

Seasonal variation in density and species richness of soil seed-banks in karst forests and degraded vegetation in central Yunnan, SW China

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Abstract

We studied seasonal variation in density and species richness of seeds in the 0–10 cm soil depth layer in primary, secondary and pine forests, and in shrubland and grassland in the Shilin Stone Forest Geographical Park, Yunnan, SW China. Soil samples were collected four times during the year at 3-month intervals. Seeds from 119 species were identified by germination tests in the soil samples. Density and species richness of seeds of herbaceous plants were greater than woody plants at all five sites throughout the year. Sampling time and site differences had significant effects on the mean number of species and on seed-bank density. Mean number of species per sample increased from February, reached the highest value in May, decreased to the lowest value in August and then increased in November. An exception was in the primary forest, where the highest number of species was found in February. Mean seed-bank density peaked in May at all five sites, and no significant differences were found between densities in February, November and August, except for the primary forest. The peak in seed-bank density in May might be due to dispersal of new seeds of spring-fruited species, combined with persistence of seeds dispersed in previous years. This seasonal variation of individual species was due primarily to differences in species phenology rather than to differences between sites. Four seasonal seed-bank strategies were identified: two transient and two persistent. At all sites, similar numbers of seeds of herbaceous species were found between seasons, but the number of species of trees and shrubs decreased in August.

Keywords: karst upland, persistent seed bank, seasonal variation in seed bank, transient seed bank

Introduction

When a seed is dispersed from the mother plant and reaches the soil surface, it may germinate immediately or persist on or in the soil until conditions become suitable for germination, thus forming a soil seed-bank (Thompson and Grime, 1979; Garwood, 1989; Baskin and Baskin, 1998; Thompson, 2000). A soil seed-bank is the total number of viable seeds in the leaf litter, on the soil surface and buried in the soil (Roberts, 1981). Density and species richness of seeds in the seed bank may peak at the end of a season, when seeds mature and are dispersed from the mother plants. This seasonal variation of the number of seeds in seed banks has led to the classification of seed-bank strategies according to seasonal germination patterns, based on carry-over of seeds from one year to the next (Thompson and Grime, 1979), or from one germination season to the next (Walck *et al.*, 2005). Transient seed banks consist of seeds that do not persist in the soil or litter for more than 1 year (Thompson and Grime, 1979) or for one germination season to the next (Walck *et al.*, 2005), whereas in persistent seed banks, some seeds persist for more than 1 year (Thompson and Grime, 1979) or until at least the second germination season (Walck *et al.*, 2005). The seed-bank strategy is more of a function of the species than of the environment (Thompson and Grime, 1979; Lavorel *et al.*, 1993; Onaindia and Amezaga, 2000). However, seed-bank strategies of many species are still unknown, and thus more research is needed to understand seed-bank strategies of individual species and of plant communities found in various environments.

There are more than 500,000 km² of karst landforms in southern China (Yan *et al.*, 1994), where various

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types of evergreen broadleaved forests grow across a wide climatic spectrum (Wu, 1980). In both natural and regenerated forests, plants frequently experience shortages of water and nutrients because of shallow discontinuous soils separated by rocks (Wu, 1980; Su and Zhu, 2000; Wang, 2002; Zhu, 2002). Plants in karst areas are also exposed to severe large-scale changes through tree cutting, pasture creation, slash-and-burn agriculture and collection of firewood (Zhou *et al.*, 2002). Despite their potential importance for the response of plant communities to these disturbances and forest degradation, few studies have investigated soil seed-banks in the karst areas of China (Liu, 2000; Shen *et al.*, 2004), and there have been no studies on the seasonal variation in their soil seed-banks.

In this study, seasonal variation in the seed banks of karst forests and of their degraded vegetation were examined. The following questions were asked: (1) Is there seasonal variation in the soil seed-bank? (2) How is the soil seed-bank pattern linked to the seasonal pattern of seed production? (3) What types of seed-bank strategies occur in plants of karst areas of SW China? and (4) Does the seasonal pattern and seed-bank strategy vary among sites covered with different vegetation types?

Materials and methods

Study sites and sampling procedure

This study was conducted at the Shilin Stone Forest Geographical Park (24°38'–24°58'N, 103°11'–103°29'E), a typical karst geo-park famous for its various stone-forests. This park is an area of approximately 900 km² with underlying Permian carbonate rocks, of which more than 400 km² have developed into karst and related landforms. These are confined to a north–south trending terrain that is more than 30 km long and 10 km wide. Altitudes range from 1600 to 2203 m above sea level. Mean annual precipitation is 967.9 mm (at 1680 m), 80% of which falls between May and October. Mean annual temperature is 16.2°C, mean maximum temperature 20.7°C (July) and mean minimum temperature 8.2°C (January) (Zhang *et al.*, 1997). The ground of the karst area consists of rock gaps, rock ditches, small rock caves and rock slots, all of which are surrounded by soil that accounts for about 30% of the land surface on slopes and about 90% in flat areas. The soil is shallow and patchily distributed on or between these various rock surfaces. Water and nutrients are the main limiting factors for plant growth. The growing season coincides with the rainy season and with moderate temperature periods from late spring into summer (Wu, 1980).

Slopes of five sites covered with different vegetation types were included in this study: (1) a primary forest;

(2) a young secondary forest; (3) a highly degraded shrubland; (4) a grassland; and (5) a *Pinus yunnanensis* plantation. The primary forest on this karst land is an evergreen broadleaved forest mixed with a few deciduous species. Dominant species include *Cyclobalanopsis glaucooides* Schottky, *Olea yunnanensis* Hand-Mazz, *Pistacia weinmannifolia* J. Poisson ex Fr., *Pistacia chinensis* Bunge, *Neolitsea homilantha* Allen and *Albizia mollis* (Wall.) Boiv. (Jin and Peng, 1998; Shen *et al.*, 2005). Over the past several decades, the primary forest has been destroyed as a result of human activities, such as firewood harvesting and clearing of land for agriculture and animal grazing. As a result, shrubland, and then grassland, were created in some areas. Through conservation activities, young forest was regenerated naturally on the degraded area; *Pinus yunnanensis* Fr. was also planted. The five vegetation types represent the main vegetation types in this area. The secondary forest is dominated by *N. homilantha* with a low tree density (780 stems per hectare with a diameter at breast height of 3–10 cm, unpublished survey results). *Spiraea martini* Levl., *Zanthoxylum armatum* DC. and *Berberis pruinosa* Franch. are the dominant species of the shrubland. Some dominant tree species of primary forest, such as *O. yunnanensis*, *P. weinmannifolia* and *N. homilantha*, also are found at low density in the shrubland. *Heteropogon contortus* (L.) P. Beauv. ex Roemer, *Oplismenus compositus* (L.) P. Beauv., *Schizachyrium delavayi* (Hack) Bor, and *Eupatorium adenophorum* Spreng. are the dominant species in the grassland. Some dominant species of the shrubland also are present at very low density in the grassland.

Soil seed-bank sampling and germination

At each of the five sites, four 50 m transects were established, and five sampling points were marked at 10 m intervals along each transect. Soil samples, 10 cm × 10 cm × 10 cm, were taken at each point in February 2003, at the end of winter. Thus, 20 samples were collected at each site. Since the soil was patchily distributed, samples were taken nearest to the marked sampling point. Seeds of some species, such as *Eupatorium adenophorum* and *Spiraea martini*, mature and are dispersed before the beginning of the rainy season, normally in May (Zhang *et al.*, 1997). For most species, however, seeds mature from September to November (end of rainy season and beginning of dry season). Consequently, we also collected soil samples from the primary forest and from the grassland in May, August and November at each sampling point, as close as possible to the previous sample, to study seasonal variations in the seed bank. Soil samples were taken from the other three sites in May and November as well, but not in August.

Each soil sample was washed through a 4 mm mesh sieve to eliminate coarse materials, and then through a 0.21 mm mesh sieve to eliminate fine materials (Ter Heerd *et al.*, 1996). The concentrated residue, which contained all seeds from the sample, was spread out evenly onto a 3 cm layer of perlite in plastic seed trays (c. 18 cm × 10 cm × 10 cm deep). Trays were placed in an unheated greenhouse in the Kunming section of the Xishuangbanna Tropical Botanical Garden (80 km away from the Park, 1892 m above sea-level), and seedling emergence was monitored. The sides of the greenhouse were covered with a double layer of fine nylon mesh cloth and the roof with a sheet of plastic. Trays with sterilized soil were placed randomly in the greenhouse to check for contamination. All trays were monitored and watered, usually twice a day. Seedlings were counted and discarded as soon as they could be identified, or they were transplanted into 15-cm-diameter pots filled with fertile soil and grown until identification was possible. Soil in the trays was stirred two to three times during the germination monitoring period, normally after a large flush of germination. Samples collected in February and May were monitored until the end of October (end of germination season), whereas those collected in August and November were monitored until the end of October of the following year. No seedlings were found in the contamination trays.

Numerical analyses

For each species, sample, site and season, the number of seedlings that emerged was transformed into seed density. Densities for the five vegetation types and for different seasons were compared using both one- and two-way analysis of variance (ANOVA) tests after logarithmic [$\log_{10}(x + 1)$] transformation. Mean number of species per sample was compared among vegetation types and seasons directly, using both one- and two-way ANOVA tests. Sorensen's similarity index was used on data pooled by vegetation type to compare seasonal seed-bank similarities.

Results

A total of 10,872 seedlings representing 112 taxa (9 trees, 17 shrubs and 86 herbs) emerged from the samples. All but nine were identified to species level. Seedling emergence varied considerably during the year among both species and sites (Table 1).

The number of species identified in each sample varied with the season. The average number of species in the soil samples ranged from 2.8 in August (grassland) to 11 in February (primary forest).

The mean number of species per sample increased from February to the highest level in May, decreased to the lowest level in August, and then increased in November (Fig. 1). A minor exception was for the primary forest, where the highest number of species was found in February. Sampling time (ANOVA, $F_{2,332} = 54.1$, $P < 0.001$) and site ($F_{4,332} = 22.4$, $P < 0.001$) had significant effects on number of species present in soil seed-bank samples. However, no significant interaction was found between sites and sampling times ($F_{8,300} = 1.8$, $P = 0.07$).

Seed-bank density ranged from 615 seeds m^{-2} (November, pine forest) to 13,650 seeds m^{-2} (May, secondary forest), averaging 3198 seeds m^{-2} across all sampling times and sites (Table 1). Mean seed-bank density peaked in May at all five sites. Other than for the primary forest, density in February, August, and November were not significantly different (Fig. 2). Sampling time ($F_{3,332} = 62.9$, $P < 0.001$) and site ($F_{4,332} = 51.5$, $P < 0.001$) had significant effects on seed-bank density. There were significant interactions between sites and sampling times ($F_{12,332} = 15.5$, $P < 0.001$).

The seasonal pattern in mean number of species coincided with the density pattern in the secondary forest, shrubland, grassland and pine forest. In the primary forest, species density peaked in May, although mean number of species peaked in February.

Seed densities of different species varied during the year at each site (Table 1). Of the tree species, *Albizia mollis* had the highest seed density, and its seeds were present in the soil seed-bank throughout the year. Seeds of the other tree species were not present in the soil seed-bank in August, which was before the seeds of the current year matured. *Spiraea martini* had the highest seed density in the shrub communities at each site, followed by *Rubus parvifolius* L. and *Ficus tikoua* Bur. Seeds of the latter two species were present in the soil seed-bank throughout the year, whereas those of the other species were present in only two or three seasons. Most trees and shrubs had their highest seed-bank density in February. Seeds of herbs dominated the seed banks at all sites, and those of *E. adenophorum*, a worldwide invasive species, made up a large portion of the soil seed-bank. *Pouzolzia sanguinea* (Bl.) Merr., *Pilea plataniflora* C.H. Wright and *Capillipedium parviflorum* (R.Br.) Stapf also contributed greatly to the seed banks. Many seeds of *E. adenophorum*, *P. sanguinea*, *P. plataniflora*, *Carex souliei* Franch., *Heteropogon contortus* (L.) P. Beauv. ex Roemer, *Gnaphalium affine* D. Don, *Senecio chrysanthemoides* DC., *Codonopsis convolvulacea* kurz, *Laggetera pterodonta* (DC) Benth., *Solanum nigrum* L. and *Acalypha australis* Linn. were present in the soil seed-banks throughout the year.

Densities of species occurring at more than one site varied between sites. However, certain similarities

Table 1. Seed density (number m⁻²) of the main species in the seed bank of the five vegetation types over four seasons in central Yunnan, SW China. Data are based on twenty 10 cm × 10 cm × 10 cm soil samples

Species ^a	Primary forest				Secondary forest			Shrubland			Grassland				Pine forest			Total
	Feb.	May	Aug.	Nov.	Feb.	May	Nov.	Feb.	May	Nov.	Feb.	May	Aug.	Nov.	Feb.	May	Nov.	
Trees																		
<i>Albizia mollis</i> (Wall.) Boiv.	75	45	20	55					5									200
<i>Ficus chapaensis</i> Gagnep.	30	20		15														65
<i>Morus mongolica</i> (Bur.) Schneid.	5	20		5			5											35
<i>Neolitsea homilantha</i> Allen	5			5		5	5											20
<i>Carpinus mobeigiana</i> Hand.-Mazz				10														10
Others (4 species)	10	5		5														20
Shrubs																		
<i>Spiraea martini</i> Levl.	15	10			15	450	10	70	1395	55	5	110		5				2015
<i>Rubus parvifolius</i> L.	445	305	400	200	20	5	20				25					10	10	1440
<i>Buddleja officinalis</i> Maxim		40			5	295	135		10	5		5				30		525
<i>Ficus tikoua</i> Bur.	35	80	25	20	5	10	10	10	70	5		5	55	10	15	70	85	510
<i>Zanthoxylum scandens</i> Bl.		5	60	5														70
<i>Zanthoxylum armatum</i> DC.	35	5		15														55
<i>Myrsine africana</i> L.										5						45	5	55
Others (10 species)	45	35				15	15	10						5		15		140
Herbs																		
<i>Eupatorium adenophorum</i> Spreng.	790	505	490	160	2970	10,975	3480	315	620	325	240	3010	770	370	105	495	255	25,875
<i>Pouzolzia sanguinea</i> (Bl.) Merr.	490	1560	875	360	640	840	290	15	65		5					10		5150
<i>Pilea plataniflora</i> C.H. Wright	785	965	870	130	10	15	35		10									2820
<i>Capillipedium parviflorum</i> (R.Br.) Stapf				105	90	15	160	65	85	260	860		255	215	140	30		2280
<i>Carex souliei</i> Franch.	5	1065	45	475	25	90	20	20	25	35				5	60	5		1875
<i>Heteropogon contortus</i> (L.) P. Beauv. ex Roemer		10	5	5	35	20	10	100	60	20	305	240	165	130	260	60	10	1435
<i>Cyperus iria</i> L.	455		480		35			10			5							985
<i>Gnaphalium affine</i> D. Don	80	65	65	5	75	75	20	65	90	35	40	60	35	15	20	100	45	890
<i>Viola delavayi</i> Franch.				275	20	10	5	5	20	330	5			10	5			680
<i>Senecio chrysanthemoides</i> DC.	210	15	175	35	20	10	5	10	15		15		5	5	20		25	565
<i>Conyza canadensis</i> (L.) Cronq.	30	65		15	15	55		10	55	5		140				135		525
<i>Codonopsis convolvulacea</i> Kurz	345	35	25	5				55			50							515
<i>Laggera pterodonta</i> (DC) Benth.	95	20	30	10	55		5	30			25	90	35	15	15	5	10	440
<i>Themeda triandra</i> Forssk var. <i>japonica</i>						35			15	10		205		130		30		425
<i>Oxalis corniculata</i> L.	5	30			25	45		25	55		25	70	80	15	20	15		410
<i>Anaphalis bulleyana</i> Chang	10			35	95			15		15	10			50	75		40	345
<i>Arthraxon hispidus</i> (Thunb.) Matino	10			10			5	5		15	105		5	75	60		10	300
<i>Carpesium nepalense</i> var. <i>lanatum</i> (HK.f.et Thoms. ex C.B. Clarke) Kitam		10		5		20			20	35		40		35		25	55	245
<i>Solanum nigrum</i> L.	40	90	25	30		10			10	10		10				10		235
<i>Acalypha australis</i> Linn.	45	30	115	10		10	10											220
<i>Gentiana rhodantha</i> Hemsl						210												210
<i>Elsholtzia cypriani</i> S. Chow et Hsu	5			10		125			15	5	5			10				175
<i>Rubia schumanniana</i> Pritz.	70	20	60						10	5			5					170

Table 1. Continued

Species ^a	Primary forest			Secondary forest			Shrubland			Grassland			Pine forest			Total
	Feb.	May	Nov.	Feb.	May	Nov.	Feb.	May	Nov.	Feb.	May	Nov.	Feb.	May	Nov.	
<i>Siegesbeckia glabrescens</i> Makino	25		40	5			20						5			150
<i>Dicliptera bupleuroides</i> Nees	25	25	55	5	5		20	20					25	10		130
<i>Emilia sonchifolia</i> (L.) DC.		5	15	55	5		15	15							20	120
<i>Siegesbeckia orientalis</i> Linn.			10	25	5	5	5	5					10	35		115
<i>Carex</i> spp.	585	250	75	150	40	155	60	60	15	15	130	60	5	65	30	110
Others (58 species)	4800	5340	3890	1870	4480	13,650	4170	1035	2580	685	5035	1160	1635	830	1370	1805
Total																

^a Species in which total germinants were ≥ 2 for trees, ≥ 10 for shrubs, and ≥ 20 for herbs.

were observed between seasonal patterns obtained at the five sites. For instance, seasonal patterns (expressed as % of total seeds year round) of *E. adenophorum*, *G. affine* and *H. contortus* were similar for all sites, except the primary forest (Fig. 3). Seasonal patterns of *F. tikoua* and *C. parviflorum* were similar, except for the grassland, and of *S. chrysanthemoides*, except at the pine forest.

The similarity index for herbs between seasons was stable at all sites, but it varied greatly for shrub and tree species (primary forest) (Table 2). Shrub and tree species indices between August and the other seasons were smaller for primary forest and grassland than for those of the other three vegetation types.

Discussion

Seed input is an important factor determining the seasonal pattern of soil seed-banks. According to long-term phenological observations by the Institute of Geography, Chinese Academy of Sciences and National Planning Commission (1989, 1992), there are two major seed maturation seasons in the study area: spring (April–May) and autumn (September–October). Seeds of the shrub *S. martini* and of the herbs *E. adenophorum*, *P. sanguinea*, *A. australis*, *Viola delavayi* Franch. and *Oxalis corniculata* L. mature in April and May. Seeds of tree species and most shrub and herb species mature in autumn (September–October) and are dispersed over a long period of time, especially in the case of small-seeded species. Seeds of spring-fruited species are dispersed immediately after ripening. However, the number of seeds produced by spring-fruited species is great, which results in very high seed-bank densities (Table 1). For example, density of *E. adenophorum* reached 10,975 seeds m⁻², which accounted for 80% of the soil seed density in the

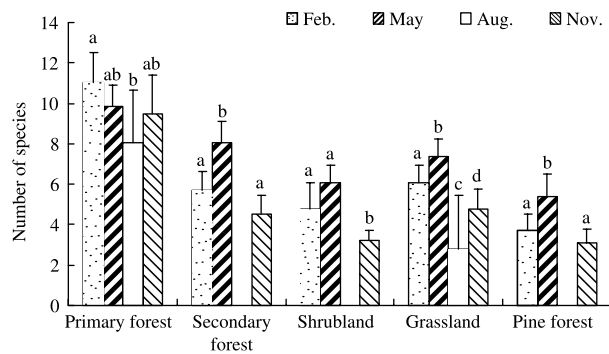


Figure 1. Mean number of species found in twenty 10 cm × 10 cm × 10 cm soil samples for each of the five vegetation types at different sampling times. Means within sites not sharing the same letter are significantly different at $P < 0.05$. Bars = 95% confidence interval.

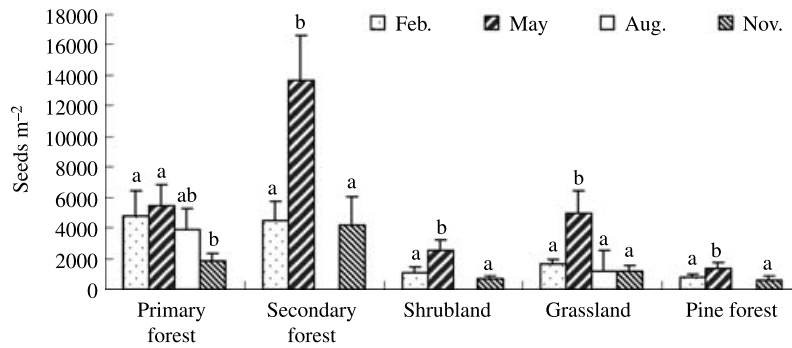


Figure 2. Seasonal variation in soil seed-bank density in each of the five vegetation types (twenty 10 cm × 10 cm × 10 cm soil samples each). Means within sites not sharing the same letter are significantly different at $P < 0.05$. Bars = 95% confidence interval.

secondary forest in May. Autumn-fruiting species may release their seeds gradually between maturation and the following spring, depending on seed dryness and wind speed. Seed densities of these species in the soil seed-bank may peak at any time from November to May of the next year, or the changes may be relatively small. For example, the size of the seed bank of *A. mollis* peaks in February (Table 1). Accumulation of

seeds from both spring- and autumn-fruiting species causes the soil seed-bank to peak in May. Germination of viable seeds during summer (rainy season), seed predation and senescence probably reduce seed numbers in the seed bank, which could explain why the lowest seed-bank values were recorded in August. The seasonal pattern of germination is one of the most important adaptations to the local environment.

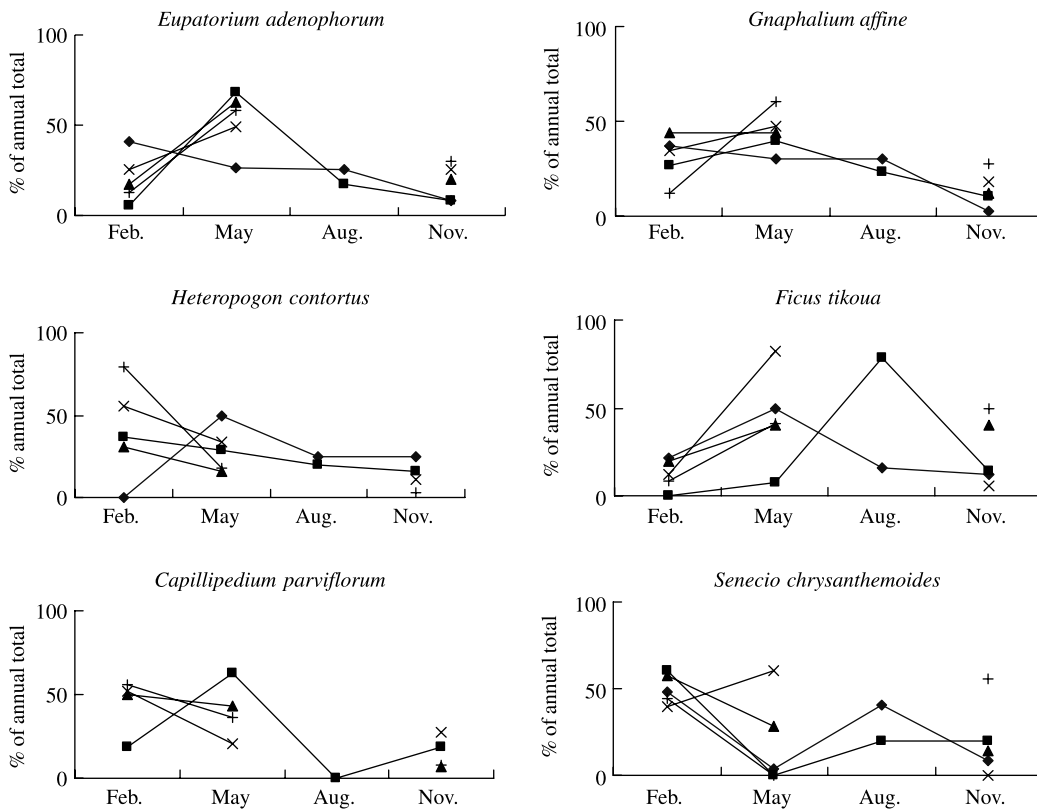


Figure 3. Examples of species with seasonal seed-bank patterns in each of the five vegetation types (◆, primary forest; ■, grassland; ▲, secondary forest; ×, shrubland; +, pine forest) in karst areas, central Yunnan, SW China.

Table 2. Sorensen's similarity index between seasons, calculated from species pooled from each soil seed-bank of each vegetation type in the karst area, central Yunnan, SW China

Vegetation	Feb. versus May	Feb. versus Aug.	Feb. versus Nov.	May versus Aug.	May versus Nov.	Aug. versus Nov.
Primary forest						
Herbs	0.58	0.64	0.61	0.55	0.65	0.58
Shrubs	0.59	0.36	0.5	0.50	0.62	0.86
Trees	0.6	0.29	0.67	0.40	0.60	0.29
Total	0.58	0.56	0.60	0.53	0.64	0.58
Secondary forest						
Herbs	0.42		0.56		0.51	
Shrubs	0.89		0.72		0.83	
Trees	0		0		0.67	
Total	0.48		0.58		0.58	
Shrubland						
Herbs	0.48		0.43		0.63	
Shrubs	0.67		0.57		0.86	
Trees	0		0		0	
Total	0.49		0.44		0.67	
Grassland						
Herbs	0.48	0.48	0.52	0.44	0.5	0.45
Shrubs	0.40	0	0.40	0.50	0.67	0.50
Trees	0	0	0	0	0	0
Total	0.47	0.44	0.51	0.45	0.52	0.46
Pine forest						
Herbs	0.47		0.64		0.44	
Shrubs	0.33		0.5		0.75	
Trees	0		0		0	
Total	0.45		0.63		0.5	

In ecosystems in which seed maturation and germination seasons are not synchronized, the ability of a species to persist in the seasonal seed-bank allows plants to delay germination until conditions are suitable for seedling survival. Other studies also found strong seasonal patterns in seed-bank composition and density. For instance, in both natural woodland and coniferous plantations in northern Spain, seed-bank richness and density in spring are higher than in summer or autumn because of the persistence of seeds from the previous years' production (Onaindia and Amezaga, 2000). In a 3-year study of Mediterranean grasslands, maximum seed density occurred each year at the time of seed maturity in late spring (May), and the minimum density occurred just before seed dispersal (April) (Russi *et al.*, 1992). A similar pattern was found in Argentinean (Bertiller, 1992; Mayor *et al.*, 2003) and Patagonian grasslands (Bertiller, 1992).

The seasonal strategy of soil seed-banks seems to be more of a function of species than of vegetation type or environment. Thus, seasonal patterns of species occurring at more than one site were similar between sites (Fig. 3), which agrees with results of studies in ecologically contrasted sites in northern England (Thompson and Grime, 1979), Mediterranean grasslands (Lavorel *et al.*, 1993) and Spanish forests

(Onaindia and Amezaga, 2000). However, seed density may be influenced by input of new seeds and by the rate at which existing seed reserves are lost through predation, senescence and germination. Thus, seed density might be influenced by site conditions that determine these factors. This is the reason why the patterns in Fig. 3 are not identical in all five sites. If site effect is great enough, it may shape the seasonal seed-bank pattern. Cabin and Marshall (2000) found that the micro-environment (subshrub versus intershrub) had a great impact on temporal seed patterns of *Lesquerella fendleri* in the soil seed-bank in a New Mexico desert.

Thompson and Grime (1979) measured seasonal variation in density of germinable seeds in ten contrasting habitats in a temperate area and classified soil seed-banks into four basic types: two transient and two persistent. This was consistent with the morphology and germination characteristics they obtained in the laboratory. However, species included in their study were annual and perennial herbs in which seeds are released mainly during late spring and summer. Since their study, additional types of persistent seed-banks have been identified in annuals and in perennials (Roberts and Neilson, 1981; Baskin and Baskin, 1984, 1985, 1986). More soil seed-bank strategies may exist in tropical than in temperate areas because reproduction occurs throughout

the year. Based on germination behaviour and temporal patterns of seed dispersal, Garwood (1989) summarized five basic seed-bank strategies (transient, persistent, pseudopersistent, seasonal transient and delayed transient) for lowland tropical species. In our study, at least four basic types of seed-bank strategies could be identified.

- (1) Transient 1. Seeds are dispersed in late spring, germinate in summer and are present in the soil seed-bank only in May, e.g. *Gentiana rhodantha* Hemsl. This is similar to type 1 in Thompson and Grime (1979) (seeds released in summer, but germinate in autumn) and to the transient seed bank in the study by Garwood (1989) (immediate germination after seed release).
- (2) Transient 2. Seeds are released in autumn and germinate in spring of the next year. Most tree and shrub species have seeds in the soil seed-bank in November, February and May, but not in August, and their total seed densities are very low, e.g. *N. homilantha* and *Carpinus mobeigiana*. Some herb species, e.g. *C. parviflorum*, *Themeda triandra* Forssk var. *japonica*, *Elsholtzia cypriani* and *Emilia sonchifolia*, have high seed densities in November, February and May, but not in August. This is comparable to type 2 of Thompson and Grime (1979) (seeds released in summer, but germinate in spring of the following year), and to a combination of the seasonal transient seed-bank and delayed transient seed-bank of Garwood (1989).
- (3) Persistent 1. Seeds are released in late spring, and a portion of them germinates after release, whereas the others are present in the soil throughout the year, e.g. *E. adenophorum*, *O. corniculata*, *S. chrysanthemoides* and *A. australis*, thus forming persistent seed-banks (Baskin and Baskin, 1998).
- (4) Persistent 2. Seeds are released in autumn, some of which germinate in spring, while others persist in the soil throughout the year. This includes some autumn-fruiting species whose seeds are still present in the soil before new seeds are released in August, e.g. the tree *A. mollis*, the shrubs *R. parvifolius* and *F. tikoua*, and the herbs *P. sanguinea*, *P. plataniflora*, *C. souliei*, *G. affine*, *C. convolvulacea*, *L. pterodonta* and *S. nigrum*.

Since we did not take soil samples in the secondary forest, shrub or pine sites in August, we may lack the information necessary to define the seed-bank strategy of some species. From the existing data, only a few tree and shrub species were present in the soil throughout the year, and thus most of them had transient soil seed-banks. On the other hand, many herbs formed persistent soil seed-banks, and their seeds were present in soil throughout the year (Table 1). This result suggests that different component groups in the

soil seed-bank (trees, shrubs and herbs) have different seasonal patterns.

Only a few tree species had seeds present in the soil seed-bank in the primary or secondary forests; many of the dominant species were present in very low numbers or absent altogether (Table 1). Tree seeds mature in autumn and are released gradually. Therefore, they lie on the soil surface or buried in the soil until suitable germination times in spring and early summer, when the rains come. Logically, these seeds may have a short transience in or on the soil before germination. However, seeds of most tree species were not determined in samples between dispersal (November) and germination (May). Possible reasons for the failure to detect tree seeds may include animal predation, dormancy, or large seeds failing to pass through the 4 mm filter. Bossuyt *et al.* (2002) also found that tree species abundant in such forests were absent in soil seed-banks, which they attributed to few tree species producing long-lived seeds. More studies need to be undertaken to determine the reason why seeds of many tree species are not found in soil seed-banks.

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