut treatment dropped to 37% while remaining above 90% where weeds were left uncut ($P < 0.01$).

3.2. Prunus cerasoides (Rosaceae)

Prunus trees fruited heavily in both years (Table 3). Seed rain, probably dispersed by birds (Table 1), was recorded in all zones. However, in the clearing centre, density was only 0.83 seeds/m^2 and frequency was only two out of six traps, half the amounts recorded in the forest (Table 4). In the edge zone all recorded seeds (55 in total) fell into a single trap located under a branch of a fruiting *Prunus* tree, but no seeds germinated in that plot, presumably because of heavy predation (Janzen, 1970). Germinants did emerge in two other edge plots with no recorded seed rain. In the clearing centre the mean density of germinants was

Table 4
Results from field observations on seed rain, germination and survival of the first year

	Forest			Edge			Centre		
	Density (per m^2)[a]	F[b]	Mortality rate[c]	Density (per m^2)	F	Mortality rate	Density (per m^2)	F	Mortality rate
Beilschmiedia									
Seeds[d]	1.17 ± 0.98	2	0.07	0	0	~	0	0	~
Germinants[e]	1.09 ± 0.98	3	0.33	0.22 ± 0.17	2	0.2	0	0	~
Yearlings[f]	0.73 ± 0.67	2		0.18 ± 0.13	2		0	0	
Prunus									
Seeds	1.67 ± 0.67	4	0.04	9.17 ± 9.17	1	0.99	0.83 ± 0.65	2	0.46
Germinants	1.60 ± 0.89	3	0.85	0.09 ± 0.06	2	0.50	0.45 ± 0.45	1	0.60
Yearlings	0.24 ± 0.14	3		0.05 ± 0.05	1		0.18 ± 0.18	1	
Engelhardia									
Seeds	225.83 ± 148.99	6	0.89	3.33 ± 1.56	4	0.92	10.67 ± 2.95	6	0.93
Germinants	23.88 ± 22.62	4	0.89	0.28 ± 0.14	3	1.00	0.79 ± 0.32	5	0.78
Yearlings	2.67 ± 2.61	2		0	0		0.18 ± 0.11	2	

[a]Mean ± SE ($n = 6$).
[b]Frequency as indicated by the number of traps or plots where seeds or seedlings were recorded out of a maximum of 6.
[c]Rate for seeds is estimated by 1 − (mean density of germinants/mean density of seed rain). The actual rate for germinants is 1 − (mean density of yearlings/mean density of germinants).
[d]Seed rain during period of ripe fruit (February–July 1995).
[e]Seedlings germinating during period May–December 1995.
[f]Germinants surviving through to May 1996 (the end of their first dry season).

54% of the mean density of seed rain. Forty percent of those germinating survived to the end of the first dry season. All germinants in the clearing centre were in one plot located in a clump of small pioneer trees (with a canopy cover of 68%). In this plot the dense litter associated with the grasses and ferns found in more open plots had been shaded out and exposed soil was 53% of the total area (mean for all clearing centre plots was 32 ± 11%, $n = 6$). However, the number of seeds caught in the clearing centre traps was insufficient to permit statistical analysis of the effects of micro-environment on percentage germination and establishment.

In the nursery, seeds started to germinate 3 weeks after planting except for the low moisture/full sunlight and low moisture/partial shade treatments, in which germination began in the fifth week when regular rainfall began. ANOVA showed a significant difference between shade treatments ($F = 28.2$, df = 2,18, $P < 0.001$), but none between watering treatments, and a significant interaction between the two ($F = 6.1$, df = 2,18, $P < 0.01$). Germination was high (89% and

Table 5
Percentage germination of seeds sown in three light and two moisture treatments (mean ± SE)

	Full sunlight			Partial shade			Heavy shade		
	High moisture	Low moisture	P[a]	High moisture	Low moisture	P	High moisture	Low moisture	P
Beilschmiedia	5 ± 5	0	NS	35 ± 6	2 ± 2	***	28 ± 9	2 ± 2	*
Prunus	67 ± 9	17 ± 7	**	93 ± 3	93 ± 4	NS	89 ± 6	91 ± 3	NS
Engelhardia	48 ± 12	42 ± 2	NS	66 ± 2	51 ± 1	*	68 ± 2	54 ± 2	*

Beilschmiedia ($n = 15$) and *Prunus* ($n = 25$): four replicates per treatment, df = 6; *Engelhardia* ($n = 50$): two replicates per treatment, df = 2.
[a]P is the significance of differences between moisture treatments within light treatments according to a t-test: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS, not significant.

Table 6

Percentage survival of seedlings planted in two treatments (weeds cut and weeds not cut)

	End of cold dry season (4 months after planting)			End of hot dry season (8 months after planting)		
	Weeds cut	Weeds not cut	P^a	Weeds cut	Weeds not cut	P
Beilschmiedia	93	97	NS	37	93	**
Prunus	97	93	NS	53	70	NS
Engelhardia	97	87	NS	27	67	*

[a]P is the significance of differences between treatments according to the χ^2-test: *$P < 0.05$; **$P < 0.01$; NS, not significant ($n = 30$, df = 2).

above) under partial and heavy shade, irrespective of moisture treatment (see Table 5). In full sunlight, germination was significantly reduced by dry season drought but remained high when seeds were watered.

In the seedling establishment experiment, survival in both treatments was over 90% throughout the cold dry season. By the end of the hot dry season (8 months after planting) survival was slightly lower in the cut than in the uncut treatment but the difference was not significant (Table 6).

3.3. *Engelhardia spicata (Juglandaceae)*

The *Engelhardia* population fruited in both years (Table 3) although some individual trees fruited supra-annually and non-synchronously. The seed rain of this wind dispersed species (Table 1) was of high density and frequency with seeds falling into all traps on the site except two along the clearing edge (Table 4). In the clearing centre and edge the mean density of germinants was 7 and 8%, respectively of the mean density of seed rain (Table 4). In both zones the small winged seeds were sometimes prevented from reaching the soil by the thick leaf and stem litter created by grasses and ferns (pers. obs.). Of those germinating in the clearing centre an average of 22% survived the first dry season, while none survived in the edge zone. There was a significant positive relationship between the percentage of exposed soil and the percentage of germinants surviving in each centre plot ($r = 0.895$, $P < 0.05$).

In the nursery, seeds in the high moisture treatment started to germinate 3–4 weeks after planting and seeds in the low moisture treatment started to germinate 3 weeks (heavy shade) to 6 weeks (full sunlight) after planting. Germination was at least 40% in all treatments showing that neither exposure to drought nor full sun totally impeded germination (Table 5). ANOVA showed significant differences in germination between moisture treatments ($F = 7.7$, df = 1,6, $P < 0.05$) and light treatments ($F = 5.6$, df = 2,6, $P < 0.05$), but no significant interaction between the two. Supplementary dry season watering significantly increased germination by 15% (under partial shade) and 14% (under heavy shade) (Table 5) but failed to make any significant difference in full sunlight. In the seedling establishment experiment, seedling survival during the hot season was significantly higher in the uncut treatment (Table 6).

4. Discussion

4.1. *Limiting factors*

Forest regeneration in abandoned agricultural clearings depends on seeds dispersed from the forest rather than remnant seeds or roots in the soil which are often destroyed through intensive agricultural use (Nepstad et al., 1990). Tree seed rain in a clearing is governed by density of reproductive individuals in nearby forest, regularity of seed production, availability of dispersal agents and distances that seeds are dispersed.

Our field observations indicated that regeneration of *Beilschmiedia* is limited in some years because seeds are not produced annually (Table 3). Supra-annual seed production is typical of many large-seeded tropical trees (Swaine and Whitmore, 1988) and may result from a combination of climatic cueing and the need for a tree to build up a certain amount of reserves before it can set seed (Janzen, 1978). By contrast, the *Prunus* and *Engelhardia* populations produced seeds annually, a pattern typical of small seeded and pioneer species (Fleming and Williams, 1990; Bazzaz, 1991; Finegan, 1996).

The distance that seeds are dispersed is limited by their method of dispersal which depends largely on their fruit morphology (van der Pijl, 1982). Large seeds of fleshy-fruited species generally need large vertebrates for dispersal (Willson, 1992). As very few, if any, large mammals or birds remain in Doi Suthep-Pui National Park (Elliott et al., 1989) it is not surprising that no *Beilschmiedia* seeds (mean fresh weight 6.7 g, Table 1) were recorded in the clearing. Even when populations of suitable dispersers are present, regeneration of large seeded tree species in clearings is still an extremely slow process (Parrotta et al., 1997). Although the seeds of *Prunus* are smaller (mean fresh weight 0.2 g, Table 1) they are still too large for many bird species; most of the tree seeds recovered from the faeces of birds and bats captured in a pasture in Brazil weighed less than 0.1 g (Nepstad et al., 1990). This may explain the very low occurrence of *Prunus* seeds in the clearing centre (Table 4). The three-winged fruits of *Engelhardia* are smaller still (fresh seed weight 0.03 g, Table 1) and were dispersed by wind throughout the clearing, where all seed traps were less than 100 m from a fruiting *Engelhardia* tree, well within the mean dispersal distances reported for many tropical wind-dispersed tree species. Theoretical mean dispersal distances of 34 such species ranged from 22 to 194 m (Augspurger, 1986) and the wind-dispersed seeds of *Toona australis* were found 100 m from the forest edge in an old field (Willson and Crome, 1989). Thus, regeneration of *Beilschmiedia* and *Prunus* was limited by low seed availability in the clearing, while regeneration of *Engelhardia* was not.

Percentage survival and germination of seeds in a clearing may be influenced by seed size. Finegan (1984) holds that when surface-sown in open sites, seeds of forest tree species (which tend to be larger than the seeds of pioneers, Foster and Janson, 1985) will not be able to withstand the heat, desiccation and predation as well as the seeds of pioneers. Results from our nursery experiments show that the large *Beilschmiedia* seeds were indeed much less tolerant of exposure to full sunlight and low moisture than the smaller seeds of *Prunus* and *Engelhardia* (Table 5), even allowing for the lower viability of *Beilschmiedia* seeds in this experiment (35%, as judged by the highest germination percentage, probably due to infestation by insect larvae, pers. obs.). The reason for this difference is not clear. Normally, tolerance of environmental extremes is linked to low seed moisture (Mayer and Poljakoff-Mayber, 1975), but the seeds of all three species in this study have similar moisture contents (Table 1). Despite the resilience of *Engelhardia* seeds to high light and low moisture, natural regeneration in the clearing centre was limited by low germination (Table 4). Thick leaf litter, low seed viability (68% according to the nursery experiments) and seed predation may have been responsible. Nepstad et al. (1990) and Osunkoya (1994) state that in general, small seeds are at greater risk of predation than large ones, but this was not tested in this study.

Potential causes of seedling mortality in a large clearing include drought and exposure to full sunlight causing high leaf temperatures (Finegan, 1984). Finegan suggests that pioneer species are more tolerant of these conditions than forest species and are therefore better suited to the old field environment. As pioneer species tend to be smaller seeded (Foster and Janson, 1985), it would be expected that a species' mean seed size would be a good predictor of its seedling performance in old fields. Our results did not support this hypothesis. When seedlings were exposed to the sun by cutting surrounding weeds, survival rate during the hot, dry season was highest for *Prunus* (Table 6), which has medium sized seeds. *Beilschmiedia*, the largest seeded species, did suffer low survival (as expected), but survival of *Engelhardia*, the smallest seeded species, was even lower. However, when shaded from direct sun by the weed canopy, *Beilschmiedia* seedlings had the highest survival rate of the three species in the hot, dry season. This result supports Nepstad et al. (1990), who state that large seeded, shade-tolerant, slow growing species are more drought resistant than pioneers, as they use the energy reserves in their seeds to develop deeper root systems which tap deep soil moisture reserves. Evidently the precise environmental conditions of an old field are of crucial importance. On an exposed site with short vegetation or bare ground, full sunlight is the most important limiting factor in the dry season (Uhl, 1987), so 'exposure tolerant' species such as *Prunus* are most suited. On shadier sites, with dense, tall herbaceous vegetation, dry season drought is the most important limiting factor and large seeded, drought tolerant, shade loving species such as *Beilschmiedia* may survive best. More research is needed on this subject.

Field observations indicated that establishment of *Engelhardia* seedlings in the clearing centre was limited by thick leaf and stem litter. This could be because the small seedlings (about 2 cm at 3 days old, pers. obs.) are covered by litter, especially in the wet season when it is heavy with moisture. Similarly, Finegan (1984) found that some species required bare ground for seedling establishment and Parrotta (1995) found a significant negative relationship between seedling density of all tree species and litter depth and dry mass in plantation understories.

4.2. Assisted natural regeneration strategies

4.2.1. Beilschmiedia sp. (Lauraceae)

Regeneration of *Beilschmiedia* in the clearing centre was limited by poor seed dispersal and by drought and direct sun at the germination stage. Thus, seeds manually broadcast into clearings would fail to germinate if sown during a long period without rainfall, although Shaw has shown that burying seeds helps to protect them (Shaw, 1968). Alternatively, the traditional system of collecting seeds and raising them in shaded, watered conditions in a nursery before transplanting into gaps would be justified here. Seeds or wildings should be collected in years of abundant fruiting and seedlings could be planted out in their first year under the protection of existing vegetation. Although at the early stages it appears that any form of shading, even from grass and ferns, is enough to reduce dry season mortality, the effect of weed competition on later growth is unknown.

4.2.2. Prunus cerasoides (Rosaceae)

Regeneration of *Prunus* in the clearing centre was limited at the seed dispersal stage. As seeds were not highly sensitive to seasonal drought and the few naturally dispersed seeds were able to germinate and establish in the clearing in the absence of thick grass and weeds, it is likely that regeneration could be significantly improved by increasing seed dispersal. Seeds could be broadcast into areas cleared of grass and fern litter, a feasible option as large quantities of seed are available each year. Further research is required to test ways of reducing seed predation, such as burying or coating seeds with unpalatable substances already developed by the agrochemical industry. Dispersal could be indirectly increased by protecting birds from hunters and improving the habitat for seed dispersing birds (providing that a seed source exists nearby). Planting nurse trees in open grassy areas or assisting those that are naturally regenerating by suppressing surrounding weeds would have the double advantage of encouraging bird dispersal of *Prunus* and improving the micro-environment for its germination and establishment by shading out grass and weeds (Parrotta, 1995).

4.2.3. Engelhardia spicata (Juglandaceae)

As dense litter appears to be a limiting factor, it is suggested that narrow openings be created in dense, ground level vegetation and litter towards the end of the dry season, enabling a higher proportion of seeds to reach the soil and establish. One way of doing this would be to amend current practice by cutting the lines for enrichment planting earlier than usual, during the hot dry season (before seeds disperse) instead of in the rainy season (after seeds have germinated). As direct exposure to the sun reduced survival of young seedlings the vegetation cover should be allowed to re-establish towards the end of the rainy season, to provide shade during the following dry season. An alternative approach would be to shade out the thatch-creating grass and ferns by encouraging existing trees and shrubs (e.g. by weeding around them) or by planting nurse tree species, providing that the trees themselves did not create thick leaf litter.

5. Conclusions

Regeneration of *Beilschmiedia* sp., *Prunus cerasoides* and *Engelhardia spicata* in deforested areas was clearly limited by various factors operating at different stages of the life-cycle. Appropriate ANR plans for each should vary accordingly. Rapid establishment of a nurse crop, either by weeding around naturally established trees and shrubs or by planting fast growing trees, may be an effective way of assisting a diverse range of species by overcoming several limiting factors at once, such as thick grass litter accumulation, lack of habitat for birds and lack of shade. However, species differ considerably in their effect on these factors (Lugo, 1988; Goosem and Tucker, 1995; Parrotta, 1995) and more research is needed to identify suitable nurse crops.

This project has shown that systematic study of regeneration processes can facilitate the identification of specific factors limiting succession in degraded areas, enabling management strategies to be devised to overcome them. However, the chosen management approach will also be influenced by such practical considerations as the end use of the restored site, available capital, facilities for collecting seeds and raising seedlings and the distance over which seeds or seedlings would have to be transported. Further research is needed to test the feasibility of the techniques suggested here and to compare their cost with traditional methods of reforestation.

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