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Spatial heterogeneity of the soil seed bank in the tropical semi-deciduous forest at Wasgomuwa National Park, Sri Lanka

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Abstract: This study examined the spatial distribution of seeds in the soil seed banks of a tropical semi-deciduous forest and adjacent grassland at Wasgomuwa National Park, Sri Lanka and some factors responsible for the spatial heterogeneity. It also evaluated how soil seed banks would contribute to forest regeneration or degeneration. Two soil seed bank types were identified in the study area: those of the forest and the grassland. In between these two, there was a narrow transitional zone, a forest-grassland ecotone, which contained large numbers of seeds of grassland species and seeds of some forest pioneer and agricultural weed species. These soil seed banks are highly heterogeneous, and clumping of seeds occured frequently. Composition of the local vegetation, fruiting season and the seed dispersal patterns greatly affected for this heterogeneity. Seeds of woody forest species were hardly found in the grassland implying that invasion of forest into grasslands would not occur spontaneously. Seeds of grassland species were frequently dispersed into the forest interior mainly by herbivores. If the forest or the forest edge gets disturbed, these seeds would germinate and establish, and this would result in the reduction of the forest cover and, subsequently, expansion of the grassland.

Resumen: En este estudio se examinó la distribución espacial de las semillas en los bancos de semillas del suelo de un bosque tropical subcaducifolio y un pastizal contiguo en el Parque Nacional Wasgomuwa, Sri Lanka, así como algunos factores responsables de la heterogeneidad espacial. También se evaluó cómo los bancos de semillas del suelo podrían contribuir a la regeneración o degeneración del bosque. En el área de estudio se identificaron dos tipos de bancos de semillas del suelo: los de bosque y los de pastizal. Entre los dos existió una estrecha zona de transición, un ecotono bosque-pastizal, donde hubo grandes números de semillas de especies de pastizal, así como semillas de algunas especies pioneras del bosque y de malezas agrícolas. Estos bancos de semillas del suelo son muy heterogéneos y con frecuencia se presentó una distribución agregada de las semillas. La composición de la vegetación local, la temporada de fructificación y los patrones de dispersión de semillas afectan en gran medida esta heterogeneidad. Apenas se encontraron unas cuantas semillas de especies forestales leñosas en el pastizal, lo que implica que la invasión del bosque hacia el pastizal no ocurriría espontáneamente. Las semillas de especies de pastizal fueron dispersadas con frecuencia hacia el interior del bosque principalmente por herbívoros. Si el bosque o el borde del bosque son perturbados, estas semillas podrían germinar y establecerse, y esto podría resultar en la reducción de la cobertura del bosque y, subsecuentemente, en la expansión del pastizal.

Resumo: Este estudo examina a distribuição espacial das sementes no banco seminal no solo de uma floresta tropical semidecídua e em pastagem adjacente no Parque Nacional de Wasgomuwa, Sri Lanka e alguns dos factores responsáveis pela heterogeneidade espacial. Avalia-se também como é que os bancos seminais no solo contribuem para a regeneração ou degenerescência da floresta. Na área estudada identificaram-se dois tipos de bancos seminais no solo: aqueles na floresta e os na pastagem. Entre estes dois, havia uma zona de transição estreita, um ecotono floresta-pastagem, que continha um grande número de sementes de espécies de capim, sementes de algumas espécies florestais pioneiras e espécies infestantes agrícolas. Estes bancos seminais no solo são muito heterogéneos mostrando frequentes agrupamentos de sementes. Esta heterogeneidade afecta fortemente a composição da vegetação local, a estação de frutificação e os padrões de dispersão de sementes. As sementes de espécies florestais lenhosas dificilmente se encontravam na pastagem implicando que a invasão das florestas nas pastagens não ocorre espontaneamente. Já as sementes das espécies da pastagem eram frequentemente dispersadas na interior da floresta principalmente pelos herbívoros. Se a floresta, ou as suas margens, forem disturbadas, estas sementes germinarão e estabelecer-se-ão, e de que resultará uma redução do coberto arbóreo e, subsequentemente, a expansão da pastagem.

Key words: Proximity to seed source, seed dispersal, spatial heterogenity, tropical semi-deciduous forest.

Introduction

Spatial heterogeneity of species and seed densities of soil seed banks is well known for some ecosystems like tropical humid forests (Whitmore 1983) and temperate grasslands (Rice 1989; Rusch 1992; Young *et al.* 1981). Grasslands often contain large number of seeds and their seed banks are persistent. For example, Young *et al.* (1981) reported 27,400 seeds m^{-2} from *Stipa* grassland in California. Tropical rain forests contain large number of seeds in the soil of many pioneer species (Whitmore 1983). In contrast, the density of seeds in tropical dry forests is found to be low. For instance, Lieberman (1979) found a maximum of 160 seeds m^{-2} in a dry forest in Ghana while Hall & Swaine (1980) reported 100 - 700 seeds m^{-2} in a dry forest in the same country. In a tropical semi-deciduous forest at Sigiriya Sanctuary, Sri Lanka, soil seed density of 166 ± 127 seeds m^{-2} was reported (Perera 2005 in press).

Soil seed banks in tropical humid forests are found to be highly heterogenous (Garwood 1989; Uhl *et al.* 1981). Some factors which results in high spatial heterogeneity of soil seed banks are the seed dispersal patterns of the different species (Hall & Swaine 1980; Nepstad *et al.* 1996; Swaine & Hall 1983; Uhl *et al.* 1981), edaphic factors (e.g. drainage) (Garwood 1989), fire and seed predation (Perera, unpublished data). Such constrains affect seed germination while the time of disturbance relative to flowering may limit the number of seeds and species that invade a site (Epp 1987). According to Geritz *et al.* (1984) and Hartshorn (1980), proximity to a seed source is important in determining the successful colonization and regeneration of species in a disturbed site. This seems to be more relevant to the colonization of small canopy gaps in forests.

Tropical semi-deciduous forests in Sri Lanka are highly disturbed and large canopy gaps occur as a result of shifting cultivation (Perera 2001). Regeneration of tree species do not occur frequently in these large gaps (Holmes 1954; Perera 2001; Rosayro 1961) and, therefore, it is necessary to assist natural regeneration (Perera *et al.* 1995; Perera 2001).

Soil seed banks play a major role in natural regeneration after disturbances such as fire, logging and overgrazing in humid environments (Grime 1981; Roberts 1981; Swaine & Hall 1983), and determining the composition and density of seed banks is considered as an essential step in artificial restoration of degraded vegetation (van der Valk 1989). Therefore, it is necessary to examine whether the disturbed tropical semi-deciduous forests of Sri Lanka could be rehabilitated by using their soil seed banks.

The objectives of this study were to examine the spatial distribution of seeds in the soil seed bank of a tropical semi-deciduous forest of Sri Lanka and factors responsible for the spatial heterogeneity. It also assesses the potential role of the soil seed bank in forest regeneration and evaluates how far the proximity to forests affects in the regeneration of forests in grasslands, which are situated adjacent to forests.

Materials and methods

Study site

The research was conducted at the Wasgomuwa National Park in the dry zone of Sri Lanka ($7^{o}34'$ - $7^{o}57'$ North and $80^{o}51'$ - $81^{o}05'$ East) (Fig. 1), which extended over 37,063 ha area (Green 1990). The forest and adjacent grassland in the southern half of the park were selected for the study. The soils in the area are reddish brown with some alluvial deposits, and the pH varies between 6 - 8 (Jayasingham 1991). Generally, the mean annual rainfall in the dry zone of Sri Lanka is about 1000-1900 mm year^{-1} (Rosayro 1950). The rain is mainly brought by the north-east monsoon between October and February. The south-west monsoon brings less rain between March and May. Dry periods occur in between monsoonal periods though intermonsoonal rains also occur. Man made fires periodically burn the grass vegetation.

The vegetation of the area is mainly characteristic of a tropical semi-deciduous forests of Sri Lanka (Jayasingham 1991). Characteristic species include *Berrya cordifolia* (Willd.) Burret, *Chloroxylon swietenia* DC, *Drypetes sepiaria* (Wight and Am.) Pax. and Hoffm. and *Diospyros* spp. Over the forested area, 155 species belonging to 47 families have been identified including 107 trees, 34 shrubs, 13 lianas and 2 climbers (Jayasingham 1991). The Euphorbiaceae, Leguminosae and Rutaceae are the dominant families (Jayasingham 1991). Some parts were heavily disturbed by a cyclone in 1978 and these areas have more light demanding forest pioneer species.

Jayasingham (1991) identified two grassland types in the area and named them as *Imperata* grasslands and *Ischemum*/*Eragrostis* grasslands. The former occurs widely over the area and is dominated by *Imperata cylindrica* while the latter occurs towards the eastern boundary and is dominated by *Eragrostis* sp. and *Ischemum* sp.

Soil sampling

Sampling was done at the early period of the main rainy season (November 1995). Four transects were established at right angles to the forest-grassland boundary in randomly selected locations across slight altitudinal gradient distances of 0, 5, 25, 125, 625 and 3125 metre were marked along these transects from the forest-grassland boundary into the forest and the grassland. In most of the places, the length of the grassland was less than 3 km from the boundary. In such transects, the soil samples were collected from the furthest available point (fp) in the grassland, which varied between 2000 to 3125 m.

At each distance along the transect, 20 m lines perpendicular to the transect were marked. Ten soil samples (surface area = 15 x 15 cm; depth = 4 cm) were collected at 2 m intervals along these lines. Soil samples were brought to the shade house thatched with transparent plastic corrugated sheets, and the 10 soil samples collected at each distance were mixed together and spread over sterilized sand beds (surface area of the sand bed was one square meter and depth of the sand layer was five centimeters). The beds were well watered using a hand held fine sprayer and germinants were observed and recorded for 110 days. Seventy days after the original spreading the soil surface was lightly scarified in order to expose buried seeds if any. Six sand beds were left without any soil to detect any contamination in the shade house. Dicot seedlings which could not be identified when very young were potted and identified after 7-8 months.

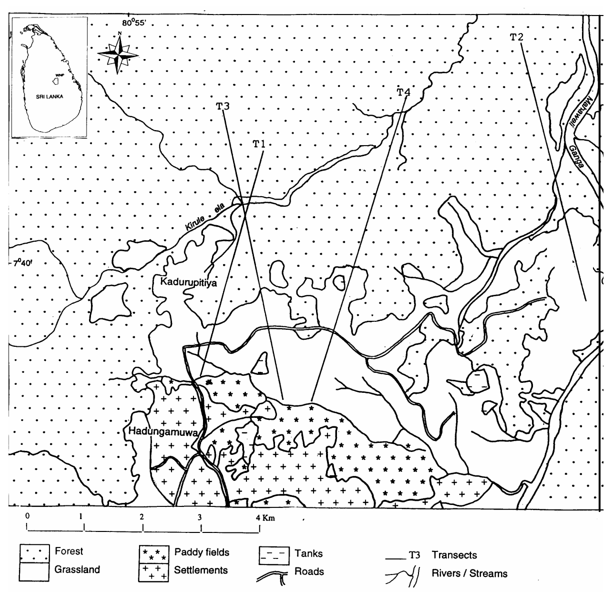

Fig. 1. Location of the study site and transects.

Results

Species composition and distribution in the soil seed banks

Three major groups of sample plots were identified in the TWINSPAN (Hill 1979) sample plot dendrogram (Fig. 2a) representing the soil seed banks of forest interior, grassland interior and a transitional area (ecotone) between these two. The group of soil samples denoted as forest interior were collected in the forest beyond 5 m from the forest grassland boundary (Fig. 2a). The grassland interior soil samples include those collected in the grassland beyond 25 m from the boundary. Soil samples taken up to 5 m in the forest and 25 m in the grassland were similar in species composition and abundance and appear as forest-grassland ecotone. The species dendrogram (Fig. 2b) clearly showed that the soil of forest-grassland ecotone contained seeds of some agricultural weeds or plants that grow in forest fringes and disturbed environments, e.g. *Ageratum conyzoides* L., *Chromalaena odorata* (L.) R.M. King and H. Robinson and *Lantana camara* L. in addition to other forest and grassland species (Table 1).

However, a few number of sample plots have shown some exceptional characteristics. In the TWINSPAN sample plot dendrogram (Fig. 2a), the grassland interior samples, G3:125; G1:125; G3:fp and G4:625 were grouped with the ecotone samples. This is due to the similarities of species abundance and composition of these samples to the soil at forest-grassland ecotone, mainly, by having many seeds of *Ageratum conyzoides* and *Lindernia crustacea*. The boundary samples G4:5 and G4:25 were grouped with grassland interior samples because of the absence of seeds of the typical grassland species *Lindernia crustacea* in them. The boundary samples F1:5; F2:5 and F4:5 showed similarities to forest interior because of the presence of seeds of *Securinega leucopyrus* (Willd.) Mueller and *Clinopodium umbrosum* (Bieb.) Koch in large amounts. In addition, the forest interior sample F1:125 lied with boundary samples mainly

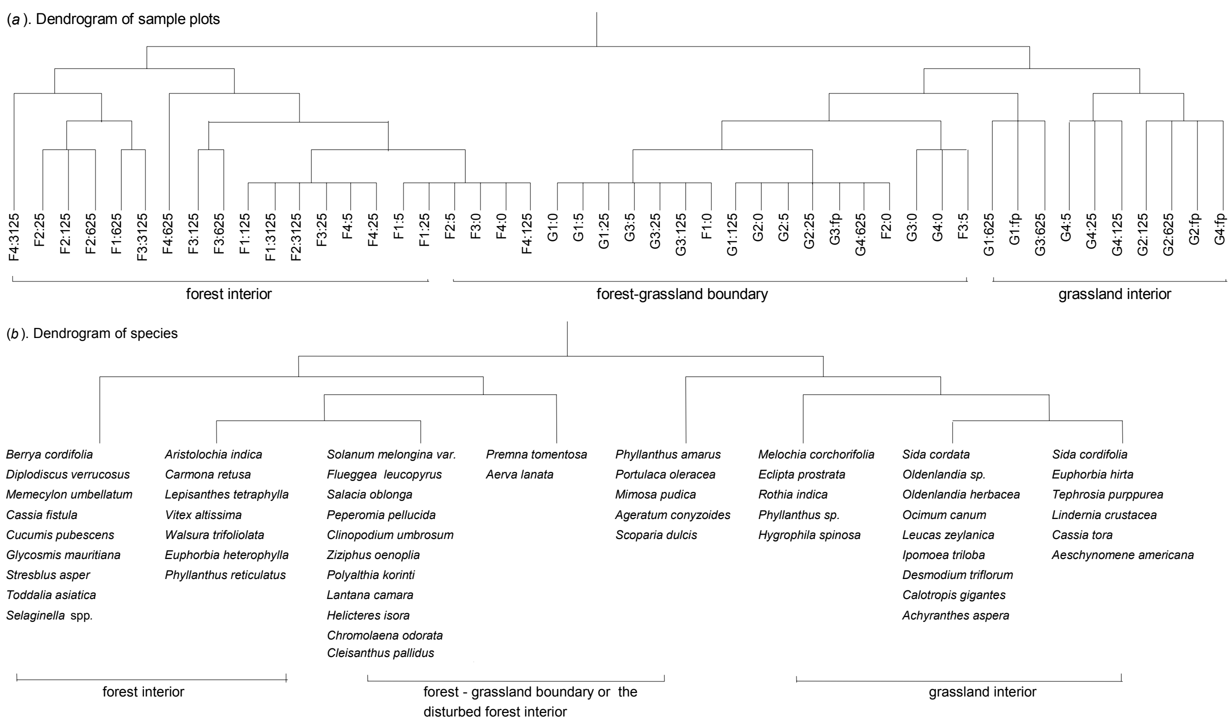

Fig. 2. Dendrogram of (a) sample plots and (b) species produced by TWINSPAN of species abundance data of the soil seed bank at Wasgomuwa National Park, Sri Lanka. Alphabets in the abbreviated names show forest (F) or grassland (G) with subsequent first numeral indicating replicate number (F1..F4) and second numeral after colon shows distance along transects from forest-grassland boundary. fp is the distance to the furthest point that sampled within the grassland.

due to abundance of *Ageratum conyzoides* seeds, a characteristic feature of the soil seed bank of the ecotone.

Seeds of forest species were, mainly, present in the forest soil seed bank although a few of them were also found in the soil seed bank of the forest-grassland ecotone (Table 1). They were, however, hardly found in the grassland soil seed bank. Most of the typical grassland species were found in the forest soil although they were found in the soil seed banks of the grassland and the ecotone in large quantities. When the woody species were considered, it became evident that seeds of the most common woody forest species were not represented in the soil seed bank except for *Diplodiscus verrucosus* (Thw.) Kosterm. and *Memecylon umbellatum* Burm. f. (Table 2).

Density of seeds in the surface soil

Seed densities in the soil varied significantly with the distance form the forest grassland boundary (one way ANOVA: $P < 0.001$). The mean seed density was higher in the grassland (8339 ± 918) and at the forest-grassland ecotone grassland (6990 ± 2751)(Fig. 3). However, there was an abrupt decline in the densities of seeds in the soil beyond 5 m distance into the forest and the density of the forest soil seed bank was 583 ± 236. There was a very high interaction between the distance and the transects (blocks), especially in the

Table 1. Distribution of typical forest and grassland species (as a percentage of the total number of plots in each category) in the two soil seed bank types and at the forest-grassland ecotone.

Species category	Species	Frequency (%)		
		Grassland interior	Forest-grassland ecotone	Forest interior
Forest species	*Diplodiscus verrucosus*	0	5	19
	Peperomia pellucida	0	10	38
	Flueggea leucopyrus	0	35	75
	Walsura trifoliolata	0	0	25
Grassland species	*Ageratum conyzoides*	33	85	38
	Phyllanthus amarus	8	10	7
	Lindernia crustacea	58	75	19
	Desmodium triflorum	25	55	0
	Oldenlandia herbacea	42	60	0
	Ocimum canum	25	25	6
	Scoparia dulcis	50	25	7
	Mimosa pudica	67	55	31

Table 2. Dominant woody species in the standing vegetation and the on the soil (Species in each category are arranged in descending order of abundance).

Forest vegetation (studied by Jayasingham 1991)	Soil seed bank estimated by the current study
Dimorphocalyx glabellus, Mallotus rhamnifolius, Glycosmis sp., *Polyalthia korinti, Diospyros ovalifolia, Diplodiscus verrucosus, Memecylon umbellatum, Drypetes sepiaria, Catunaregam spinosa, Phyllanthus polyphyllus*	Forest interior *Flueggea leucopyrus, Chromolaena odorata, Diplodiscus verrucosus, Memecylon umbellatum, Salacia oblonga, Walsura trifoliolata, Phyllanthus reticulatus*
	Forest - grassland ecotone *Flueggea leucopyrus, Chromolaena odorata, Phyllanthus reticulatus, Diplodiscus verrucosus*
	Grassland interior *Aristolochia indica, Calotropis gigantea*

grassland despite that it was not statistically significant (Fig. 4).

A total of 42,054 seeds germinated from all soil samples, 64% of which were grasses. The mean densities of seeds of grass species were significantly higher in the grassland and at the ecotone (Fig. 3; one way ANOVA: $P < 0.001$). The densities of seeds of other species except grasses, (i.e., other herbs, shrubs and trees) also varied significantly with the distance along transects (Fig. 5; one way ANOVA: $p = 0.003$ for herbs; $P < 0.001$ for both shrubs and trees). Tree and shrub seeds were found at the forest-grassland ecotone in small numbers (Fig. 5) but they were also commonly found in the forest soil seed bank. No tree seeds were found in the grassland interior but a few seeds of *Calotropis gigantea* (L.) R. Br. in Ait. f., a semi-woody shrub species, were found in the grassland.

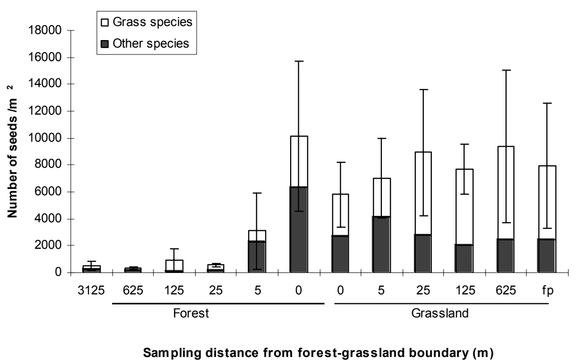

Fig. 3. Mean density of seeds in the soil at each distance from the forest-grassland boundary with 95% confidence limits (n = 4, but each sample is a mixture of 10 sub-samples; fp is the distance along transects to the furthest point that sampled within the grassland).

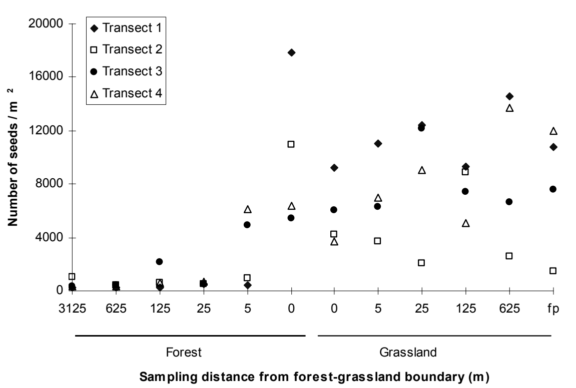

Fig. 4. Interaction between the seed density and the distance from the forest-grassland boundary. (fp is the distance along transects to the furthest point that sampled within the grassland).

Diversity of the soil seed banks

Fifty eight dicotyledonous species were identified in the collected soil samples belonging to 33 families. Seven herbaceous plants could not be identified to the species level as they died before being identified. No seeds germinated in the control sand beds in the shade house implying that no contamination took place. Poaceae was the dominant family in all seed banks. Seeds of plants belong to the families Asteraceae and Scrophulariace were also common in all seed banks. The species richness of forest interior samples was significantly higher than the ecotone area and the grassland interior (one way ANOVA: $P < 0.001$; Fig. 6).

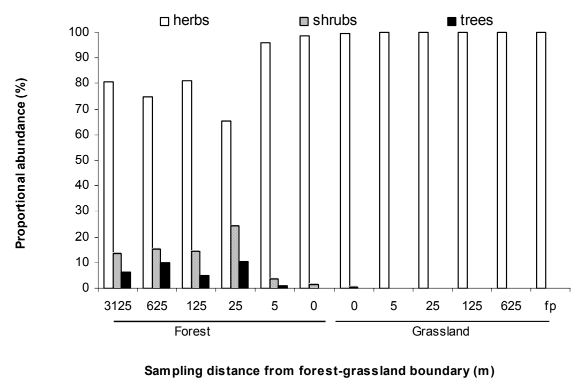

Fig. 5. Proportional abundance of (a) dicotyledonous herb, (b) shrub and (c) tree seeds in the soil. (fp is the distance along transects to the furthest point that sampled within the grassland).

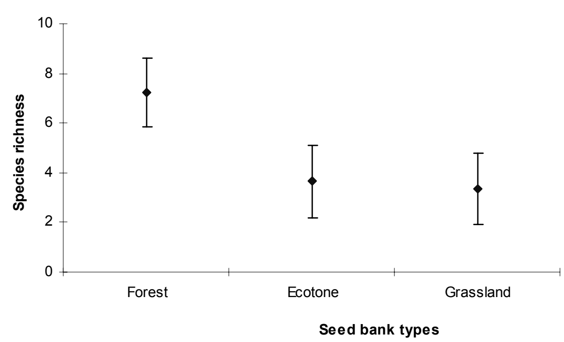

Fig. 6. Species richness at the two soil seed banks and the ecotone in samples of 20 individuals, which detected

by Hurlburt's rarefaction method with 95% confidence limits (Also see the Figure 2a for the soil seed bank types).

Ecology and seed dispersal patterns of forest species

All woody species found at the forest-grassland ecotone area were forest pioneer species (*sensu* Whitmore 1990), but seeds of both pioneer and climax species were found in the forest interior (Table 3). Seeds of wind dispersed-pioneer stem twiner *Aristolochia indica* L. were found in both forest and grassland. Seeds of most woody forest species were dispersed by animals and they were not found in the grassland interior (Table 3). In contrast, the grassland species were dispersed by both wind and animals, and these were also found in the forest and at the forest edge. Seeds of invasive agricultural weed species: *Chromalaena odorata* and *Lantana camara* L. were present at the ecotone area in large quantities.

Table 3. Abundance of seeds of woody species in the soil seed bank along transects, the ecology of seeds and their major dispersal agent (The first digit indicates the frequency of seeds out of 4 replicated (transects) while the latter digit indicates the total number of seeds found). fp is the distance to the furthest point that sampled within the grassland.

			Sampling distance from forest-grassland boundary (m)											
Species	Ecology	Dispersal	Forest						Grassland					
		Agent	3125	625	125	25	5	0	0	5	25	125	625	fp
Trees														
Lepisanthes tetraphylla	Climax	Mammal	2/3											
Streblus asper	Pioneer	Bird	1/1											
Berrya cordifolia	Climax	Wind	2/4	1/1										
Cassia fistula	Climax	Mammal		1/1										
Vitex altissima	Climax	Bird	1/1	2/3	1/1	1/2								
Walsura trifoliolata	Climax	Bird	2/3	1/5		1/3								
Diplodiscus verrucosus	Pioneer	Bird	1/3		1/2	1/10	1/15							
Premna tomentosa	Pioneer	Bird			1/2				1/2					
Shrubs														
Memecylon umbellatum	Climax	Bird	1/4	2/7										
Salacia oblonga	Pioneer	Bird/ Mammal	3/9	1/1		1/1								
Helicteres isora	Pioneer		1/2		1/1	1/2								
Glycosmis mauritiana	Climax	Bird		1/1										
Toddalia asiatica	Pioneer	Bird		1/1										
Carmona retusa	Climax	Bird		1/2	2/3									
Flueggea leucopyrus	Pioneer	Bird/ Mammal	3/11	3/6	3/11	3/15	3/48	3/26	1/7					
*Chromolaena odorata**	Weed	Wind	1/7			2/17	2/23	3/55						
Polyalthia korinti	Climax	Mammal				1/1								
Ziziphus oenoplia	Pioneer	Bird/ Mammal					1/1	1/1						
Lantana camara	Weed	Bird						1/1						
Phyllanthus reticulatus	Pioneer	Mammal	2/2	1/2	2/2	1/4	1/14	3/10		1/1	1/1			
*Calotropis gigantea**	Pioneer	Wind										1/1		
Climbers														
*Aristolochia indica**	Pioneer	Wind	2/2		1/1		1/2							1/1

* semi-woody speices

Discussion

Two distinct soil seed bank types could be identified in the study area, namely the forest and the grassland soil seed banks. Between these two seed banks, there was a transitional zone, which included samples collected at the forest-grassland ecotone, i.e. the samples collected between 5 m into the forest and 25 m into the grassland form the forest-grassland margin. The ecotone soil seed bank was formed due to the accumulation of seeds of grassland species (grasses and herbs) with some forest pioneer and agricultural weed species.

As in temperate grasslands (Rice 1989; Rusch 1992) the seed density in the soil of the tropical grassland at Wasgomuwa was very high (8399 ± 918). This can be explained by the high seed production of grasses and herbs, their long viability and capability to withstand harsh environments. More than 50% of the seeds in the soil of the grassland were grasses. The only shrub found in the grassland interior was *Calotropis gigantea*, which is not a forest species.

As in other tropical semi-deciduous forests in Sri Lanka (Perera 2005 in press) and in Ghana (Hall & Swaine 1980; Lieberman 1979), the average density of seeds in the soil seed bank of the forest at Wasgomuwa was low (583 ± 236) and contained seeds of grass and dicotyledonous herbs in large quantities (Figs. 3 & 5). Some parts of the forest interior had been disturbed by the cyclone in 1978 and the seed bank of such disturbed patches contained some species, which characterize the forest - grassland boundary, i.e. seeds of some agricultural weeds such as *Chromalaena odorata* and *Lantana camara*.

Seeds of tree and shrub species were found in samples collected inside the forest and at the ecotone while those of climax species were only found from the forest interior (Table 3). The species richness is also high in the forest soil seed bank (Fig. 6). As in humid rain forests, (Whitmore 1983), most of the woody forest species of the standing vegetation were not represented in the soil seed bank (Table 2). However, *Diplodiscus verrucosus* and *Memecylon umbellatum* were represented both in the standing forest vegetation and the soil seed bank. This may be due to the ability of the species to produce a plethora of seeds and/or because sampling was done in the fruiting season. The fruiting season of these species is between September to January and, therefore, viable seeds of these species may be available in the soil when sampling was done in late November. Some other species like *Chromolaena odorata* and *Flueggea leucopyrus* have long lived seeds and they may form a persistent seed bank.

In agreement with reports of Garwood (1989) and Uhl *et al*. (1981), soil seed banks of Wasgomuwa National Park are highly heterogeneous, and local variations were also observed in a given soil seed bank type (Figs. 2a & 4). In the sample plot dendrogram (Fig. 2a), some grassland interior samples have been grouped with the forest-grassland ecotone sample group because these samples contained seeds of *Lindernia crustacea* and *Ageratum conyzoides* abundantly, which is a characteristic of the ecotone area. Similarly, two of the ecotone soil samples have been grouped with grassland interior samples due to the absence of seeds of *Lindernia crustacea* in them. According to Garwood (1989), such situations may arise due to localized seed dispersal patterns such as presence of drainage flows.

As in typical forest interior samples, the presence of *Flueggea leucopyrus* and *Clinopodium umbrosum* seeds in a large quantity has caused some forest edge samples to be grouped with forest interior samples. Such situations are caused by the local composition of the standing vegetation in addition to localised seed dispersal patterns. Aubréville (1938) has described the spatial heterogeneity and mosaic nature of standing vegetation, and similarly spatial heterogeneity of the seed bank may occur.

In the sample plot dendrogram, the forest interior sample F4:125 was grouped with ecotone soil samples and the presence of *Ageratum conyzoides* seeds in a large quantity, which is a characteristic feature of the soil of the forest-grassland ecotone area. This implies that the particular sampling point, which situated in the forest, may be a resting site of mega-herbivores, or situated beside a foot path of herbivores who feed on grasslands. Droppings of these herbivores add *Ageratum conyzoides* seeds to the soil at the site.

As the soil seed banks are very heterogeneous, even over a small area, collection of several smaller samples (sub-samples) per location is, therefore, more effective and accurate than collecting fewer bigger samples.

Although Geritz *et al.* (1984) and Hartshorn

(1980) have shown that proximity to a seed source is important in determining the successful colonization and regeneration of a species, this study has shown that proximity to the forest has little influence on the re-invasion of forests in the grasslands at Wasgomuwa National Park of Sri Lanka. Dispersal of seeds of fleshy fruits into grassland is determined by several factors such as whether the new site is of interest to birds by having perching sites and fruits (Janzen & Vázquez-Yanes 1991; Nepstad *et al.* 1996). In contrast, close proximity to a seed source may be important for wind dispersed tree seeds. Then, some other factors such as the wind speed and the direction may affect in the process (Janzen 1986; Janzen & Vázquez-Yanes 1991). A few wind dispersed forest tree and shrub seeds might reach to the grassland in their fruiting season but, these are predated or destroyed by unfavourable climate or by grazing soon after germination. Also, these grasslands are burnt periodically in the dry season and this results in the destruction of the vegetation and the soil seed bank. Therefore, re-invasion of forests in grasslands will not take place spontaneously.

However, dispersal of seeds of grassland species into forest occurs frequently. This is partly by passive dispersal (by wind) and partly by herbivores. Wind carries seeds only a short distance as the air movement under a forest canopy is not strong. Therefore, most of the wind dispersed seeds of grassland species accumulate at the forest-grassland boundary forming an ecotone region. Also, grassland species are very effectively dispersed over longer distances by herbivores. In the Wasgomuwa National Park, the grasslands are feeding areas for wild elephants, wild buffaloes, deer and other herbivores, which feed during the evenings and nights and spend the day inactively in the forest. Animal droppings contain seeds many of which may still be viable and add grassland seeds to the forest soil. This may also lead to the clumping of seeds in the soil. Mega-herbivores are well recognised as seed dispersal agents in other areas of the world as they take seeds of grassland species long distances into the forest (Janzen 1986; Schüle 1992).

Seeds of grassland species, which are accumulated in the forest can germinate and establish if a disturbance occurs in the forest. With frequent disturbances, grassland species may become well established leading to degeneration of high forest and as a result, open savanna forests or grasslands may be formed. The boundary of the forest is at a high risk as it is always disturbed both by natural (e.g. strong wind) and anthropogenic factors (fire). Then grass and herbaceous seeds, which are present in the soil at the forest boundary may germinate and establish, and this will result in gradual shrinking of the forest cover.

Conclusions

Two distinct soil seed banks were identified in the study area as: the forest and the grassland soil seed banks. The species richness of the forest seed bank was higher compared with that of the grassland while the density of seeds was lower. Seeds of pioneer species and a few climax forest species were available in the forest soil seed bank but were absent in the adjacent grassland. Between the soil seed banks of the forest and grassland, there was a narrow ecotone, which contained seeds of grasses and herbs of grassland species in very high densities. Some seeds of pioneer shrubs and agricultural weeds were also present at the ecotone.

The soil seed banks were highly heterogeneous and clumping of seeds occured frequently. Species composition of the parent vegetation, the fruiting season and seed dispersal patterns affect the spatial heterogeneity of the soil seed bank.

The soil seed banks of tropical semi-deciduous forests were highly influenced by adjacent land use types and contained seeds of grasses and herbs in very large quantities since these seeds are efficiently dispersed into the forest by herbivores. Wind carries small seeds of grassland species to short distances, probably up to the forest-grassland boundary. In contrast, seeds of forest species are not accumulated in the grassland due to poor dispersal and destruction by predation, natural death and anthropogenic activities.

Owing to the lack of forest seeds, grasslands would not develop into forests unless intensive silvicultural methods, e.g. protection from fire and grazing, sowing of seeds or planting, are applied. As seeds of many grassland species were common in the soil seed banks of the forest interior and forest-grassland ecotone, they may germinate and establish after a catastrophe. Therefore, there is a risk of gradual conversion of forests into grasslands with frequent disturbances.

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