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Assessing weed impacts in tropical cropping systems through a functional trait-based approach : a case study on sugarcane

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ABSTRACT

Context: Yield losses due to weeds arise from competition for light, water, and nutrients. Beyond abundance, weed impact could also depend on their resource acquisition strategies. This study aims to evaluate how different weed species, characterized by distinct functional traits, may affect sugarcane agronomic performances under varying environmental and management conditions.

Methods: Two field trials were conducted in Réunion Island (2021 – 2023) under contrasting irrigation and fertilization conditions. Different weed management treatments (unweeded, fully weeded, and selectively weeded) leading to distinct weed communities dominated by climbers, perennials, grasses, or small dicotyledons were compared. Sugarcane growth and yield, and weed ground cover were measured over both cropping seasons. Dominant weed species were characterized by functional traits related to competition for resources. Linear mixed models assessed treatment effects while multivariate analyses (PCA, clustering, RLQ and fourth-corner) were used to group species by traits and link them to crop performance.

Results: Reduction of sugarcane biomass and stem density was related to weeds to an extent that varied by year and selected weed communities. Weed cover alone did not explain sugarcane biomass reduction. Trait-based groups revealed that climbers exhibited leaf acquisitive and root conservative traits, while dicotyledons showed the opposite pattern. Sugarcane biomass reduction seems mainly related to Climbers due to leaf acquisitive traits under high-input conditions and small dicotyledons due to root acquisitive traits under low-input conditions.

Conclusions: These results provide insights into how weed harmfulness may be linked to species-specific strategies and may vary depending on the environmental context, supporting the idea of more targeted, trait-informed weed management strategies in cropping systems.

1. Introduction

Herbicides are the most widely used pesticides globally, accounting for over 50% of pesticide applications (FAO, 2024). This heavy reliance reflects the significant challenge posed by weeds, which are responsible for the greatest yield losses among biotic constraints (Oerke, 2006). The

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problem is particularly severe in tropical environments, where weeds can grow rapidly all year round and may cause yield losses ranging from 20% to over 50% (Marnotte and Le Bourgeois, 2018; Oerke, 2006). In Reunion Island, this is particularly relevant to sugarcane cultivation, where weeds represent the main biotic constraint and are considered a major threat by industry stakeholders (DAAF La Réunion, 2016a; Martin et al., 2012b). In contrast, other pests and diseases cause relatively minor damages, as they are effectively controlled through biological treatments (e.g., *Hoplochelus marginalis* white grubs control) or mitigated by the development of resistant crop varieties for diseases (Antoir et al., 2016; DAAF La Réunion, 2016b). In France and the French overseas departments and territories (DOM-TOM), the number of herbicides legally available for use on sugarcane has been continuously declining in the last ten years (ANSES, 2023). Non-chemical alternatives exist, but their use is more constraining to farmers: manual weeding is effective but costly and arduous, mechanical weeding faces terrain challenges (steep slopes and rocky terrain) (Chetty et al., 2023), and cover crops remain under study with inconsistent results (Soulé et al., 2024). Consequently, weeds will become harder to control.

Within the flora on sugarcane fields in Reunion Island, some specific weed groups are recognized as being particularly problematic: species with a climbing growth habit - which can climb on the stems and cause physical constraints - (Martin et al., 2012b), and tall grasses - which are perceived to compete strongly and reduce yield - (Le Bourgeois et al., 2004). Although little studied in the context of Reunion Island, perennial weeds are also often highlighted in the scientific literature as being particularly harmful in organic no-till systems in temperate climates (Andert et al., 2023; Turner et al., 2007). With the current search for herbicide alternatives, these species may also represent a potential challenge in Reunion Island's cropping systems. These growth habits define weed groups expected to differ in competitive potential, reflecting differences in their ability to compete with the crop.

The negative impact of weeds mainly stems from their sharing the same trophic resource pool with crops: light, water, and nutrients (Colbach et al., 2023). At the scale of the agroecosystem, limiting resources lead to competition among plants and, thus, between crops and weeds, resulting in yield losses (Caussanel, 1989; Colbach et al., 2020). The competitive effect of the weed community depends on the traits and strategies of the individual plants within it. Each weed species, and each individual, contributes to the overall level of competition with the crop. At the individual plant scale, trade-offs in resource allocation between growth and reproduction occur and can vary among species and environmental contexts. Analysing these trade-offs a species makes in different contexts reflects its strategy for maintaining itself in a competitive context (Reich, 2014; Westoby, 1998). For example, Wright et al. (2004) highlighted the "leaf economic spectrum" theory, which demonstrates a fundamental trade-off between rapid acquisition and efficient conservation of resources in the aboveground parts. Similarly, Roumet et al. (2016) demonstrated a "root economic spectrum" associated with the belowground parts. The functional approach allows these trade-offs to be described with a combination of functional traits, i.e., any morphological, physiological, or phenological characteristic measurable at the individual level and significantly influencing the plant fitness indirectly via its effect on growth, reproduction, and survival (Violle et al., 2007). The combination of trait values observed in a given context enables the comparison of multiple species within that context (Garnier and Navas, 2013; Lavorel et al., 1997). As an example, Wright et al. (2004) associated plants with acquisition strategies at the leaf level with high values of specific leaf area (SLA), allowing an increased light interception area for a given leaf biomass and low leaf dry matter content (LDMC), indicating low resource conservation within leaf tissues and the mobilization of these nutrients for leaf growth. Roumet et al. (2016) associated plants with an acquisitive root strategy with high specific root length (SRL) and small root diameter (RD), increasing root water uptake capacity. Conversely, species with conservative strategies could be characterized by opposite combinations of these trait values. Reich (2014) also showed that this "fast-slow" (or acquisitive - conservative) economic spectrum could be extended to the whole plant, linking leaf and root strategies into a single integrated strategy. Assessing plant traits to characterize resource exploitation strategies of a species thus helps to evaluate its competitive potential, with acquisitive strategies likely being more competitive (Bourgeois et al., 2019).

Understanding how these strategies vary among weed species and weed functional groups is crucial to assess their behaviour and effects on crop production. It could help define better weed management priorities and the solutions best suited to each context, contributing to reduce the use of herbicides while avoiding yield losses due to weed competition with the crop. However, most studies assessing weed impacts on crops rely on abundance-based metrics - weed density, ground cover, or biomass - (Cordeau et al., 2018; Oerke, 2006; Ripoche et al., 2024) and rarely consider the functional characteristics of weed species that determine how they acquire and use resources. Functional trait approach has recently been applied to crop–weed interactions in agroecosystems (Martin and Isaac, 2015; Navas, 2012; Romillac et al., 2023), focusing mainly on crops grown in temperate climates, while tropical cropping systems remain poorly documented (Damour et al., 2015). In Reunion Island, weed communities are relatively well described in terms of taxonomic diversity, but their ecological behaviour and functional characteristics remain largely unexplored (Le Bourgeois et al., 2022, 2004; Marnotte and Le Bourgeois, 2018).

The objectives of this study were to (i) assess the response of sugarcane yield to different weed communities, (ii) associate weed species or weed functional groups into strategies based on their functional traits related to the competition for resources, and (iii) link these strategies to effects on sugarcane yields. We hypothesized that (i) different weed groups defined according to their clade, growth habit, and life cycle would exhibit consistent functional trait patterns at the leaf and root levels, reflecting different strategies for resource acquisition and use, and that (ii) these weed groups would have different effects on sugarcane growth and yield, partly explained by their functional traits and associated resource strategies, rather than by their abundance.

To achieve these objectives, we performed two independent field trials on Reunion Island between 2021 and 2023. While the water and nutrients provided differed between the two trials, the goal was to investigate how functional traits of naturally occurring weed communities affect sugarcane growth and yield in different conditions. In these trials, we artificially created different weed communities using weed control interventions (chemical and manual) to promote specific combinations of plant clades, growth habits, and biological cycles, thus considering four weed groups, i.e., "Small dicotyledons", "Climbers", "Grasses", and "Perennials". To assess the relationship between the functional characteristics of weeds and sugarcane production, we measured various functional traits on the most abundant weeds and sugarcane growth and yield variables.

2. Material and methods

2.1. Site and trials description

Field trials were conducted over two cropping seasons (2021–2022 and 2022–2023) at CIRAD's La Mare experimental station in Sainte-Marie in the north of Reunion Island (France) (20°54'10.80'' S, 55°31'51.60''W, 50 m a.s.l.). A first trial was planted in November 2021 and harvested in July 2022. A second trial was planted in December 2022 and harvested in August 2023 on an adjacent field in the same experimental site. Mean temperatures were similar over both trials, with 24.9°C in 2021–2022 and 24.6°C in 2022–2023. The first trial was drier than the second, with 1707 and 1276 mm of annual cumulative rainfall, respectively. The soil at the experimental site was a Hypereutric Nitisol according to the WRB classification (IUSS Working Group WRB, 2022) with the following properties down to 30 cm: soil pH 6.2, total N 1.86 g kg^{-1}, organic C 21.93 g kg^{-1}, total P 114.9 mg kg^{-1}, and CEC

11.89 cmol kg^{-1}. The soil texture was silt loam (17% clay, 55% silt, 28% sand; bulk density 1.16 g cm^{-3}).

Both trials consisted of three main treatments regarding weed control: 1) "totally weeded" where all weeds were totally suppressed (weeded as frequently as necessary), 2) "unweeded" where all weeds were left (no weeding at all), and 3) "selectively weeded" where weeds were selectively suppressed, with manual weedings. This latter treatment was subdivided into four sub-treatments corresponding to different combinations of the following criteria: plant clade (dicotyledonous *vs*. monocotyledonous), plant habit (climbing/twining *vs*. upright/spreading), and biological cycle (perennial with or without vegetative reproduction *vs*. annual), based on the traits from Reich et al. (2003) and expert knowledge about the weed harmfulness on sugarcane in Reunion Island (Antoir et al., 2016). We defined and named these sub-treatments, hereafter referred to as selected groups, as follows: "Small dicotyledons", "Climbers", "Grasses", and "Perennials" (Table S1). As an example, in Small dicotyledons plots, small dicotyledons species were left in the field and all other weeds were manually weeded. In the first trial, the "Grasses" sub-treatment was not included as no grasses were present in the field.

In both trials, the R579 sugarcane cultivar was planted in single rows, with an inter-row spacing of 1.5 m. The layout of both trials is illustrated in the supplementary materials (Fig. S1). In the first trial, the field was divided into three strips of four sugarcane rows each. Each strip corresponded to one of the three main treatments, i.e., unweeded, totally weeded, or selectively weeded. Each strip was divided into 12 plots of 7 × 4.5 m each, resulting in 12 plots per treatment, with four plots per weed group in the selectively weeded strip. Within each of these plots, a 3 × 3 m subplot was delimited for the sugarcane measurements. The same design was used in the second trial but with two blocks of three strips and seven plots in each strip, resulting in 14 plots per treatment. Four plots per weed group were set up in the selectively weeded strip except for "Grasses" for which only two plots were set up due to the low presence of grasses in the field. In addition, the plots (15 ×4.5 m) and subplots (6 ×3 m) were larger. In both trials, the plots for selectively weeded sub-treatments were located according to the observed weed flora in the field between two and three months after sugarcane planting. Each treatment plot was separated by one row and two inter-rows of sugarcane, serving as a partial buffer.

Several cropping practices differed between the two trials. The first trial was conducted to maximize sugarcane's advantage over weeds: irrigation, fertilization, and two weeding operations (an herbicide application one month after planting and a mechanical weeding in the inter-rows two months later in all treatments). In contrast, the second trial was conducted to minimize sugarcane's advantage over weeds: no irrigation, no fertilization, and no herbicide application after planting over the selective weeded and the unweeded treatments. In the first trial, sugarcane was irrigated three times per week using sprinklers operating in a full-coverage overhead irrigation system with in-line sprinkler spacing along the rows. Fertilization was applied on the row, with a first application at planting (192 kg N ha^{-1} and 312 kg P ha^{-1}) and a second in April (252 kg N ha^{-1} and 156 kg P ha^{-1}). Fertilization doses were determined to be non-limiting according to recommendations provided by the Serdaf software based on soil analysis (Versini et al., 2018). In both trials, selective weed groups were weeded manually approximately once a month, suppressing all the weeds not belonging to the selected group and taking care to minimize disturbance to the remaining weed flora. The totally weeded treatment was weeded chemically or mechanically, aiming to keep the weed ground cover below 5% as frequently as required, resulting in three operations in each trial. Chemical weeding was performed using selective herbicides for sugarcane, with a mixture of Dicopur 600 (2,4-D), Camix (bénoxacor, S-metolachlore, and mesotrione), Sencoral (metribuzin), and Merlin (isoxaflutole, cyprosulfamide).

2.2. Sugarcane measurements

The economic return to farmers of growing sugarcane depends on the harvested biomass of millable stalks, which is the predominant part of the overall aboveground biomass, and on the sugar content of these stalks. However, in this study, we focused only on aboveground dry biomass as a key indicator of sugar cane's response to environmental variation, especially since previous studies showed that weed pressure had very little influence on stalk sugar content (Christina et al., 2026). In both trials, sugarcane aboveground dry biomass (Mg ha^{-1} DM) was evaluated twice non-destructively, at four and six months after planting, through an allometric relationship linking the plant aboveground dry biomass to stem height, as proposed by (Poultney et al., 2020) in a context similar to that of our study. Aboveground dry biomass was also measured directly at harvest, *i.e.*, 8 – 9 months after planting. For the two non-destructive measurements, the height of each sugarcane stem and the total number of stems were recorded in all subplots of each strip. Stem density was then calculated as the number of stems per square metre. Sugarcane height was defined as the height of the terminal visible dewlap and was measured using a measuring tape mounted on a rigid pole to ensure vertical measurements in the field. At the same time, 30 sugarcane stems were taken outside the subplot in the totally weeded and unweeded treatments (15 from each treatment). The sugarcane height was measured for each stem, and the stems, green, and senescent leaves components were separated and oven-dried at 60°C until constant mass (approximately 72 h for the leaves and one week for the stems). Then, they were weighed using an electronic balance (OHAUS Pioneer, capacity 5200 g, readability 0.01 g) to establish the parameters of the allometric relationship for calculating sugarcane biomass from the height observed in the subplots. At harvest, the fresh sugarcane biomass was harvested by hand and weighed in each subplot using a portable field balance (OHAUS Valor 2000 W, model V22PWE15T, maximum capacity 15 000 g). A sample of three sugarcane stems was collected in each subplot, separated, and oven-dried similarly to the non-destructive measurements to determine the dry matter content and estimate the sugarcane aboveground dry mass of the subplot.

2.3. Weed community assessment and measurements of weed functional traits

The percentage of soil ground covered by each weed species was estimated in each subplot using a visual notation method according to a rating scale from 1 to 9 converted to 0–100% following Le Bourgeois et al. (2022) and Marnotte (1984) (see Supplementary Materials, Table S1). Total weed ground cover was also estimated. In these estimations, only weed species were considered, meaning that 100% ground cover refers exclusively to weeds and excludes sugarcane.

The major weed species were identified based on the first floristic surveys made four months after planting (Table 1) according to the following criteria: they should represent a cumulative 80% of the community in terms of cover (Pakeman and Quested, 2007), be present throughout more than half of the totally unweeded plots, and be present in the selectively weeded subplots corresponding to its group of weeds (Small dicotyledons, Climbers, Grasses, and Perennials). Among the 13 monitored species in each trial, eight were common in both trials (Table 1).

In the first trial, 12 individual plants per major species were randomly sampled in the different plots in the selectively weeded strip and 12 in the different plots in the totally weeded strip. In the second trial, the number of sampled plants per species was reduced to six, only randomly sampled in the different plots in the selectively weeded strips. All plants were sampled outside the subplots on which sugarcane and weed flora were monitored. In the first trial, all the individuals were sampled during the fifth month of sugarcane growth, a key phenological stage when sugarcane has a high need for resources, irrespective of weed stages. In the second trial, the weeds were sampled according to their

Table 1
Weed species observed in the selectively weeded and unweeded treatments in both trials and their mean ground cover (%). Species EPPO code and weed groups (Small dicotyledons = S.dicots, Climbers, Grasses, and Perennials) are indicated.

EPPO code	Species	Selected group	1st trial (2021-22)		2nd trial (2022-23)	
			Selectively weeded	Unweeded	Selectively weeded	Unweeded
AESAM	*Aeschynomene americana* L.	S.dicots	0.0	0.0	13.8	20.6
AMASS	*Amaranthus sp*	S.dicots	60.8	21.0	0.0	0.0
CLEVI	*Cleome viscosa* L.	S.dicots	6.6	6.9	13.9	9.1
DEDTO	*Desmodium tortuosum* (Sw.) DC.	S.dicots	15.2	10.5	26.5	39.5
DEMVI	*Desmanthus virgatus* (L.) Willd.	S.dicots	0.0	0.0	9.9	19.2
EPHHL	*Euphorbia heterophylla* L.	S.dicots	21.5	14.0	24.3	18.7
EPHHS	*Euphorbia hyssopifolia* L.	S.dicots	5.5	8.6	0.0	0.0
MIMPU	*Mimosa pudica* L.	S.dicots	11.7	6.7	0.0	0.0
PYLAM	*Phyllanthus amarus* Schumach. & Thonn.	S.dicots	8.8	11.5	5.2	3.0
PYLNO	*Phyllanthus niruroides* Müll.Arg.	S.dicots	7.1	6.4	0.0	0.0
CONAE	*Distimake aegyptius* (L.) A.R. Simões & Staples	Climbers	36.9	42.3	31.1	18.3
CRIMI	*Cardiospermum microcarpum* Kunth	Climbers	9.7	9.8	0.0	0.0
IPOTR	*Ipomoea triloba* L.	Climbers	22.4	17.2	12.0	10.7
MOMCH	*Momordica charantia* L.	Climbers	0.0	0.0	11.5	17.0
MUCPR	*Mucuna pruriens* (L.) DC.	Climbers	0.0	0.0	29.9	26.6
COMBE	*Commelina benghalensis* L.	Perennials	34.1	18.3	25.6	14.3
CYPRO	*Cyperus rotundus* L.	Perennials	16.1	9.0	11.9	7.0
ROOEX	*Rottboellia cochinchinensis* (Lour.) Clayton	Grasses	0.0	0.0	60.0	13.4

phenological stage at flowering (50–100% of the flowers in bloom). In both trials, sampling was conducted during the same period of the crop cycle and year.

Each major species was characterized by the three discrete traits (clade, plant habit, and biological cycle) and then assigned to one of four selectively weeded sub-treatments based on a combination of these traits (Table S1). Fourteen traits were measured on each individual plant (Table 2). They were selected based on the literature about strategies of resource acquisition and use (water, light, nitrogen; Fort et al., 2013; Gaba et al., 2017; Garnier and Navas, 2013; Perez-Harguindeguy et al., 2013; Tardy, 2015; Violle et al., 2009). All aboveground traits were measured following standardized protocols developed by Perez-Harguindeguy et al. (2013), and adapted based on the methodology of Fort et al. (2013). A root-system sample of each plant was extracted in the field with a spade from a cube of 25 × 25 × 25 cm. Roots were cleaned, sorted, scanned at a resolution of 600 dpi (Epson Perfection V850 Pro scanner), and analyzed via WinRHIZO™ software (Regent Instruments, Quebec, Canada) to measure the average root diameter (RD) and the specific root length (SRL), i.e., the ratio of root length to dry biomass of fine roots. They were then oven-dried for 72 h at 60°C and weighed - using a precision electronic balance under laboratory conditions (readability 0.001 g) - to calculate the root mass ratio (RMR), i.e., the ratio of root biomass to total plant biomass.

2.4. Data analysis

2.4.1. Effect of weed management treatment

The two trials were jointly analysed to assess the effects of weed management treatments (unweeded, selectively weeded, and totally weeded) on sugarcane dry biomass, stem density, and average height. Due to the lack of full randomization in the experimental design and the differences between trials, linear mixed models were used to account for both fixed treatment effects and the hierarchical structure of the data. These models allow testing the effects of weed management treatments over time while accounting for trial-specific conditions and spatial dependencies among observations. Trial, weed management treatment, and date were considered as fixed effects because they correspond to specific experimental conditions whose influence on sugarcane growth was explicitly assessed and they contain two and three levels respectively which is not enough to infer accurately a random effect variance. Because the experimental design was not fully randomized, strip and plot were included as random effects to partially account for spatial structure and reduce potential confounding effects, assuming normally distributed random effects. The statistical model is specified as the following linear mixed model:

$$Y_{ijklmn} = T_i + D_j + W_k + TD_{ij} + TW_{ik} + DW_{jk} + TWD_{ijk} + s_l + p_m + \varepsilon_{ijklmn}$$

Table 2
Mean trait values (± standard-errors) measured per weed species labelled with their EPPO codes (see Table 1) over the two trials (when present in both).

Trait	Definition	Unit	AESAM	AMASS	CLEVI	DEDTO	DEMVI	EPHHL	EPHHS	MIMPU	PYLAM	PYLNO	CONAE	CRIMI	IPOTR	MOMCH	MUCPR	COMBE	CYPRO	ROOEX
H	Plant height	cm	32.4 (± 17.9)	65.7 (± 18.6)	74.2 (± 33.2)	79.7 (± 26.1)	54.4 (± 10.8)	43.6 (± 18.8)	50.8 (± 18.4)	31.3 (± 17.1)	37.1 (± 10.2)	39.7 (± 16.2)	NaN (± NA)	43.2 (± 40.3)	175.3 (± 13.6)	NaN (± NA)	NaN (± NA)	62.9 (± 29.1)	29.9 (± 14.5)	85.5 (± 28.7)
LCC	Leaf carbon content	g 100 g^{-1} DM 60°C	42.9 (± 0.0)	36.2 (± 0.5)	44.0 (± 1.5)	42.5 (± 0.7)	44.0 (± 0.0)	42.6 (± 0.5)	45.2 (± 0.5)	47.0 (± 0.9)	45.3 (± 1.0)	46.1 (± 0.3)	40.4 (± 0.6)	43.1 (± 1.6)	42.3 (± 0.9)	41.7 (± 0.8)	44.3 (± 0.7)	38.8 (± 2.0)	40.7 (± 1.4)	37.8 (± 0.9)
LDMC	Leaf dry matter content[a]	g g^{-1}	0.29 (± 0.04)	0.23 (± 0.07)	0.11 (± 0.07)	0.27 (± 0.08)	0.37 (± 0.07)	0.24 (± 0.04)	0.31 (± 0.14)	0.15 (± 0.03)	0.25 (± 0.07)	0.21 (± 0.03)	0.11 (± 0.04)	0.22 (± 0.14)	0.14 (± 0.05)	0.19 (± 0.08)	0.21 (± 0.02)	0.14 (± 0.10)	0.14 (± 0.04)	0.29 (± 0.03)
LMF	Leaf mass fraction[b]	g g^{-1}	0.41 (± 0.07)	0.31 (± 0.07)	0.29 (± 0.18)	0.32 (± 0.13)	0.31 (± 0.04)	0.27 (± 0.13)	0.31 (± 0.09)	0.43 (± 0.05)	0.32 (± 0.08)	0.32 (± 0.06)	0.23 (± 0.11)	0.36 (± 0.18)	0.23 (± 0.11)	0.42 (± 0.18)	0.49 (± 0.05)	0.20 (± 0.08)	0.31 (± 0.20)	0.53 (± 0.10)
LNC	Leaf nitrogen content	g kg^{-1} DM 60°C	40.2 (± 0.0)	33.8 (± 3.2)	43.6 (± 4.8)	45.1 (± 4.8)	32.7 (± 0.0)	27.8 (± 3.9)	35.4 (± 4.1)	46.9 (± 4.9)	31.5 (± 7.1)	45.9 (± 6.0)	38.3 (± 11.6)	39.2 (± 6.8)	39.5 (± 5.0)	32.1 (± 3.9)	31.5 (± 2.0)	34.9 (± 9.0)	21.8 (± 5.0)	18.1 (± 2.3)
RD	Mean root diameter	mm	0.25 (± 0.03)	0.36 (± 0.08)	0.44 (± 0.19)	0.45 (± 0.15)	0.49 (± 0.12)	0.42 (± 0.15)	0.44 (± 0.13)	0.32 (± 0.05)	0.24 (± 0.07)	0.25 (± 0.05)	2.33 (± 0.95)	0.40 (± 0.19)	0.71 (± 0.28)	1.05 (± 0.32)	0.99 (± 0.32)	0.55 (± 0.07)	0.44 (± 0.11)	0.35 (± 0.08)
RMR	Root-mass ratio[c]	g g^{-1}	0.16 (± 0.07)	0.09 (± 0.04)	0.15 (± 0.03)	0.12 (± 0.07)	0.22 (± 0.05)	0.13 (± 0.05)	0.11 (± 0.03)	0.10 (± 0.03)	0.17 (± 0.09)	0.10 (± 0.02)	0.02 (± 0.01)	0.10 (± 0.06)	0.06 (± 0.04)	0.03 (± 0.02)	0.02 (± 0.02)	0.06 (± 0.05)	0.68 (± 0.21)	0.12 (± 0.05)
SCC	Stem carbon content	g 100 g^{-1} DM 60°C	43.1 (± 0.0)	35.2 (± 1.1)	44.4 (± 1.2)	43.2 (± 0.4)	44.4 (± 0.0)	40.0 (± 0.7)	44.4 (± 0.4)	43.1 (± 0.5)	43.0 (± 0.5)	41.6 (± 0.6)	40.8 (± 1.0)	42.7 (± 0.3)	42.5 (± 0.5)	42.1 (± 0.7)	43.6 (± 0.3)	33.2 (± 1.7)	NaN (± NA)	41.4 (± 0.5)
SLA	Specific leaf area	m^2 kg^{-1}	36.5 (± 7.2)	25.2 (± 8.0)	89.1 (± 67.8)	53.3 (± 23.2)	26.6 (± 3.3)	28.2 (± 7.0)	35.6 (± 11.0)	48.2 (± 9.8)	50.0 (± 13.4)	68.5 (± 16.9)	29.9 (± 9.3)	79.0 (± 19.8)	36.7 (± 5.3)	38.1 (± 8.4)	23.0 (± 3.3)	74.5 (± 49.9)	21.5 (± 8.5)	23.1 (± 2.6)
SNC	Stem nitrogen content	g kg^{-1} DM 60°C	16.5 (± 0.0)	14.9 (± 4.3)	8.7 (± 2.5)	10.0 (± 1.8)	7.9 (± 0.0)	10.3 (± 2.4)	10.0 (± 1.1)	17.8 (± 3.1)	11.7 (± 3.4)	21.3 (± 4.3)	13.6 (± 5.8)	15.8 (± 3.9)	10.2 (± 3.0)	13.8 (± 1.2)	12.0 (± 0.6)	18.8 (± 7.1)	NaN (± NA)	7.2 (± 1.8)
SRL	Specific root length[d]	m g^{-1}	75.6 (± 53.6)	8.3 (± 5.1)	21.3 (± 30.4)	10.8 (± 9.6)	7.7 (± 6.5)	46.1 (± 54.1)	9.6 (± 7.8)	18.1 (± 9.7)	54.1 (± 56.6)	49.6 (± 34.9)	1.1 (± 2.0)	22.8 (± 24.1)	6.6 (± 7.1)	2.8 (± 1.3)	1.8 (± 0.7)	23.7 (± 7.4)	8.9 (± 6.3)	28.9 (± 15.5)
TLA	Total leaf area	cm^2	41.4 (± 29.8)	502.3 (± 346.4)	371.3 (± 341.8)	531.0 (± 366.5)	141.5 (± 48.8)	76.4 (± 59.2)	88.1 (± 78.6)	174.8 (± 175.2)	63.8 (± 36.1)	73.8 (± 47.8)	22741.3 (± 16698.2)	225.6 (± 425.7)	3479.7 (± 2991.7)	9685.8 (± 7263.2)	77934.3 (± 48347.6)	2342.3 (± 2359.1)	29.2 (± 17.8)	390.5 (± 177.2)

[a] Oven-dry biomass of a leaf / water-saturated fresh biomass; [b] leaf dry mass / total plant dry biomass; [c] roots dry biomass / total plant dry biomass; [d] root length / dry biomass of fine root

Where Y is the response variable, T is the effect of trial, D is the effect of date, W is the effect of weed management treatment, TD the interaction effect of trial and date, TW is the interaction effect of trial and weed treatment, DW is the interaction effect of date and weed treatment, TDW is the interaction effect of trial, date and weed treatment, s is the effect of the strip, p is the effect of the plot and ε is the residual. The indices i, j, k, l and m are associated to the trial, date, weed treatment, strip and plot respectively. The index n is related to the observation.

To satisfy the assumptions of the linear mixed model, certain observations were excluded, and trial-specific weights were applied to account for residual variance heterogeneity between the two trials. The procedure was as follows: (i) fit an unweighted model with all observations and detect outliers using the quantile–quantile plot of residuals, (ii) refit the unweighted model after outlier removal, compute weights as the inverse of the trial-specific residual variances, and normalize the resulting weights to sum to the total number of observations, (iii) fit the weighted model, verify model assumptions, perform ANOVA, and obtain the estimated marginal means.

2.4.2. Effect of specific weeds (four selected groups)

The analysis of sub-treatment effects was conducted separately for each trial because the Grasses sub-treatment was not present in the first trial. For each trial, we used a linear mixed model in which date and weed sub-treatment were included as fixed effects. Because measurements were repeated over time within the same plots, plot was included as a random effect to account for the repeated-measures structure and the non-independence among observations. In practice, this model structure allowed testing differences between weed sub-treatments while partially accounting for temporal dependency within plots and variability among plots. The statistical model is given by:

$$Y_{jkmn} = D_j + W_k + DW_{jk} + p_m + \varepsilon_{jkmn}$$

Where Y is the response variable, D is the effect of date, W is the effect of weed sub-treatment, DW is the interaction effect of date and weed treatment, p is the effect of the plot and ε is the residual. The indices j, k, and m are associated to the date, weed sub-treatment and plot respectively. The index n is related to the observation. The plot effect has been considered as random effect following a Gaussian distribution. The Above Dry Biomass variable was transformed using the Box-Cox function (powerTransform function from car R package Fox et al., 2012) based on a Gaussian law to ensure residue normality.

Statistical analyses were performed using R software version 4.4.1 (R Core Team, 2024), linear mixed models were fitted using the lme4 package (*lmer* function of the *lme4* package; Bates et al., 2015), anova using lmerTest package (Kuznetsova et al., 2017) and estimated marginal means were computed using the emmeans package (*emmeans* R package, Lenth et al., 2024).

All statistical models' variance homogeneity and residual normality assumptions were checked graphically using histograms of residuals, quantile-quantile plots of Pearson's residuals *vs*. standardized Gaussian sample, plots of residuals against fitted values and statistical tests (Levene and Shapiro Wilk). The marginal and conditional R square of each model used were detailed in Table S3. Pairwise comparisons among treatments were performed using the *emmeans* function with a Sidak p adjustment method and a 0.05 probability threshold (*emmeans* R package, Lenth et al., 2024).

2.4.3. Weed species cluster

A principal component analysis (PCA) was performed on the weed trait values using the *FactomineR* package in R software version 4.4.1 (Lê et al., 2008) for each trial to cluster weed species with similar traits and analyse their strategies. The fourteen traits were introduced as quantitative variables, and two qualitative variables (species and selected group) were included as additional information variables. Then, a Hierarchical Principal Component Classification (HCPC) was performed to cluster species with similar trait values on the first five PCA dimensions. The number of dimensions was decided according to the Kaiser criteria and the explained variance distribution, searching for the breakpoint and cumulative variance between 70% and 90%.

RLQ and fourth-corner analyses were performed in each trial to analyse the link between weed functional traits and sugarcane growth indicators (aboveground dry biomass, stem height, and stem density) at the second biomass measurement, using the package *ade4* in R software version 4.4.1 (Chessel et al., 2004). These methods were initially used in ecology studies to link cropping practices of monitored fields (R matrix) to weed species traits (Q matrix) via weed species abundances observed in these same fields (L matrix). RLQ analyses consist of running a correspondence analysis on the L matrix (weed-species densities) to determine co-occurring weed species, followed by principal component analyses: one on the R matrix (cropping practices), weighted by the line weights of the correspondence analysis, and the other on the Q matrix (weed traits), weighted by the column weights of the correspondence analysis. Then, a fourth-corner analysis is run using the *fourthcorner* function (Dray et al., 2014) to establish Pearson correlation coefficients (and test their significance) between cropping practices and weed traits.

This method was adapted by Colbach et al. (2019) using weed-impact indicators on crop production (e.g., yield loss or field infestation) and biodiversity (e.g., trophic resources for bees) in the R matrix instead of the cropping practices, to link them to the most influential weed traits. Here, we applied the same method to link sugarcane growth indicators to the most influential weed traits. The R matrix contained the sugarcane-growth indicators: above dry biomass, average height and stem density (sugarcane indicators observed in plots). The L matrix included the maximal ground cover of each weed species in each plot from crop sowing to harvest. The Q matrix consisted of the functional traits of the 13 weed species averaged over all plots, and the three discrete traits in binary form: dicotyledonous clade, climbing plant habit, and perennial biological cycle were assigned a value of 1, with other traits assigned to 0. Then, the fourth-corner analysis was run to establish Pearson correlation coefficients between sugarcane yield components and weed species traits.

3. Results

3.1. Effect of treatments and selected weed groups on sugarcane growth

In the first trial, aboveground dry biomass differed between treatments, starting from the second measurement in May (Fig. 1a, Table 3). The lowest aboveground dry biomass was observed in the unweeded treatment, with −36.9% compared to the totally weeded treatment at harvest. In July, the selectively weeded treatment showed a lower biomass than the totally weeded treatment (–36.6%), but the difference was not significant. No differences in stem density or in stem height were found between treatments (Fig. 1b, Fig. 1c). Although not statistically significant, stem density tended to be lower under unweeded treatment (Fig. 1b).

In the second trial without irrigation or fertilization, sugarcane had a similar response but with a more pronounced decrease in aboveground dry biomass between the totally weeded treatment and the two other treatments (−94.8% and −68.7% in the unweeded and the selectively weeded treatments, respectively, at harvest). The same decrease was observed considering the sugarcane stem density at two months of measurement. Moreover, sugarcane stems were significantly smaller in the selectively weeded treatment than in the other two treatments at the second measurement date (Fig. 1f).

Sub-treatments within the selectively weeded treatments did not result in differences between sugarcane stem height but did result in significant differences in sugarcane aboveground dry biomass at harvest and stem density (Fig. 2, Table 4). In the first trial, no significant differences among sub-treatments were detected early in the crop cycle (March and May), but at harvest, aboveground dry biomass was

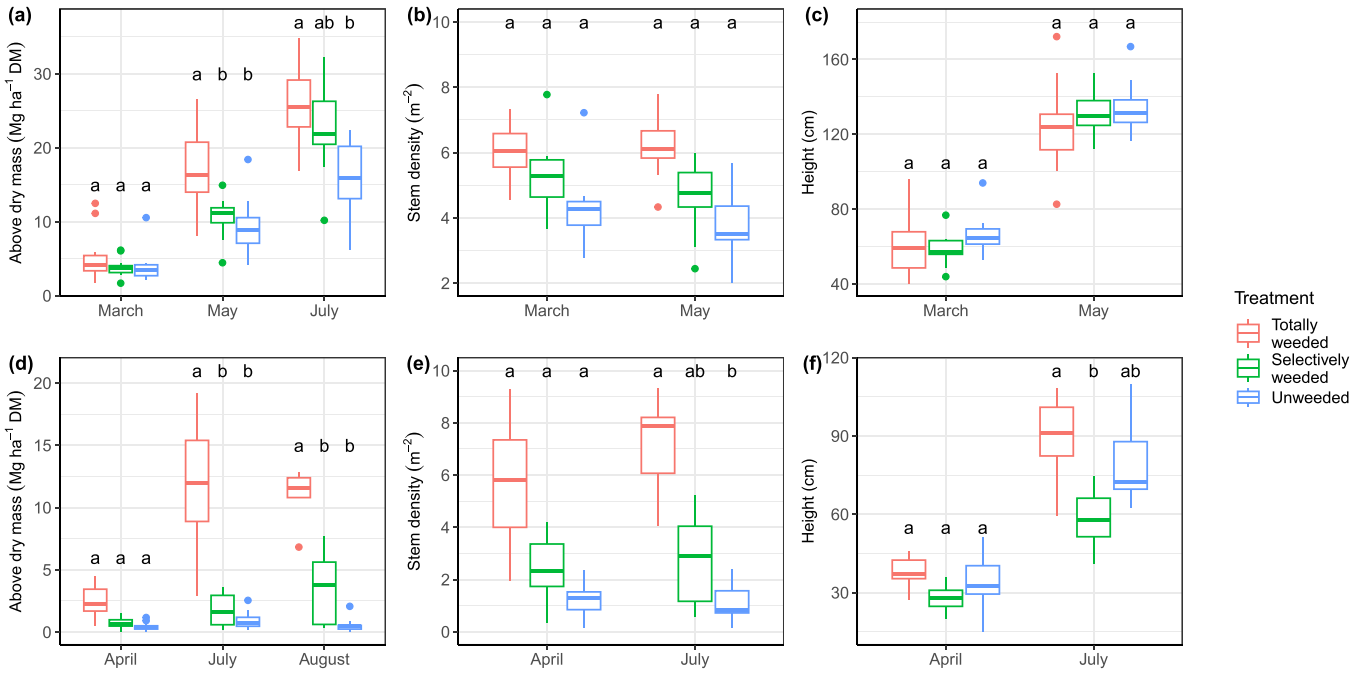


Fig. 1. Effect of weeding treatments on sugarcane aboveground dry biomass (Mg ha^{-1}), stem density (number of stems m^{-2}), and height (cm) depending on the month of measurement, during the first (a, b, c) and second trial (d, e, f). Boxplots show the median (thick line), interquartile range (box), range excluding extreme values (whiskers), and extreme values (dots). Letters indicate significant differences at $p = 0.05$ in the pairwise comparisons.

Table 3
Analysis of the effect of the trial, the treatment (unweeded, totally weeded, and selectively weeded), the measurement month and their interactions, on sugarcane aboveground dry biomass, height, and stem density, with associated F and p-values and marginal R_M^2 of the model. Details on conditional and marginal R^2 are given in Table S3.

	Aboveground dry biomass	Height	Stem density
Trial	$F = 45.003$ **$p < 0.001$**	$F = 80.582$ ***$p < 0.001$***	$F = 0.413$ $p = 0.565$
Treatment	*$F = 17.990$* **$p = 0.033$**	*$F = 2.357$* $p = 0.285$	$F = 4.912$ $p = 0.118$
Measurement month	*$F = 681.356$* ***$p < 0.001$***	*$F = 1893.428$* ***$p < 0.001$***	$F = 1.614$ $p = 0.207$
Trial: Treatment	*$F = 1.410$* $p = 0.389$	*$F = 5.148$* $p = 0.149$	$F = 2.367$ $p = 0.247$
Treatment: Measurement month	$F = 68.793$ ***$p < 0.001$***	$F = 1.488$ $p = 0.230$	$F = 21.063$ ***$p < 0.001$***
Trial: Measurement month	$F = 226.727$ ***$p < 0.001$***	$F = 99.358$ ***$p < 0.001$***	$F = 12.086$ ***$p < 0.001$***
Trial: Treatment: Measurement month	*$F = 5.372$* ***$p < 0.001$***	*$F = 14.085$* ***$p < 0.001$***	$F = 10.553$ ***$p < 0.001$***
R_M^2	0.891	0.901	0.637

significantly lower in the Climbers sub-treatment than in the Small dicotyledons sub-treatment (−30.6%, Fig. 2a). The stem density followed the same pattern, with a significantly lower stem density in the Climbers sub-treatment in May, compared to other groups (Fig. 2b). In the second trial, differences among sub-treatments were more pronounced, but the highest aboveground dry biomass was observed in the Perennials group and the lowest in the Small dicotyledons sub-treatment (−93.1% compared to Perennials, Fig. 2d). As in the first trial, stem density followed the same pattern as aboveground dry biomass, being significantly lower in the Small dicotyledons sub-treatment than in the Perennials sub-treatment (−77.3% in July, Fig. 2e). Stem height also followed a similar pattern, with significantly smaller height in the Small Dicots sub-treatment compared to the other sub-treatments.

3.2. *Weed ground cover variations across treatments and their correlation with sugarcane biomass*

The relative weed ground cover of treatments and sub-treatments were similarly ranked in both trials (Fig. 3). The unweeded treatment had a higher estimated weed ground cover than the selectively weeded one, while the totally weeded treatment had the lowest (close to 0%, Fig. 3a,c). The Small dicotyledons sub-treatment had a higher weed ground cover than the other sub-treatments, while Perennials had the lowest (Fig. 3b,d).

In the first trial, the weed cover in the unweeded treatment was dominated by a single species, *Distimake aegyptius* (L.) A.R. Simões & Staples (42.3%), with two relatively abundant other species: *Amaranthus sp.* (21%) and *Commelina benghalensis* L. (18.3%, Table 1). Conversely, in the second trial, weed composition in unweeded treatment plots was more diverse, with six species whose ground cover varied from 18% to 39.5%. In the selectively weeded treatment, the dominant species in the Small dicotyledons sub-treatment differed among trials. In the first trial, *Amaranthus sp.* (Table 1) dominated with 60.8% ground cover, with *Euphorbia heterophylla* L. less abundant. The composition was more balanced in the second trial, with *E. heterophylla* and *Desmodium tortuosum* (Sw.) DC. covering 26.5% and 24.3%, respectively. In the Climbers sub-treatment, the dominant species was *D. aegyptius* in both trials. However, the secondary species differed between trials: *Ipomoea triloba* L. in the first trial and *Mucuna pruriens* (L.) DC. in the second one. The perennial species were the same in both trials, with *C. benghalensis* and *Cyperus rotundus* L. being dominant. Finally, the Grasses sub-treatment in the second trial consisted of a single dominant species, *Rottboellia cochinchinensis* (Lour.) Clayton, with 60.0% of ground cover.

Variations of mean weed cover across the treatments were strongly related to the sugarcane biomass response (Fig. 4). More specifically, mean weed ground cover statistically explained 38% and 73% of the aboveground dry biomass variations in the first and the second trials,

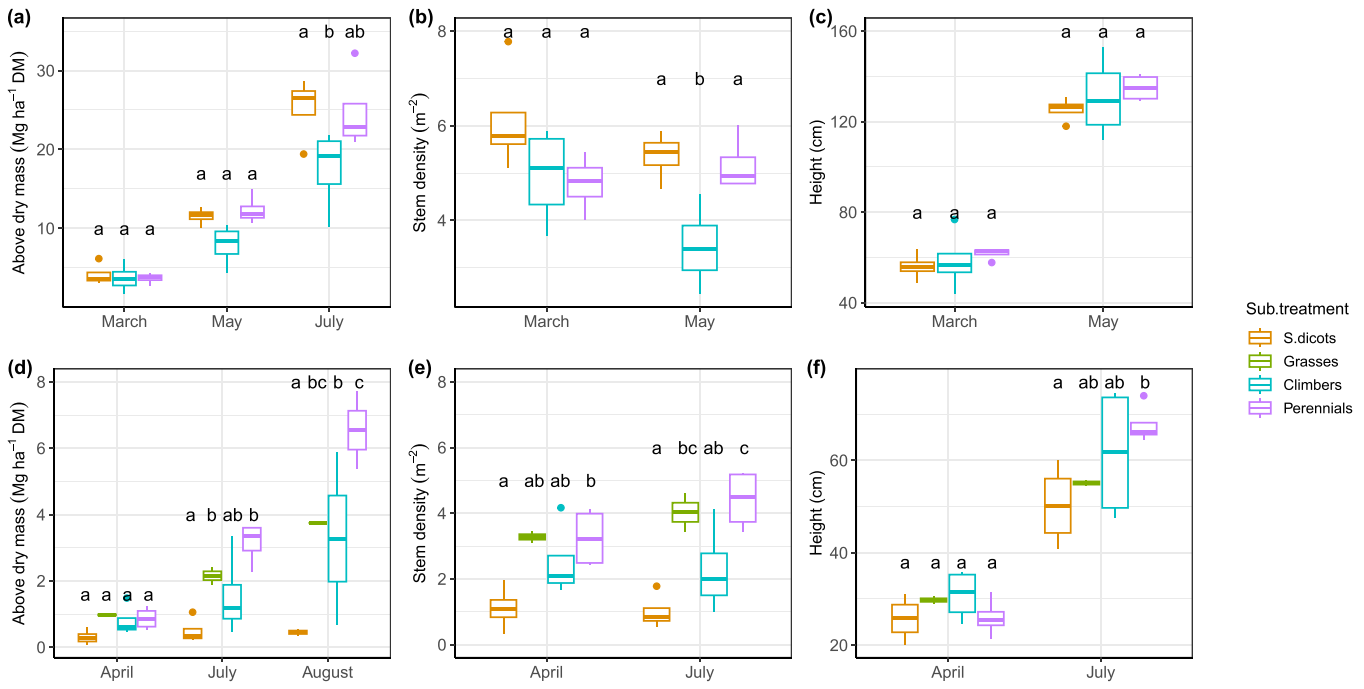


Fig. 2. Effect of selected weed groups (Small dicotyledons – S. dicots, Climbers, Grasses, and Perennials) on sugarcane aboveground dry biomass (Mg ha^{-1}), stem density (number of stems m^{-2}), and height (cm) depending on the month of measurement, during the first (a, b, c) and second trial (d, e, f). Boxplots show the median (thick line), interquartile range (box), range excluding extreme values (whiskers), and extreme values (dots). Letters indicate significant differences at $p = 0.05$ in the pairwise comparisons.

Table 4
Analysis of the effect of the sub-treatment (Small dicotyledons, Climbers, Grasses, and Perennials), in interaction with the measurement month on sugarcane stem density, height, and aboveground dry biomass, with associated F and p-values and marginal R_M^2 of the model. Details on conditional and marginal R^2 are given in Table S3.

	Aboveground dry biomass		Height		Stem density	
	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2
Sub-treatment	$F = 2.435$	$F = 8.828$	$F = 0.607$	$F = 1.354$	$F = 5.412$	$F = 8.234$
	$p = 0.1428$	$\mathbf{p = 0.003}$	$p = 0.566$	$p = 0.312$	$\mathbf{p = 0.029}$	$\mathbf{p = 0.005}$
Measurement month	$F = 525.411$	$F = 73.188$	$F = 2228.255$	$F = 397.239$	$F = 4.521$	$F = 4.035$
	$\mathbf{p < 0.001}$	$\mathbf{p < 0.001}$	$\mathbf{p < 0.001}$	$\mathbf{p < 0.001}$	$p = 0.062$	$p = 0.072$
Sub-treatment:	$F = 4.179$	$F = 7.319$	$F = 0.582$	$F = 7.594$	$F = 3.542$	$F = 3.452$
Measurement month	$\mathbf{p = 0.015}$	$\mathbf{p = 0.001}$	$p = 0.579$	$\mathbf{p = 0.006}$	$p = 0.073$	$p = 0.059$
R_M^2	0.888	0.714	0.929	0.834	0.491	0.631

respectively. In both trials, the sugarcane aboveground dry biomass significantly decreased with an increasing mean weed ground cover.

3.3. *Weed functional groups and competitive resource strategies*

The hierarchical clustering using the coordinates of PCA of each trial based on the trait values divided the weeds into groups with significantly different functional profiles. Four functional groups were formed in the first trial and five in the second. In both trials, some selected groups or species (Fig. 5b,e) were homogeneously clustered together (Fig. 5c,d, Table S4), indicating that cluster formation was not independent of the initial groups or species ($p < 0.001$).

In the first trial, the first two axes of the PCA explained 27.5 and 22.3% of weed trait variability (Fig. 5a). They represented two distinct gradients of functional traits, capturing major functional variations among weeds. The first PCA axis reflected a gradient along root diameter (RD), total leaf area (TLA), and height (H) (Fig. 5a, Fig. S2, S3). The root diameter (RD) was also positively correlated with the total leaf area (TLA) (Spearman correlation; $\rho = 0.69$) and the height (H) ($\rho = 0.48$) but negatively with the specific root length (SRL; $\rho = -0.85$). In other words, tall species also tended to have a large leaf area and thick roots. Some of the individual plants in the Climbers group (mainly *D. aegyptius* species) distributed along the right end of this first dimension (Fig. 5b) had these characteristics (high RD, TLA, and H values, Table 2), being more competitive for light acquisition than for soil water and nutrients uptake. All the *D. aegyptius* individuals were grouped in an isolated cluster (Cluster 4 in the first trial). The other species of the Climbers group (*I. triloba* and *Cardiospermum microcarpum* Kunth) were included in either cluster 1 or 2 (Fig. 5c, Table S4). Cluster 1 was located on the opposite lower part of this first dimension axis, composed mainly of individuals from the Small dicotyledons group and characterized by thinner roots (higher SRL and lower RD) and lower leaf area and height than the other clusters (Table S4).

The second PCA dimension represented a second trait gradient along the stem nitrogen content (SNC) and leaf nitrogen content (LNC). Conversely, this dimension was negatively correlated with the root biomass ratio (RMR). The group of Perennials was distributed almost exclusively along this gradient (Fig. 5b). However, the hierarchical classification divided this group into clusters 2 and 3 (Fig. 5c). Cluster 2 was composed mainly of individuals from *C. rotundus* and other species from the Small dicotyledons group (Table S4), characterized by higher mean RMR values and lower mean LNC values compared to the other

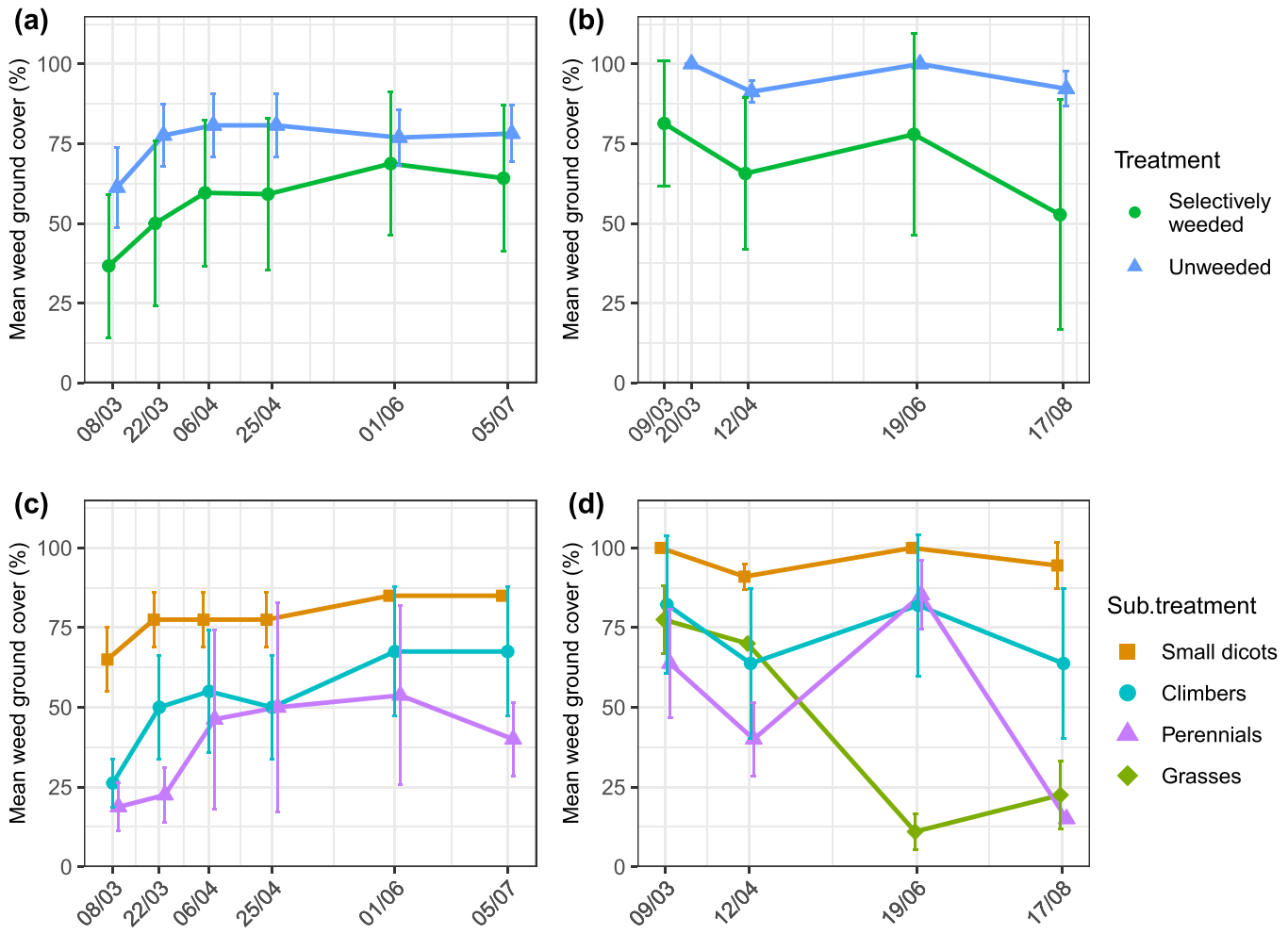


Fig. 3. Mean weed ground cover (%, error bars indicate standard errors) in the first (a, c) and second trial (b, d), depending on the treatments (selective weed control and unweeded; a, c) and sub-treatments (selected group: Small dicotyledons – S. dicots, Climbers, Grasses, and Perennials; b, d).

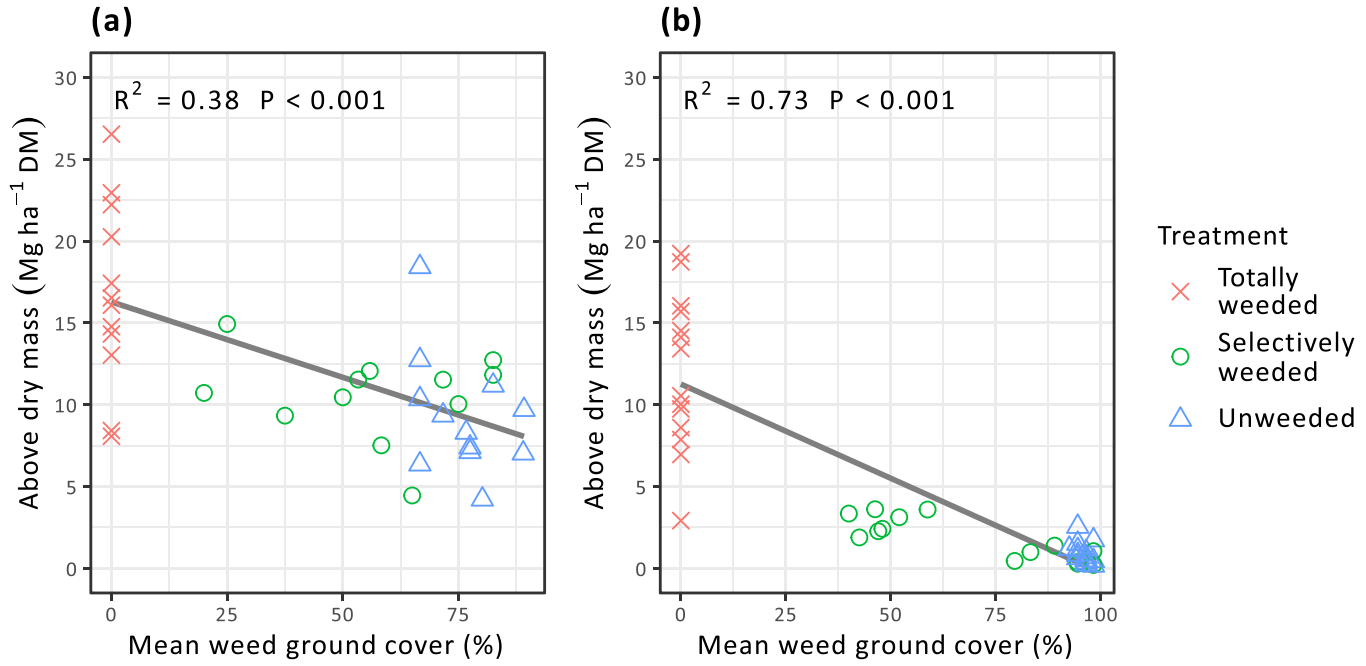


Fig. 4. Relationship between sugarcane aboveground dry biomass at the second measurement (Mg ha^{-1}) and mean weed ground cover (mean from the first weed measurement to harvest, %), differentiated by treatment (totally weeded, selective weed control, and unweeded), in the first trial (a) and second trial (b).

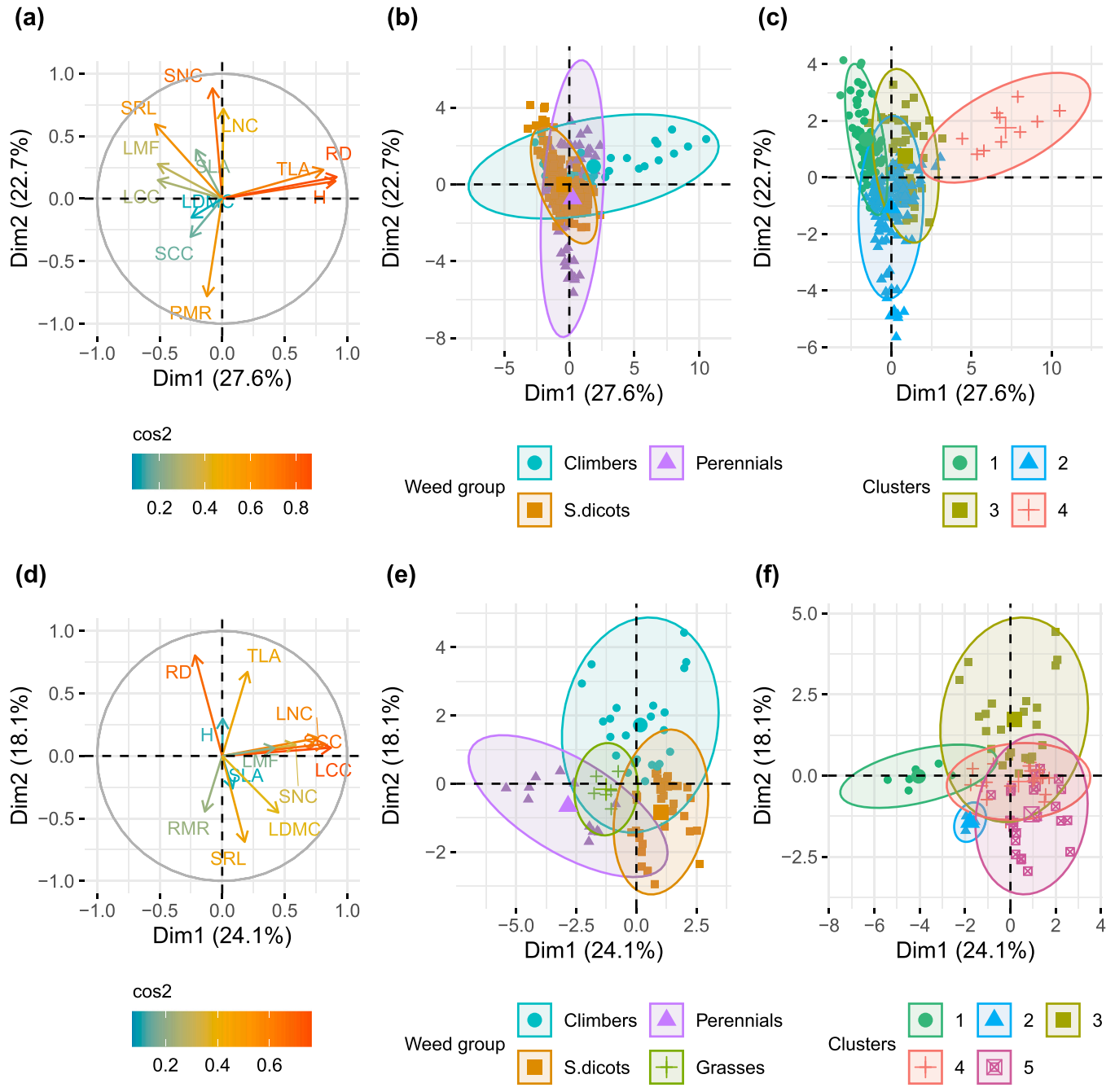


Fig. 5. Principal component analysis (PCA) performed on weeds traits values measured during the first (a, b, c) and second trial (d, e, f): (a, d) correlation circle between traits on the first two axes; (b, e) observations on the first two axes with the selected groups represented (Small dicotyledons - S. dicots, Climbers, Grasses, and Perennials); (c, f) observations on the first two axes with the new HCPC clustering analysis represented. Details on weed trait abbreviations are given in Table 2.

clusters. On the other side, cluster 3 was constituted by *C. benghalensis* (Perennials) and *Amaranthus sp.* (Small dicotyledons), characterized by lower RMR values than cluster 2 (Table 2, Table S4).

In the second trial, the same two trait gradients were observed in the first two PCA axes, explaining 24.1% and 18.1% of weed trait variances. Nonetheless, they were inverted compared to the first trial: TLA, RD, H, and SRL along the second-dimension axis; and leaf nitrogen content (LNC), leaf carbon content (LCC), stem nitrogen content (SCC) and stem nitrogen content (SNC) along the first-dimension axis (Fig. 5d). As in the first trial, most climber species also grouped in one cluster (cluster 3), with higher TLA and RD values and the lowest SRL values compared to the other clusters (Fig. 5e,f, Table S4). Conversely, cluster 5, located in the lower part of the second-dimension axis, included many Small dicotyledon species and was characterized by low RD and high SRL values. Cluster 5 was also characterized by higher values of LNC and SNC than the other clusters (Table S4). Individuals from the Perennials selected group were distributed along the low part of the first dimension axis and isolated in two clusters (clusters 1 and 2), splitting the *C. rotundus* and *C. benghalensis* species. These two clusters had the lowest mean values of LNC, LCC, SNC, and SCC (Table S4).

3.4. Weed traits and relation with sugarcane growth

For each trial, the RLQ analysis grouped weed species into clusters based on their abundance in plots (Fig. 6b,e). These clusters can be associated with dominant functional traits and sugarcane growth

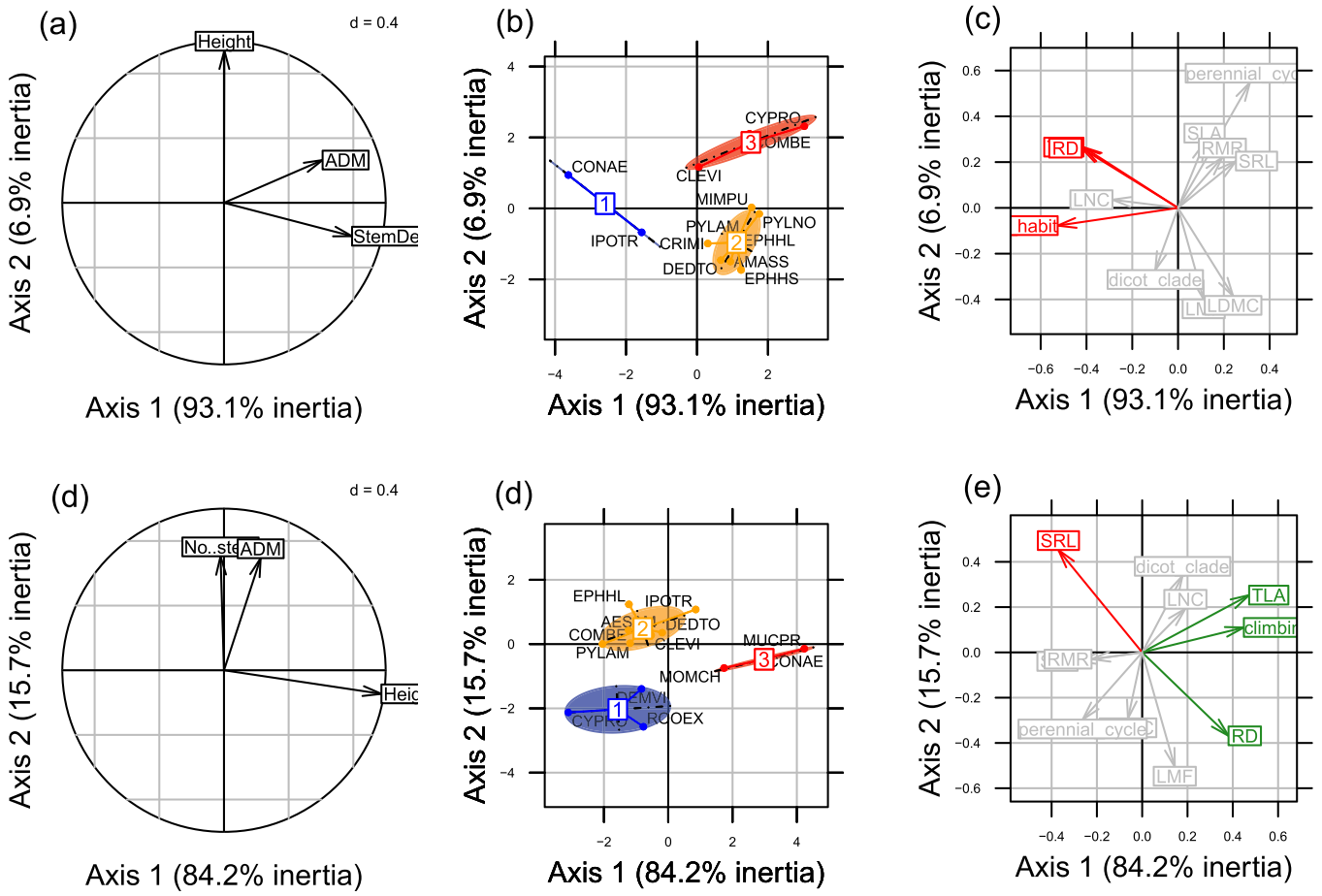


Fig. 6. Links between weed species (shown with EPPO codes, listed in Table 1), species traits, and sugarcane growth indicators (aboveground dry mass – ADM, Height and stem density – StemDens). Synthetic representation of the RLQ results with sugarcane aboveground dry biomass, height, and stem density as R matrix (a, d), maximum weed ground cover as L matrix (b, e), and values of weeds functional trait values (trait abbreviations in Table 2) as Q matrix (c, f), for the first (a, b, c) and second trial (d, e, f). Red and green arrows show negative and positive correlations between weed traits and sugarcane growth variables (aboveground dry biomass and stem density in trial 1, height in trial 2). Parameters in grey are not significantly correlated to sugarcane growth variables based on fourth-corner analysis (details in Supplementary materials Fig. S4).

indicators (aboveground dry biomass, number, and height of stems). The fourth-corner analysis tested the significance of the relationship between functional traits and sugarcane growth indicators.

In the first trial, weed species mainly differed regarding their relation with sugarcane aboveground dry biomass and stem density. The first axis captured the majority of the cross-variance between weed traits and sugarcane yield indicators (93.1% inertia; Fig. 6a). In contrast, the relation between weed traits and sugarcane height was low (6.9% of inertia, Fig. 6a). Three clusters of weed species were identified. Cluster 1, composed of two climber's species and located on the left side of the first axis, was associated with lower sugarcane aboveground dry biomass and stem density compared to the other two clusters (Fig. 6c). In addition, root diameter and total leaf area were negatively correlated with the aboveground sugarcane dry biomass and the stem density in the fourth-corner analysis ($p < 0.01$; Fig. S4). In other words, species like *D. aegyptius* and *I. triloba*, with thick roots and an important leaf area, tended to reduce sugarcane biomass and stem density.

In the second trial, the weed species mainly differed in their relation with sugarcane height, biomass, or stem density. The first RLQ axis, mainly correlated with sugarcane height, captured most of the cross-variance (84.2% inertia; Fig. 6d). Again, the biomass and stem density arrows were perpendicular to the height arrow, meaning that there was no systematic link between weed relation with sugarcane height on the one hand and weed relation with sugarcane biomass and density on the other hand. As in the first trial, the weed species were grouped into three clusters, and one of them (Cluster 3; Fig. 6f) included almost all Climbers species, except *I. triloba.* This cluster, positioned on the right side of the first-dimension axis, was associated with greater sugarcane height. Moreover, root diameter and total leaf area were significantly correlated with sugarcane height in the fourth corner analysis ($p < 0.01$; Fig. S4), meaning that the two weed traits linked with a reduction in sugarcane biomass and stem density in the first trial were associated with an increased sugarcane height in the second trial. Conversely, cluster 2 was located on the other side of the first-dimension axis and characterized by a high specific root length (SRL). This cluster was composed mainly of Small dicotyledon species and also of one Perennial species (*C. benghalensis*), and one Climber species (*I. triloba*) (Fig. 6f). The specific root length trait was significantly negatively correlated with the sugarcane stem height ($p < 0.01$; Fig. S4) meaning that species with thinner roots tended to reduce the sugarcane stem height.

4. Discussion

4.1. Study contributions

To our knowledge, this is the first study analyzing specifically functional traits of tropical weed species and the potential link with their harmfulness on crop production. The link between weed functional traits and crop growth impact has recently been investigated in temperate environments (Colbach et al., 2023, 2019). In tropical

cropping systems, most of the studies focused on the responses of weed communities to cropping systems or practices (Lal et al., 2014; Leon et al., 2017; Neyret et al., 2020; Ranaivoson et al., 2018) while weed harmfulness remains poorly documented (Rafenomanjato et al., 2023; Ripoche et al., 2024). Previous research on functional traits in tropical agrosystems mainly focused on characterizing traits of cover crop plants (Damour et al., 2014; Tardy et al., 2017, 2015) without directly linking them to their impact on crops.

Our study also jointly analyses weed leaf and root functional traits, which are usually studied separately in most weed functional trait studies (Reich et al., 2003). Very few studies have measured root functional traits under field conditions, primarily due to the lack of standardized protocols and the technical challenges associated with their implementation. Variations in root sampling methods across studies may also explain differences between our results and those reported in other studies (Tardy et al., 2017). Tardy et al. (2017) measured root diameter and specific root length (SRL) from three 10 × 10 × 10 cm soil cubes collected at different positions around each plant and subsequently pooled. In contrast, our study measured root traits from a single 25 × 25 × 25 cm soil cube centred at the base of each plant, without spatial replication. In addition, SRL in our study was calculated based on fine roots only, whereas Tardy et al. (2017) do not explicitly report such a distinction. These differences in sampling design and root fraction considered may contribute to variations in SRL and RD values.

Although the two trials differed in sampling strategy in this study —fixed at a given stage of sugarcane development in the first trial and at weed flowering in the second— the sampling were carried out during the same crop cycle and period (April–June, four to six months after planting), which helps limit potential biases. Moreover, trait analyses were performed separately for each trial rather than directly compared, thereby reducing risks of misinterpretation. As expected, greater variability in trait values was observed in Trial 1 than in Trial 2, but values in the two trials remained relatively consistent within species and weed groups as shown by cluster formation. Our results enrich this discussion by providing data and demonstrating that weed resource acquisition strategies cannot be considered independently of the specific conditions in which they are expressed.

4.2. Sugarcane response to weed treatment depending on environmental conditions

Our study highlights a decrease in aboveground sugarcane growth under an increasing weed pressure. These results may reflect the negative impact of weeds on sugarcane growth, as previously shown in various studies (Ibrahim, 1984; Marion and Marnotte, 1991; Suganthi et al., 2019). In line with previous studies (Ibrahim, 1984), tillering was the sugarcane growth phase most affected by weed occurrence, with a reduction in stem density early in the growth cycle. To a lesser extent, the reduction in sugarcane growth may also be linked to sugarcane height, but only in the second trial with no fertilizer inputs or herbicides. The difference in sugarcane biomass reduction between both trials may highlight the difference in sugarcane weed competition sensitivity depending on environmental conditions. Under non-limiting irrigation and fertilizer conditions (first trial), the competition between sugarcane and weeds may be less than under limiting conditions (second trial). This difference in sensitivity to limiting environmental conditions aligns with observations made on sugarcane intercropping systems (Viaud et al., 2023) and crop-weed interactions in many crops under increasing limiting conditions (Little et al., 2021). Adequate nutrients and water supply supports robust tillering and canopy expansion (Zhao et al., 2017), allowing sugarcane to out-compete weeds for light and space more effectively, creating an “asymmetric” competition situation between crop and weeds (Little et al., 2021).

Secondly, our study provides insights into the contrasting effects of different weed communities on sugarcane growth. Two main hypotheses may explain the differences in sugarcane responses to weeds observed in the selected weed groups. A first hypothesis could be that the higher the weed ground cover, the lower the sugarcane aboveground biomass, with weed ground cover representing a proxy of the competition exerted by weeds on the crop. Our results confirm the negative relationship between weed ground cover and sugarcane biomass, as observed in previous studies (Ibrahim, 1984; Marion and Marnotte, 1991; Suganthi et al., 2019). The higher the weed ground cover, the lower the sugarcane aboveground dry biomass. A second hypothesis could be that different weed species or communities may have a different effect on yield, regardless of their ground cover. In our study, weed ground cover alone did not statistically explain all the sugarcane dry biomass variations observed, and the ranking of sub-treatments by aboveground dry biomass and average weed ground cover did not follow the same consistent pattern as for treatments. In the first trial, the lowest sugarcane aboveground dry biomass was observed in the plots of weeds from the Climber group despite not having the highest weed ground cover. These differences could thus be related to different resource acquisition strategies.

4.3. Weed resource acquisition and use strategies

Our study highlights relationships between functional traits associated with key trade-offs between acquisitive and conservative resource-use strategies, both above- and belowground, within the weed species studied.

Correlations between height and total leaf area, on the one hand, and between specific leaf area and leaf nitrogen content, on the other hand, reflect resource acquisition strategies at the leaf level, as described by Wright et al. (2004). According to previous studies (Tardy et al., 2015; Tribouillois et al., 2015), weeds with high values for these traits can be associated with a better capacity to acquire light resources, more efficient photosynthesis, and thus a greater light competition, illustrating a leaf acquisitive strategy (by opposition to a conservative one, characterized by higher leaf dry matter content for example). The trade-off between rapid acquisition and efficient conservation of resources in the aboveground parts was highlighted as the “leaf economic spectrum” by Wright et al. (2004). As observed by Tardy et al. (2015) and in both our trials, weeds associated with a high nutrient investment in both support structures for lateral growth (stems) and light acquisition structures (leaves), i.e., with a leaf acquisitive strategy, are primarily twining and climbing species.

The trade-off between an acquisitive and conservative root strategy is illustrated by the negative correlation between specific root length (SRL) and root diameter (RD), also observed in previous studies (Fort et al., 2013; Tardy et al., 2017). This negative correlation highlights an opposition between the rapid acquisition of root resources (high SRL) and resource conservation at the root level (high RD), described by Roumet et al. (2016) as a “root economic spectrum”. In our study, high root diameter, i.e., conservative root strategy, was associated with twining and climbing species in both trials. At the opposite end, a high specific root length, i.e., acquisitive root strategy, was associated with clusters of a majority of weed species from the Small dicotyledon group in both trials. Similar patterns have also been reported in a recent work on service crops in Mediterranean vineyards, in which SRL and root diameter were negatively correlated and strongly contributed to the differentiation of plant functional strategies (Garcia et al., 2026).

Unlike the findings of Reich et al. (2003) or Fort et al. (2013), our analyses reveal distinct weed strategies between leaf and root compartments, meaning that species do not have the same leaf and root acquisition strategies simultaneously. On the contrary, the negative correlation between total leaf area and root mass ratio, or specific root length, highlights the trade-off between weed leaf and root acquisitive strategies, as previously observed by Tardy et al. (2017), Chanteloup (2013) and Carmona et al. (2021). Moreover, total leaf area was also strongly positively correlated with root diameter in both trials, indicating that species with a conservative root strategy may adopt an

acquisitive strategy at the leaf level. This divergence between aboveground and belowground traits aligns with findings by Garcia et al. (2026), who identified distinct functional clusters: one with high values of specific leaf area (SLA), leaf nitrogen concentration, and root diameter, predominantly Fabaceae; and another with high values of specific root length (SRL) and leaf dry matter content, dominated by Poaceae. As in our study, these results highlight contrasting combinations of leaf and root traits across plant groups, reflecting trade-offs between acquisitive and conservative strategies at different plant compartments.

The observed divergence between leaf and root trait patterns across studies and species aligns with Weigelt et al. (2021), who demonstrated that leaf–root trait relationships are context-dependent, precluding a single universal coordination pattern between aboveground and belowground organs. The authors proposed an integrated conceptual framework that extends beyond the simple fast–slow gradients for aboveground parts and roots, incorporating a shared conservation axis across organs, a root-specific collaboration axis, and independent size-related dimensions such as plant height and rooting depth.

In addition, the range of trait values differs between studies. For example, the highest SLA in our study (89.1 m^2 kg^{-1}) exceeds that reported by Garcia et al. (2026); 21.66 m^2 kg^{-1}), and root diameter in our clusters (0.25–2.33 mm) is generally higher than in their study (0.18–0.24 mm). These differences in orders of magnitude suggest that trait relationships should be interpreted with caution when comparing studies conducted in different contexts, and raise the question of to what extent direct comparisons between temperate and tropical weed communities are meaningful.

4.4. Sugarcane sensitivity to weed growth strategy

While weed strategies were similar across both trials in our study, their statistical effects on sugarcane growth varied depending on the trial, and thus potentially, depending on the environmental conditions. Under irrigated and fertilized conditions (trial 1), species with a leaf acquisitive strategy (high leaf area) and root conservative one (high root diameter) were associated with the most significant reduction of sugarcane growth, expressed in stem density as well as aboveground mass (RLQ analysis). Such observation is supported by the prominent effect of twining and climbing weeds, as observed in similar conditions (Martin et al., 2012a), despite not having the highest ground cover. Under fertilized and irrigated tropical conditions, light competition appears thus to be predominant (Little et al., 2021; Tardy et al., 2015). On the contrary, under non-irrigated and non-fertilized conditions (trial 2), sugarcane grown with species from the Small dicotyledons group showed as the lowest biomass, height, and stem density. Most of these species adopted a conservative strategy at the leaf level (high leaf dry matter content) but an acquisitive one at the root level (high specific root length). While sugarcane biomass tended to be reduced in the presence of Small Dicots, the RLQ analysis indicated that weed root traits were associated only with stem height, suggesting a limited effect of root traits on sugarcane biomass. As Small dicotyledon was the sub-treatment with the highest ground cover, their root acquisitive strategy may allow them to increase their root development under resource-limited conditions, thus increasing root competition with the main crop (Christina et al., 2025; Tardy et al., 2017).

In the second trial, increasing sugarcane height was associated with the weed climbing habit clade and higher weed total leaf area. A first explanation could be linked to the “climbing plant syndrome” of twining and climbing plant species which, when adjacent vegetation provides physical support to access the upper canopy, tend to allocate more resources to light-acquisition structures (e.g., leaves) rather than to self-supporting structures (e.g., stems), relying instead on the surrounding plants (Tardy et al., 2015; Wyka et al., 2013). Specifically, the taller and more robust the neighbouring vegetation, the more pronounced the development of the aerial parts in climbing species. A second explanation could be the sugarcane response to the smothering strategy of the climber’s species (Tardy et al., 2015), as plants tend to increase their height in response to light competition (Colbach et al., 2019). For example, Bezuidenhout et al. (2003) proposed a mechanistic model incorporating the hypothesis that, under increasing light competition, sugarcane plants tend to reduce tillering rates while promoting stem elongation (Bezuidenhout et al., 2003). This change in sugarcane development, noted initially by Van Dillewijn (1952), could explain why sugarcane may prioritize vertical growth to escape shading created by the climber’s weed leaf.

These trials were conducted with a single sugarcane cultivar. Yet, sugarcane cultivars are known to differ in traits such as early growth rate, leaf architecture, and resource use efficiency, which could influence their competitive ability against weeds (Yirefu et al., 2012). The competitive relationships observed in this study may therefore be partly specific to the cultivar tested, and their magnitude could vary with other commonly grown cultivars. While assessing cultivar × weed interactions was beyond the scope of this study, future research could explore how cultivar choice modulates weed–crop competition and thereby influences the links between weed functional traits and sugarcane growth variables.

4.5. Limitations and prospects of the study

The two trials differed in environmental and management conditions (mainly irrigation and fertilization), which may have influenced sugarcane responses. Yet, these contextual variables were not monitored with sufficient resolution to be formally included in the models. In addition, the experimental design was not fully randomized due to logistical constraints, including field size and the row structure of sugarcane. Implementing a fully randomized block design would have required separate field sections as independent blocks, which was not feasible under our conditions. For the selectively weeded sub-treatments, assigning plots to specific species would have required sowing weeds, which is currently impossible due to the lack of seeds and the unknown germination requirements of most weed species. To address these design limitations, fixed effects reflecting the experimental structure were retained in the models, and a random effect of plot was included to partially control for spatial variation. Therefore, our results should be viewed as indicating probable trends and generating hypotheses about context-dependent weed impacts, rather than providing strong causal inferences or broadly generalizable conclusions. Observed effects of treatment and sub-treatment on sugarcane growth should also be interpreted as associations rather than strict causal relationships as observed crop responses may also reflect underlying gradients in soil conditions. Despite these constraints, each treatment was replicated, and the random effect had minimal impact on aboveground dry biomass (difference between conditional vs. marginal R^2 <0.1). Moreover, consistent responses across the two trials support the interpretation of treatment-related trends.

The different management practices (fertilization and irrigation) in the two trials prevented direct assessment of the effects of these practices on crop performance, weed functional traits, or their interactions Nevertheless, the combined analysis allows identification of relevant trends and hypotheses for future research. Regarding the RLQ analysis linking weed functional traits to sugarcane response, the lack of full randomization may introduce co-occurrence effects rather than strict causality. While environmental variability could influence both trait values and crop performance, it appears unlikely that the treatments and field condition gradients would produce the same patterns of co-occurrence between weed trait values and sugarcane performance across both trials.

Despite the limitations of this study, a potential effect of management on the relationship between weed traits and sugarcane response emerges. To further investigate these interactions, future studies on the functional traits of tropical weeds are crucial and should be designed

specifically to assess the effects of cropping practices in combination with weed functional traits on sugarcane performance. Given the experimental challenges associated with such investigations, process-based crop models that dynamically simulate weed–crop interactions and their impacts on agroecosystem performance—such as FLORSYS Colbach et al., 2021, 2019)—represent a promising approach. These models can be used to evaluate different weed management strategies under varying cropping practices and climate scenarios, and to identify management solutions suitable for specific agro-ecological conditions in tropical sugarcane systems.

5. Conclusion

Using an approach based on functional characteristics, this study aimed to investigate whether different weeds groups have different resource utilization strategies and whether these strategies can lead to different effects on sugarcane growth. This study provides new insights into weed-crop interactions in tropical agroecosystems by analyzing the link between weed functional traits and crop growth under field conditions for sugarcane.

Our results showed that weed harmfulness may not be determined only by weed ground cover but also by specific resource acquisition and use strategies, which differ across weed functional characteristics. Based on the acquisitive vs. conservative strategies at the leaf and root level of weed species, we highlighted how these strategies may affect sugarcane growth differently depending on environmental conditions. Species with leaf acquisitive strategy (i.e., mainly climbers) potentially have a greater impact under irrigated and fertilized conditions, while species with a root acquisitive strategy (i.e., mainly small dicotyledons) may have a greater impact under non-irrigated and non-fertilized conditions. These results suggest that the impact of weed communities on sugarcane could be context-dependent and determined by both environmental cropping conditions and the functional strategies of the weed species. Despite the limitations related to our experimental design, the patterns observed provide a basis for formulating hypotheses for future research.

Future studies should aim to test these hypotheses through additional field trials with more precise monitoring of environmental variables and cropping practices, potentially focusing on the key leaf (total leaf area and specific leaf area) and root traits (root diameter and specific root length) identified as particularly informative in this exploratory study. Crop models represent a promising alternative to explore a wide range of scenarios at lower cost. Overall, this work provides a first step towards context-dependent weed management strategies in tropical sugarcane systems, highlighting the importance of considering both environmental conditions and weed functional traits in designing sustainable systems.

CRediT authorship contribution statement

E. Lainé: Writing – original draft, Formal analysis, Data curation, Investigation, Visualization, Writing – review and editing. **N. Colbach:** Writing – original draft, Formal analysis, Data curation, Investigation, Visualization, Writing – review and editing. **M. Ponsart:** Data curation, Investigation, Formal Analysis, Writing – review and editing. **A. Horain:** Data curation, Investigation, Formal Analysis, Writing – review and editing. **M. Christina:** Methodology, Formal Analysis, Supervision, Visualization, Validation, Writing – original draft, Writing – review and editing. **G. Damour:** Methodology, Supervision, Writing – review and editing. **M. Schwartz:** Validation, Investigation, Writing – review and editing. **B. Heuclin:** Methodology, Formal Analysis, Validation, Writing – review and editing. **P. Letourmy:** Methodology, Formal Analysis, Validation, Writing – review and editing. **F. Fort:** Methodology, Formal analysis, Writing – review and editing. **F. Affholder:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review and editing. **A. Ripoche:** Conceptualization, Methodology, Formal Analysis, Validation, Investigation, Data curation, Supervision, Writing – original draft, Funding acquisition, Project administration, Writing – review and editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Elise Lainé reports financial support was provided by eRcane. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.fcr.2026.110570.

Data availability

Data will be made available on request.

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