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Weed Seed Banks Are More Dynamic in a Sod-Based, Than in a Conventional, Peanut–Cotton Rotation

Ramon G. Leon, David L. Wright, and James J. Marois*

Crop rotation promotes productivity, nutrient cycling, and effective pest management. However, in row-crop systems, rotation is frequently limited to two crops. Adding a third crop, especially a perennial crop, might increase crop-rotation benefits, but concerns about disruption of agricultural and ecological processes preclude grower adoption of a three-crop rotation. The objective of the present research was to determine whether weed seed banks differ between a sod-based rotation (bahiagrass–bahiagrass–peanut–cotton) and a conventional peanut–cotton rotation (peanut–cotton–cotton) and the importance of crop phase in weed seed-bank dynamics in a long-term experiment initiated in 1999 in Florida. Extractable (ESB) and germinable (GSB) seed banks were evaluated at the end of each crop phase in 2012 and 2013, and total weed seed or seedling number, Shannon-Weiner's diversity (H'), richness, and evenness were determined. ESB increased in H' (36%), richness (29%), and total number of weed seeds (40%) for sod-based compared with conventional rotation, whereas GSB increased 32% in H', 27% in richness, and 177% in total number of weed seedlings. Crop phase was a determinant factor in the differences between crop rotations. The first year of bahiagrass (B1) exhibited increases in weed seed and seedling number, H', and richness and had the highest values observed in the sod-based rotation. These increases were transient, and in the second year of bahiagrass (B2), weed numbers and H' decreased and reached levels equivalent to those in the conventional peanut–cotton rotation. The B1 phase increased the germinable fraction of the seed bank, compared with the other crop phases, but not the total number of weed seeds as determined by ESB. The increases in H' and richness in bahiagrass phases were mainly due to grass weed species. However, these grass weed species were not associated with peanut and cotton phases of the sod-based rotation. The results of the present study demonstrated that including bahiagrass as a third crop in a peanut–cotton rotation could increase weed community diversity, mainly by favoring increases in richness and diversity, but the structure and characteristics of the rotation would prevent continuous increases in the weed seed bank that could affect the peanut and cotton phases.

Nomenclature: Bahiagrass, *Paspalum notatum* Fluegg; cotton, *Gossypium hirsutum* L.; peanut, *Arachis hypogaea* L.

Key words: Community, dormancy, germination, integrated weed management, long-term research, populations.

Diversification of crop rotations is beneficial to maintain crop productivity over time, promote nutrient cycling, and decrease insect pest and disease problems (Davis et al. 2012; Liebman and Dyck 1993). Crop rotation has also been shown to be a critical component for effective weed management and, more recently, for herbicide-resistance management (Beckie 2006; Chauvel et al. 2001; Owen 2008). However, crop diversity in a rotation has been limited, in many cases, to two crop species. For example, in the Midwest United States corn (*Zea mays* L.)–soybean [*Glycine max* (L.) Merr.] rotation has been predominant for many decades (Gibson et al. 2006; Karlen et al. 2006), and cotton–peanut rotation is common in row-crop production in the southeast United States (Katsvairo et al. 2006). It has been proposed that the addition of a third crop to those rotations would further increase the benefits described above and even allow the reduction of external inputs (Liebman and Dyck 1993; Westerman et al. 2005). To introduce such a change into well-established agricultural systems, it is critical to assess the effect of adding a crop on productivity, profitability, and environmental and agricultural management aspects.

From the weed-management perspective, the introduction of a third crop into a two-crop rotation creates at least three possible outcomes: (1) weed management improves by adding new weed-control tools that will more effectively reduce existing weed populations (Liebman and Dyck 1993; Owen 2008); (2) weed problems might be

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exacerbated, and other weed species might be introduced and be allowed to thrive, especially if control practices of the additional crop are not as effective as the ones of the crops currently in rotation; and (3) weed species number and populations might increase, but because of the characteristics of the added crop and how weed-control practices may complement each other throughout the rotation, the increase in weed populations might not negatively affect weed management in the phases of the traditional crops and may allow better control of herbicide-resistant weeds (Beckie 2006; Liebman and Dyck 1993; Liebman and Staver 2001; Owen 2008).

Design of a crop sequence that properly manages weed communities is not an easy task. Liebman and Staver (2001) and Westerman et al. (2005) proposed that introducing a perennial forage into a two-crop rotation would help reduce herbicide inputs and maintain relatively stable weed populations over time. Also, these researchers showed that the replacement of herbicides by mechanical control (e.g., frequent mowing) plus higher seed loss from animal predation in the perennial forage could partially compensate for increases in the seed bank triggered by a higher reproductive success because of the absence or less-intensive use of herbicides in the forage phase. Crop phases that can effectively reduce the weed seed bank could further ensure that the more-diverse crop rotation will be able to prevent weed population increases. These "weed suppressive" components of the crop rotation might be a very competitive crop that limits light access to weeds or a crop phase in which highly effective weed-control tools can be implemented or both.

In north Florida, row-crop growers rely predominantly on a peanut–cotton rotation (Katsvairo et al. 2009). The peanut phase lasts generally a single year and is followed by 2 yr of consecutive cotton (Zhao et al. 2009). The main reason for this rotational sequence is that peanut should be grown only every 3 yr in the same field to avoid buildup of soil-borne pathogens (i.e., fungi and nematodes), which could significantly reduce peanut yield (Katsvairo et al. 2006). Florida has an important beef-cattle industry, which relies on pastures for animal nutrition. Therefore, it is not uncommon to find row-crop farms and cattle ranches intermixed in the southeast US landscape. For this reason, a sod-based rotation was proposed to introduce bahiagrass as a third crop into the cotton–peanut rotation for this area (Katsvairo et al. 2006, 2009). Bahiagrass is the most-common grass species used on cattle ranches because of its adaptation to southeast soils and climate. Bahiagrass is a warm-season, perennial grass that can be established from seed and grows very rapidly during the summer (Sollenberger et al. 1988); it is used for hay and for grazing, thus giving the growers more flexibility in farm management (Katsvairo et al. 2006).

A long-term experiment was established in Quincy, FL, in 1999 to compare the proposed sod-based rotation with the conventional peanut–cotton rotation. The results of this experiment demonstrated that peanut and cotton yields were similar or higher in the sod-based rotation than they were in the conventional peanut–cotton rotation (Katsvairo et al. 2007, 2009). Additionally, in the cotton phase weed populations in the sod-based rotation were lower than in the conventional rotation (Katsvairo et al. 2009). No information about weed populations in the other crop phases of the rotation had been generated, partially because of the implementation of intensive and effective herbicide programs (Katsvairo et al. 2009), making it difficult to assess whether the inclusion of bahiagrass changed weed communities in comparison with the conventional peanut–cotton rotation. Seed banks can provide a direct measurement of population dynamics in response to agricultural management (Menalled et al. 2001) and are especially useful when herbicide use cannot be avoided. Therefore, the objective of the present research was to determine whether after 13 yr, weed seed banks differ between the sod-based rotation and the conventional peanut–cotton rotation and to determine the importance of each crop phase in weed seed-bank dynamics.

Materials and Methods

A field experiment was established at the University of Florida's North Florida Research and Education Center in Quincy, FL (84.55°W, 30.6°N), in 1999. The soil was a Dothan sandy loam (fine-loamy, kaolinitic, thermic Plinthic Kandiudult). Before the crop experiment was initiated, the entire experimental area had been managed as a uniform unit, so weed management practices were identical over the site. The rotations established were conventional peanut–cotton–cotton (P_{conv}–C1–C2) and sod-based bahiagrass–bahiagrass–peanut–cotton (B1–B2–P_{sod}–C_{sod}). Cotton and peanut agronomic management followed Extension Service recommendations (Katsvairo et al. 2007) and was the same regardless of rotation. During the winter, oats (*Avena sativa* L. 'Fla 501') were grown as a cover crop in all plots for both

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Table 1. Herbicides and key agronomic practices for different crop phases of a sod-based and a conventional peanut–cotton rotation.[a,b]

Crop	Date	Agronomic practice	Description	Timing	Product/formulation
Peanut	January	Weed control	800 g ai ha^{-1} 2,4-D	POST	2,4-D amine, 456 g ae L^{-1}, UCPA, Eagan, MN
	March	Weed control	1,263 g ae ha^{-1} glyphosate		Roundup WeatherMax, 540 g ae L^{-1}, Monsanto Co., St. Louis, MO
	May	Planting			
		Weed control	420 g ai ha^{-1} pendimethalin	PRE	Prowl H2O, 455 g ai L^{-1}, BASF Corp., Research Triangle, NC
			31 g ai ha^{-1} diclosulam	PRE	Strongarm, 84% ai w/w, Dow AgroSciences, Indianapolis, IN
			1,263 g ae ha^{-1} glyphosate	PRE	
	June	Weed control	74 g ai ha^{-1} bentazon	POST	Basagran, 480 g ai L^{-1}, Arysta LifeScience North America, LLC, Cary, NC
			296 g ai ha^{-1} metolachlor	POST	Stalwart, 960 g ai L^{-1}, SipcamAgro USA, Inc., Durham, NC
			9 g ae ha^{-1} imazapic	POST	Cadre, 240 g ae L^{-1}, BASF
	November	Cover crop planted			
Cotton	January	Weed control	800 g ai ha^{-1} 2,4-D	POST	
	March	Weed control	1263 g ae ha^{-1} glyphosate	POST	
			140 g ai ha^{-1} flumioxazin	PPI	Valor SX, 51% ae w/w, Valent U.S.A. Corp. Walnut Creek, CA
	April	Planting			
		Weed control	1,263 g ae ha^{-1} glyphosate	PRE	
			420 g ai ha^{-1} pendimethalin	PRE	
			180 g ai ha^{-1} fluometuron	PRE	Cotoran 4L, Makhteshim Agan of North America, Inc., Raleigh, NC
	May	Weed control	1,263 g ae ha^{-1} glyphosate	POST	
	June				
		Weed control	204 g ai ha^{-1} linuron	Directed	Linex 4L, 480 g ai L^{-1}, Tessenderlo Kerley, Inc., Phoenix, AZ
			296 g ai ha^{-1} metolachlor	Directed	Sipcam Agro USA
			1,263 g ae ha^{-1} glyphosate	Directed	
	November	Cover crop planted			
Bahiagrass 1	January	Weed control	800 g ai ha^{-1} 2,4-D	POST	
	February	Weed control	1,263 g ae ha^{-1} glyphosate	POST	
	March	Planting			
	July	Weed control	Mowing		
	August	Weed control	Mowing		
	November	Cover crop planted			
Bahiagrass 2	January	Weed control	800 g ai ha^{-1} 2,4-D	POST	
	July	Harvest	Mowing and hay		
	August	Harvest	Mowing and hay		
	November	Burn down	1,263 g ae ha^{-1} glyphosate	POST	
	November	Cover crop planted			

[a] Abbreviation: UCPA, Universal Crop Protection Alliance.
[b] The sod-based rotation was bahiagrass–bahiagrass–peanut–cotton, and the conventional rotation was peanut–cotton–cotton. Peanut and cotton inputs were the same regardless of rotation.

Table 2. Significance of main factors and interactions in ANOVA for Shannon-Weiner's diversity index (H'), richness (S), evenness (J), and the total number of seeds or seedlings per 100 g of soil, based on germinable (GSB) and extractable (ESB) seed-bank tests.

		GSB				ESB			
Factor	df	H'	S	J	Total	H'	S	J	Total
		P value[a]							
Year	1	0.288	**< 0.0001**	**< 0.0001**	0.099	0.211	0.129	0.813	**< 0.0001**
Crop phase	6	**0.018**	**0.0007**	0.226	**< 0.0001**	**< 0.0001**	**0.001**	**0.004**	0.204
Irrigation	1	0.946	0.1928	0.683	**< 0.0001**	0.705	0.704	0.357	0.443
Crop phase × irrigation	6	0.224	**0.010**	0.180	**< 0.0001**	0.221	0.666	0.557	0.373
Year × crop phase	6	0.692	0.127	0.117	0.254	0.318	0.601	0.055	0.056
Year × irrigation	1	0.915	0.588	0.518	0.167	0.716	0.209	0.322	0.302
Year × crop phase × irrigation	6	0.245	0.301	0.411	0.364	0.870	0.835	0.932	0.644

[a] Bolded values are significant.

rotations. All crop-rotation phases were included each year, so specific comparisons between crops could be conducted avoiding year effects. Each crop was grown under either irrigated or nonirrigated conditions. Weed management was based on herbicide control relying on PRE and POST herbicides and on mowing for bahiagrass phases (Table 1). The experiment was a randomized complete-block design with three replications arranged as a split-plot, with irrigation as the main plot and crop phase as the subplot. Main plot and subplot size was 128 m by 24 m and 24 m by 18 m, respectively.

Seed banks were sampled the spring following each crop phase. Therefore, data represented the seed banks at the end of each crop phase. Sampling was conducted the second week of April, in 2012 and 2013, after the winter cover crop was eliminated and before summer crop planting and PRE herbicide application. Eight soil cores (3.5 cm in diameter and 20 cm deep) were collected from each plot by following a serpentine pattern and collecting samples spaced at least 2 m apart. The soil cores were combined to form one composite sample per plot. Composite samples were mixed and homogenized manually, and soil structure was destroyed. Samples were stored at 4 C until seed-bank tests were initiated the third week of May. For the germinable seed bank (GSB) test, a subsample from each composite sample was weighed and placed in a tray (average sample weight was 650 ± 10 g). Trays were placed in a greenhouse and watered twice a day to ensure proper soil moisture for weed-seed germination. Temperature was 28 ± 5 C for the duration of the test. Emerged seedlings were identified, counted, and eliminated weekly. This was done for 3 wk, when irrigation was stopped for 1 wk. Then, the soil of each tray was mixed manually to simulate soil disturbance, and irrigation was reinstated, and weed-seedling emergence was evaluated for another 3 wk.

For the extractable seed bank (ESB) test, another subsample weighing 300 g was washed manually in a sieve retaining only particles > 150 µm to eliminate most of the clay and silt. At the end of the washing step, mainly sand and organic materials were left. Repeated sampling and evaluation of the material that was not retained in the sieve indicated that no identifiable weed seeds were lost during the washing process. Washed samples were air dried for several days and then divided into 10 fractions.

Table 3. Shannon-Weiner's diversity index (H'), richness (S), evenness (J), and the total number of seeds or seedlings per 100 g of soil in a sod-based and a conventional peanut–cotton rotation based on germinable (GSB) and extractable seed bank (ESB) tests.

Test	Crop rotation	H'	S	J	Total No. 100 g^{-1} soil
ESB	Conventional	0.89	5.2	0.55	30
	Sod-based	1.21	6.7	0.65	42
	P value[a]	**< 0.0001**	**< 0.0001**	**0.0003**	**< 0.0001**
GSB	Conventional	0.79	4.13	0.65	1.59
	Sod-based	1.04	5.23	0.69	4.41
	P value[a]	**0.0013**	**0.0002**	0.25	**< 0.0001**

[a] Bolded values are significant.

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Under a stereoscope, weed seeds that did not show any visible damage were identified based on morphology, and counted. Damaged seeds or empty seed coats were not counted to reduce the risk of misidentification and overestimation of the viable seed bank. Weed seeds that were not identified based on morphology were germinated, and the resulting plant was used for species identification. If the seed could not be germinated, the morphology was noted, and it was treated as an "other species."

Data from the ESB and GSB tests were used to estimate seed-bank density (i.e., total weed number), richness (*S*), evenness (*J*), and H', as described by Sosnoskie et al. (2006). Results were analyzed with ANOVA using PROC MIXED in SAS software (SAS Institute, Cary, NC), considering crop rotation or crop phase, irrigation, year, and their interactions as fixed effects, and block and block-by-irrigation interaction as random effects. Crop rotation and crop phase were not included simultaneously in the same ANOVA because of the difference between rotations in the number of crops and crop phases. Tukey-Kramer Honestly Significant Difference ($\alpha = 0.05$) was used for separation of crop phase means. Because normality was not achieved for all species, the Wilcoxon rank-sum test was used to conduct nonparametric analyses comparing the frequency of individual species in each crop rotation and crop phase (Ramsey and Shafer 2002). This was done using NPAR1WAY PROC in SAS software, and the Kruskal-Wallis test was used for mean separation ($\alpha = 0.05$). Canonical correspondence analyses were conducted with CANOCO software (version 4.53, Wageningen University, Wageningen, The Netherlands) to determine association between weed species and crop phases and irrigation for ESB and GSB data. Monte Carlo permutation tests were conducted with a minimum of 499 permutations to determine the significance ($\alpha = 0.05$) of the canonical axes. Biplots were graphed using the two canonical axes that significantly explained most of the variability observed.

Results and Discussion

There was no significant interaction between year and any of the other main factors ($P > 0.05$) (Table 2), so results were pooled over years. This indicated that seed-bank responses to the irrigation and crop phases were consistent, even after agricultural practices changed in a given plot from year to year. Irrigation regime only affected seedling number and richness in the GSB test (Table 2), so, with the exception of these two variables, irrigation treatments were pooled for data analyses.

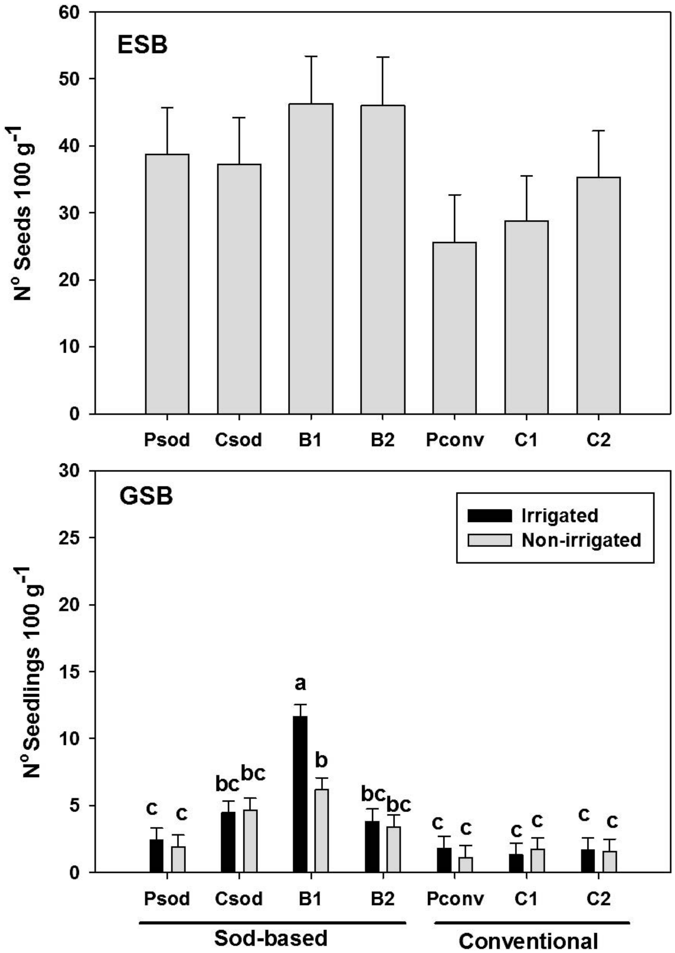

Figure 1. Total number of seeds or seedlings per 100 g soil in the different crop phases of a sod-based and a conventional peanut–cotton rotation under irrigated and nonirrigated conditions based on extractable (ESB) and germinable (GSB) seed bank tests. Crop phases with the same letter were not significantly different based on Tukey-Kramer's Honestly Significant Difference test ($\alpha = 0.05$). No differences between crop phases were observed for ESB. Irrigation effect was only significant for the GSB, so irrigation treatments were pooled for ESB.

In both GSB and ESB tests, the sod-based rotation exhibited more-dense and diverse weed seed banks than did the conventional rotation (Table 3). H' was 36 and 32%, richness 29 and 27%, and total number of weeds 40 and 177% higher in the sod-based than in the conventional plots, for ESB and GSB, respectively. Evenness was higher in the sod-based rotation only for the ESB test. Therefore, the introduction of bahiagrass to a peanut–cotton rotation modified weed community structure.

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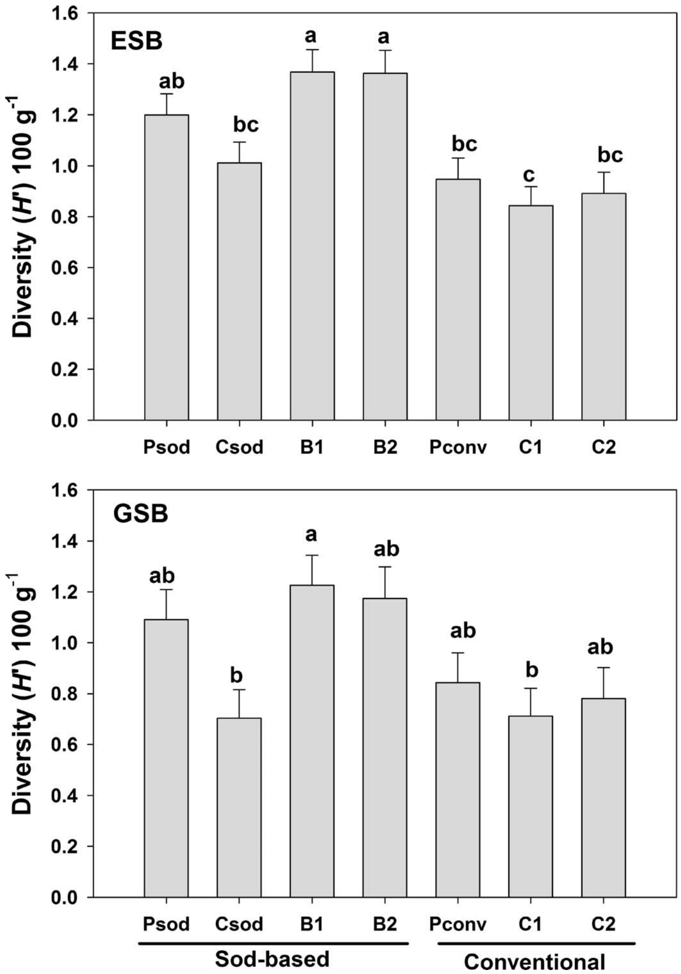

Figure 2. Weed diversity (H') in the different crop phases of a sod-based and a conventional peanut–cotton rotation based on extractable (ESB) and germinable (GSB) seed bank tests per 100 g soil. Crop phases with the same letter were not significantly different based on Tukey-Kramer's Honestly Significant Difference test ($\alpha = 0.05$).

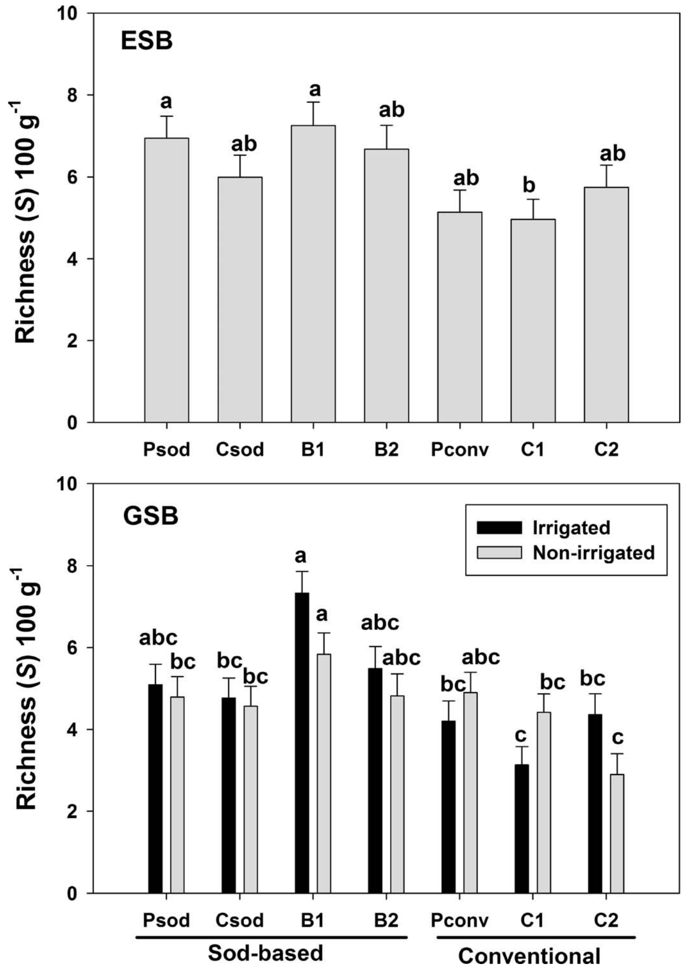

Figure 3. Weed richness (S) in the different crop phases of a sod-based and a conventional peanut–cotton rotation under irrigated and nonirrigated conditions, based on extractable (ESB) and germinable (GSB) seed bank tests per 100 g soil. Crop phases with the same letter were not significantly different based on Tukey-Kramer's Honestly Significant Difference test ($\alpha = 0.05$). Irrigation effect was only significant for the GSB, so irrigation treatments were pooled for ESB.

To determine whether the changes in weed communities were consistent throughout the entire rotation, crop phases were compared. No statistical differences in seed number were observed in the ESB (Figure 1). Conversely, differences among crop phases were identified in seedling number in the GSB. In this case, all crop phases of the conventional rotation had similar seedling numbers. In contrast, in the sod-based rotation, there was a substantial increase in seedling number in B1, which was approximately 10 and 5 times higher for plots with and without irrigation, respectively, when compared with the conventional rotation. However, by the end of B2, seedling numbers were equivalent for both rotations.

Weed H' was influenced by crop phase and crop rotation (Tables 2 and 3). In the conventional rotation, all crop phases had similar H', regardless of the estimation system (e.g., 0.9 and 0.7 for ESB and GSB, respectively) (Figure 2). In the sod-based rotation, both B1 and B2 had the highest H', P_{sod} had intermediate H', and the $C_{sod}H'$ was the lowest.

Richness results varied more than diversity did. In the ESB, most crop phases, regardless of crop rotation, had similar richness (Figure 3). However, B1 richness was significantly greater than C1 richness. In the GSB test, a similar trend was observed, but B1 exhibited greater richness than any cotton phase, regardless of the rotation and irrigation regime. Also, B1 had greater richness than peanut did, depending on irrigation, but the interaction with irrigation was not consistent when

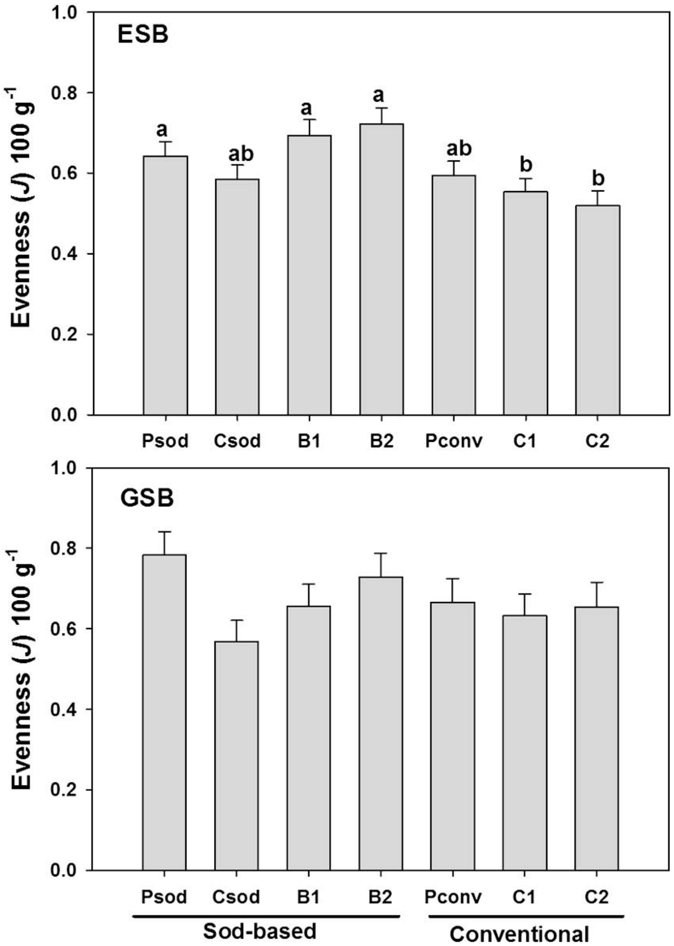

Figure 4. Weed species evenness (*J*) in the different crop phases of a sod-based and a conventional peanut–cotton rotation under irrigated and nonirrigated conditions based on extractable (ESB) and germinable (GSB) seed bank tests per 100 g soil. Crop phases with the same letter were not significantly different based on Tukey-Kramer's Honestly Significant Difference test (α = 0.05). No differences between crop phases were observed for GSB.

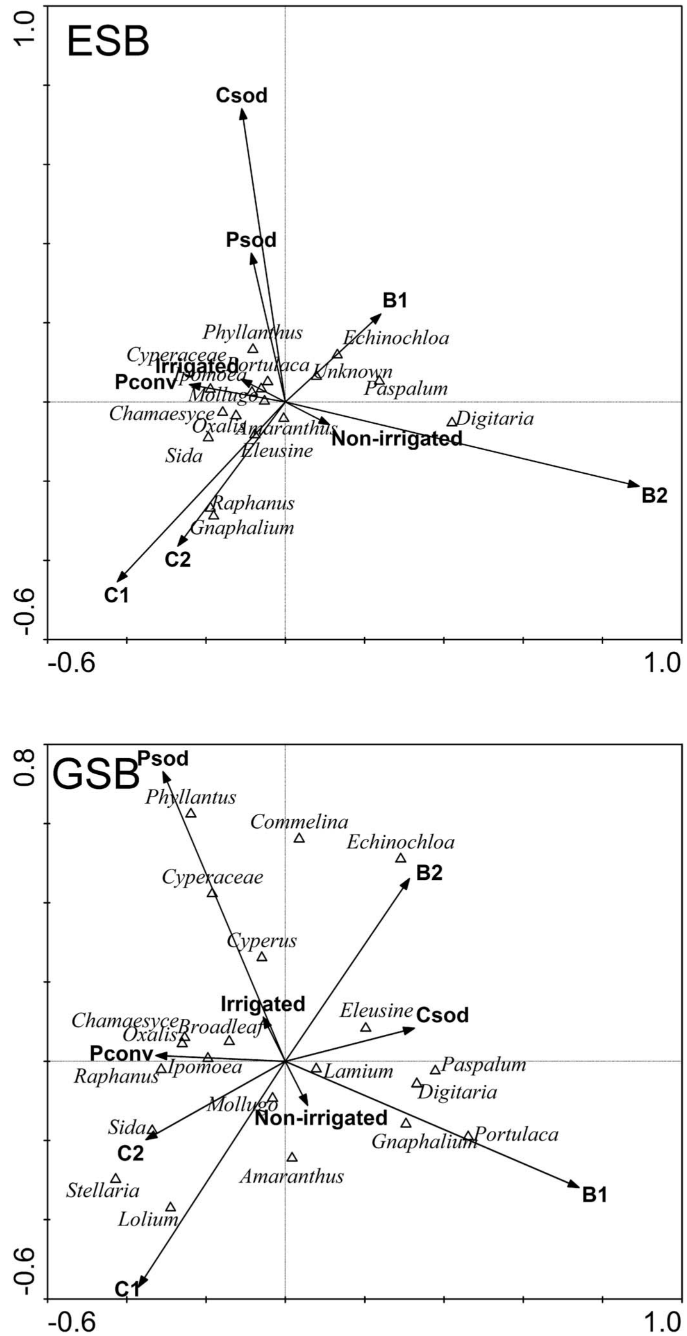

Figure 5. Canonical correspondence-analysis ordination showing associations among weed species, crop phase, and irrigation regime in a sod-based bahiagrass–peanut–cotton rotation (B1–B2–P_{sod}–C_{sod}) and a conventional peanut–cotton rotation (P_{conv}–C1–C2), based on extractable (ESB) and germinable (GSB) seed bank (ESB) tests.

comparing rotations. Overall, B2 richness was consistently intermediate between B1 and peanut and cotton phases.

In the ESB, weed evenness was lowest in the cotton phases of the conventional rotation and highest in the bahiagrass phases of the sod-based rotation. However, no differences in evenness were found in the GSB (Figure 4).

Canonical correspondence analysis indicated that the first two axes explained 52 and 71% of the variance, for GSB and ESB, respectively ($P = 0.002$). Irrigation treatments did not influence weed community structure. However, there was a clear separation between crops from the conventional and sod-based rotations (Figure 5). Species such as Palmer amaranth (*Amaranthus palmeri* S. Wats.), spurge (*Chamaesyce* sp.), morningglory (*Ipomoea* sp.), carpetweed (*Mollugo verticillata* L.), woodsorrel (*Oxalis* sp.), and wild radish (*Raphanus raphanistrum* L.) were more closely associated with the conventional crop rotation in both GSB and ESB tests. Conversely, grass weeds, such as large crabgrass [*Digitaria sanguinalis* (L.) Scop.] and

Table 4. Number of individuals per 100 g of soil for the most-predominant weed species in a sod-based and a conventional peanut–cotton rotation and in their respective crop phases based on germinable (GSB) and extractable seed banks (ESB).

		Amaranthus palmeri		*Chamaesyce* sp.		*Cyperus compressus*		*Digitaria sanguinalis*	
Crop rotation	Crop phase[a]	GSB	ESB	GSB	ESB	GSB	ESB	GSB	ESB
		No. 100 g^{-1} soil							
Conventional		0.04	0.68	3.19	0.16	2.83	3.94	0.38	0.46
Sod-based		0.43	1.00	1.96	0.07	10.71	4.36	4.18	8.80
P value[b]		**0.03**	0.23	0.17	0.86	**< 0.001**	0.35	**< 0.001**	**< 0.001**
	P_{conv}	0	0.64	6.50	0.14	0.50	3.36	0.25	0.07
	C1	0.05	0.88	3.50	0.23	4.85	4.69	0.75	0.42
	C2	0.05	0.94	2.10	0	2.20	4.38	0.10	0.75
	B1	**1.42***[c]	1.92	0.17	0	**8.83***	3.08	2.83	**10.33***
	B2	0.42	0.92	1.25	0	4.83	3.83	**12.75***	**28.42***
	P_{sod}	0	0.50	1.92	0.25	1.42	4.56	2.5	1.50
	C_{sod}	0.10	0.10	3.5	0	1.13	4.6	0.85	0.30
	P value	**< 0.001**	0.09	0.75	0.23	**0.003**	0.97	**< 0.001**	**< 0.001**

barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.], in the GSB, and goosegrass [*Eleusine indica* (L.) Gaertn.] in the ESB test, were associated with the sod-based rotation crops, specifically with the bahiagrass phases. These results were confirmed when comparing the incidence of individual species in each crop rotation and crop phase (Table 4). The sod-based rotation had higher weed frequency for all monocotyledonous species and broad-leaved species, such as Palmer amaranth and carpetweed, especially in GSB. The only exception was sida (*Sida* sp.) in GSB, which had a higher frequency in the conventional rotation, specifically in C1. When comparing crop phases, B1 and B2 exhibited the highest frequencies of weed species, explaining the differences between crop rotations. However, with the exception of large crabgrass, these differences were observed predominantly in GSB and not in the ESB. Palmer amaranth, one of the most important weed species in the southeast United States because of its high reproductive rate and resistance to several herbicide mechanisms of action (Ward et al. 2013), was more frequent in the sod-based, than the conventional, rotation in the GSB test (Table 4). This difference was mainly due to an increase in Palmer amaranth populations in the B1 phase of the sod-based rotation, which was subsequently eliminated in the B2 phase when Palmer amaranth populations returned to the same levels observed in the cotton and peanut phases of both rotation systems. Therefore, the implementation of a sod-based rotation does not represent a risk for the management of this important weed species.

The results of our research indicate that adding a third crop to a peanut–cotton rotation increased weed communities, mainly by favoring richness and diversity. However, such increase is likely to be transient and dependent on the crop species and the management associated with it. B1 was the crop phase in which not only weed *H′* increased but also weed seedling number. This is explained by the absence of weed control actions (i.e., herbicides and cultivation) to allow bahiagrass establishment (Table 1). This finding could raise concerns about the possibility of continuously increasing the weed seed bank, making weed control more difficult in following crop phases. However, after B2, weed seed-bank structure and density were equivalent to crop phases managed conventionally. Therefore, once bahiagrass was established, a dense permanent canopy combined with mowing was enough to suppress weed growth and, more important, favor seed-bank reductions. The processes responsible for the decreases observed in B2 in the GSB were not determined. However, it has been reported that increased seed-predator activity might result from higher vegetation ground cover, such as that provided by bahiagrass, which could compensate for increased seed inputs as a result of the reduction of herbicide applications (Gallandt et al. 2005; Sanguankeo and Leon 2011; Westerman et al. 2005).

The dynamics in weed seed bank *H′* and density observed in the sod-based rotation raise a question about the source of more seeds and weed species. Increases in *H′* in B1 are difficult to explain because the differences between C_{sod} and B1 phases were present in both ESB and GSB (Table 3). One

Table 4. Extended.

Eleusine indica		*Ipomoea* sp.		*Mollugo verticillata*		*Oxalis* sp		*Portulaca oleracea*		*Sida* sp.	
GSB	ESB	GSB	ESB	GSB	ESB	GSB	ESB	GSB	ESB	GSB	ESB
No. 100 g^{-1} soil											
2.5	6.86	0.06	1.38	14.85	39.12	2.60	0.82	0	1.24	0.31	0.10
13.16	6.12	0.07	0.09	40.55	47.46	3.14	1.39	0.11	1.55	0	0.04
< 0.001	0.38	0.77	0.88	**0.03**	0.22	0.72	0.35	0.34	0.53	**0.001**	0.53
3.17	4.64	0	1.64	18.33	36.21	3.33	1.36	0	0.93	0	0
2.25	9.38	0.15	1.77	17.30	47.46	3.05	2.08	0	1.35	**0.55***	0.15
2.35	8.56	0	0	10.30	43.44	1.70	0.56	0	1.44	0.25	0.12
5.58	5.17	0.08	0.08	**82.58***	49.33	4.92	1.17	0	2.92	0	0
30.83*	4.92	0.08	0.08	56.25	36.42	1.50	0.25	0.50	0.75	0	0
12.75	7.00	0	0.19	18.33	56.88	0.25	0.88	0	1.25	0	0.06
7.35	**0.70***	0.10	0	18.55	23.90	4.8	0.60	0	1.40	0	0
< 0.001	**0.04**	0.43	0.83	**0.01**	0.10	0.39	0.64	0.24	0.15	**0.004**	0.52

[a] Abbreviations: P_{conv}, conventional peanut; C1, first cotton crop; C2, second cotton crop; B1, first sod-based bahiagrass; B2, second sod-based bahiagrass; P_{sod}, sod-based peanut crop; C_{sod}, sod-based cotton crop.
[b] Statistical analysis was conducted using Wilcoxon rank-sum scores, and P-values were based on Kruskal-Wallis test ($\alpha = 0.05$). Bolded values were significant.
[c] Values with an asterisk within species and seed bank test are significantly higher than values without an asterisk.

possible explanation is that there are rare species present at very low numbers in most crop phases, but they are favored in B1. Therefore, it is possible that the change in soil conditions and agricultural practices introduced with the added crop (e.g., B1) facilitated the germination, establishment, and reproduction of those rare species that are not commonly observed in conventional systems. Another explanation is migration, in which B1 could have provided a hospitable environment for weed species introduction to the seed bank. However, richness differences between crop phases were not consistent between GSB and ESB tests. The cotton phase in the sod-based rotation had fewer species than did bahiagrass phases in the GSB test, but in the ESB, richness was similar for all crop phases. Furthermore, seed-bank density determined with ESB was almost 10 times higher than the estimation obtained with GSB, and only the latter exhibited differences between crop phases in the total number of weeds (Figure 1).

GSB tests have a strong bias towards nondormant seeds and species with germination requirements similar to the conditions provided in the test (Brown 1992; Gross 1990). If the differences between GSB and ESB were due to a bias of the GSB test, no differences across crop phases should have been detected for the GSB test. Seedling number increase after B1 might be explained by a higher weed survival and reproductive success in the absence of weed control actions. Another explanation for the differences between GSB and ESB is that a large proportion of the ESB was not viable. We tried to minimize this potential problem, and although we did not test for seed viability in the ESB, most of the counted weed seeds did not present evident external damage and were not empty (i.e., seed coats without embryo or endosperm). Therefore, these results suggest that crop phase modified the germinable fraction of the seed bank. Thus, in B1, although the total number of seeds did not change (ESB) compared to other crop phases, the fraction that was germinable (i.e., less dormant or greater germination vigor) increased (GSB). This was true even at the individual species level for those weed species that were favored by bahiagrass phases (Table 4). The mechanisms that control changes in the germinable fraction are not clear. It has been proposed that crop phase can influence the size and composition of the germinable fraction by controlling weed survival and seed inputs to the bank (Menalled et al. 2001; Smith and Gross 2006). However, in the present case, because total ESB did not change, lower weed-seed dormancy levels or greater germination vigor or both in B1 might be at least partially responsible for the results observed.

Although our seed-bank analysis was conducted after 13 yr of establishing the rotations, and the differences reported here between rotations and crop

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phases were consistent across 2 yr, we acknowledge that weed-community structure can vary significantly over long periods (Hernandez Plaza et al. 2011). Therefore, future evaluations will be necessary to confirm our findings and that the observed weed seed bank dynamics had reached a "stable" state. Because aboveground weed vegetation was not assessed in the present study, the effects of the observed weed seed bank dynamics on crop–weed competition cannot be determined. However, previous studies conducted on the same experiment demonstrated that yields in the peanut and cotton phases were similar in both rotations (Katsvairo et al. 2007, 2009). Additionally, Katsvairo et al. (2009) reported that in the same experimental site only 2 of 7 yr exhibited moderate weed pressure to justify weed counts. In those 2 years, for the cotton phase, weed populations were one-half in the sod-based, compared with those in the conventional, rotation. Thus, it seems that increases in weed communities in B1 did not threaten yields or the effectiveness of weed-management practices in peanut and cotton.

Our results demonstrated that crop phase has a key role in determining changes in weed seed bank structure. Furthermore, the changes in weed populations and community observed in the sod-based rotation illustrate how increases in the germinable fraction of the seed bank favors seedling recruitment, but with new seed production being contained via management in the following crop phases, the increases in the aboveground weed populations (i.e., emerged weeds) do not necessarily represent a loss of weed control at the end of the rotation cycle. Finally, although weed communities increased overall in the sod-based rotation, the increase was limited to the first year of bahiagrass, and that increase was transient. Therefore, the introduction of bahiagrass as a third crop did not change weed management for the cotton and peanut phases, in which weed seed banks were similar in both rotations.

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