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Effects of Sorgoleone on Soil Microbial Communities and Soybean Nodulation

Laiane Barbosa de Medeiros[1], Maria Eduarda Borges Rodrigues Silva[2], Gabriel Duarte da Costa[2], Cícero Donizete Pereira[3], Fábio Santos Matos[2] & Talles Eduardo Borges dos Santos[2]

[1] University of Brasilia, Brasília-DF, Brazil

[2] State University of Goiás, UnU Ipameri-GO, Brazil

[3] Brazilian Agricultural Research Corporation (Embrapa - Cerrados), Planaltina-DF, Brazil

Correspondence: Talles Eduardo Borges dos Santos, State University of Goiás, UnU Ipameri-GO, Brazil. E-mail: talles.eduardo@ueg.br

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Abstract

Bioinputs offer a promising alternative to synthetic herbicides, reducing environmental impacts, but their effects on soil microbial communities are not well understood. This study assessed the effects of aqueous sorghum extract on soil microbial communities and nodulation in soybean cultivated on sorghum and maize crop residues. The experiment was conducted in a completely randomized split-plot design with five replications, with sorghum or maize crop residues in the plots, and weed control with or without aqueous sorghum extract application in the subplots. Microbial biomass carbon (MBC), basal soil respiration (BSR), microbial quotient (*q*MIC), metabolic quotient (qCO_2), mycorrhizal colonization, and number of viable nodules were measured. Aqueous sorghum extract application reduced MBC (77.92 mg C kg^{-1} soil) and BSR (40.58 mg C-CO_2 kg^{-1} soil day^{-1}) under sorghum residue treatments, increased qCO_2 (indicating higher microbial stress), and reduced *q*MIC, suggesting lower carbon use efficiency. Soybean mycorrhizal colonization was unaffected, but nodulation was significantly reduced under sorghum residue treatments (37 viable nodules per plant), suggesting an inhibitory effect on soybean-rhizobium symbiosis. These findings indicate that phenolic compounds and quinones in sorghum alter soil microbial activity and impair biological nitrogen fixation, particularly when combined with sorghum crop residues.

Keywords: allelopathy, soil microbial biomass, biological nitrogen fixation, arbuscular mycorrhizal fungi

1. Introduction

Agriculture significantly contributes to Brazil's gross domestic product (GDP), with soybean leading in both production and export since 2019 (Boschiero, 2023). The seventh monitoring survey of the 2024–2025 crop season, with 81.4% of the planted area harvested, reported a soybean production of 167.8 million Mg over 47.5 million hectares, with an average yield of 3,533 kg ha^{-1}, representing the highest recorded soybean production in Brazil (CONAB – Companhia Nacional de Abastecimento, 2025). These results were influenced by environmental conditions, human resources, technological advancements, and financial investments, as effective management of these factors through the application of production and management technologies, enhances agricultural competitiveness (Lopes-Assad et al., 2021; Turtt and Toledo, 2023).

In soybean production, bioinputs support sustainability by enhancing plant growth, improving resilience to biotic and abiotic stresses, and promoting soil health through physicochemical and biological processes (BRASIL, 2020; Vidal and Dias, 2023). In this context, bioinputs serve as an alternative to mitigate the adverse effects of excessive agrochemical use. Studies indicate that agrochemical accumulation in soil significantly reduces the diversity of microorganisms essential for nutrient cycling (Rodrigues et al., 2020). Although agrochemicals primarily target weeds or pests, their indirect effects disrupt soil microbial communities by altering plant physiological processes, such as photosynthesis and hormone biosynthesis, which subsequently affect plant–microorganism interactions (Ruuskanen et al., 2023; Mauprivez, 2019).

Zheng et al. (2022) demonstrated that imazethapyr, applied for weed control, reduced chlorophyll content and photosynthetic efficiency in *Arabidopsis thaliana* and altered the structure of its rhizosphere microbial community. These effects persisted in the subsequent plant generation, accompanied by changes in soil microbial communities.

These findings highlight the need to reduce herbicide use in modern biorational agriculture by prioritizing safer, cost-effective alternatives, such as plants with allelopathic properties (Matos et al., 2020).

Sorghum (*Sorghum bicolor* [L.] Moench), an annual Poaceae species cultivated as a second crop in Brazil's Central-West region following soybean, is recognized for its allelopathic properties. Its primary allelochemical, sorgoleone, a brownish oily exudate containing lipid benzoquinones, accounts for over 90% of the hydrophobic components in sorghum root exudates (Sarr et al., 2020). Allelochemicals occur in various plant tissues, including bark, stems, leaves, and roots (Pantoja et al., 2023).

The allelopathic effect of sorgoleone inhibits weed germination and growth (Queiroz et al., 2024), reducing shoot biomass of invasive and susceptible species, such as lettuce and other vegetables, by more than 50% (Gomes et al., 2018). Sorgoleone is used as a natural herbicide, offering a sustainable approach with multiple environmental benefits. Sorgoleone modifies soil microbial communities by inhibiting nitrification through the suppression of ammonia monooxygenase and hydroxylamine oxidoreductase in nitrifying bacteria and archaea, which convert ammonia to nitrate (Sarr et al., 2020; Wang et al., 2021).

Arbuscular mycorrhizal fungi, obligate biotrophic fungi of the order Glomerales (Glomeromycota), are an important group of soil microorganisms, forming symbiotic associations with vascular plant roots. These mycorrhizal fungi can expand the absorption surface area of the root system by up to 20-fold, enhancing the uptake of low-mobility nutrients such as phosphorus, zinc, and copper, from the soil solution (Liu et al., 2018; Jansa et al., 2019; Soares, 2022).

Recent studies indicate that sorgoleone significantly increases plant biomass and phosphorus content in mycorrhizal plants compared to non-mycorrhizal plants under low-phosphorus conditions (Oliveira et al., 2021; Sarr et al., 2021). However, research on the allelopathic effects of sorghum has mainly focused on weed suppression, with limited understanding of its impacts on soil microbial communities.

In addition to mycorrhizal fungi, biological nitrogen fixation is a critical symbiotic process supporting sustainability in soybean production systems in Brazil, as soybean roots form symbiotic associations with bacteria that convert atmospheric nitrogen (N_2) into ammonium (NH4+) via nitrogenase activity (Prando et al., 2023; Andreola, 2021). Thus, the objective of this study was to evaluate the effects of aqueous sorghum extract on soil microbial communities and nodulation in soybean cultivated on sorghum and maize crop residues.

2. Material and Methods

The experiment was conducted at the experimental farm of the State University of Goiás, Ipameri Campus, Goiás, Brazil (17°43'19"S, 48°09'35"W, 773 m altitude). This region has a tropical climate characterized by a rainy summer and a dry winter (Alvarez et al., 2013). The experimental area was in its second year of no-tillage cultivation, with aqueous sorghum extract applied for post-emergence weed control. The soil was classified as a Typic Hapludox (Latossolo Vermelho-Amarelo Distrófico típico; Santos et al., 2018) with a medium texture. Fertilizers were applied based on soil analysis (Table 1) and technical recommendations for the crop, with liming determined by a preferred soil Ca to Mg ratio of 2 to 3 (Procópio et al., 2022).

Table 1. Chemical properties of soil in the experimental area (0.00–0.20 m layer). Ipameri, Goiás, Brazil

Soil layer	pH	OM	P [(1)]	K	Ca	Mg	H+Al	BS
(m)	($CaCl_2$)	(%)	(mg dm^{-3})	(mmolc dm^{-3})				(%)
0.00–0.20	6.1	1.6	6.7	0.45	3.7	1.3	1.1	54.5

OM = organic matter; BS = base saturation. [(1)] Extractor: Mehlich-1.

The experiment was conducted in a completely randomized split-plot design with five replications, with sorghum (*Sorghum bicolor* cv. DOW 1G100) or maize (*Zea mays* cv. SHS 7990 PRO3) crop residues in the plots, and and weed control with or without aqueous sorghum extract application in the subplots. Each experimental unit measured 1.5 × 5 m. The experimental area was divided into two sections: one with sorghum and the other with maize, both cultivated as a second crop to produce residues. During the main crop season, soybean (*Glycine max* cv. FOCO Brasmax) was planted in both sections. Weed control treatments, applied in subplots, consisted of aqueous sorghum leaf extract application to weeds or no weed control.

The aqueous sorghum extracts were prepared from leaves of 30-day-old sorghum plants grown under field conditions. Leaves were washed with running water, placed in paper bags, and dried in a forced-air circulation

oven at 70 °C for 72 hours. Dried leaves were ground in a hammer mill, mixed with ethanol at a ratio of 3 g to 60 mL (3% w v^{-1}), incubated at 40 °C for 72 hours, and filtered (Hien et al., 2016). The extract was diluted to 75% (v v^{-1}) with water (750 mL extract to 250 mL water), and applied using a calibrated backpack sprayer delivering 150 L ha^{-1}. Aqueous sorghum extract was applied as a directed spray to weeds at three soybean phenological stages: V3, R1, and R5. Soybean plants were evaluated 15 days after the last application, and weed assessments were performed at the soybean phenological stage R9.

Maize (*Zea mays* cv. SHS 7990 PRO3) and sorghum (*Sorghum bicolor* cv. DOW 1G100) seeds were planted as a second crop in the first week of March each year, and after completing their growth cycle, plants were cut with a manual brush cutter and left on the soil as crop residues. An indeterminate-growth soybean cultivar (*Glycine max* cv. FOCO Brasmax), with a growth cycle of 110 to 115 days, was planted in October and November of the first and second years, respectively, following a minimum of 100 mm accumulated rainfall. Soybean seeds were treated with a fungicide–insecticide product containing pyraclostrobin, thiophanate-methyl, and fipronil, and inoculated with *Bradyrhizobium japonicum* at a minimum concentration of 12×10^{-5} cells per seed. A fungicide containing fluxapyroxad and pyraclostrobin was applied at the phenological stage R2.

Soil samples (0.00–0.20 m layer) were collected at the soybean R6 stage for microbiological analyses and transported to the Soil Microbiology Laboratory at the State University of Goiás, Ipameri Campus, where they were homogenized and sieved through a 2-mm mesh. Soil samples were immediately analyzed for Microbial biomass carbon (MBC), basal soil respiration (BSR), metabolic quotient (qCO_2), microbial quotient (qMIC), whereas soybean plants were assessed for mycorrhizal colonization and number of viable nodules.

MBC was quantified using the irradiation–extraction method with 0.5 mol L^{-1} potassium sulfate, followed by oxidation with 0.066 mol L^{-1} potassium dichromate and titration with 0.033 mol L^{-1} ammonium ferrous sulfate, with values expressed as mg C kg^{-1} soil (Islam and Weil, 1998; Vance et al., 1987). BSR was measured as the amount of $C\text{-}CO_2$ released from the soil, following Anderson and Domsch (1993), using 100 g of soil samples incubated in glass jars with a central flask containing 10 mL of 0.1 mol L^{-1} NaOH. After incubation (duration determined by a calibration curve), the NaOH was titrated with 0.1 mol L^{-1} HCl, and values were expressed as mg $C\text{-}CO_2$ kg^{-1} soil day^{-1}.

The metabolic quotient (qCO_2) was calculated as the ratio of BSR to MBC, expressed as mg $C\text{-}CO_2$ mg^{-1} Cmic day^{-1}, and qMIC was determined as the ratio of MBC to total organic carbon, expressed as a percentage (Anderson and Domsch, 1993). Total organic carbon for qMIC calculations was quantified by wet oxidation following Mendonça and Matos (2005). A 0.2 g sample of bulk soil was placed in digestion tubes and treated with 5 mL of potassium dichromate solution and 7.5 mL of concentrated sulfuric acid. This solution was heated in a digestion block at 170 °C for 30 minutes. After digestion, the solution was titrated with 0.2 mol L^{-1} ammonium ferrous sulfate.

Mycorrhizal colonization was assessed by collecting the finest roots of each plant, washing them with running water, and preserving them in a 50% ethanol solution. Roots were clarified and stained using the method of Phillips and Hayman (1970), involving 0.5 g of roots heated in 10% KOH, acidified with diluted HCl, and stained with 0.05% trypan blue. Colonization was quantified using the gridline intersect method under a stereoscopic microscope, as described by Giovannetti and Mosse (1980), by distributing roots evenly on a grid plate with 1.1 × 1.1 cm quadrants and counting segments with and without fungal structures (arbuscules and vesicles) intersecting the grid lines. The percentage of mycorrhizal colonization was calculated using the equation: $MC = (sc / (sn + sc)) \times 100$, where MC is the mycorrhizal colonization, sn is the number of non-colonized segments, and sc is the number of colonized segments. The number of viable nodules was determined by washing soybean roots, collecting all nodules with a diameter ≥2 mm, and assessing viability by cutting nodules in half with a scalpel to confirm pink coloration.

Data were analyzed using analysis of variance (ANOVA), with means compared by Tukey's test at a 5% significance level for both plots and subplots. All statistical analyses were conducted using SISVAR software (Ferreira, 2011).

3. Results and Discussion

Analysis of variance (ANOVA) results (Table 2) revealed significant interactions between crop residues and aqueous sorghum extract for microbial biomass carbon (MBC) and basal soil respiration (BSR) at $p < 0.01$, and for microbial quotient (qMIC) and number of viable nodules at $p < 0.05$. The aqueous sorghum extract had a significant ($p < 0.05$) effect on the metabolic quotient (qCO_2) (Table 2), while neither crop residues nor the extract significantly affected mycorrhizal colonization.

Table 2. Analysis of variance (ANOVA) and F-values for microbial biomass carbon (MBC), basal soil respiration (BSR), metabolic quotient (qCO_2), microbial quotient (qMIC), mycorrhizal colonization (MC), and number of viable nodules per plant (NVN) in soybean grown on maize or sorghum crop residues, with or without aqueous sorghum extract application for weed control

Source of Variation	F-values						
	DF	MBC	BSR	qCO_2	qMIC	MC	NVN
Residues (R)	1	3.926^{ns}	138.339^{**}	0.556^{ns}	0.222^{ns}	1.529^{ns}	14.151^{**}
Error 1	8	-	-	-	-	-	-
Extract (E)	1	112.086^{**}	9.893^{ns}	39.490^{**}	178.489^{**}	1.122^{ns}	0.001^{ns}
R × E	1	19.169^{**}	13.064^{**}	4.266^{ns}	11.005^{*}	0.008^{ns}	10.569^{*}
Error 2	8	-	-	-	-	-	-
Total	19	-	-	-	-	-	-
CV_1(%)	-	16.45	4.45	10.61	16.83	6.84	10.92
CV_2 (%)	-	12.45	9.99	16.68	13.83	9.64	18.53

CV = coefficient of variation; DF = degrees of freedom; *, **, and ^{ns} = significant at 5%, 1%, and not significant by the F-test, respectively.

Sorghum residues combined with aqueous sorghum extract significantly reduced MBC to 77.92 mg C kg^{-1} soil (Table 3). Sarr et al. (2020) demonstrated that sorgoleone alters amoA gene expression in ammonia-oxidizing bacteria, thereby reducing nitrification rates. Additionally, under favorable soil moisture and pH conditions, sorgoleone can also modify the composition of bacterial and archaeal communities, reducing the abundance of *Nitrospirae* bacteria, which may help explain the observed decrease in MBC.

BSR, an indicator of microbial activity and organic matter decomposition, was reduced to 40.58 mg C-CO_2 kg^{-1} soil day^{-1} under sorghum residues with aqueous sorghum extract application (Table 3). This reduction can be attributed to changes in the structure and function of the soil microbial community (Carballido and Poulson, 2017). Similarly, Tesfamariam et al. (2014) and Wang et al. (2021) reported that allelochemicals, including sorgoleone, suppress the metabolic activity of soil microbial communities.

Table 3. Effect of maize (MR) and sorghum (SR) crop residues on microbial biomass carbon (MBC), basal soil respiration (BSR), microbial quotient (qMIC), and number of viable nodules (NVN) in soybean grown with (WE) or without (NE) aqueous sorghum extract application for weed control

Source of variation	MBC (mg C kg^{-1} soil)		BSR (mg C-CO_2 kg^{-1} soil day^{-1})		qMIC (%)		NVN	
	WE	NE	WE	NE	WE	NE	WE	NE
SR	77.92Bb	208.74Aa	40.58Bb	57.32Aa	0.54Ab	1.64Aa	37.00Bb	51.00Aa
MR	138.73Ab	193.00Aa	62.51Aa	61.35Aa	0.72Ab	1.39Ba	60.00Aa	46.00Ab

Means followed by the same uppercase letter in the columns, or lowercase letter in the rows, are not significantly different by the Tukey's test at a 5% significance level.

Aqueous sorghum extract application reduced the carbon use efficiency of soil microbial communities, regardless of the residue type, resulting in a qMIC of 0.54% and 0.72% under sorghum and maize residues, respectively (Table 3). This effect may be attributed to a higher proportion of quinone rings relative to methoxy groups in the extract. Gimsing et al. (2009) evaluated the mineralization of sorgoleone in soils from the United States and Denmark and reported that quinone rings in sorgoleone inhibited carbon incorporation by the soil microbial communities, whereas the methoxy group was readily mineralized.

qMIC is an important bioindicator of soil quality, reflecting carbon use efficiency by microbial communities and

providing insights into the quality of soil organic matter and the persistence of allelopathic substances like sorgoleone in soil (Vieira, 2019; Gimsing et al., 2009). Weed control with aqueous sorghum extract increased CO_2 loss per unit of microbial biomass by 36.88% compared to the treatment without extract application (Figure 1). Melo et al. (2025) also reported an increase of approximately 42% in metabolic quotient (qCO_2) with aqueous sorghum extract application in first-year cultivation compared to the control, supporting the findings of this study.

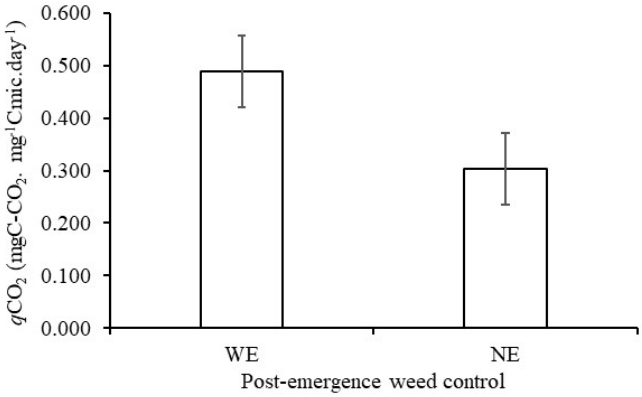

Figure 1. Mean metabolic quotient (qCO_2) in soybean grown with (WE) or without (NE) aqueous sorghum extract application for weed control. Ipameri, Goiás, Brazil, 2023

An increase in BSR, coupled with a significant decrease in MBC, was attributed to allelochemicals serving as a carbon source for soil microorganisms, thereby altering microbial community composition (Xu et al., 2023). Allelochemicals can either enhance or reduce the abundance and diversity of soil microbial communities (Zhu et al., 2017). Mardani-Korrani et al. (2021) reported that allelopathic effects of *Vicia villosa* root exudates reduced populations of *Proteobacteria* and *Acidobacteria*.

The response of the metabolic quotient (qCO_2) to allelochemicals varies depending on factors such as compound type and concentration, soil properties, and environmental conditions (Carvalho et al., 2019). Aqueous sorghum extract application on sorghum residues significantly reduced the mean number of viable nodules to 37 nodules per plant, differing statistically from the 60 nodules per plant under maize residues (Table 3). This result suggests that compounds in aqueous sorghum extract may inhibit nodulation when combined with sorghum residues but not with maize residues. Recent studies indicate that phenolic compounds and quinones, such as sorgoleone, in sorghum residues exert allelopathic effects that can suppress the symbiotic interaction between legumes and nitrogen-fixing bacteria (Sowiński et al., 2020).

Finally, as illustrated in Table 2, no significant effects of the residue, extract, or their interaction on arbuscular mycorrhizal (AM) colonization in soybean were observed. This result is consistent with recent findings suggesting that the allelopathic influence of sorgoleone may be strongly dependent on soil and climatic conditions, especially soil phosphorus availability (Figueiredo de Oliveira et al., 2025; de Oliveira et al., 2021). At moderate concentrations, sorgoleone can promote mycorrhizal colonization and phosphorus uptake, while higher levels or variations in soil management may decrease or nullify these effects (de Oliveira, 2024; Tibugari, 2024).

4. Conclusions

Aqueous sorghum extract application negatively affected soil microbial communities, reducing both soil microbial biomass and activity, but did not influence soybean mycorrhizal colonization.

Aqueous sorghum extract application inhibited soybean–rhizobium symbiosis, particularly under sorghum residues.

These findings indicate that sorghum crop residues and aqueous sorghum extract should be managed cautiously to minimize adverse effects on soil biological quality.

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Authors contributions

Prof. Dr. Talles Eduardo Borges dos Santos and Prof. Dr. Fábio Santos Matos were responsible for the design and review of the study. Maria Eduarda Borges Rodrigues Silva, Laiane Barbosa de Medeiros and Gabriel Duarte da Costa were responsible for data collection. Laiane Barbosa de Medeiros and Maria Eduarda Borges Rodrigues Silva wrote the manuscript. Prof. Dr. Talles Eduardo Borges dos Santos and researcher Dr. Cícero Donizete Pereira reviewed it. All authors read and approved the final manuscript.

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