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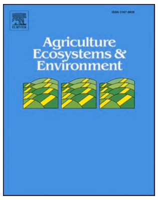

Do rotation and fertilization practices shape weed communities and affect rice yield in low input rainfed agroecosystems in the Malagasy highlands?

Aude Ripoche [a,b,c,d,e,*,1], Karim Barkaoui [f,g,2], Nina Allouch [h], Mathias Christina [b,i,3], Benjamin Heuclin [b,i,4], Antsa Rafenomanjato [b,e,j,5], Anna-Camilla Moonen [j,6], Patrice Autfray [b,e,i,7], Pascal Marnotte [a,b,8]

[a] *CIRAD, UPR AIDA, 97743 Saint-Denis Cedex 9, La Réunion, France*
[b] *AIDA, Univ Montpellier, CIRAD, Montpellier, France*
[c] *CIRAD, UPR GECO, 97743 Saint-Denis Cedex 9, La Réunion, France*
[d] *GECO, Univ Montpellier, CIRAD, Montpellier, France*
[e] *FOFIFA, Antsirabe BP 230, Madagascar*
[f] *CIRAD, UMR AMAP, Montpellier F-34398, France*
[g] *AMAP, Univ Montpellier, CNRS, CIRAD, INRAE, IRD, Montpellier, France*
[h] *Institut Pasteur de la Guadeloupe, Les Abymes, Guadeloupe, France*
[i] *CIRAD, UPR AIDA, Montpellier F-34398, France*
[j] *Group of Agroecology, Institute of Plant Sciences, Scuola Superiore Sant'Anna, Pisa, Italy*

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ABSTRACT

Weeds are a major threat in tropical regions where climate conditions favor their growth and development. This is particularly true in low-input rice-based cropping systems in the Malagasy highlands, where weed management is mainly done by manual removal. Crop rotation is often promoted as an efficient way to control weed infestations, while the role of fertilization is more controversial. In this study, we compared rice monoculture to three rainfed rice-based two-year rotations: rice followed by groundnut, rice followed by sorghum-cowpea mixture, and rice followed by a velvet-bean crotalaria mixture. Each rotation was tested with two levels of fertilization (5 t DM ha^{-1} organic manure, sole or in combination with mineral fertilizer - 400 kg ha^{-1} NPK + 200 kg ha^{-1} urea). We assessed the effect of rotation and fertilization on weed composition, diversity, biomass and rice yield. Additionally, the farmers' perception of weed harmfulness and the relation between their assessment of weed harmfulness and rice production was tested. Our results showed that weed biomass significantly decreased rice yield but only under the low fertilization level. The rotation of rice with the velvet bean-crotalaria mixture was efficient in reducing weed biomass, modified weed community composition and allowed to achieve the highest rice yield. A significant negative relationship was found between weed community harmfulness index and weed species richness. Yet, the lowest rice yield was observed under rice monoculture despite a higher species richness over years and under high fertilization level. The lack of significant correlation between the harmfulness index and the actual rice yield is probably because our index is partly based on farmer's perception, and only on major weeds. More studies on tropical weed harmfulness are needed to support the design of ecologically intensified cropping systems.

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* Correspondence to: Persyst - UPR AIDA/UPR GECO, Station de La Bretagne - 40 chemin de Grand Canal - CS 12014, 97743 Saint-Denis Cedex 9 Réunion, France
E-mail address: aude.ripoche@cirad.fr (A. Ripoche).

[1] 0000-0001-6756-9777
[2] 0000-0002-5787-3748
[3] 0000-0003-3618-756X
[4] 0000-0002-0488-032X
[5] 0000-0003-3207-4699
[6] 0000-0002-4472-1665
[7] 0000-0002-3637-7366
[8] 0000-0002-6904-1682

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1. Introduction

Weeds are among the most damaging pests in agroecosystems if they are not correctly managed, particularly for annual food crops (Oerke, 2006). In tropical regions, temperature and rainfall are favorable to their development and reproduction, whatever the season, resulting in constant pressure on crops all year round. The pressure is even increasing due to climate change in these regions (Wan and Wang, 2019). For farmers who do not have access to mechanization or herbicides, weeds are the major threat to their crop production, and weeding is the most time-consuming cropping practice (Ogwuike et al., 2014). Weed harmfulness has emerged as a concept to assess and rank the severity of the various negative impacts weeds can have not only on crop yield loss, but also on harvest pollution, harvesting difficulties, short- and long-term field infestation, or an increase of crop pathogen attractiveness (Mézière et al., 2015). Yet, the determinants that cause harmfulness and the quantification of harmfulness remain little studied at the species- and community levels (*e.g.* Rafenomanjato et al., 2023).

Crop management practices such as soil preparation, crop and variety choice, sowing time and depth, and soil amendments, together with the direct weed control tactics determine the weed community composition and structure (Fried et al., 2019). They act as ecological filters and select the most adapted species to the local environment and disturbance regime, modifying weed communities' harmfulness and impact on crop production (Bopp et al., 2022; Gaba et al., 2017). For instance, a recent synthesis showed that crop diversification (rotation, crop mixtures, agroforestry) could significantly contribute to weed regulation and thus improve crop production (Beillouin et al., 2021). Indeed, crop diversification may regulate weed infestation in the field, reducing weed biomass and resource competition during the crop cycle (Weisberger et al., 2019) with weed-regulating effects depending on how diversification is implemented. In this study, we focus on crop rotation diversification with a service or cash crop.

The magnitude of the effect of crop rotation on weed abundance (weed density or biomass) varies significantly according to the cropping system (main crops, soil, climate, and management practices). The rotation effect depends on several factors such as the crop species, the rotation duration (number of crop sequences involved), and, especially, the functional differences between the crops, which determine their respective sowing date, crop cycle length, and way of using resources interacting with the weed communities (Mahaut et al., 2019). In some systems crop rotation reduced weed density (Liebman and Dyck, 1993; Weisberger et al., 2019), but the effect was in general limited compared with conventional weed management practices such as mechanical or chemical weeding (Bàrberi et al., 1997; Doucet et al., 1999). In contrast, significant weed biomass reductions were repeatedly observed in rotations (Buhler, 2002; Gu et al., 2021), even without herbicides (Jastrzębska et al., 2019). However, the meta-analysis by Weisberger et al. (2019) revealed that crop rotations did not systematically affect weed biomass despite a significant reduction in weed density, regardless of the climate conditions (temperate or tropical).

Crop rotation may also affect weed species richness independently from weed abundance as shown by Neyret et al. (2020) in a tropical mountainous context. In their study, the number of alternating crops during the rotation promoted weed richness more than the crop type itself. Weed diversity may also increase when weed management is extensive, inefficient, or varies over time and between crops in the rotation (Adeux et al., 2022; Doucet et al., 1999). As hypothesized by Storkey and Neve (2018) and observed by Adeux et al. (2019), a higher weed diversity could mitigate yield losses and be a desirable result for agroecological weed management.

The effect of fertilization on weed density, biomass, or diversity is highly context-dependent (field age, crop type, cropping practices) and therefore responses are difficult to predict. The response to various types of nutrients and nutrient availability is weed species specific (Santín-Montanyá et al., 2013; Tang et al., 2014). Some studies showed that a high level of fertilization, especially N-rich fertilizers, lead to an impoverishment of weed communities due to the selection of nutrient-responsive species (Lal et al., 2014). These nitrophilous species are generally harmful to crop production due to their high competitive ability, while the less competitive species are outcompeted by these weeds and by competition with the crop (Pyšek and Lepš, 1991; Storkey and Neve, 2018). In addition, weed density and biomass may vary differently according to the type of fertilization (mineral or organic) and the weed species considered (Blackshaw et al., 2003; Gao et al., 2022).

In the Malagasy highlands, upland rainfed rice-based cropping systems recently expanded and the main part of rainfed rice is produced on low fertility soils, with no or limited access to mechanization and external inputs. In these conditions, yields remain dramatically low (1.6 – 2 t ha^{-1} on average; Razafimahatratra et al., 2017) and weeds may lead to substantial yield losses (until 30 kg ha^{-1} per day of delay in the weeding, Rafenomanjato, 2018). In a previous study, Ripoche et al. (2021) showed that diversified rotations could promote ecosystem services (soil fertility, soil macrofauna diversity and activity, and pests and weed regulation) while maintaining rice production, despite the low level of soil fertility and nutrient supply in the Vakinankaratra region (mid-west of Madagascar). There still is a need to understand how different crops that can be used to diversify the rotation, affect the weed community composition and weed abundance, and eventually, if and how the crop choice can moderate the harmfulness of tropical weed species (Le Bourgeois et al., 2022; Rafenomanjato et al., 2023).

The objectives of this study were to assess how diversified rice-based rotations through the inclusion of legumes and legume mixtures and the interaction with fertilization regimes affect weed biomass, species richness, and weed community harmfulness, and how it affects rice grain yield. The same field experiment established by Ripoche et al. (2021) was used, where three types of rotations, including legume species alone or in mixture with a cereal or another legume species, were assessed in comparison with rice monoculture under two contrasted levels of fertilization, organic manure alone or combined with mineral fertilizer (Ranaivoson et al., 2022). To our knowledge, it is one of the few tropical studies relating crop management to weed communities and their harmfulness in relation to crop production in herbicide-free cropping systems.

2. Material and methods

2.1. Study site

We conducted a field experiment at the Ivory station, mid-west of Vakinankaratra (19°33'18.90'' lat. S, 46°24'53.83'' long. E, 930 m.a.s.l.) during four successive cropping seasons, in 2015/2016, 2016/2017, 2017/2018 and 2018/2019 hereafter referred to as year 1, year 2, year 3 and year 4, respectively. The cropping season corresponds to the rainy season from November to April, while fields remain uncropped from May to October during the dry and cold season. We started the experiment in late October 2015 and ended it in June 2019. An automatic weather station (CIMEL, Electronique, Paris, France) near the experimental field recorded daily weather data. The average minimum and maximum temperature during the four cropping seasons were 18.1 ± 1.1 °C and 31.3 ± 1.0 °C, respectively, and the average annual rainfall was 1295 ± 94 mm (Supplementary Material, Fig. S1). The soil type was a sandy-clay-loamy Ferralsol (FAO classification) with a clay-silt-sand composition of 32–18–50 % in the 0–40 cm soil layer and a low inherent fertility (0.1 % N and 3 % of organic matter). Physical and chemical soil properties are detailed in the Supplementary Material (Table S1).

2.2. Experimental design and crop management

The experiment was carried out on a field previously cropped with maize and cassava. We used a factorial randomized block design with four replications to compare a rainfed rice/rice monoculture (*Oriza sativa* L.) (RR) to three rice/legume rotations: (i) rice after groundnut (*Arachis hypogaea* L.) (RG), (ii) rice after a mixture of sorghum (*Sorghum bicolor* L. Moench*)* and cowpea (*Vigna unguiculata* (L.) Walp.) (RSC), and (iii) rice after a mixture of velvet bean (*Mucuna pruriens* (L.) DC) and crotalaria (*Crotalaria spectabilis* Roth.*)* (RVC). The cultivars of the experiment were the rice cultivar "Nerica 4", the groundnut cultivar "Marabe", the sorghum cultivar "IS 2787", the cowpea cultivar "Farimaso" (Malagasy cultivar), and the velvet bean cultivar "Utilis", commonly used in the region. The monoculture and the three rotations were combined with two contrasted levels of fertilization: (i) a low fertilization level (LF) based on manure only (LF = 5 t DM ha^{-1} with 0.6 % N) and (ii) a high-fertilization level (HF) based on the same amount of manure as in LF combined with mineral fertilizer (HF = LF + 400 kg ha $^{-1}$ NPK (11/22/16) and 200 kg ha^{-1} urea). Additionally, each rotation x fertilization combination was repeated twice, with half of the plots starting with rice the first year (2015/2016) and the other half with the rotation crop (or mixture). Consequently, rice and each rotation crop (or mixture) were present each year of the experiment. Thus, two complete rotations were conducted on each plot at the end of the experiment in 2019 corresponding to four cropping cycles. Crops were grown on individual plots of 5.1 m * 9 m, resulting in 64 plots in total (4 rotation x 2 fertilization levels x 2 rotation sequences x 4 blocks, Fig. 1). After harvest, crop residues, whether of rice or rotation crop(s) were left on the soil until buried at the following soil tillage before sowing of the subsequent crop. All crop management practices were done manually (tillage, sowing, weeding, and harvest), and no herbicide was used, in line with the management farmers perform in their fields. Depending on rainfall, soil tillage was done 3–6 weeks before sowing. Five to eight rice seeds were sown in a hole with 30 and 20 cm between and within rows, respectively. Manure and mineral fertilizer were applied at sowing, while urea was applied at 45 and 75 days after sowing (DAS). The amount and characteristics of manure and cropping practices are detailed in Supplementary Material (Table S2 and S3) and fully described in Ripoche et al. (2021) and Ranaivoson et al. (2022).

2.3. Weed biomass and composition

We measured weed total biomass twice a year (just before hand-weeding) in the plots cultivated with rice from year 1 to year 4 (Table S3). In year 1, weed biomass was assessed on the entire plot. From year 2–4, we harvested weed aboveground biomass at ground level from three 0.9 m * 0.6 m quadrats in each plot, weighted fresh biomass, and then one sub-sample per quadrat (around 200 g) was collected and oven-dried at 65°C for 72 h to obtain dry matter content.

We assessed weed species composition in each rice plot each year just before rice flowering. In year 1, weed species composition was assessed considering the proportion of grasses, broadleaved species and sedges in each plot. From year 2–4, weed species abundance was assessed visually measuring weed cover by species (%) in the whole plot (Braun-Blanquet, 1932; Le Bourgeois et al., 2022). Only genus was considered for *Digitaria* and *Cyperus* species, as it was not possible to distinguish species without flowers. We estimated weed species richness as the number of species observed at the sampling date.

2.4. Weed harmfulness on crop production at the community level

We calculated a harmfulness index (HC) for each surveyed weed community. To do this, we used a weed species harmfulness score (0−10) based on a farmer surveys in which 20 men and 20 women were interviewed and asked to evaluate the harmfulness for rice production of 15 major weed species commonly observed in rainfed rice fields near our study site (Rafenomanjato et al., 2017). A score of 10 indicated that the weed species was of major concern regarding rice cultivation, while a score of 0 indicates that the species was perceived as not damaging. In our study, 13 of the species rated were observed over the four years of the experiment. We calculated the HC index as follows:

$$HC_{r,f,y} = \sum_{i=1}^{n} Cov_{i,r,f,y} * H_i$$

where $Cov_{i,r,f,y}$ is the cover of species *i* (0–100 %), in rotation or in the rice monoculture *r*, under the fertilization *f*, in year *y*, and H_i is the harmfulness rating for species *i* based on the above mentioned farmer survey.

2.5. Rice yield

Rice yield was measured at harvest based on a five m^2 quadrat (16–17 weeks after sowing). Rice panicles were collected manually from

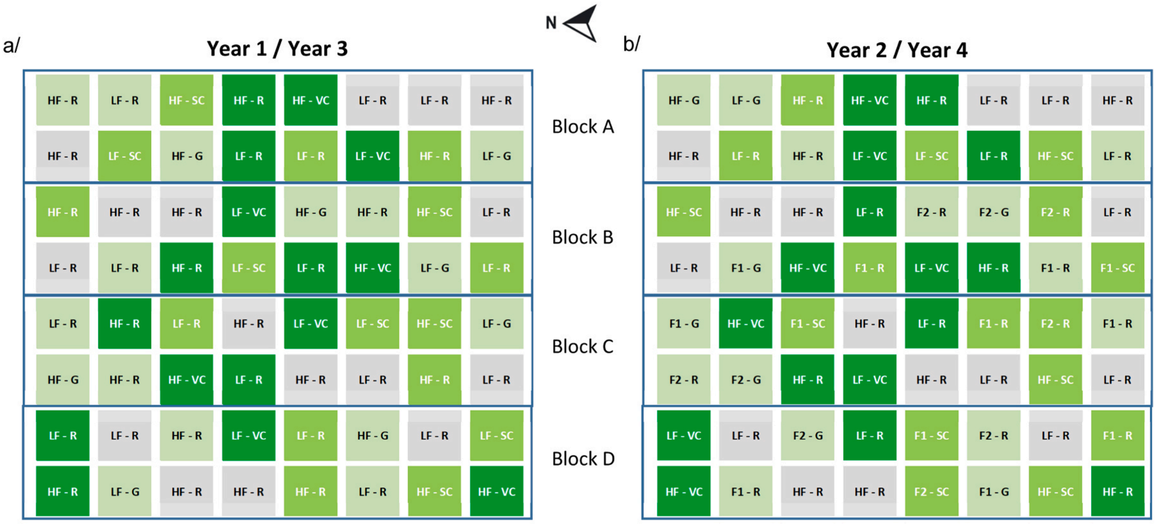

Fig. 1. Experimental design over two complete rotations in year 1 and 3 (a, 2015/2016 and 2017/2018) and year 2 and 4 (b, 2016/2017 and 2018/2019) on the experiment at Ivory station, Mid-West region in Madagascar. Crop sown and fertilization level are indicated in each plot. Grey cells correspond to rice monoculture, light green ones to rice followed by groundnut, green ones to rice followed by sorghum - cowpea mixture and dark green ones to rice followed by velvet bean - crotalaria mixture. R= rice; G = groundnut, SC = sorghum – cowpea mixture, VC = Velvet bean – crotalaria mixture; LF = low fertilization level (5 tDM ha^{-1} of organic manure), HF = High fertilization level (LF + 400 kg ha^{-1} NPK (11/22/16) + 200 kg ha^{-1} urea).

this quadrat and hand-threshed by stripping the spikelets from the panicles. Unfilled spikelets were removed, and filled spikelets were weighed to estimate grain yield. Filled spikelets were oven-dried at 65°C for 72 h to obtain dry matter content. Grain yield was adjusted to 14 % moisture content on an oven-dry basis.

2.6. Statistical analyses

The first year was excluded of the analysis because the trial had to settle and no differences were detected in rice yield nor on weed biomass (Ripoche et al., 2021), neither considering proportions of the different weed life forms (grasses, broadleaved species and sedges).

We performed all statistical analyses using R version 4.3.2 (R Core Team, 2023). We performed a non-metric multidimensional scaling (NMDS) using the 'metaMDS' function to further examine the changes in weed species composition in response to rotation, fertilization level, and year from *vegan* package (Oksanen et al., 2022). We performed a permutational ANOVA using the 'adonis2' function with the Bray-Curtis distance calculation method paired with a posthoc test from the *pairwiseAdonis* package (Martinez Arbizu, 2017) to test for significant differences among factors and modalities. We then used the 'multipatt' function from the *indicspecies* package (De Cáceres and Legendre, 2009) to identify weed species significantly associated with each rotation type, fertilization level, and cultivation year.

Weed species richness, total weed biomass, and community harmfulness were subjected to analysis of variance (ANOVA) with a linear mixed effects model using *lme4* package (Bates et al., 2015). Fixed effects were rotation (RR, RG, RSC, RVC), fertilization level (LF, HF), year (year 2, 3, and 4), and their interactions for all variables. Species richness and weed biomass were also tested as fixed effects on weed community harmfulness. Plot was considered as a random factor. Normality and variance assumptions were tested using Bartlett's and Shapiro's tests. Data were log-transformed (weed biomass and species richness) when assumptions were not respected. Finally, we tested the effects of the different weed variables on rice yield, including total weed biomass, weed community harmfulness, species richness and rotation, fertilization, year and their interactions as fixed effects, with the plot being a random effect. The fixed effects of the models were then tested and with post-hoc tests (Tukey's HSD) to compare and determine significant differences between means using *emmeans* (Lenth, 2022) and *multcomp* (Hothorn et al., 2008) packages.

3. Results

3.1. Weed cover and species richness

In year 1, proportion of grasses, broadleaved species, and sedges were 90, 3 and 4 % respectively with few differences between monoculture and rotations (from 90 % to 96 % of grasses, from 1 % to 5 % of broadleaved species and 2–5 % of sedges; data not shown). From year 2–4, thirty different weed species belonging to 13 botanical families, mostly Poaceae (7 species) and Fabaceae (6 species), were observed in rice plots (Table 1). Most species were annuals (24 species) and/or were broadleaved species (21 species). Despite the low number of perennial species (5 species), they were among the 13 most abundant ones. On average, the individual species cover was around 13 % and *Digitaria spp.*, *Eleusine indica,* and *Striga asiatica* had the highest cover, respectively 30, 22.6 and 19.3 % (Table 1, Fig. S2). Two-thirds of the species from 10 different botanical families, among which all Fabaceae species, ranked between 10 % and 20 % of cover. The abundance of the eight other species, mainly Poaceae, was below 10 % (Table 1).

On average, 5.54 weed species were observed in individual rice plots. Species richness varied between years ($p < 0.05$) and rotations ($p < 0.05$), and was also significantly affected by the rotation x fertilization (p

Table 1
Weed species and their average weed cover (%) observed over the three years of the experiment (all treatments combined), with their EPPO code, family, cycle and life form. The thirteen species rated by farmers for their harmfulness on rice crop production are in bold.

Weed species	EPPO Code	Family	Cycle & life form	Average weed cover	Harmfulness score
Digitaria sp.	**DIGSP**	**Poaceae**	**A, G**	**30.0**	**6.2**
Eleusine indica	**ELEIN**	**Poaceae**	**A, G**	**22.6**	**8**
Striga asiatica	**STRLU**	**Orobranchaceae**	**A, B**	**19.3**	**10**
Mollugo nudicaulis	**MOLNU**	**Molluginaceae**	**A, B**	**16.5**	**1.5**
Stylosanthes guianensis	**STYGN**	**Fabaceae**	**P, B**	**14.4**	**1.6**
*Crotalaria spectabilis**	CVTSP	Fabaceae	P, B	14.4	-
Melochia pyramidata	MEOPY	Malvaceae	P, B	14.3	-
Cleome hirta	**CLEHI**	**Cleomaceae**	**A, B**	**14.3**	**4.9**
Mitracarpus hirtus	**MTCVI**	**Rubiaceae**	**A, B**	**13.8**	**4.2**
Sida acuta	**SIDAC**	**Malvaceae**	**P, B**	**13.7**	**1.6**
Acanthospermum hispidum	**ACNHI**	**Asteraceae**	**A, B**	**12.7**	**3.3**
Cyperus sp.	**CYPSP**	**Cyperaceae**	**P, S**	**12.4**	**4.5**
*Mucuna pruriens**	MUCPR	Fabaceae	A, B	12.0	-
Rottboellia cochinchinensis	ROOEX	Poaceae	A, G	11.9	-
Richardia scabra	**RCHSC**	**Rubiaceae**	**A, B**	**11.8**	**8.2**
*Arachis hypogea**	ARHHY	Fabaceae	A, B	11.6	-
Indigofera hirsuta	INDHI	Fabaceae	A, B	11.3	-
Celosia argentea	CEOAR	Amaranthaceae	A, B	11.1	-
Bidens pilosa	**BIDPI**	**Asteraceae**	**A, B**	**11.1**	**2.3**
Corchorus olitorius	CRGOL	Malvaceae	A, B	10.4	-
Aeschynomene americana	AESAM	Fabaceae	A, B	10.2	-
Euphorbia hetereophylla	EPHHL	Euphorbiaceae	A, B	10.0	-
Ageratum conyzoides	**AGECO**	**Asteraceae**	**A, B**	**9.9**	**1.9**
Urena lobata	URNLO	Malvaceae	P, B	9.7	-
Echinochloa sp.	ECHSP	Poaceae	A, G	9.1	-
Setaria pumila	SETPU	Poaceae	A, G	9.1	-
Commelina benghalensis	COMBE	Commelinaceae	A, G**	8.9	-
Pennisetum polystachion	PESPO	Poaceae	A, G	8.4	-
Perotis patens	PRRPA	Poaceae	A, G	6.7	-
Portulaca oleracea	POROL	Portulacaceae	A, B	6.7	-

A = Annual, P = Perennial; G = Grasses, B = Broadleaved species, S= Sedges
*indicates crop from the rotation which is a volunteer crop during the rice growing cycle therefore considered a weed.
** *Commelina benghalensis* is a monoctyledon with broad leaves.

< 0.01) and year x rotation interactions ($p < 0.05$; Table 2). Species richness in the rice monoculture was significantly higher than in the rotation with groundnut during year 2 ($p < 0.05$, 6.4 vs. 4.6 respectively) or under high fertilization levels ($p < 0.01$, 6.12 vs. 4.42, Table S4). No difference was observed during years 3 or 4 or under low fertilization levels (Table S4).

Table 2

Variance analyses on weed species richness, weed community harmfulness, weed biomass, and rice yield, with the plot as random effect.

	Fixed effects	Chi^2	Degree of freedom	p-value
Species Richness	**Intercept**	**130.37**	**1**	***<2.2e-16***
	Block	1.02	3	0.795
	Rotation	**8.58**	**3**	***0.035***
	Fertilization	1.8	1	0.179
	Year	**6.56**	**2**	***0.038***
	Rotation * Fertilization	**11.45**	**3**	***0.009***
	Year * Fertilization	1.07	2	0.586
	Year * Rotation	**13.98**	**6**	***0.029***
	Year * Rotation * Fertilization	12.28	6	0.056
Weed Community Harmfulness	**Intercept**	**280.41**	**1**	***<2.2E-16***
	Block	**17.48**	**3**	***<0.001***
	Rotation	52.82	1	0.056
	Fertilization	0	1	0.955
	Year	7.56	3	0.134
	Rotation * Fertilization	1.99	3	0.574
	Year * Fertilization	3.31	2	0.191
	Year * Rotation	3.76	6	0.709
	Year * Rotation * Fertilization	7.64	6	0.265
	Species richness	**52.82**	**1**	***3.66E-13***
Weed biomass	**Intercept**	**9.7**	**1**	***0.002***
	Block	**31.54**	**3**	***6.55E-07***
	Rotation	**25.21**	**3**	***1.39E-05***
	Fertilization	0.37	1	0.545
	Year	**46.39**	**2**	***8.45E-11***
	Rotation * Fertilization	2.34	3	0.504
	Year * Fertilization	4.97	2	0.083
	Year * Rotation	10.79	6	0.095
	Year * Rotation * Fertilization	6.57	6	0.362
Rice yield	**Intercept**	**45.13**	**1**	***1.85E-11***
	Block	**25.56**	**3**	***1.18E-05***
	Rotation	7.29	3	0.06
	Fertilization	**60.73**	**1**	***6.55E-15***
	Year	**18.39**	**2**	***0.0001***
	Rotation * Fertilization	**11.67**	**3**	***0.009***
	Year * Fertilization	**31.46**	**2**	***1.47E-07***
	Year * Rotation	**14.3**	**6**	***0.026***
	Year * Rotation * Fertilization	11.98	6	0.062
	Weed biomass	**22.13**	**1**	***8.46E-07***
	Weed Community Harmfulness	0.65	1	0.419
	Species richness	0.9	1	0.341

Significant effects are indicated in bold.

3.2. *Weed community composition and indicator species in the rice crop*

Weed community composition differed between years ($p < 0.001$, Fig. 2a) and was significantly affected by the fertilization level ($p = 0.001$, Fig. 2b), rotation ($p < 0.001$, Fig. 2c) but not by their interactions (Table 3). Each year significantly differed from each other ($p < 0.001$), low fertilization level differed from the high one ($p < 0.05$), and the rotation with a legume mixture differed from the rice monoculture (RR, $p < 0.001$), the rotation with groundnut (RG, $p < 0.001$) and the one with a cereal-legume mixture (RSC, $p < 0.05$). Some species were significantly associated with some years, one particular fertilization level or with some rotation types. For instance, *Corchorus olitorius* ($p = 0.001$) and *Commelina benghalensis* ($p = 0.021$) were associated with year 2 (2016/17), *Striga asiatica* ($p = 0.001$), *Mitracarpus hirtus* ($p = 0.001$) and *Ageratum conizoides* ($p = 0.027$) with year 3 (2017/18) and *Cyperus spp.* ($p = 0.001$), *Bidens pilosa* ($p = 0.001$) and *Richardia scabra* ($p = 0.009$) with year 4 (2018/19). *Bidens pilosa* ($p = 0.003$) was also associated with the low fertilization treatment. *Rottboellia cochinchinensis* ($p = 0.039$) was associated with the rotation with a cereal-legume mixture while *Mucuna pruriens* ($p = 0.001$) and *Crotalaria spectabilis* ($p = 0.001$) (volunteer crops) were with the rotation with a legume mixture. Finally, other species like *Sida acuta* ($p = 0.001$), or *Mollugo nudicaulis* ($p = 0.001$) and *Melochia pyramidata* ($p = 0.012$), were associated with two different years, year 3 and 4 or 2 and 3 respectively.

3.3. *Total weed biomass*

Total weed biomass was significantly affected by rotation ($p < 0.001$) and year ($p < 0.001$), without any effect of the fertilization level and none of the interactions was significant (Table 2). Total weed biomass was almost halved in the rotation with a legume mixture compared to the other rotations and the rice monoculture, i.e., on average 0.25 vs 0.50 t ha^{-1} respectively ($p < 0.001$, Fig. 3a). Each year differed from the other ($p < 0.001$, Fig. 3b), the highest weed biomass being observed in year 4 (around 0.75 t ha^{-1}) while the lowest was observed in year 3 (around 0.15 t ha^{-1}).

3.4. *Weed community harmfulness*

Farmers considered *Striga asiatica* the most noxious species before *Richardia scabra* and *Eleusine indica*, with a harmfulness score of 10, 8.2, and 8, respectively (Table 1). *Digitaria spp*. had an intermediate score (6.2), while the other species obtained a score lower than 5.

The weed community harmfulness index (HC) was neither affected by rotation, year, or fertilization nor by their interactions (Table 2, Fig. 3c, d). Weed community HC tended to be higher during year 4 than years 2 or 3 (around 5.4 vs. 4.6), higher under the rotation with groundnut and lower under the rotation with a legume mixture (5.4 *vs.* 4.4), while it remains similar under the low and high fertilization level (4.7 vs 4.9). Additionally, weed community HC was negatively affected by species richness ($R^2 = 0.35$, $p < 0.001$, Fig. 4).

3.5. *Effect on rice yield*

Rice yield was significantly affected by weed biomass ($p < 0.001$), fertilization ($p < 0.001$), year ($p < 0.001$), year × rotation interaction ($p < 0.05$), rotation × fertilization ($p < 0.001$), and year × fertilization ($p < 0.001$, Table 2). No effect of rotation, weed community harmfulness (Fig. 5a,b), or species richness on rice yield was revealed.

Under low fertilization, rice yield was significantly lower in rice monoculture (RR = 2.4 t ha^{-1}) than the rotation with a legume mixture (RVC = 4.3 t ha^{-1}; $p < 0.001$), while rotations with cereal-legume mixture or groundnut had intermediate yields (RSC = 3.3 and RG = 3.2 t ha^{-1}, Table S5). Moreover, rice yield significantly decreased over the years, rice yield being the highest in year 2 (3.47 t ha^{-1}) and the lowest in year 4 (2.66 t ha^{-1}; $p < 0.05$), year 3 being similar to both

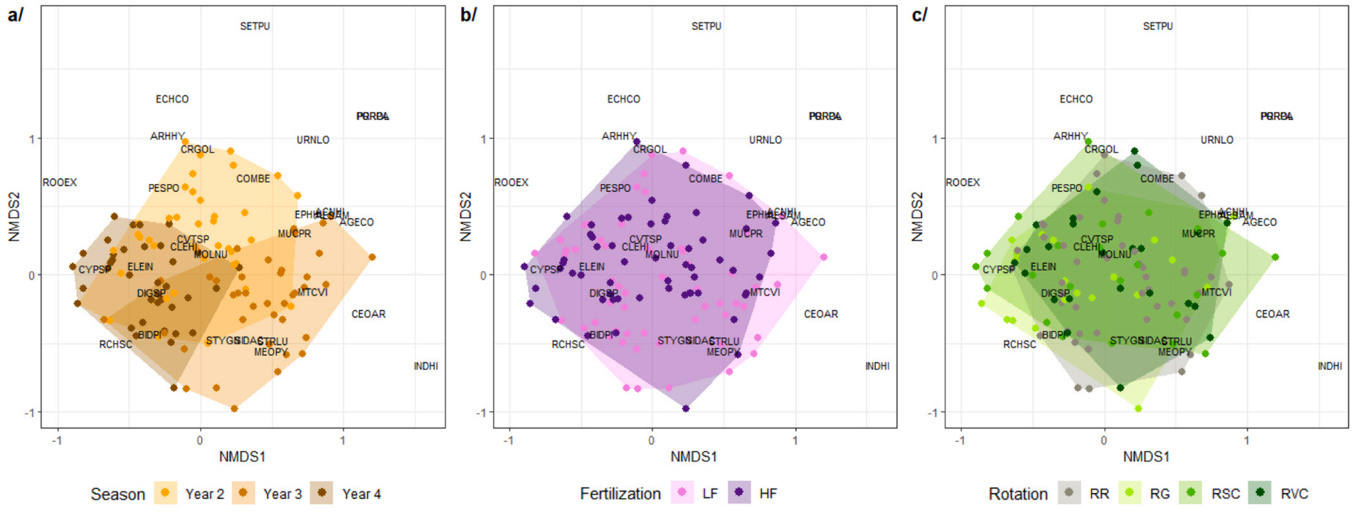

Fig. 2. Non-metric multidimensional scaling (NMDS) showing the variability in weed community composition in the sampled plots (dots in the diagrams) projected on the first two ordination dimensions. Colored polygons delimitate the variability in weed community composition for the different levels of the experimental factors (year (a), fertilization (b) and rotation (c)). Year 2 = orange, year 3 = brown, year 4 = dark brown; low fertilization level (LF = 5 tDM ha^{-1} of organic manure) = pink, high fertilization level (HF = LF + 400 kg ha^{-1} NPK (11/22/16) + 200 kg ha^{-1} urea) = violet; Rice monoculture (RR) = grey, rotation of Rice followed by Groundnut (RG) = light green, rotation of Rice followed by a Sorghum-Cowpea mixture (RSC) = green, rotation of Rice followed by a Velvet bean - Crotalaria mixture (RVC) = dark green. Species are projected and indicated with EPPO codes (see Table 1 for species full names).

Table 3
Results from the adonis procedure to test the effect of rotation, fertilization, year and their interactions on the weed community composition over the experiment.

Factors	Degree of freedom	Sum of Squares	R^2	F	p-value
Residual	96	9.97	0.52		
Rotation	**3**	**1.16**	**0.06**	***3.721***	***0.001***
Fertilization	**1**	**0.52**	**0.03**	***4.994***	***0.001***
Year	**2**	**5.26**	**0.28**	***25.336***	***0.001***
Fertilization * Year	2	0.33	0.02	1.579	0.108
Fertilization * Rotation	3	0.49	0.03	1.585	0.077
Rotation * Year	6	0.61	0.03	0.986	0.514
Rotation * year * Fertilization	6	0.78	0.04	1.254	0.177

Significant effects are indicated in bold.

(3.07 t ha^{-1}; $p > 0.05$; Table S5). Under high fertilization, rice yield under rice monoculture and the rotation with a cereal-legume mixture was significantly lower (RR = 5.58 and RSC = 5.37 t ha^{-1} respectively, $p < 0.01$) than under the rotation with a legume mixture (RVC = 7.27 t ha^{-1}; Table S5). In addition, the rice yield of each year significantly differed from each other (year 2 or 3 *vs*. year 4, $p < 0.001$; year 2 *vs*. year 3, $p < 0.05$). The ranking of the rice yield was the following: year 4 (6.9 t ha^{-1}) > year 2 (5.8 t ha^{-1}) > year 3 (5.3 t ha^{1}). At last, we observed that rice yield decreased significantly with increasing weed biomass under low fertilization ($p < 0.001$, R^2=0.21, Fig. 5c) while no trend was detected under higher fertilization (Fig. 5d).

4. Discussion

Our main objective was to assess whether rice-based crop rotations could regulate weeds, mitigate their impact on rice yield under rainfed conditions, and determine if this is affected by fertilization regime. Our results showed that rotation and fertilization both affect weed composition, diversity and biomass, and that weed biomass has the strongest negative impact on rice yield.

4.1. *Contrasting effects of years and management practices on weeds*

Weed communities are shaped by the interaction between environmental factors, resource availability, and crop management. In this experiment, the composition of weed communities was primarily determined by the year and most probably by the variations in annual rainfall and temperature patterns. Weeds are highly responsive to short-term weather conditions and can therefore compete strongly with crops (Patterson, 1995). Here, we identified eight species particularly associated with years, among which six were broadleaved species. Some studies indicated that broadleaved species could be promoted by alternation in wet and dry periods, which is currently observed in tropical regions (Huxley and Turk, 1966). For instance, some species, like *Bidens pilosa* or *Richardia scabra*, are known to be able to germinate relatively easily under light, disturbed conditions, or poorly fertile soils (Fenner, 1980; Mhlanga et al., 2015). Another reason for year-to-year variation in species composition can be explained by the stochasticity of weed emergence (Perronne et al., 2015), which complicates predictions of weed community dynamics, especially under tropical conditions where climate and weather are less seasonalized than under temperate climates, promoting more randomness. Besides the effect of year, rotation and fertilization level had only little effect on weed species composition, explaining less than 10 % of the variability observed. This result is not very surprising since crop management did not differ between rotations and the rice monoculture in our study, with similar timing for the different management practices (tillage, sowing, weeding). Indeed, the cropping season is restricted to the rainy season in each case, and only a few crop sequences (two-year rotation) have been tested. Nevertheless, we showed that the legume polycultures (RVC) transformed weed communities more than the other rotations we tested. The differences were modest due to the persistence/ regeneration of *M. pruriens* and *C. spectabilis* in the following rice crop cycle.

Similar to the results for the weed community composition, the magnitude of the effect of rotation on weed biomass strongly depended on the rotation crops, and a significant decrease was only observed in the rotation that included a legume mixture (RVC). This aligns with studies highlighting the importance of crop identity when proposing crop rotations (Mhlanga et al., 2015; Smith and Gross, 2007). This variation of weed control efficiency could be explained mainly by the ability of the rotation crops to compete with weeds for light and

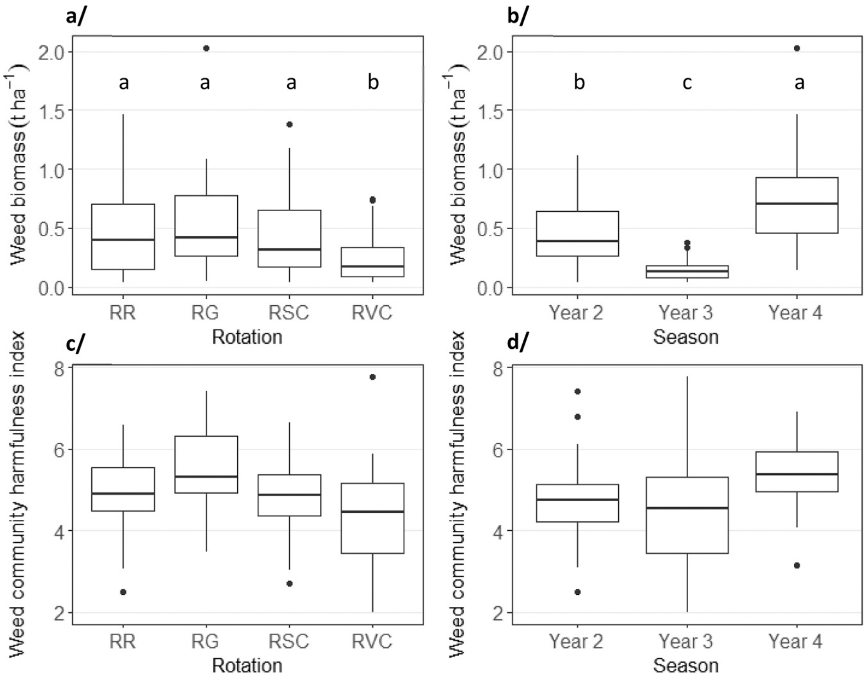

Fig. 3. Rotation and year effect on total weed biomass (t ha^{-1}, a and b respectively) and weed community harmfulness index (c and d respectively).RR = Rice monoculture, RG = Rice followed by Groundnut, RSC = Rice followed by a Sorghum-Cowpea mixture and RVC = Rice followed by a Velvet bean - Crotalaria mixture. Different lowercase letters indicate significant differences between treatments.

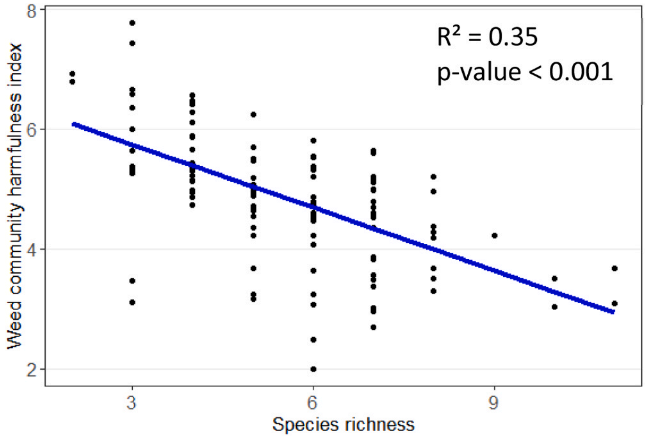

Fig. 4. Correlation between weed community harmfulness index and species richness pooled for the three years of the experiment. Bold blue line indicates a significant negative relationship between weed community harmfulness and species richness with R^2 and its level of significance.

nutrients during their cropping cycle, thus affecting germination and growth conditions for weeds (Liebman and Dyck, 1993; Smith and Gross, 2007). Indeed, legumes in the mixture were chosen for their complementarity of growth habit and to produce biomass, based on the assumption that the higher the crop biomass, the lower the weed one. The legume mixture achieved the highest biomass until 8 t ha^{-1}, which was up to 2–5 times more than groundnut or the cereal-legume mixture on this study site (Ranaivoson et al., 2022). Furthermore, this suppressive effect on weeds may have been combined with a legacy effect of the legume mixture residues buried in the soil prior to rice sowing, this green manure then benefiting the rice growth cycle as shown on the same study site (Ranaivoson et al., 2022; Ripoche et al., 2021). This may have limited the growth of competitive weed species with rice such as *Digitaria sp.* and *Eleusine indica*.

Management practices' effect on weed diversity was also relatively weak as species richness only differed between rice monoculture and the rotation, with only one additional legume species, and only under high fertilization or during the second year of the experiment. More surprisingly, species richness was the highest under monoculture in this case. Various studies showed that rotation may increase weed diversity (Liebman and Dyck, 1993; Storkey and Neve, 2018). This effect is mainly explained by the number of crop sequences or alternations between crops during the rotation (Neyret et al., 2020; Weisberger et al., 2019), which in our case were very low. As for weed composition, we may argue that the short duration of our rotation, the similarity of crop management, and the short duration of the experiment (two entire rotation cycles) have limited the impact of filters that weed management practices have on weed species. This may have delayed a potential rotation effect on the richness (Bàrberi et al., 1997; Fried et al., 2019) on an abundant weed seedbank (Ranaivoson et al., 2018). This could also explain the presence of perennials among the most abundant species in all treatments, favored by few disturbances in the cropping systems but not particularly selected by any factors (year, rotation or fertilization) as observed for example in cropping systems under conservation agriculture (Derrouch et al., 2021).

4.2. Rice yield and weed community harmfulness

As expected, weed biomass was a significant determinant of rice grain yield. Weed biomass is a better predictor of yield loss than weed density because it relates more accurately to the ability of the weed community to compete with crops (Colbach and Cordeau, 2018; Milberg and Hallgren, 2004). Moreover, different patterns were observed according to the level of fertilization. An increased weed biomass decreased rice yield under low fertilization levels, while no trend was detected with a high nutrient supply. Under high fertilization, we may suppose that rice and weeds to grow, which limited the competition between them. Moreover, given the fact that weed biomass did not increase in this case, rice more than weeds may have benefited from the nutrients supply (fertilizers and mineralization of the residues from previous crop cycle buried before sowing; Ripoche et al., 2021). Consequently, rice may have out-competed weeds, leading to high rice

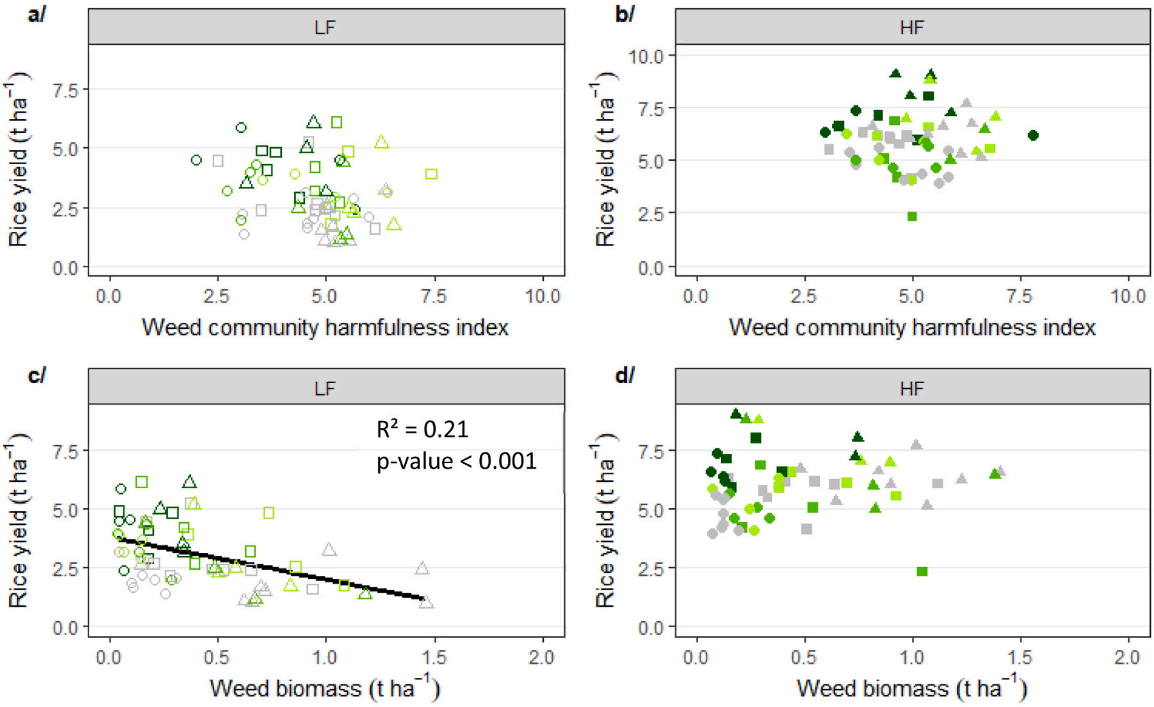

Fig. 5. Correlation between rice yield (t ha^{-1}) and weed community harmfulness index (a, b) and weed biomass (t ha^{-1}, c, d) under low (a, c) and high (b, d) fertilization for the four rotations over the years 2–4 of the experiment. Bold line indicates a significant negative relationship between rice yield and weed biomass with R^2 and its level of significance. RR = Rice monoculture (grey), RG = Rice followed by Groundnut (light green), RSC = Rice followed by a Sorghum-Cowpea mixture (green), RVC = Rice followed by a Velvet bean - Crotalaria mixture (dark green). LF (low fertilization level) = 5 tDM ha^{-1} of organic manure (empty symbols), HF (high fertilization level) = LF + 400 kg ha^{-1} NPK (11/22/16) + 200 kg ha^{-1} urea (filled symbols). Year 2 = □, Year 3 = ○, Year 4 = Δ.

grain yields (until 8 t ha^{-1}), close to the potential of the cultivar used. Furthermore, organic and mineral fertilizer were applied in the hole drilled for the rice seed, and was therefore directly available for the rice crop, but not for the weeds in the inter and intra row space.

In line with what was observed by Adeux et al. (2019), the harmfulness of weed communities was negatively correlated to species richness. However, no clear links appeared between weed community harmfulness and rice yield in our study, and a more diversified weed community under rice monoculture did not mitigate yield losses and led to the lowest rice grain yields. Several hypotheses may explain that. First, the weed harmfulness assessment was based on an *ex-situ* farmers' survey, gathering their knowledge and perception of the weed species. Second, there may be selection effects: the most diverse communities in rice monoculture were more likely to host at least one highly competitive species. Third, this harmfulness assessment included the most common weeds observed in the study area, but not all the most abundant at our study site. Consequently, it could lead to an important bias, under- or over-estimating harmfulness at both levels, species, and community, and this may explain the lack of significant differences between rotations, fertilization or year.

Currently, harmfulness at the species level remains poorly studied and frequently focused on the most aggressive species, aiming to define some thresholds to implement weed control practices (Colbach et al., 2020). Yet, characterizing weed harmfulness more precisely, for example, taking into account for the strategies weeds may have to compete for resources and their dynamics at individual and community level, will help to develop management strategies to suppress them (Ferrero et al., 2017) or alternatively, to promote 'neutral weed communities' (Esposito et al., 2023), at least "acceptable weed communities" with an intermediary competition level. Indeed, even if management practices like crop and, more generally, plant diversification are highly valued to enhance ecological processes and ecosystem functions and services in agroecosystems, optimal conditions are not always achievable, particularly for farmers working on low-inputs cropping systems (soil nutrients availability, access to seeds, human resources or mechanization, technical advice, etc.). Improving our knowledge of weeds and their potential harmfulness according to farmers' constraints, objectives and local context (practices, climate, …), could contribute to the promotion of adaptive weed management limiting yield losses, particularly in tropical contexts where too little is known and farmers' expectations considering weed management are high.

5. Conclusion

In low-input cropping systems in Malagasy highlands, weeds are a major threat, and crop diversification appears to be a pivotal component in regulating weed infestation and improving crop production. Our study showed that short rotations, including crop mixtures, slightly modified the weed communities in the Malagasy production context, where climate and stochastic events probably interfered with the management practices. Weed composition, diversity, and biomass were little affected by rotation or fertilization, at least on the short term. Effectiveness of rotation appeared to depend highly on crop species. The rotation that included a legume mixture was the most efficient to reduce weed infestation. Interestingly, weed biomass increase did not reduce rice yield under high but localized fertilization, indicating that an adequate nutrient supply, applied near the rice seed, combined with crop diversification could enhance crop production in the challenging conditions of rainfed rice production. Despite a link between weed harmfulness and species richness, the farmers' perception of weed harmfulness was not reflected in crop yield reduction in this study. Much work remains to be done to assess properly weed communities' response to cropping practices and their harmfulness on crop production, this contributing to propose adapted cropping systems supporting smallholder farmers in these regions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109136.

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