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Diversity and dynamics of the soil seed bank in tropical semi-deciduous forests of Sri Lanka

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Abstract: The nature and the magnitude of the soil seed bank of tropical semi-deciduous forests at Sigiriya, Sri Lanka were examined in 41 experimental plots established along a chronosequence of forest age to reveal the potential role of the soil seed banks in forest regeneration and succession following a large-scale disturbance. Species composition and abundance in the soil seed banks were influenced by the time of the year and the structure of forests where the latter is highly determined by the age of forests after a large-scale disturbance. Clumping of seeds in the soil seed bank was commonly seen in all studied forests. Soil seed banks of young successional forests were dominated by agricultural weeds, and their seeds were mainly dispersed by wind. Therefore, such seed banks do not often contribute to the forest regeneration. After about 20 years, the diversity of the soil seed bank increased and the seed banks contained some forest tree and shrub seeds. Since the microclimate of such forests are more favourable for seed germination and seedling establishment, seeds which reach these forests might germinate and establish well, contributing to successful forest regeneration and succession. Seed bank of mature forests contain less number of seeds but are also dominated with grass and agricultural weed species. Therefore, these seed banks cannot support the natural regeneration of tropical semi-deciduous forests after a large-scale disturbance. Instead, seeds of grass and agricultural weed species would germinate and establish if a disturbance occurs. Therefore, such forests are under a threat of degeneration with frequent disturbances.

Resumen: Se examinó la naturaleza y la magnitud del banco de semillas del suelo en bosques tropicales subcaducifolios en Sigiriya, Sri Lanka, en 41 parcelas experimentales establecidas a lo largo de una cronosecuencia de edad del bosque; la finalidad fue revelar el papel potencial de los bancos de semillas del suelo en la regeneración del bosque y la sucesión después de un disturbio de gran escala. La composición y la abundancia de las especies en los bancos de semillas del suelo estuvieron influenciados por el momento del año y la estructura de los bosques, estando esta última fuertemente determinada por la edad del bosque después de un disturbio de gran escala. En todos los bosques estudiados se observó que es común que las semillas en el banco de semillas estén agregadas. Los bancos de semillas del suelo de los bosques sucesionales jóvenes estuvieron dominados por malezas agrícolas, cuyas semillas fueron dispersadas principalmente por viento. Por lo tanto, tales bancos de semillas frecuentemente no contribuyen a la regeneración del bosque. Después de unos 20 años, la diversidad del banco de semillas en el suelo aumentó y los bancos de semillas contuvieron algunas semillas de árboles y arbustos. Como el microclima de tales bosques es más favorable para la germinación de semillas y el establecimiento de plántulas, las semillas que llegan a estos bosques pueden germinar y establecerse bien, contribuyendo a la regeneración exitosa del bosque y la sucesión. El banco de semillas de bosques maduros contienen un menor número de semillas, pero también están dominados por pastos y especies de malezas agrícolas. Por lo

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tanto, estos bancos de semillas no son capaces de soportar la regeneración natural de los bosques tropicales subcaducifolios después de un disturbio de gran escala. Por el contrario, las semillas de pastos y de malezas agrícolas podrían germinar y establecerse si ocurre un disturbio. Por lo tanto, estos bosques están bajo la amenaza de degenerarse ante la presencia de disturbios frecuentes.

Resumo: A natureza e a dimensão dos bancos seminais no solo das florestas semidecíduas de Sigiriya, Sri Lanka, foram examinados em 41 blocos experimentais estabelecidos ao longo de uma sequência de idades da floresta e sucessão por forma a revelar o papel dos bancos seminais no solo na regeneração da floresta e na sucessão a seguir a um distúrbio em grande escala. A composição das espécies e a sua abundância nos bancos seminais no solo eram influenciados pela época do ano e a estrutura da floresta e onde, esta última, é fortemente determinada pela idade da floresta depois do distúrbio em grande escala. Agrupamentos de sementes nos bancos seminais de sementes no solo eram vulgarmente observados em todas as florestas estudadas. Bancos seminais no solo de florestas secundárias jovens eram dominadas por infestantes agrícolas e as suas sementes eram fundamentalmente dispersas pelo vento. Consequentemente, tais bancos seminais no solo frequentemente não contribuem para a regeneração da floresta. Depois de cerca de 20 anos, a diversidade do banco seminal no solo aumentou e os bancos seminais continham algumas sementes de árvores florestais e sementes de arbustos. Uma vez que o microclima de tais florestas é mais favorável para a germinação das sementes e para o estabelecimento das plântulas, as sementes que atinjam estas florestas podem germinar e estabelecer-se bem, contribuindo para o estabelecimento favorável da regeneração da floresta e da sucessão. O banco seminal de florestas adultas contem menor número de sementes sendo dominado por gramíneas e infestantes agrícolas. Por isso, estes bancos seminais não podem suportar a regeneração das florestas tropicais semidecíduas depois de um distúrbio em grande escala. Em vez disso as sementes das gramíneas e das infestantes agrícolas germinarão e estabelecer-se-ão se ocorrer um distúrbio em grande escala. Estas florestas estarão, consequentemente, sob ameaça de degeneração se sujeitas a distúrbios frequentes.

Key words: Disturbance, ecology, regeneration, succession.

Introduction

Soil seed banks play an essential role in regeneration of tropical rain forests (Hopkins & Graham 1983; Hopkins & Graham 1984 a & b; Kellman 1970; Symington 1933; Whitmore 1983) as well as in temperate (Archibold 1989) and boreal forests (Pickett & McDonnell 1989), although the role of these in tropical dry forests have not been fully understood.

Seed banks in successional forests tend to be larger (Ewel *et al.* 1981; Hopkins & Graham 1984b; Saulei & Swaine 1988) and consist mainly of pioneer seeds (Guevara & Gomez-Pompa 1972; Hopkins & Graham 1983; Hopkins & Graham 1984 a & b; Nepstad *et al.* 1996; Ross 1954; Symington 1933; Whitmore 1983) but, seed banks reflecting human-dominated disturbance regimes are likely to contain species that evolved under similar natural disturbance regimes or have originated in similar human-dominated landscapes elsewhere (Pickett & McDonnell 1989). These seeds may stay in the soil for a longer period and form a persistent seed bank where as seeds of most of the climax forest species form a transient seed bank (Whitmore 1983).

Guevara & Gomez-Pompa (1972) stated that older successional communities have a greater storage of seeds due to the longer period of time for seed deposition but, decrease in seed density and species richness with increasing age of old fields is often observed in temperate forests despite that there may be small seed banks in some young forests (Pickett & McDonnell 1989). The density of seeds in soils of mature tropical dry forests is believed to be low. For instance, Lieberman (1979) found 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.

Limited seasonal variation in rain forest soil seed banks has been recognised (Enright & Cameron 1988; Guevara & Gomez-Pompa 1972). In contrast Chandrashekara *et al.* (1993) showed that the density of germinable seeds in a humid forest seed bank of western Ghats of Kerala, India, fluctuates considerably with time of the year, and the seed density was high during the monsoon season.

Density of seed banks decline with increasing depth of the soil (Pickett & McDonnell 1989; Saulei & Swaine 1988). Buried seed banks appear to be an important source of plant colonists in some secondary successions in the tropics (Kellman 1970; Symington 1933). They are regarded as 'persistent' (*sensu* Grime 1979) as demonstrated by seed longevity in experimental trials (Hopkins & Graham 1987; Perez-Nasser & Vázquez-Yanes 1986).

Swaine & Hall (1983) stated that the composition of the forest following a disturbance may be partly predicted from the knowledge of the soil seed bank prior to the disturbance although the importance of seeds in dry forest regeneration is greatly affected by the environmental requirements for germination. Seed viability and dormancy are genetically controlled characters while the damp moist climates may break seed dormancy (Vázquez-Yanes & Orozco-Segovia 1990).

The natural regeneration in dry forests of Sri Lanka is very poor (Holmes 1956; Perera 1998, 2001a & b; Perera *et al.* 1995; Rosayro 1961), and the regrown forests do not possess most of the valuable timber tree species (Holmes 1956). In tropical semi-deciduous forests of Sri Lanka, regeneration immediately after a disturbance mainly takes place from root sprouts and cut stumps (Perera 1998 & 2001b). Soil seed bank might play an important role in a latter stage of vegetation succession but, when and how would this happened is poorly understood.

This study examined the size and the diversity of the soil seed bank in tropical semi-deciduous forests of Sri Lanka, their annual and successional variations and the microclimate of the soil seed bank. It also investigated some of the factors that govern the existence of seeds in the soil at different stages of succession.

Materials and methods

Study site

The study was carried out in successional and natural high forests at Sigiriya sanctuary (7° 57' N & 80° 45' E) in the northern dry zone of Sri Lanka (Fig. 1). The mean annual rainfall is 1334 mm and highly seasonal. The major rainy season is from October to January/ February of the following year by north-eastern monsoonal rain. It is followed by a short dry spell, and then a minor rainy season from March/April to May/June, which is again followed by a longer dry period. The mean annual air temperature in the study area is 27° C. The evaporation from a free water surface ranges from 1900 - 2030 mm per year (Alwis & Eriyagama 1969).

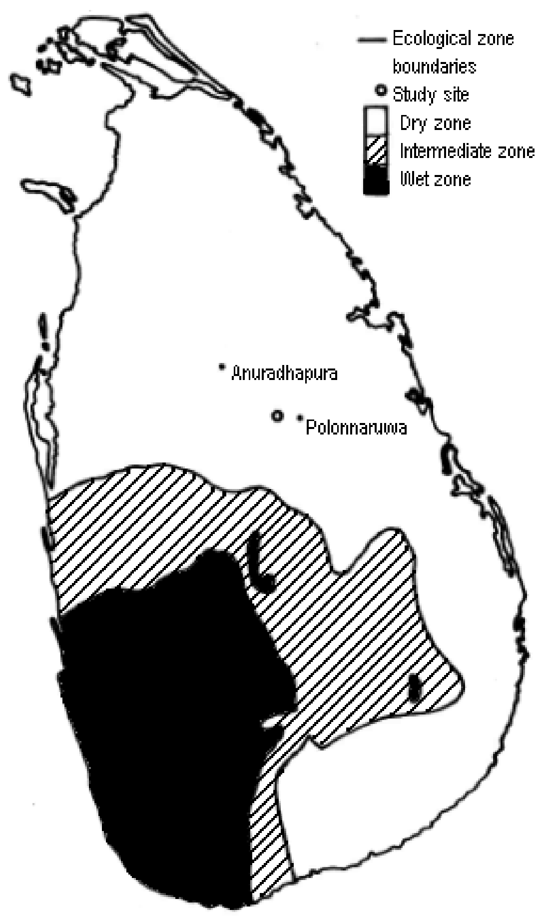

Fig. 1. Location of the study site and the major ecological zones of Sri Lanka.

Sampling the surface soil seed bank

Forty one 20 x 20 m experimental plots were established in mature and successional forests in a chronosequence of forest age (Table 1). Soil samples were collected from the experimental plots at 4 months interval over a period of one year. The first sampling was done in July 1995, i.e., at the beginning of the long dry period. A random location was selected along one of the axes of each experimental plot. A string was pulled from that point to the opposite side across the plot. Ten soil samples of 15 x 15 cm surface areas to a depth of 4 cm were carefully removed at 2 m intervals along the line and put in labelled polythene bags. The soil samples were taken to a shade house with a transparent roof where they were mixed together, spread over prepared sand beds (that had been heat sterilized) and kept well watered. Sixty days after original spreading, the soil layer was scarified in order to expose any buried seeds. Germinants were marked and recorded (code number and the date of germination) every two days for 110 days from the date of spreading. Germinants that could not readily be identified were potted and grown for later identification. Grasses and ferns were not identified to the species level. Five sand beds were left without any soil in order to detect contamination, if any.

This procedure was repeated on two further occasions, at the beginning of the long rainy period (November, 1995) and at the end (February, 1996). One month old forest was only sampled in February because shifting cultivation areas are always abandoned after cultivation in late January or in early February.

Table 1. Nature of forest types and number of replicates.

Forest type	Age after a large scale disturbance	Number of experimental plots established
Young successional forest	1 month	3
	1 year	9
	4-7 years	9
	12-25 years	8
	20-25 years	6
Natural high forest	>100 years	3
	Not cleared before	3

Sampling of the sub-surface soil seed bank

The above procedure was followed for soil samples collected at 4-8 cm depth but, the sampling was done only once, in July 1995, at the same time of sampling the 0-4 cm soil depth. One month old forests have not been sampled because, they were not available at that time of the year.

Forest microclimate

Soil moisture was estimated by gravimetric analysis at the beginning of the short dry period (early February, 1996). Two soil samples per experimental plot were collected from the forest floor after removing the surface litter layer for the purpose at randomly chosen locations and weighed immediately. The depth of the soil core was 8 cm. There was no rain for 10 days prior to sampling which was all done within two days. The samples were oven dried at 70° C until they received a constant weight. The percentage soil moisture was calculated using the formula:

Percentage soil moisture = $[W_I - W_A / W_I]$ 100

where, W_I = initial weight of the soil sample

W_A = weight after oven drying

Soil temperatures in two selected plots in each forest type were recorded in January and February of 1996 using 'TINYTALK II' temperature data loggers. The sensors of the temperature data loggers were kept on the forest floor about 1-2 cm below the soil surface.

The canopy openness in the plots was estimated from hemispherical photographs taken using a fisheye-Nikkor 8 mm lens during January-February 1996 and 3-8 photographs of the canopy were taken in each plot. Images were digitised (Canon Still Video Camera RC-5CO and dedicated Canon ION software) and the grey scale threshold set in Flamingo software (version 1.2 © Hamlet Software Systems ApS) before being analysed for canopy openness using Winphot (version 4.0). In this study, hemispherical photographs were taken only once within a two month period but, it is adequate for the comparison of different aged forests.

Results

Surface soil seed bank

Species composition and the density of germinable seeds along a chronosequence of forest age

Thirty four woody species and forty non-woody species were identified from all the surface soil samples during the three sampling times but three woody and eight non-woody species died before being identified. The density of viable seeds in the soil seed bank varied significantly with the age of the forest (one way ANOVA: $P < 0.001$ for all three sampling times; Fig. 2). Also, a clear seasonal variation in the soil seed bank was observed in the study sites (one way ANOVA: $P = 0.031$).

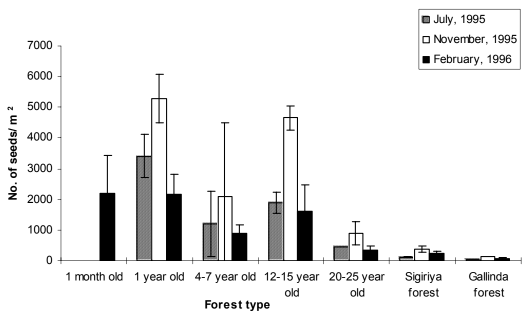

Fig. 2. The mean density of germinable seeds in the surface soil (0-4 cm) in different aged forests of the chronosequence at three sampling times with 95% confidence limits.

The seed density was high in young successional forests at all three sampling times (Fig. 2). The two most common herbaceous dicot species in these seed banks were *Chromolaena odorata* (L.) R.M. King and H. Robinson and *Ageratum conyzoides* L., and they dominate the soil in other forests too throughout the year. After about 15 years, the seed density decreased and older successional (20-25 year old) and natural high forests showed very low seed densities. The seed density in mature high forests is 166 ± 121 m^{-2}.

DCA scattergrams (Fig. 3 a-c) show that most of the soil samples collected from younger successional forests (less than 15 year old) are positioned separately form those of mature high forest and older successional (20-25 year old) forest plots despite the fact that some 12-15 year old forest sample plots are also positioned among older successional and mature high forest samples at some times of the year. These confirm that the seed bank in 1 month, 1 year, 4-7 year old forests and 12-15 year old forests are somewhat similar in species composition and abundance. Table 2 shows the percentage variance accounted for the four axes and the eigen values for the three sampling times. Seeds of mono- and di-cotyledonous herbaceous species were always present in very high numbers in the seed banks, especially in younger successional forests (Table 3). Tree seeds are mostly present in older successional (20-25 years old) and natural high forests only in some periods of the year.

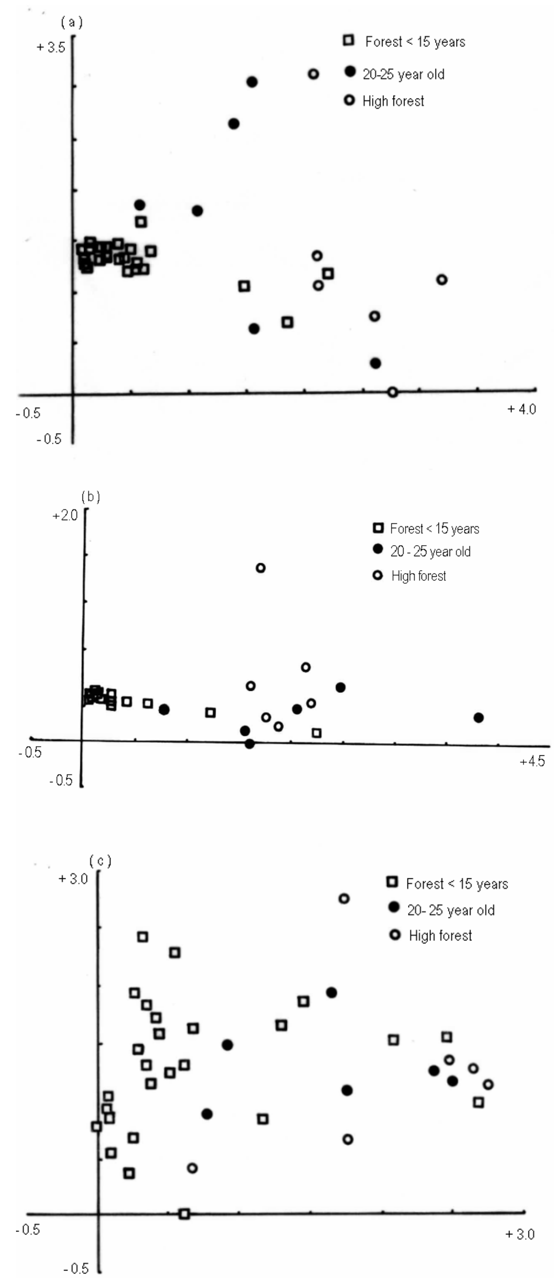

Fig. 3. DCA's sample plot scattergrams for the species abundance data of the soil seed banks collected at three sampling times: (a). at the beginning of the long dry season, (b). at the beginning of the long rainy season and (c). at the end of the long rainy season.

Table 2. Summary of DCA for all three sampling times.

Sampling time		Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
July, 1995	Eigenvalues	0.687	0.235	0.210	0.074	3.16
	Cumulative percentage variance of species data					
	Sum of all unconstrained eigenvalues	21.7	29.2	35.8	38.2	3.16
Nov., 1995	Eigenvalues	0.636	0.334	0.188	0.129	3.407
	Cumulative percentage variance of species data					
	Sum of all unconstrained eigenvalues	18.7	28.5	34.0	37.8	3.407
Feb., 1996	Eigenvalues	0.757	0.264	0.211	0.076	3.423
	Cumulative percentage variance of species data					
	Sum of all unconstrained eigenvalues	22.1	29.8	36.0	38.2	3.423

Table 3. Density of seeds in the soil seed bank according to life-form categories.

Life form	Sampling time	Seed density m^{-2} with the standard deviation						
		1 month	1 year old	4-7 year old	12-15 year	20-25 year	Sigiriya	Gallinda
Tree	First sampling	--	0	1±2	2±4	3±4	0	2±3
	Second sampling	--	1±3	6±19	17±31	53±81	3±3	3±5
	Third sampling	0	1±2	2±6	2±5	7±10	10±7	7±13
Shrub	First sampling	--	2197±1342	394±207	1079±1121	92±56	6±7	0
	Second sampling	--	1086±817	1035±893	1996±1705	154±148	18±9	58±31
	Third sampling	18±8	1292±950	296±214	464±204	79±37	28±16	12±10
Herbaceous dicots	First sampling	--	936±1601	684±833	656±770	268±491	46±38	16±9
	Second sampling	--	2529±2229	532±491	1849±2043	284±294	203±154	56±51
	Third sampling	253±199	543±360	469±230	963±1330	201±150	159±22	40±16
Monocots	First sampling	--	274±183	119±118	148±75	87±82	62±34	12±5
	Second sampling	--	1676±1173	524±246	789±287	403±199	142±204	31±16
	Third sampling	1133±761	319±305	126±93	171±154	62±25	52±51	25±16

Ecology of seeds

In ecological terms, most of the herbaceous dicot and shrub seeds present in the soil seed bank are 'non-forest early colonizers (or agricultural weeds) (Fig. 4), which germinate and establish well in disturbed open areas. The two most common non-forest early colonizers in the seed banks were *Chromolaena odorata* (L.) R.M. King and H. Robinson and *Ageratum conyzoides* L. These non-forest early colonizers dominate the soil in all forests throughout the year (Kruskal-Wallis test: P = 0.237). In all three sampling times, their abundance varied significantly with the age of forests (for the first and second sampling times: Kruskal-Wallis test: P < 0.001; for the third sampling time: one way ANOVA: P < 0.001). Their high abundance in younger successional forests was the reason for high total seed density in the soil, which varied little with the time of the year.

Few seeds of forest pioneer species were present in almost all studied forest soil seed banks (Fig. 4). Their abundance did not vary significantly with the time of the year (one way ANOVA: P = 0.219) but varied significantly with the forest age (one way ANOVA: for the first sampling time: P = 0.021; for the second sampling time: P < 0.001; for the third sampling time: P = 0.012). Their abundance was higher in 12 - 15 and 20 - 25 year old forests (Fig. 4).

Few seeds of climax forest species were found in natural high forest soils in some times of the year (Kruskal-Wallis test: P = 0.045). Their abundance varied significantly with the forest age during the second and third sampling times (Kruskal-Wallis test: for both second and third sampling times: P < 0.001). During the first sampling time, i.e., at the beginning of the long dry period, climax forest seeds were not available anywhere as it was not the fruiting season and, therefore, a significant variation of the abundance of climax forest seeds could not be observed with the forest age (Kruskal-Wallis test: P > 0.999).

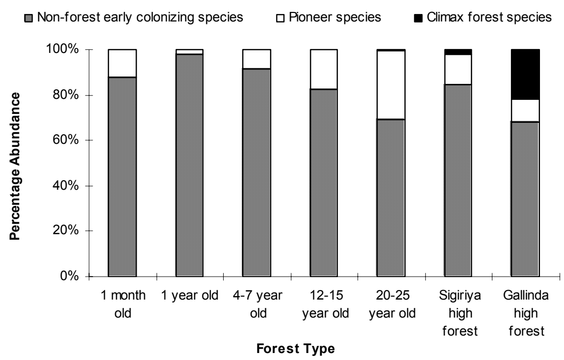

Fig. 4. Percentage abundance of plant ecological groups in different forests.

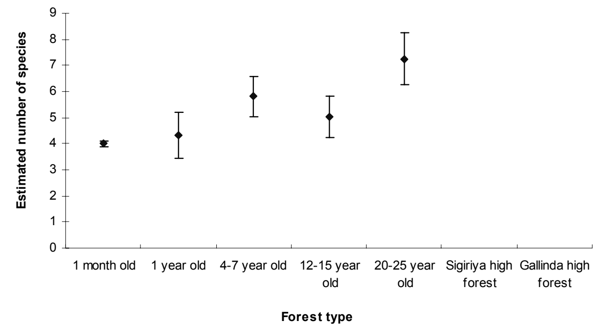

Fig. 5. Estimated number of species found in a sample of 30 individuals in different aged forests estimated by Hurlbert's (1971) rarefaction method with 95% confidence limits. Species richness in natural high forests could not be estimated by the rarefaction method because the method has a shortcoming that the selected sample size should be within the range of the total number of seeds of most abundant species.

Diversity of the surface-soil seed bank

Species diversity

The species richness in the surface soil seed bank, which determined by the rarefaction method (Hurlbert 1971), is given in Fig. 5. There is a gradual trend of increase of species richness with the forest age (for the first sampling time: Kruskal-Wallis test: P = 0.056; for the second sampling time: Kruskal-Wallis test: P = 0.012; for the third sampling time: one way ANOVA: P = 0.003). The species richness was low in one month and one year old forests. It increased to very high levels in the 20 - 25 year old successional forest (Fig. 5). The species richness also varied significantly with the time of the year (Kruskal-Wallis test: P < 0.001). Species richness in natural high forests could not be estimated by the rarefaction method because the method has a shortcoming that the selected sample size should be within the range of the total number of seeds of most abundant species.

The evenness of species distribution as indicated by the value of the slope coefficient of the species rank-log abundance curves (Tokeshi 1993) for the surface soil seed banks is given in Fig. 6. It varied significantly with the age of forests at all three sampling times (for the first sampling time: one way ANOVA: P = 0.006; for the second and third sampling times: Kruskal-Wallis test: probabilities were 0.016 and 0.050 respectively). There was a general trend of increase in species evenness with increasing age of successional forests despite that, there was a significant seasonal variation (Kruskal-Wallis test: P < 0.001). The evenness in 20 - 25 year old forests is high throughout the year. It was also exceptionally high in one month old fallow forest.

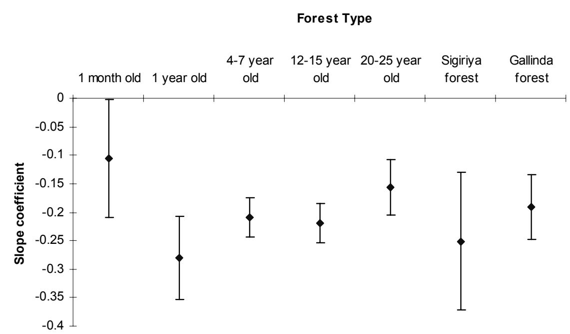

Fig. 6. Evenness of species distribution of the surface soil seed banks of different aged forests of the chronosequence with 95% confidence limits.

Habitat diversity

As shown in the Fig. 7, the value of mean similarity between plots varied significantly with the age of forest (for the first sampling time: one way ANOVA: P < 0.001; for the second sampling time: Kruskal-Wallis test: P = 0.009; for the third sampling time: one way ANOVA: P < 0.001). The value of mean similarity between plots was high in 1 month, 1 year and 4-7 year old successional forests. This implies the low habitat diversity in them. It was low in 12-15 and 20-25 year old forests implying higher habitat diversity. However, the mean similarity between plots did not vary with the time of year (One way ANOVA: P = 0.959). In high forests, the habitat diversity in the surface soil seed bank was somewhat high and it fluctuated seasonally although the fluctuation was not statistically significant, probably due to high standard deviation values (Fig. 7).

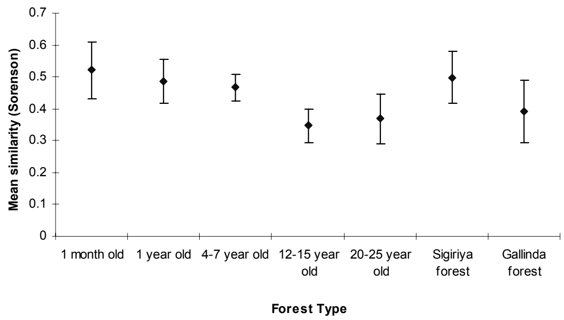

Fig. 7. Mean similarity estimated by the Sørenson index for different aged forests of the chronosequence with 95% confidence limits.

Seed dispersal patterns

It is evident from Fig. 8 that wind dispersed seeds dominated the soil seed banks of all studied forests. In all three sampling times, the abundance of wind- and animal-dispersed seeds varied significantly with the forest age (one way ANOVA: P < 0.001 for both wind- and animal dispersed seeds at all three sampling times). The dispersal mechanisms of a few non-woody species could not be identified and, therefore, indicated as 'unidentified' in Fig. 8 while in some other herbaceous dicots, any specialized seed dispersal mechanism could not be observed.

The proportional abundance of wind- and animal-dispersed seeds in the surface soil varied significantly with the time of the year (for wind dispersed seeds: one way ANOVA: P = 0.001; for animal dispersed seeds: one way ANOVA: P = 0.009).

Seed bank of the sub-surface soil

Seventeen woody and forty two non-woody species were found in the sub-surface soil (4-8 cm depth) seed banks. In successional forests, the seed density of the sub-surface soil was lower than that on the surface soil and highly varied with the age of the forest (two way ANOVA: soil depth, P = 0.035; forest type, P < 0.001; Fig. 9). As in the surface soil, dicotyledonous herb and shrub seeds were very abundant in the sub-surface soil and it varied significantly with the forest age (Fig. 10; two way ANOVA: soil depth: P = 0.452; forest type: P < 0.001). Most of these dicotyledonous herb and shrub species are ecologically known as non-forest early colonizing (agricultural weed) species. More than 80% of seeds in the soil seed banks of younger successional forests was non-forest early colonizing species while more than 60% of seeds in the soil seed banks of older successional and natural high forests were non-forest early colonizing species.

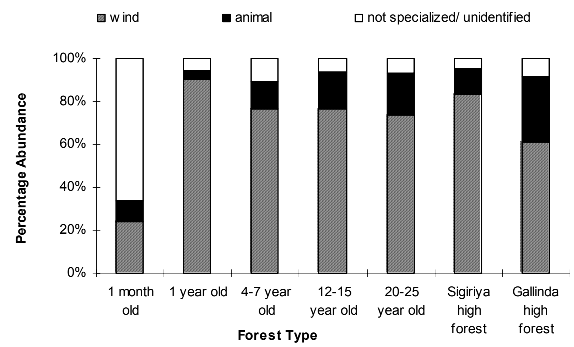

Fig. 8. Proportional abundance of seeds according to their major agent of seed dispersal.

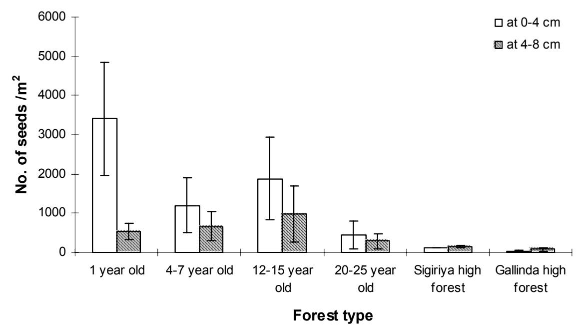

Fig. 9. Mean density of germinable seeds in the surface and sub-surface soil in different aged forests at the beginning of the long dry season (first sampling time) with 95% confidence values.

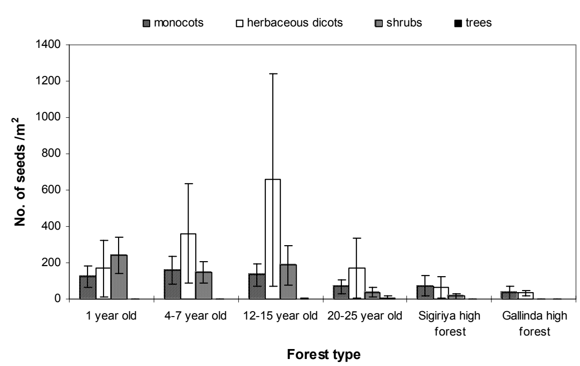

Fig. 10. The density of seeds of different life form categories in the sub-surface soil (4-8 cm) in different aged forests at the beginning of the long dry season (first sampling time) with 95% confidence values.

Microclimate of the soil seed bank

Canopy openness of the vegetation

The canopy openness changed significantly with the forest age (Kruskal-Wallis test: P = 0.025; Table 4). The land immediately after the abandonment of cultivation was very open but the canopy openness decreased abruptly after 3-4 years.

Soil temperature

Both mean and maximum surface soil temperatures varied significantly with the forest age (Kruskal-Wallis test: for mean soil temperature, P = 0.026 and for maximum soil temperature, P = 0.008; Table 4). It was higher in recently abandoned shifting cultivation land (one month old fallow forest) where the ground is open while comparatively lower in older forests.

Soil moisture

The percentage soil moisture in different aged forests were significantly different (One way ANOVA: P = 0.002). At early stages of succession, moisture content in the surface soil increased with the forest age (Table 4). It was at a maximum in 20-25 year old forests but slightly lower in mature high forests.

Discussion

The density of soil seed banks of the studied tropical semi-deciduous forests varied with the forest age. It is higher in younger successional forests and lower in older successional and natural high forests. Seeds of grass, herb and some shrub species dominated all studied soil seed banks. These seeds are mainly dispersed by wind (Fig. 8). In ecological terms, most of the herb and shrub seeds present in the soil seed bank were 'non-forest early colonizers' (or agricultural weeds) (Fig. 4).

Forest structure and the species composition in the vegetation mainly affect the quality and quantity of the soil seed banks in younger successional forests. Density of mature individuals of 'non-forest early colonizers' was higher in these forests, which produce enormous quantities of seeds annually or continuously (Perera, unpublished data). Also, these forests are open and as a result, wind-borne seeds of 'non-forest early colonizers' are efficiently dispersed. *Ageratum conyzoides* L. and *Chromolaena odorata* (L.) R.M. King and H. Robinson are two common 'non-forest early colonizers' in these forests. The longevity of seeds of *Chromolaena odorata* (L.) R.M. King and H. Robinson is about 2 years in humid environments (Epp 1987) and the persistent seed bank of *Chromolaena odorata* is another reason for the high seed density in the soil seed bank. These seeds germinate and establish well in open areas. Similar situations have also been identified elsewhere in the world (e.g. Pickett & McDonell 1989).

In the DCA ordination (ter Braak 1995), the location of two sample plots close to each other on a scattergram reflects the similarity between these two plots in terms of species composition and abundance. As depicts by the scattergrams (Fig. 3 a-c), soil seed banks of younger successional forests were positioned separately from those of 20-25 year old (older successional) and natural high forests, which could be attributed to the differences in species composition and abundance in soil seed banks. For instance, younger successional forests contain seeds of grasses, herbs and the semi-woody shrub *Chromolaena odorata* in very high numbers (Table 3) resulting in a high total seed density in the soil. In contrast, some seeds of climax forest species were present in 20 -

Table 4. Forest microclimate (Average values with the standard deviation).

	1 month old forests	1 year old forests	4-7 year old forests	12-15 year old forests	20-25 year old forests	Natural high forests at Sigiriya	Natural high forests at Gallinda
Canopy openness (%)	69.4(±5.1)	52.3(±9.7)	11.7(±3.7)	8.6(±2.6)	8.6(±3.4)	5.0(±1.3)	6.0(±1.5)
Max. soil temperature (°C)	35.30(±1.60)	25.12(±1.03)	25.37(±1.28)	24.24(±0.59)	23.71(±0.59)	24.11(±0.89)	23.25(±0.50)
Mean soil temperature (°C)	26.24(±0.44)	23.13(±0.47)	22.83(±1.42)	21.72(±0.79)	22.47(±0.20)	22.03(±1.01)	22.79(±0.37)
Soil moisture (%)	2.3(±1.2)	3.2(±1.6)	3.5(±1.4)	4.4(±2.1)	8.8(±3.2)	5.0(±2.2)	4.5(±2.9)

25 year old (older successional) and high forests but not in young successional forests.

The DCA scattergrams (Fig. 3a-c) also show that the sample plots for a given forest age are rather scattered, and this may be due to the high standard error of mean values which, resulted in clumping of seeds in the soil. On the forest floor, seeds form clumps, and this depends on the distance from the seed source, wind direction, animal behaviour and the surface run off. Although these results agree with those of numerous other authors who pointed out that the seed banks of younger successional forests are larger (e.g. Ewel 1981; Hopkins & Graham 1984b; Saulei & Swaine 1988), they fail to confirm the prediction of Chandrashekara & Ramakrishnan (1993) that density of seeds increases with forest age.

Most of the shrub species that were present in 12 - 15 year old forests can be described as forest pioneer species. Some shrub species such as *Lantana camara* L. can produce seeds throughout the year. Therefore, their abundance did not vary significantly with the time of the year. Seeds of some forest pioneer species (e.g. *Flueggea leucopyrus* (Willd.) Mueller) have hard seed coats, which can be long lived and accumulate in the soil for a long period.

Seed densities in older successional (20-25 year old) and natural high forests were very low. In natural high forests, the density was as low as 166 ± 121 seeds m^{-2} and this is comparable with those reported for Ghanian dry forests, i.e. 100 - 700 seeds m^{-2} (Hall & Swaine 1980). This was due to low number of seeds of agricultural weeds and grasses in the soil which resulted in their poor occurrence in the vegetation or due to the death of these seeds after a long period of accumulation. Wind cannot carry seeds long distances in a closed forest because of the weak air movement. Therefore, the dispersal of grass and herb seeds into natural high forests is rather random. Tree seeds are mostly present in older successional and natural high forests but they are available only in some periods of the year.

Seeds of climax forest species were especially found in natural high forest soil seed banks. Seeds of climax forest shrub species were found in their fruiting season but those of tree species were rare even during their fruiting season. Most of these seeds have originated from the site, but a few may be brought in by animals from out side. Interestingly, one seed of *Madhuca longifolia* (L.) Macbride germinated in one of the sand bed of 20 - 25 year old forest soil, but no mature individuals were present within the relevant experimental plot or nearby. *Madhuca longifolia* is a riverine tree species and bats act mainly as the dispersal agents implying that very few seeds can be dispersed from long distances as these forests attract animals by having food and roosting sites in older successional and natural high forests.

A clear seasonal variation in the soil seed bank was observed in this study, and similar situations have been observed for other areas such as the tropical humid forests of the western Ghats of India (Chandrashekara & Ramakrishnan 1993). The high seasonal variation in the soil seed bank could often be seen in areas with seasonal climates where flowering, seed production, seed germination and seedling establishment are highly seasonal. The seed density was high if sampling was done at the beginning of the long rainy period (November) (Fig. 2) because most of the monocots and herbs have produced mature fruits by then. The shrub seed density is high throughout the year (Table 3). However, it was the highest at the beginning of long dry period, i.e. during the first sampling time particularly in one and 12 - 15 year old forests. This is due to the presence of seeds of the invasive semi-woody shrub species: *Chromolaena odorata* (L.) R.M. King and H. Robinson, which is efficiently dispersed by wind.

Tree seed density also showed a high seasonal variation, which was higher at the beginning of the long rainy period (November). This seasonal variation is attributed to the seasonal production of seeds and their recalcitrant nature due to the seasonal seed dormancy. At the end of the rainy period, tree seed density was low. Seed germination during the wet period, destruction by fungal attacks and predation are the most probable reasons for this (personal observation). Most climax forest tree species in tropical humid forests form a transient seed bank (Whitmore 1983) but in dry forests of Sri Lanka, seeds of many climax forest species posses thick seed coats and are dormant for 2-3 months under dry climatic conditions (Perera, unpublished data). The abundance of seeds of forest pioneer species did not show a seasonal variation and this may be due to the persistent seed bank of forest pioneer species.

The diversity of soil seed bank was low in younger successional forests while the species richness was also somewhat higher in the soil seed bank of 12 - 15 year old forests only in some times of the year. The species diversity (both species richness and the evenness of species distribution) was the highest in older successional (20 - 25 year old) forests (Figs. 5 & 6). This may be partly a result of high species richness of the standing vegetation at this stage (Perera, unpublished data) and *in situ* seed production. These forests contain natural forest species with some small patches of agricultural weeds in the vegetation (Perera, unpublished data) and may have seeds of all these species. It was obvious that seeds of new species may also reach the site resulting in an increase in species richness with increasing forest age. There was one seed of the riverine species, *Madhuca longifolia* (L.) Macbride, in a 20 - 25 year old forest plot, which might have been dispersed by bats. It should be noted, however, that only a single seed of a so called 'rare' species is adequate to contribute to a species richness score, although this does not imply a high seed density.

The habitat diversity of younger successional forests was lower but was comparatively higher in 12-15 year and 20-25 year old forests throughout the year. This is another reason for these forest plots to be positioned among older successional and natural high forest plots in Fig. 3 b. However, 12 - 15 year old forests contained seeds of agricultural weed species in very high quantities. Therefore, there was a clear sequential dominance in the soil seed bank resulting in lower evenness of species distribution. In contrast, the evenness of species distribution was high in 1 month old forest at the last sampling time, but the species richness was low in that forest. This is because most of the seeds in such forests have been destroyed by cultivation so that no sequential dominance could be observed. In mature forests, the habitat diversity is also somewhat high but fluctuates with the seed rain throughout the year although this fluctuation was not statistically significant due to high standard error mean values.

Seed density of the sub-surface soil of successional forests is lower than that in the surface soil and highly varied with the age of the forest (Fig. 9) and such situations have also been observed in other forests in the world (Pickett & McDonnell 1989; Saulei & Swain 1988). The seed density and composition of the sub-surface soil depends on that of the surface and the rate of soil mixing. Natural (e.g. surface run-off) and artificial (e.g. mixing of soil by animals) causes result in seeds being buried although the process might probably be slow. Because seeds of herbaceous dicots and some non-forest early colonizing shrubs prevailed in the surface soil, especially in younger successional forests, they get buried with time resulting in high seed densities in the sub-surface soils.

Agricultural practices accompanying shifting cultivation may destroy some of the seeds in the sub-surface soil. Therefore, the seed density is low in recently abandoned agricultural land, but it increases slowly with time. After about 8-10 years, non-forest early colonizing species which produce persistent seed banks would accumulate in the soil and may get buried resulting in higher seed densities (Figs. 10 & 11). However, by about 15 - 20 years, such species in the vegetation are already replaced by more shade tolerant species with recalcitrant seeds and, therefore, the seed input becomes lowers. Those seeds that have already accumulated in the soil may loose their viability after a long time leading to a decrease in the seed density of the sub-surface soils.

In mature high forests, the density of seeds in the sub-surface soil is more or less similar to the surface soil as seeds of grass and herbs which have high seed longevity are able to accumulate over a long period in the absence of disturbances such as 'burning'. Seeds of monocots and herbs of non-forest early colonizing species were mostly available in the sub-surface soil in high forests (Figs. 9 & 10). Tree seeds were not available in the sub-surface soil implying the weak potential contribution of sub-surface soil seed banks in forest regeneration. Seasonal seed production, recalcitrant nature of some forest tree seeds and high seed predation are some of the possible reasons for this.

The microclimate of soil seed banks highly varied with the canopy openness and the insolation that reached the forest floor, which is highly governed by the age of the forest. However, the root distribution patterns of the parent vegetation may also affect the microclimate especially the soil moisture content. A close relationship between the canopy openness and solar radiation has already found by using hemispherical photographs (Mitchell & Whitmore 1993). This suggests that the high canopy openness in one month and one year old forests resulted in high amounts of solar radiation reaching the forest floor. In recently abandoned shifting cultivation land, the ground is exposed to the sunlight, and, therefore, evaporation was high.

In mature dry forests, the light reaching the ground varies with time of the year because some canopy trees were deciduous.

The soil moisture content in 20 - 25 year old successional forests was higher compared to the rest of the forests, and this may be attributed to several factors. Firstly, the pattern of root distribution of individuals may have changed. The death of most pioneer shrubs, which may have shallow roots and absorb water from the surface saves some water at the surface soil. Long-lived trees which dominated at this stage have roots which grow deep into the soil to absorb water. The reduced shrub density also reduced the transpiratory water loss. Secondly, evaporation of water is low due to the low canopy openness and high levels of soil organic matter and leaf litter in these forests. Mature high forests that appear at the end of successions contain dense shrub flora with surface spreading roots and, therefore, the surface soil moisture levels decrease slightly again.

Surface soil moisture may also vary considerably with time of the year though it was not studied. The soil moisture differences between different forests are possibly conspicuous during the early parts of dry season. It is because, in the wet season, the soil is almost saturated with water due to impervious bed rock (Rosayro 1961) while towards the end of dry seasons, surface soil is almost dry everywhere (personal observations). That is why the sampling was done at the end of the long rainy season.

Mean and maximum soil temperatures were higher in one month old forest plots where the ground is very much open (Table 4). Once the canopy closes, the soil temperature is not much affected by forest age and the variations in soil temperatures in different forests are not great. Soil temperature under a forest cover is largely controlled by air temperature, and soil temperature appears to be practically unaffected even by considerable differences in soil texture and in the amount of soil moisture (Schulz 1960).

Management implications

The results of this study revealed that the soil seed banks of tropical semi-deciduous forests of Sri Lanka are very fragile. Seeds of monocots, herbaceous dicots and shrubs of agricultural weed species dominate all the seed banks regardless of the forest age. Densities of those seeds were enormously higher in younger successional forests, i.e. the vegetation up to about 15 years old. Therefore, those seeds may germinate and establish if a disturbance occurs in such vegetation. Tree seeds of climax forest species were not available in the sub-surface soil of young successional forests implying their weak potential contribution in forest regeneration.

Therefore, with frequent disturbances, these forests may easily convert into grasslands or scrublands. Therefore, it is very essential to protect these young successional forests by fire and other anthropogenic disturbances not only to protect biodiversity in them but also to support the ongoing successional process or to the perpetuity of tropical semi-deciduous forests of Sri Lanka. However, at present, it should not be forgotten that these forests are frequently disturbed by swidden farmers and, therefore, it is necessary to formulate and implement suitable policies to prevent shifting cultivation and other illegal human activities.

Soil seed bank of natural high forests are also in a vulnerable stage as they contain less number of seeds, especially, of climax forest tree species. The diversity in natural high forests was also low and grass and agricultural weed seeds dominated both surface and sub-surface soil seed banks. Therefore, these forests may also degenerate easily with frequent disturbances.

Compared to other forest ages, 20-25 year old forests can be assisted to promote natural regeneration and for biodiversity conservation more easily than others, because soil seed banks of these forest have comparatively higher species and habitat diversities, higher numbers of tree and shrub seeds and favourable soil microclimate for seed germination and establishment. Also, the seed dispersal is comparatively more efficient in these forests.

Natural regeneration in these forests could be assisted by suitable management practices, which may include protection practices and practices to assist natural regeneration. The former includes management practices such as prevention of seed predation or disturbances like fire and cultivation while the latter includes cutting trenches to reduce root competition for water (Holmes 1957) or sowing of seeds etc. However, these should be further experimented.

Conclusions

Forest structure and vegetation composition are determined by the age of the forest after a large-scale disturbance and the quantity and quality of seeds that are available in the forest soil seed banks. Open canopy forests not only support the growth of pioneer and agricultural weed species, which possess light seeds but also facilitate the air movement and thereby the efficient dispersal of wind-dispersed seeds. Older successional and natural high forests contain many individuals of climax forest tree and shrub species in the vegetation, which can produce seeds while encouraging the visits of seed dispersing animals by providing food and roosting sites.

The density of seeds at the surface soil of tropical semi-deciduous forests of Sri Lanka varies with the time of year. Clumping of seeds could be commonly seen in all forest soil seed banks. As both surface and sub-surface soil seed banks of younger successional forests are dominated by herbs and shrubs of non-forest early colonizing species (agricultural weeds), such seed banks are less important in forest regeneration after disturbances.

Both species and habitat diversities were high in older successional forest surface soil throughout the year ,and there are considerable quantities of seeds of forest pioneer species in addition to herbaceous dicots and shrubs of non-forest early colonizing species. The microclimate in these forests is also favourable for seed germination and seedling establishment. Therefore, the seeds in the soil seed bank of older successional forests may contribute to successful forest regeneration and succession.

In mature forests, both surface and sub-surface soil seed banks were dominated by seeds of monocotyledonous and dicotyledonous herbaceous species, and a few seeds of climax forest shrub species were encountered during their fruiting season. Seeds of climax forest tree species are rare in the soil. If a disturbance occurs in a mature forest, monocotyledonous and dicotyledonous herbaceous species, which form persistent soil seed bank, would germinate and invade the site. Therefore, there will be a risk of forest degeneration and formation of grasslands with frequent disturbances.

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