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Influence of fallow type and land-use intensity on weed seed rain in a forest/savanna transition zone

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Weed seed rain was monitored in field plots under three fallow types and four land-use intensities in Ibadan, Nigeria, in 1994 and 1995. The fallow types were natural bush, planted *Leucaena leucocephala*, and *Pueraria phaseoloides*. The land-use intensities consisted of continuous cropping, involving *Zea mays*/*Manihot esculenta* and fallowing for 1, 2, and 3 yr, with each fallow period followed by 1 yr of *Z. mays*/*M. esculenta* cultivation. In 1994, seed rain in plots cropped after *P. phaseoloides* fallow was significantly lower than in plots cropped after bush or *L. leucocephala* fallow. *Pueraria phaseoloides* plots had similar seed rain as bush fallow plots in 1995, and the seed rain in these plots was significantly lower than in *L. leucocephala* plots. Weed seed rain was significantly higher in continuously cultivated plots across all fallow types than in plots that were cultivated after one or more years of fallow. The lowest seed rain was in plots that were cropped once after a 3-yr fallow. The largest quantity of weed seed input in the plots occurred in either August or September, reflecting the life cycle of the annual weeds that dominated the vegetation. Individual species differed in pattern and duration of shedding seeds within the fallow systems and land-use intensities. Annual weeds dominated the seed rain in continuously cropped plots, and seeds of perennial weeds were dominant in plots fallowed for more than 1 yr before cultivation. Weeds flowered earlier in continuously cropped plots than in plots that were cropped after 2 or 3 yr of fallow. Increased land-use intensity caused an increase in seed rain and consequently increased the soil seed bank. *Pueraria phaseoloides* fallow was more effective in shading weeds and probably reducing the quantity of light reaching them than the natural bush and planted *L. leucocephala* fallow systems, and this may have been the basis of the significantly lower seed rain in *P. phaseoloides* plots.

Nomenclature: *Leucaena leucocephala* (Lam.) de Wit LUAGL, leucaena; *Manihot esculenta* Crantz 'TMS 30572', cassava; *Pueraria phaseoloides* (Roxb.) Benth. PUEPH, tropical kudzu; *Zea mays* L. 'TZSRW', corn.

Key words: Fallow management, cropping frequency, bush fallow, seed bank.

Mature weeds shed their seeds on agricultural land and thus add to the population of weed seeds in or on the soil. Harper (1977) has described this periodic weed seed supply as seed rain. Weed seed rain is of major interest in weed management because it is the main source of seeds to replenish the seed bank in agricultural land. More than 95% of seeds entering the seed bank in arable land is produced by annual weeds growing on that land (Cavers 1983; Hume and Archibold 1986; Louda 1989; Roberts 1981). Seed rain is one of the factors that affects the dynamics of the weed seed bank (Kitajiman and Tilman 1996). Use of cover crops and some tillage practices have also been shown to cause rapid decline in the soil seed bank (Akobundu 1984; Bhowmik and Bekech 1993; Froud-Williams et al. 1983). The existence of a soil seed bank in highly disturbed arable land has been linked to yearly input of seeds from seed rain (Cavers and Benoit 1989). Annual weeds that produce a large quantity of seeds that are dispersed by wind have the best chance to contribute to the seed rain.

Despite the obvious importance of weed seed rain as a biological factor that can affect weed control, there is a lack of data on weed seed input into arable fields in West Africa. Weed control by smallholder farmers in this zone is mostly done in intercropping settings. These weed control methods have been discussed at length by Akobundu (1987) and in-

clude bush fallowing, hand weeding, burning, crop rotation, and use of animal-drawn cultivators. Studies in the West African subregion have so far not incorporated weed seed input and dispersal when designing weed management strategies. Progress in weed management will increase with improved understanding of weed seed dispersal and the contribution of weed seed rain to weed infestation in arable fields.

Data on changes in weed seed input into different cropping systems will be needed to understand and design appropriate weed management packages for smallholder farmers in West Africa. Wilson (1988) has shown that in developed agriculture, farming practices influence weed population dynamics and species composition by affecting the quantity of seeds returned to and removed from the soil. There is a need to understand how weed seed input into smallholder farms interacts with traditional land-use and weed control practices to affect weeding frequencies and the drudgery associated with smallholder agriculture in the tropics.

Planted fallows, especially herbaceous cover crop-based fallows, have been advocated as a better alternative to natural bush fallow systems because of their efficiency in protecting the soil from erosion, restoring nutrients, and improving weed control (Akobundu 1992; Mulongoy and

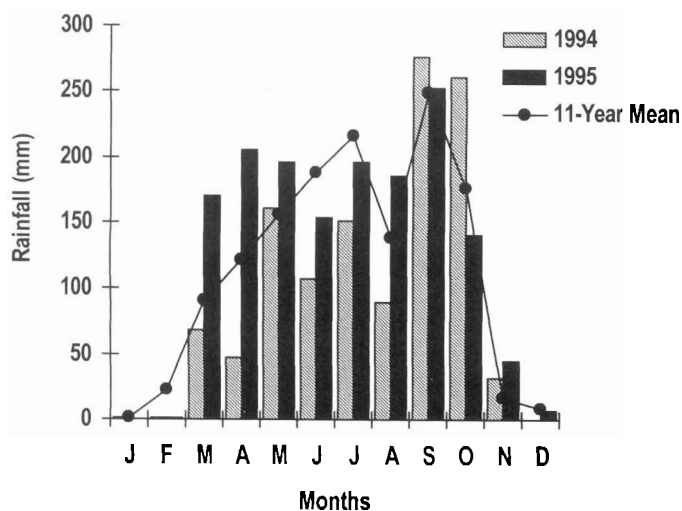


FIGURE 1. Monthly rainfall at the IITA fallow plots in southwestern Nigeria.

Akobundu 1990). Planted fallows, especially *Pueraria phaseoloides*, have also been reported to lower the annual weed population and the size of the soil seed bank over time (Akobundu et al. 1999, Chikoye et al. 1997). In one variant of planted fallow technology known as alley cropping, *Leucaena leucocephala* fallow has been shown to cause a greater decline in weed density over time than arable fields without alley cropping (Akobundu et al. 1992). The ability of planted fallows to reduce weed pressure in arable fields could be due to reduced seed input in the system. The objective of this study was to assess and quantify the influence of different fallow types and land-use intensities on weed seed rain in arable fields.

Materials and Methods

Site Description

Field studies were conducted during wet and dry seasons in 1994/1995 and 1995/1996 (June to February) at the research farm of the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria (7°30'N, 3°54'E). The experimental site is located in the humid forest/savanna transition zone with a mean annual temperature of 26 C. The annual rainfall of 1,250 mm has a bimodal distribution pattern with major peaks in July and September (Figure 1). The period November through February/March constitutes the dry season. The soil type was a sandy loam (Oxic Paleustalf) with approximately 68% sand, 13% silt, and 17% clay, organic matter < 2%, and pH 6.2 (0 to 15 cm deep). Description of this site, experimental design, plot layout, crop husbandry and management procedures have been reported previously (Akobundu et al. 1999).

Data Collection

Weed seed input into cropland was studied by collecting dispersed seeds during the wet and dry seasons in both years. The seeds were collected in traps that were placed randomly in a permanent 4- by 4-m microplot located in each of the subplot treatments. Each microplot was divided into 1- by 1-m grid cells. Ten seed traps were placed

randomly in each grid cell in the permanent quadrat in May in each year of the study, but seed collection commenced in June. Each trap was kept in its position throughout the study. Seed traps were modeled after Werner (1975) and Rabinowitz and Rapp (1980). Each trap was made up of a square petri dish (9.5 by 9.5 cm) with a piece of transparent paper sprayed with an aerosol,¹ TanglefootTM, a permanently sticky petroleum gel that held weed seeds that dropped onto it. Trapped weed seeds were not blown away by wind or picked up by insects. Each petri dish was nailed to a small wooden board and pushed approximately 2 cm into the soil. Tanglefoot and paper were replaced every week. The exposed paper was examined in the laboratory and seeds that were trapped on it were sorted into types and counted under a dissecting StereoZoom[®] microscope.² The seeds were identified to species level by comparing them with seeds from fruits collected from the field. The data obtained from the counts were used to estimate seed rain per square meter for each species. Total seed rain for each treatment was obtained by summing the number of seeds of each species trapped on each sampling date. Total seed rain for each species was also aggregated on a monthly basis. *Zea mays* canopy cover was estimated at 6 and 8 wk after planting (WAP) in 1994 and 1995, respectively, using a LAI-2000 plant canopy analyzer.³ The canopy analyzer was placed 40 cm above ground level during the measurement. Photosynthetically active radiation transmitted through the crop canopy was measured with a Decagon sunfleck ceptometer.⁴ Light measurement was done 6 wk after the crops were planted in both years.

Data were subjected to analysis of variance (ANOVA) to assess the effect of fallow type and land use on total seed rain. Differences between means were tested using Fisher's Protected LSD at $P = 0.05$.

Results and Discussion

Weed Seed Rain for all Species

The number of seeds for all species caught in each fallow type and land-use intensity in 1994 and 1995 is shown in Table 1. The number of dispersed weed seeds in the *P. phaseoloides* fallow plot was significantly lower than that in either bush or *L. leucocephala* fallow plots in 1994. In 1995 seed rain in *P. phaseoloides* plots was similar to that in natural bush fallow but lower than that from *L. leucocephala* plots. There was no significant difference in weed seed rain of natural bush and *L. leucocephala* plots in both years. Seed rain in *P. phaseoloides* plots averaged 14,308 seeds m^{-2} over 2 yr. In the bush fallow and planted *L. leucocephala* fallow plots, it averaged 24,714, and 24,883 seeds m^{-2} , respectively for the same period. Although there are no published data on seed rain in the humid forest/savanna transition zone, these seed rain values are comparable to those reported by Forcella et al. (1996) in the northern *Z. mays* belt of the United States. Weed seed rain in cropped *P. phaseoloides* plot was 45 and 38% less than in the natural bush fallow in 1994 and 1995, respectively. Total seed rain within the various fallow types was significantly higher in continuously cultivated plots than in plots fallowed for 1 to 3 yr before cultivation in both 1994 and 1995.

Zea mays growth was better in *P. phaseoloides* plots than

TABLE 1. Effect of fallow type (*Pueraria phaseoloides* or *Leucaena leucocephala*) and land-use intensity on weed seed rain in 1994 and 1995.

Land-use intensity	Seed rain							
	1994			1995				
	Bush fallow	<i>P. phaseoloides</i> fallow	<i>L. leucocephala</i> fallow	Mean	Bush fallow	<i>P. phaseoloides</i> fallow	<i>L. leucocephala</i> fallow	Mean
Continuous cropping	43,478	26,108	38,444	36,010	42,108	21,240	35,899	33,082
1-yr fallow/1-yr crop	30,049	19,331	32,661	27,347	15,959	11,169	13,942	13,690
2-yr fallow/1-yr crop	20,778	7,291	15,885	14,651	13,403	11,778	15,900	13,694
3-yr fallow/1-yr crop	16,158	7,571	14,666	12,799	15,778	9,979	31,667	19,141
Mean	27,616	15,075	25,414		21,812	13,542	24,352	
LSD (0.05) fallow type			5,521				9,127	
LSD (0.05) land-use intensity			6,029				10,538	

- seeds m⁻²

the other fallow types. For example, *Z. mays* leaf area indices (LAIs) in *P. phaseoloides* plots were 1.33 and 1.78 in 1994 and 1995, respectively (Table 2). *Zea mays* LAI values were 1.08 and 1.52 in 1994 and 1995, respectively, for natural bush and 1.22 in 1994 and 1.46 in 1995 in *L. leucocephala* fallow plots. Averaged over fallow type, the *Z. mays* LAI in plots cultivated after 3 yr of fallow was 1.53 in 1994 and 2.02 in 1995 compared to 0.86 in 1994 and 1.08 in 1995 in continuously cultivated plots. The photosynthetically active radiation (PAR) reaching the weed community was 27% in *P. phaseoloides*, 33% in *L. leucocephala*, and 37% in natural bush plots before *Z. mays* was harvested in 1995 ($P = 0.0157$). The PAR at weed canopy level was 72% in continuously cultivated plots, 65% in plots cropped every other year, 59% in plots cropped every 2 yr, and 49% in plots cropped every 3 yr in 1994 ($P = 0.0093$). LAI and PAR measured in this study suggest better crop canopy cover in plots cropped every 3 yr relative to the other land-use intensities. The combined effect of increased shading and reduced light quality may partially explain why seed rain was lower in *P. phaseoloides* plots relative to other fallow types in plots cropped every 3 yr than in the continuously cropped plots.

Reduction in weed seed rain increased as cropping frequency decreased. Up to 65% reduction in weed seed rain was observed after 3 yr of fallow in 1994. This result agrees with those of Zanin and Sattin (1988), who reported up to 50% reduction in seed rain of *Abutilon theophrasti* Medicus (velvetleaf) in the presence of *Z. mays*. Reduction in seed rain is also affected by weed density. Any factor that adversely affects weed density, growth, flowering, seed production, maturation, or dispersal will in turn affect the seed rain. Results of several studies confirm these consequences of interference with weed growth and development. For instance, Buhler et al. (1997) noted that weeds in agricultural fields produce fewer seeds as a result of competition from the crop, damage from herbicides, and other factors. They showed that *Xanthium strumarium* L. (common cocklebur) suffered up to 84% reduction in seed production in competition with *Glycine max* L. (soybean). Bhowmik and Bekech (1993) noted that the presence of a crop canopy could change the competitive ability of weed species, change the subsequent growth and development of weed species, and reduce seed production. Akobundu et al. (1999) reported that *P. phaseoloides* was better than natural bush and *L. leucocephala* fallow systems in reducing weed density. Rao et al. (1998) reported that planted fallow smothered weeds by the combined effect of reduced light, a thick litter layer on the soil surface, and a large leaf canopy. These reductions in weed density would in turn affect the quantity of seeds produced and dispersed.

Phenology of Seed Rain of Individual Species

Seed rain characteristics of weeds in different fallow types and land-use intensities in 1994 and 1995 are shown in Figure 2. Weed seeds were dispersed throughout the sampling period, especially in 1995. In the natural bush fallow system, weed seed rain in the continuously cultivated plots peaked in September 1994 and there was a second minor peak in November, after which the seed rain declined (Figure 2a). Seed rain in plots that were fallowed for 1 to 3 yr before cultivation was generally less than the continuously

TABLE 2. Corn leaf area index (LAI) and light transmittance in different fallow types (*Pueraria phaseoloides* or *Leucaena leucocephala*).

Land-use intensity	Corn LAI (photosynthetically active radiation) ^a							
	1994				1995			
	Bush fallow	<i>P. phaseoloides</i> fallow	<i>L. leucocephala</i> fallow	Mean	Bush fallow	<i>P. phaseoloides</i> fallow	<i>L. leucocephala</i> fallow	Mean
Continuous cropping	0.63 (80)	0.81 (68)	1.14 (67)	0.86 (72)	0.92 (60)	1.20 (37)	1.13 (48)	1.08 (49)
1-yr fallow/1-yr crop	0.95 (67)	1.40 (62)	0.87 (66)	1.07 (65)	1.41 (33)	1.98 (20)	1.55 (38)	1.64 (30)
2-yr fallow/1-yr crop	1.29 (57)	1.41 (54)	1.44 (66)	1.38 (59)	1.68 (32)	1.91 (23)	1.19 (24)	1.59 (26)
3-yr fallow/1-yr crop	1.44 (44)	1.70 (57)	1.45 (49)	1.53 (49)	2.06 (23)	2.02 (27)	1.98 (21)	2.02 (24)
Mean	1.08 (62)	1.33 (60)	1.22 (62)	1.53 (49)	1.52 (37)	1.78 (27)	1.46 (33)	1.59 (26)
LSD (0.05) fallow type			0.21 (11)				0.34 (7)	
LSD (0.05) land-use intensity			0.24 (12)				0.39 (8)	

^a Values in parentheses are photosynthetically active radiation as a percentage.

cropped plots at all sampling dates. Peak seed rain in these plots occurred in August rather than in September, as was the case in the continuously cropped plots. Generally, the least seed rain occurred in plots that were kept fallow for 3 yr. Seed rain in continuously cropped plots had identical peaks in July, September, and November 1995 (Figure 2b). Seed rain peaked in August and February in the 1-yr fallow/1-yr crop subplot treatment, in October in the 2-yr fallow/1-yr crop subplot, and in December and February in the 3-yr fallow/1-yr crop subplot. Seed deposition in the 3-yr fallow/1-yr crop subplot did not start until October, indicating that late-maturing weeds must have contributed to the seed rain in this treatment.

Seed rain in the *P. phaseoloides* fallow system in 1994 and 1995 are shown in Figures 2c and 2d. The largest deposition of weed seeds occurred in the continuously cropped plots in August and November. Seed rain in the 1-yr fallow/1-yr crop peaked in July and September in 1994 and 1995, respectively. Although there was a distinct peak in seed rain in 1995 in the 2- and 3-yr fallow treatments, such peaks were absent in these treatments in 1994.

The seed rain pattern in *L. leucocephala* fallow plots in 1994 was similar to that of the bush fallow system (Figures 2a and 2e). Seed rain in the continuously cropped plots peaked in September, and the seed rain in plots cropped after 1 to 3 yr of fallow peaked in August. This pattern is identical to the pattern noted for the natural bush fallow plots. Seed rain in 1995 peaked in September (Figure 2f) in all land-use intensities except in the 3-yr fallow/1-yr crop, in which the seed rain peaked in October. A consistent trend in all treatments is that seed rain is least in the *P. phaseoloides* fallow system and in land-use intensities, in which a year of cultivation alternates with 3 yr of fallow.

The contribution of different weed types to seed rain in all the three fallow types is shown in Figures 3–5. Seventeen major species occurred in plots cropped after natural bush fallow over the 2 yr of the study (Figure 3). The number of major species in plots cropped after *P. phaseoloides* and *L. leucocephala* were 18 and 16, respectively (Figures 4 and 5). Seeds of broadleaf weeds *Ageratum conyzoides* L. (tropical ageratum), *Synedrella nodiflora* Gaertn. (nodeweed), *Euphorbia hirta* L. (garden spurge), *Chromolaena odorata* (L.) R.M. King and Robinson (siamweed), and *Talinum triangulare* (Jacq.) Willd. (waterleaf); grass weeds *Digitaria horizontalis* Ohwi non Willd. (crabgrass) and *Brachiaria deflexa* (Schumacher.) C.E. Hubbard ex Robyns (wild paragrass); and the sedge *Mariscus alternifolius* Vahl. (mothergrass) dominated the seed rain.

The onset and duration of seed rain varied considerably among individual weed species within the different fallow management systems. Seed shed by *E. hirta* occurred mostly in June and July (Figures 3a, 4a, 4c, 4e, and 5a). *Ageratum conyzoides* and *S. nodiflora* had a longer duration of seed shed than the other species in treatments where they occurred. The duration of seed shed by the two weeds ranged from 5 to 8 mo (July to February), and *A. conyzoides* accounted for 30 to 70% of seeds in the seed rain. *Ageratum conyzoides* is an ephemeral, prolific, and ubiquitous weed of newly cleared rejuvenated land and of home gardens throughout West Africa (Akobundu and Agyakwa 1998). It has been reported as a major weed in slash-and-burn *Oryza sativa* L. (rice) fields (Rafey and

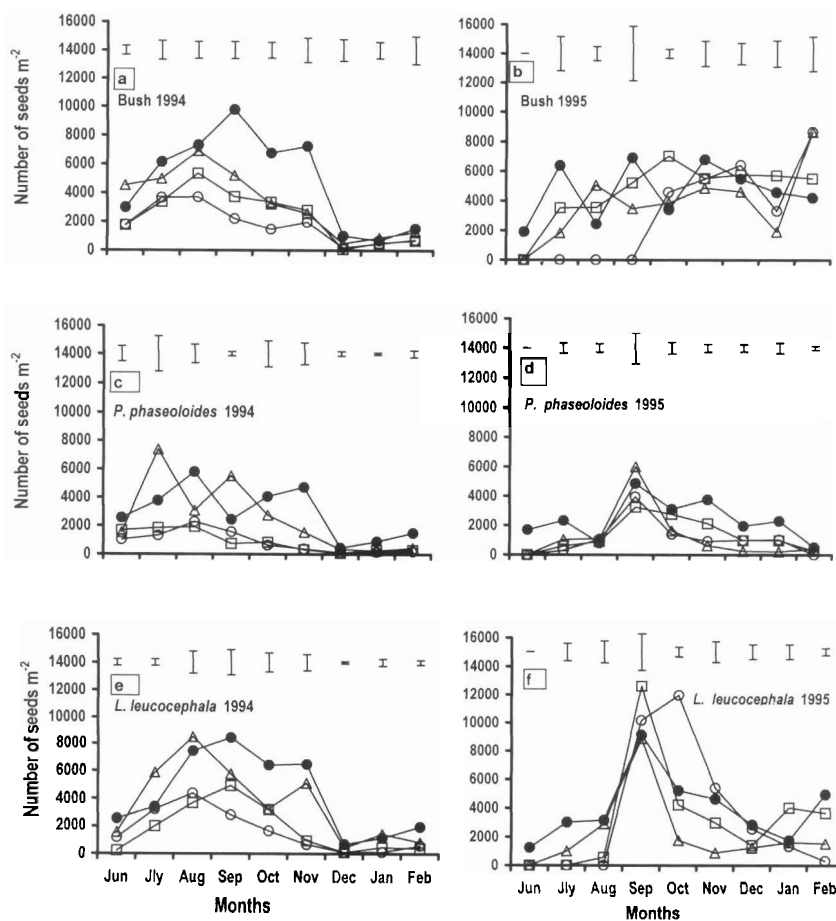


FIGURE 2. Effect of fallow type and land-use intensity on total seed rain in 1994 and 1995. Land-use intensities are represented as ● continuous cropping, △ 1-yr fallow/1-yr crop, □ 2-yr fallow/1-yr crop, and ○ 3-yr fallow/1-yr crop. Each vertical bar is the standard error of the mean.

Prasad 1995; Roder et al. 1997) and also hosts plant diseases (Pabitra et al. 1997). The pattern of seed shed by *S. nodiflora* was similar in continuously cropped natural bush and *P. phaseoloides* plots (Figures 3 and 4). *Synedrella nodiflora* seeds outnumbered all other weed seeds during the dry season in continuously cropped *L. leucocephala* and natural bush plots in 1994 and 1995 (Figures 3a, 3b, 5a, and 5b). *Synedrella nodiflora* is a late-maturing annual weed of humid environments and has been reported to grow under shade (Akobundu et al. 1992). *Chromolaena odorata*, a perennial broadleaf weed of fallow vegetation, dominated the seed rain in February in both years of study (Figures 3 and 4). In plots cropped after *L. leucocephala*, fallow seeds of perennial weeds occurred in all land-use intensities with increasing number from 1-yr fallow to 3-yr fallow subplot treatments (Figures 5c–5h). Seeds of *Panicum maximum* Jacq. (guinea grass), a perennial grass weed, increased in number relative to the other weed seeds during the rainy season with peak seed deposition in August. The number of *P. maximum* seeds declined until *S. nodiflora* seeds became dominant in December (Figure 5h). The effect of increasing seeds of perennial weeds in the fallow plot is consistent with the reduced land-use intensities in these plots that have distinct but varying fallow periods.

Time of flowering among weeds varied with cropping

intensity and fallow type. Flowering was early in continuously cultivated plots compared to plots cultivated after 1 to 3 yr of fallow. In natural bush fallow plots, *A. conyzoides* flowered at 9 wk after emergence (WAE) in the continuously cropped plots, compared to 14 WAE in plots cropped after 2 yr of fallow. Early seed rain generally correlated with early flowering. Early flowering and varied seed set and maturation needs of different weed types may have been responsible for the staggered seed rain observed in this study. Environmental stress and competition from crops also may have played a role in influencing seed production, maturation, and dispersal. According to Patterson (1995), all environmental factors that influence plant growth can potentially affect the ability of weeds and crops to exploit those environmental resources for which plants compete. Early flowering and seed production in some species may have occurred to ensure seed production before the end of the growth cycle. Various weed species have been reported to show phenotypic plasticity in flowering and seed production in different cropping systems and under different environments (Ghersa and Holt 1995; Mohler and Callaway 1995; Mortimer 1989; Sans and Masalles 1995). For example, Mortimer (1989) showed that *A. conyzoides* can complete its life cycle in less than 2 mo and can flower over a wide range of temperatures and display extraordinary plasticity. The present study confirmed this observation.

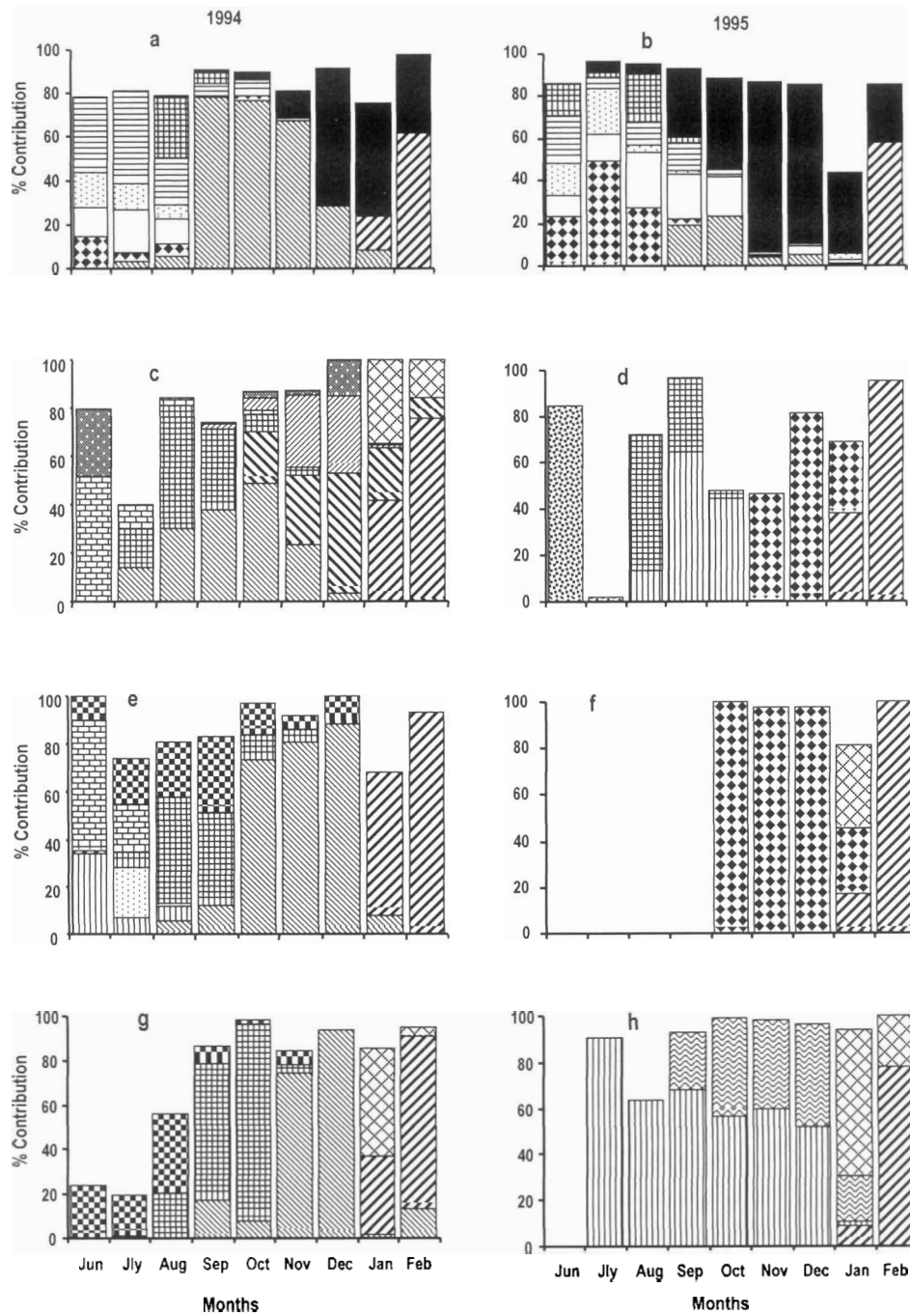


FIGURE 3. Individual species seed rain as influenced by fallow type and land-use intensity in plots cropped after natural bush fallow. Land-use intensities are represented as a and b, continuous cropping; c and d, 1-yr fallow/1-yr crop; e and f, 2-yr fallow/1-yr crop; and g and h, 3-yr fallow/1-yr crop. Species legends are as follows.

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|--------------------------------|------------------------------|------------------------------|---------------------------------|-------------------------------|-------------------------------|
| <i>Triumfetta cordifolia</i> , | <i>Celosia trigyna</i> , | <i>Tridax procumbens</i> , | <i>Cynodon dactylon</i> , | <i>Corchorus sp.</i> , | <i>Digitaria horizontalis</i> |
| <i>Euphorbia hirta</i> , | <i>Ageratum conyzoides</i> , | <i>Panicum maximum</i> , | <i>Mariscus alternifolius</i> , | <i>Synedrella nodiflora</i> , | <i>Spigelia anthelmia</i> , |
| <i>Pouzolzia guineensis</i> , | <i>Chromolaena odorata</i> , | <i>Talinum triangulare</i> , | <i>Brachiaria deflexa</i> , | <i>Physalis angulata</i> . | |

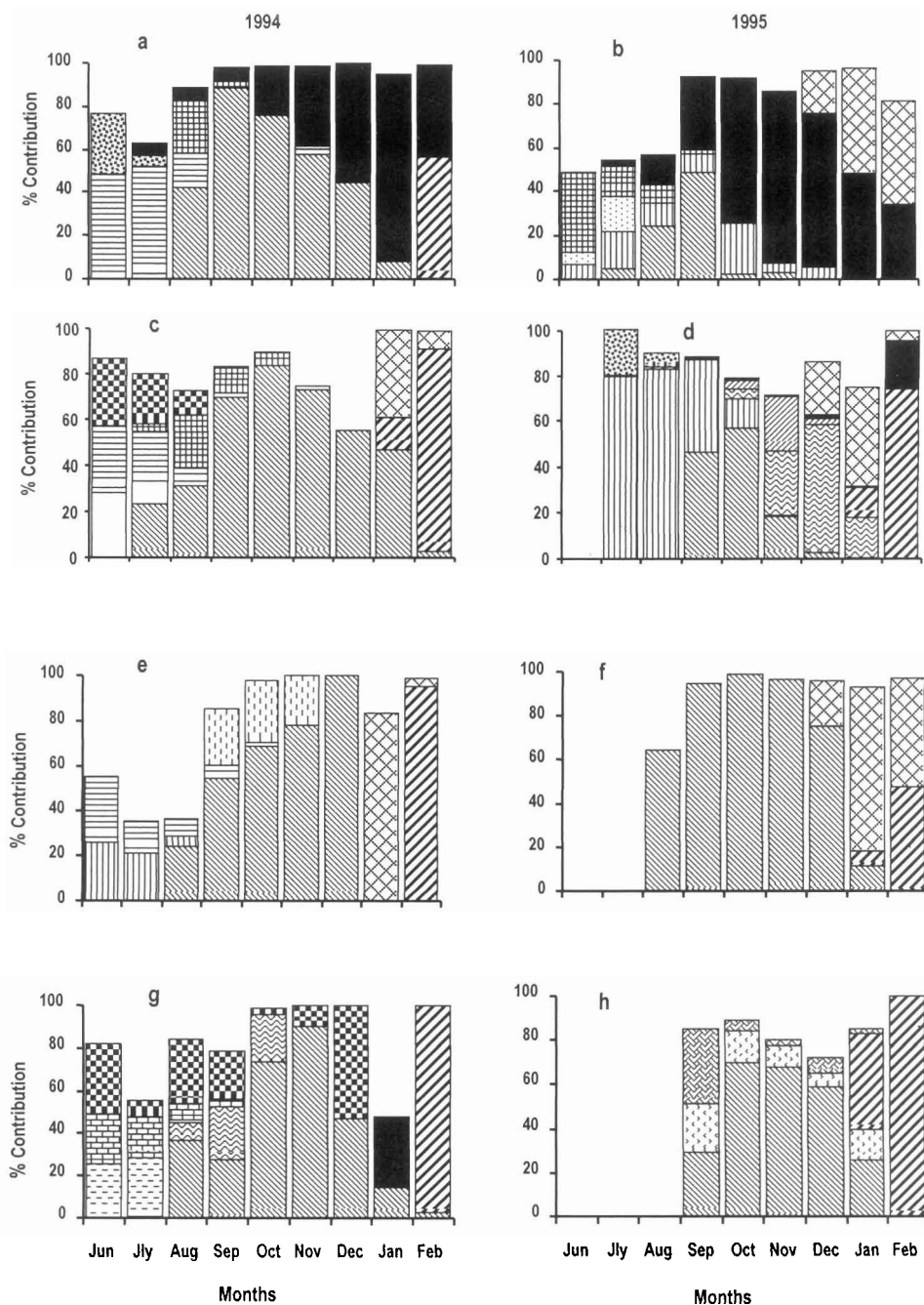


FIGURE 4. Individual species seed rain as influenced by fallow type and land-use intensity in plots cropped after *Pueraria phaseoloides* fallow. Land-use intensities are represented as a and b, continuous cropping; c and d, 1-yr fallow/1-yr crop; e and f, 2-yr fallow/1-yr crop; and g and h, 3-yr fallow/1-yr crop. Species legends are as follows.

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Our study shows that fallow type and land-use intensities affected seed rain throughout this study and that cover crop fallow systems such as *P. phaseoloides* are more effective in reducing the size of the seed rain in short fallow systems than tree-based fallow systems. It also

shows that peak periods of weed seed deposition were August and September (for most annual weeds) and December to February (for most perennial weeds). These peak periods could be targeted for managing weeds to the advantage of the crop. Because annual seed rain is an im-

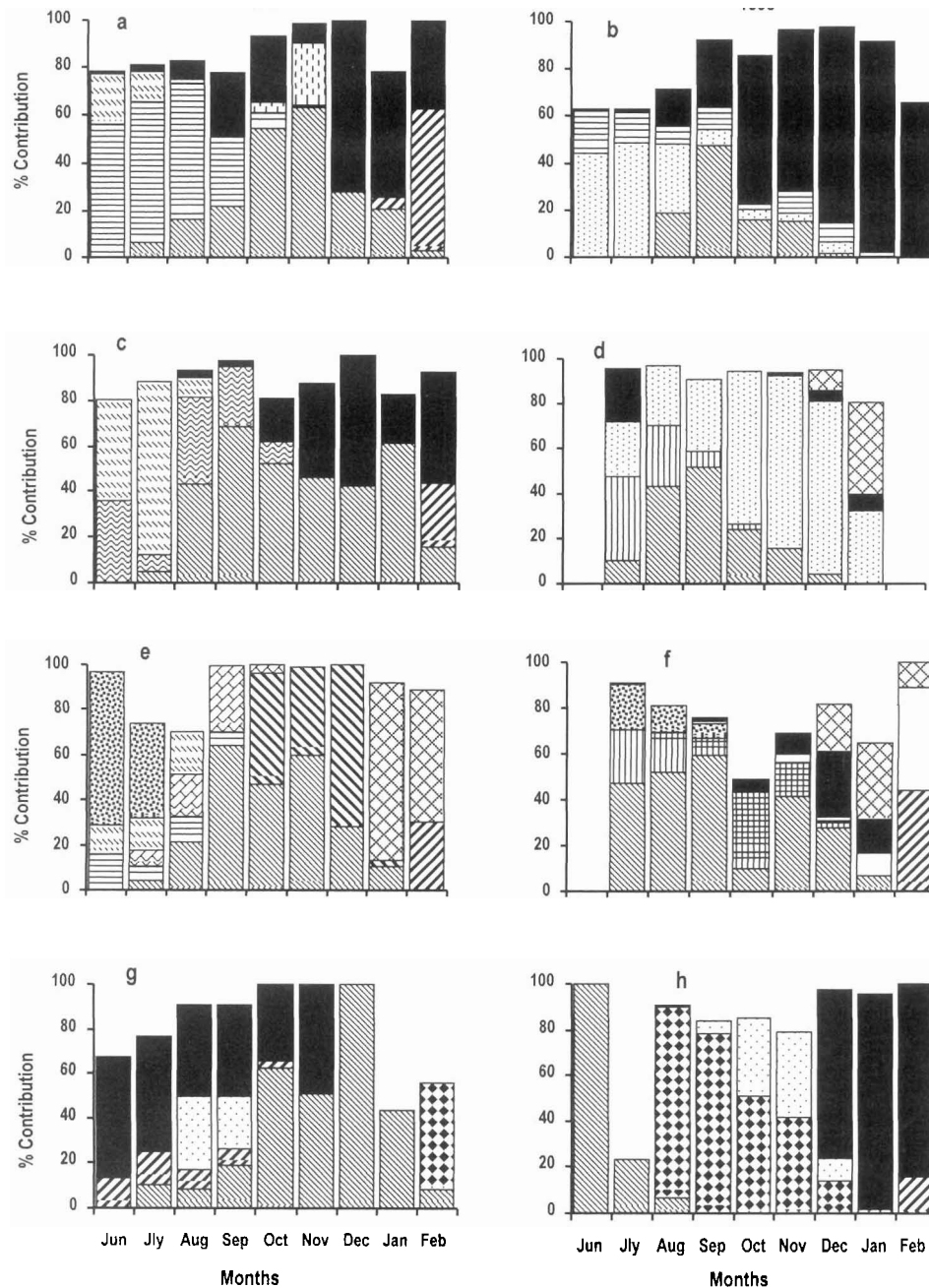


FIGURE 5. Individual species seed rain as influenced by fallow type and land-use intensity in plots cropped after *Leucaena leucocephala* fallow. Land-use intensities are represented as a and b, continuous cropping; c and d, 1-yr fallow/1-yr crop; e and f, 2-yr fallow/1-yr crop; and g and h, 3-yr fallow/1-yr crop. Species legends are as follows.

- | | | | | | |
|--------------------------------|-----------------------------|------------------------------|---------------------------------|---------------------------------|--------------------------------|
| <i>Triumfetta cordifolia</i> , | <i>Celosia trigyna</i> , | <i>Cynodon dactylon</i> , | <i>Corchorus</i> sp., | <i>Digitaria horizontalis</i> , | <i>Euphorbia hirta</i> , |
| <i>Ageratum conyzoides</i> , | <i>Phyllanthus amarus</i> , | <i>Panicum maximum</i> , | <i>Mariscus alternifolius</i> , | <i>Synedrella nodiflora</i> , | <i>Oldenlandia corymbosa</i> , |
| <i>Setaria barbata</i> , | <i>Spigelia anthelmia</i> , | <i>Chromolaena odorata</i> , | <i>Talinum triangulare</i> , | <i>Brachiaria deflexa</i> , | <i>Physalis angulata</i> |

portant supplement to the buried seed reserve and because *P. phaseoloides* has been shown to be effective in reducing the size of this seed rain, integrating this legume cover crop in smallholder agriculture has the potential of reducing weed pressure in this agricultural system.

Sources of Materials

¹Tanglefoot[®]. The Tanglefoots Company, Grand Rapids, MI 49504.

²StereoZoom[®] microscope. Bausch & Lomb, Rochester, NY 14692.

³LAI-2000 plant canopy analyzer. LI-COR, Inc., P.O. Box 4425, Lincoln, NE 68504.

⁴Decagon Sunfleck ceptometer. Decagon Devices Inc., P.O. Box 835, Pullman, WA 99163.

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