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Mycorrhizal Fungal Inoculum Potential in Crop Rotation Soil With Different Levels of Irrigation

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Abstract

Research indicates arbuscular mycorrhizal fungi (AMF) inoculum potential and AMF biomass production in agricultural soil are strongly influenced by both soil moisture availability and crop rotation (CR) strategies. We hypothesized that AMF biomass production in and inoculum potential of Wyoming semiarid agricultural soil would increase when managed using CR and irrigation. To test this hypothesis, we examined AMF activity (AMF biomarker fatty acid, and AMF infection of roots) in two differently managed soils (no-CR soil and two-year CR soil) in a field experiment. Furthermore, in a greenhouse experiment, we examined AMF activity in the same two CR treatment soils under different irrigation regimes (wet, irrigated to 60% field capacity, and dry, irrigated to 15% field capacity). Notably, the two-year CR soil had greater amounts of AMF biomarker fatty acid and greater inoculum potential, and higher percentage of AMF root colonization compared to no-CR soil. Despite the fact that the CR soil had more AMF propagules, it was less than the undisturbed non-agricultural native sage-grassland soils previously reported. Overall, the findings suggest that high levels of irrigation can inhibit the activity of AMF adapted to semiarid soil conditions and CR can increase activity of AMF in soils from semiarid regions.

Keywords: mycorrhizal root colonization, phospholipid fatty acid (PLFA), irrigation, field capacity, inoculum potential

1. Introduction

Enhancing agroecosystem functions often involve changes in soil microbial activity, particularly mycorrhizae, which facilitate nutrient uptake by plants. Arbuscular mycorrhizal fungi (AMF), the most prevalent type of mycorrhizae on annual crop plants, play a crucial role in maintaining stable soil-plant systems (Aalipour et al., 2021; Askari et al., 2018). Research has demonstrated that AMF can form an extensive extraradical mycelium network in the soil, enhancing nutrient availability and plant mineral nutrient uptake (Alsunuse et al., 2021; Huang et al., 2021). Crops inoculated with selected AMF show improved nutrient uptake, produce greater yields, and require less fertilizer (Cely et al., 2016; Pellegrino et al., 2011; Roesti et al., 2006; Tawaraya, 2003). Additionally, AMF can persist in soils, benefiting subsequent crops in rotation (Higo et al., 2010; Pellegrino et al., 2011).

Agricultural management practices including cover crop (Jian et al., 2020), biochar (Thapa et al., 2024; Zaid et al., 2024) crop rotation (Goyal et al., 2019; Chu et al., 2016), and reduced tillage (Toth et al., 2024) have positive effects on soil health. Crop rotation systems with high diversity tend to increase soil microbial richness and diversity, thereby enhancing plant resistance to biotic and abiotic stresses (Goyal et al., 2019; Han et al., 2017)

However, findings by Douds and Millner (Douds Jr. & Millner, 1999) and Tian et al. (2013) suggest that AMF inoculum potential may not be significantly influenced by rotation systems alone and that plant species selection and sequence can impact the benefits derived from CR. High-input practices like irrigation management can diminish AMF abundance and diversity (Gosling et al., 2006). In semiarid regions, water availability is a growing concern due to drought stress affecting plant physiological and biochemical responses (Mahajan & Tuteja, 2005; Yousefzadeh Najafabadi & Ehsanzadeh, 2017). Mycorrhizal plants provide energy to fungal symbionts for growth and reproduction, while the fungal partner enhances water and nutrient uptake by the plant. During drought, plants can tolerate water stress up to a threshold level, beyond which growth declines, also, limiting AMF growth and proliferation. The effectiveness of soil under CR on AMF development is closely related to the dynamics of root-associated microbial communities (Gan et al., 2011). Soil-available water also influences AMF communities, with optimal water availability promoting AMF development (Caravaca et al., 2005; Entry et al., 2002; Jansa et al., 2006). However, there is a limited understanding of the interaction between soil under CR and water availability regimes on AMF activity in soil. This study aims to examine how the CR and irrigation affect AMF biomass production, as determined by analysis of AMF-specific fatty acid content, and the mycorrhizal inoculum potential, measured by most probable number (MPN) methods using soil dilution in agricultural soils of Wyoming's semiarid region. We hypothesize that CR and adequate irrigation will significantly enhance AMF biomass production and mycorrhizal inoculum potential in the soil.

2. Materials and Methods

2.1. Field Study Site and Soil Sample Collection

The CR field experiment was conducted at Powell Research and Extension Center, University of Wyoming in a field designated for replication of CR treatments. In the first year, barley, beans, and sugar beets were initially planted without CR. Over the next two years, barley was planted after bean (bean-barley; treatment 1) and bean was planted after sugar beet (sugar beet-bean; treatment 2) in crop rotation.

Soil samples were collected in June during various CR periods, including non-CR and after two-year of CR with beans, barley, and sugar beets. The sampling took place at the University of Wyoming Powell Research and Extension Center (PREC), Powell, WY (44°45′32″ N latitude, 108°45′30″ W longitude, and an elevation of 1333 m). The region, characterized by cold, dry winters and warm, dry summers receives an average annual precipitation and temperature of 157 mm per year and 6.7 °C. The soil has clay loam characteristics (Garland fine-loamy, mixed, super active, mesic Typic Haplargid).

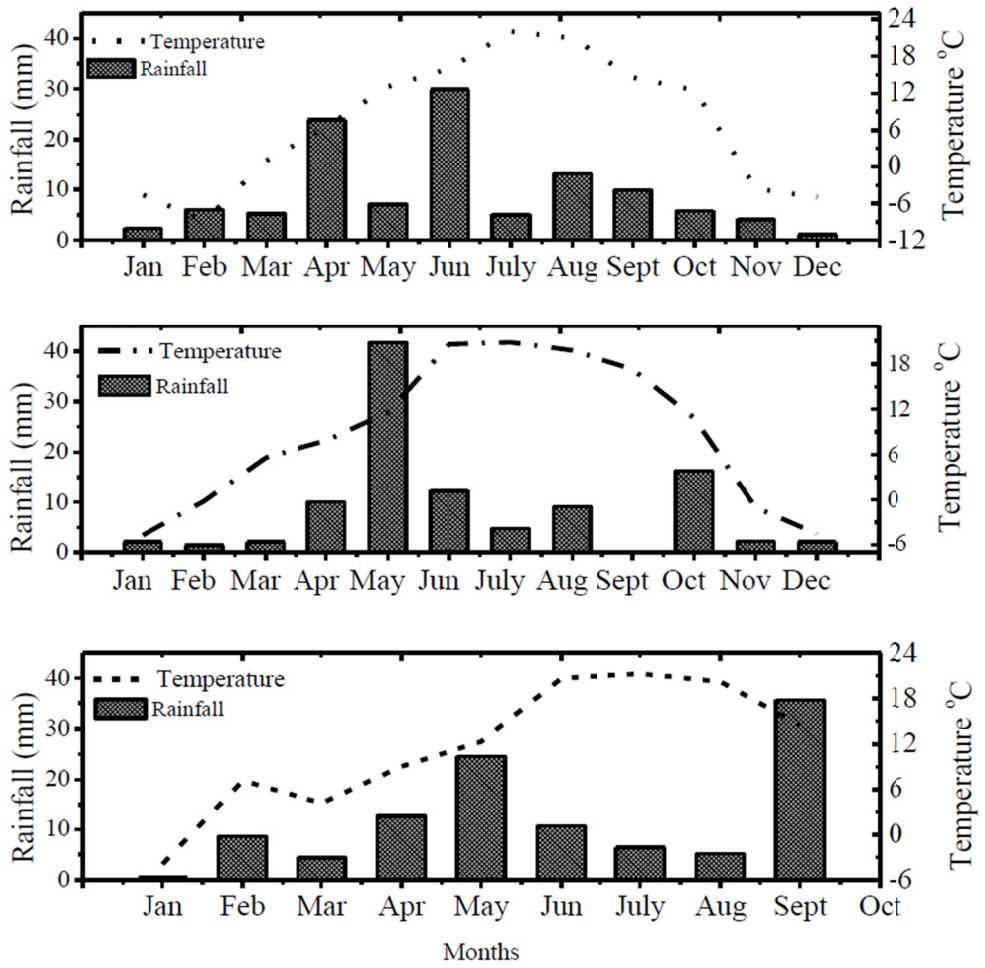

Figure 1. Cumulative monthly rainfall (mm) and temperature (°C) for Powell Research and Extension Center (PREC) of University of Wyoming over three years (2014, 2015 and 2016)

Soil and plant root samples were collected from a depth of 0-20 cm each summer to determine the AMF phospholipid-fatty acid contents (PLFA) in the soil and to examine the presence of AMF on bean and barley roots. Physical and chemical properties of the collected soil samples were determined by using the standard testing procedures, and the testing was performed at Ward Laboratories, Inc. (Omaha, Nebraska, USA, www.wardlab.com). Physical and chemical properties of the collected soil samples are shown in Table 1.

Table 1. Physical and chemical properties of the collected soil samples

Soil properties	Test results
Texture	Loam
pH	7.8±1.4
Electrical Conductivity (ds m^{-1})	0.7±0.3
Phosphorus (mg Kg^{-1})	7.3±2.3
Organic carbon (mg g $soil^{-1}$)	0.8±0.5
Total carbon (mg g $soil^{-1}$)	1.2±0.6
Total nitrogen (mg g $soil^{-1}$)	0.1±0.01
Calcium Carbonate (%)	5.5±2.6
Bulk density (g/cm^3)	1.4±0.5
Carbon: Nitrogen ratio	13±6

Note. ± indicates the Standard deviation.

2.2 Greenhouse Experiment Treatments

An experimental study was carried out at the greenhouse complex of the University of Wyoming Laramie Research and Extension Center (LREC), Laramie, WY (41°18′40″ N latitude, 104°35′37″ W longitude, elevation of 2184 m).

Soil samples from CR fields were air-dried, sieved through a 2 mm mesh, and mixed with autoclaved sand (121 °C for 30 minutes on two consecutive days) in a 1:1 ratio. Approximately 350 g of the mixed soil was transferred into nursery plastic pots and firmed (using the fist) to reduce air pockets, leaving about 1.5-2 cm of watering space at the top. Each pot had an upper diameter of 2 cm, a depth of 11.5 cm with perforations at the bottom for drainage. To prevent soil loss, the bottom of each pot was covered with a paper towel.

The treatments included (i) 2 soil types (no-CR soil and two-year CR soil), (ii) 2 water availability regimes (wet [60% field capacity] and dry [15% field capacity]).

Soil dilutions were prepared as follows: (a) control (100% soil-no dilution); (b) 10^{-1} (10% soil and 90% autoclaved sand); (c) 10^{-2} (1% soil and 99% autoclaved sand); (d) 10^{-3} (0.1% soil and 99.9% autoclaved sand); and (e) 10^{-4} (0.01% soil and 99.99% autoclaved sand).

Ten sweet clover (*Melilotus officinalis* L.) seeds were hand-sown in each pot. After uniform emergence (3-7 days after planting), the seedlings were thinned down to three plants per pot by removing excess seedlings.

2.3 Mycorrhizal Inoculum Potential Bioassay

The mycorrhizal inoculum potential (MIP) of the soil was assessed using the methods outlined by Powell (1980). A bioassay was conducted under two soil water availability regimes to compare mycorrhiza development under wet and dry conditions. The pots were maintained at different field capacities: approximately 60% field capacity (150 ml H_2O per 350 g dry soil) for wet, and 15% field capacity (70 ml H_2O per 350 g dry soil) for drier conditions. The bioassays were monitored daily in the greenhouse for 30 days to maintain the desired water levels. Pots under wet conditions received 42 ml H_2O every 2 days, while pots under dry conditions received 10.5 ml H_2O every 2-3 days. The MPN of mycorrhizal propagules was determined according to Alexander (1965) as the number of plants that become mycorrhizal at increasing dilution levels. The number of propagules per vial of undiluted inoculum, divided by the dry weight of soil per pot (350 g), yielded the numbers of mycorrhizal propagules g^{-1} soil. The plant roots from the MIP assay were examined for the presence of arbuscular mycorrhizae (AM), an indicator of AM inoculum density and fungi activity. The roots were washed, treated with 10% KOH, stained using a lactoglycerol (1:1:1; 85% lactic acid: water: glycerin) along with 0.066% trypan blue, and then destained in clear lactoglycerol (Phillips & Hayman, 1970). Microscopic examination of the roots revealed AM infection, which was quantified as the percentage of 1 mm root segments colonized by AMF, following the method illustrated by E. B. Allen and M. F. Allen (1980).

2.4 Arbuscular Mycorrhizal Biomass

The biomass of arbuscular mycorrhizal fungi (AMF) in soil samples collected from the field was estimated using PLFA techniques. The phospholipid-fatty acids were extracted from 0.5 g soil samples through a modified Bligh-Dyer approach (Buyer et al., 2010) which involved direct extraction using a 1:2:0.8 solution of chloroform, methanol, and phosphate buffer. Neutral and glycolipid fatty acids were separated from PLFA using a solid-phase extraction column. The PLFA samples were then analyzed qualitatively and quantitatively with an Agilent 6890 gas chromatograph, equipped with an autosampler, split-splitless injector, and flame ionization detector, following moderate alkaline methanolysis. The system was controlled by MIDI Sherlock software and an Agilent Chemstation. The fatty acid biomarkers 16:1 ω5c and 20:1ω9c within the individual PLFA profiles were employed to quantify the abundance of AMF in the soil.

2.5 Statistical Analysis

2.5.1 Field Experiment

Data for AMF biomass and AMF root colonization were subjected to a Student T-test analysis with six replications.

2.5.2 Greenhouse Experiment

This experiment tested two factors: soil treatment and soil moisture level, each tested at two levels, using a completely randomized factorial design (CRD) with six different replications. The results were analyzed using ANOVA.

The main effect of the response variables was tested against the error term and significance was declared when the *P* value was less than 0.05. Post-hoc mean separation was conducted with the Tukey HSD procedure. Data analyses were performed using the R statistical software (version 3.5.1 R Core Team, 2018).

3. Results

3.1 Mycorrhizal Root Colonization

In the field experiment, plants grown with CR had significantly higher AM root colonization ($P < 0.05$) than those without CR (Table 2). Barley following beans exhibited a greater mycorrhizal formation (45%) compared to barley without CR (29%) as shown in Table 2. The lowest mycorrhizal formation (22%) was observed in bean plants without CR.

Table 2. Effects of CR on percentage of AMF colonization on bean and barley in the field experiment

Crop rotation	AMF root colonization (%)	
	Bean	Barley
No-rotation soil	22 ± 4^{b}	29 ± 5^{b}
2yr-rotation soil	39 ± 6^{a}	45 ± 8^{a}

Note. ± indicates the Standard deviation and values with different letters in it are significantly different at $P < 0.05$. AMF root colonization was represented based on the % of 1 mm affected root segments.

The experimental greenhouse results for the AMF root colonization of sweet clover grown in soils under CR and no-CR at different conditions of moisture and different soil dilutions are presented in Table 3. The results revealed that soil subjected to a two-year CR had a significantly ($P < 0.05$) greater percentage of AMF root colonization compared to soil without CR (Table 3). The soil type and water availability significantly ($P < 0.05$) influenced the MIP of the soil (Table 3). Notably, the percentage of root colonized by AMF was highest in the two-year CR soil under dry conditions (15% field capacity) and lowest in the no-CR soil under wet conditions (60% field capacity). This trend was consistent across undiluted soil and soil diluted to 10^{-1} and 10^{-2} levels. However, AMF root colonization was absent in higher dilutions (10^{-3} and 10^{-4}) for both soil types under dry and wet regimes. Overall, the no-CR soil exhibited lower AMF root colonization compared to the two-year CR soil.

Table 3. The percentage of AMF root colonization for sweet clover roots grown in soils at different moisture regimes under different CR periods

Soil dilution	No-rotation soil		2yr-rotation soil	
	Dry†	Wet‡	Dry†	Wet‡
	---------- % ----------			
Undiluted	48.2 ± 3^{a}	24.6 ± 6^{b}	51.1 ± 4^{a}	50.5 ± 4^{a}
10^{-1}	23.0 ± 6^{bc}	16.0 ± 5^{c}	40.5 ± 6^{a}	28.7 ± 7^{b}
10^{-2}	9.6 ± 3^{ab}	6.2 ± 6^{a}	17.9 ± 2^{a}	16.4 ± 5^{ab}
10^{-3}	0.0^{a}	0.0^{a}	0.0^{a}	0.0^{a}
10^{-4}	0.0^{a}	0.0^{a}	0.0^{a}	0.0^{a}

Note. † Dry (15% field capacity) and ‡ Wet (60% field capacity); Means followed by same letter within a row are not significantly different at $P < 0.05$.

3.2 Mycorrhizal Infectivity

The MIP bioassay technique was employed to evaluate the impact of CR on AMF propagule density in the treated soils (Powell, 1980). The results showed no significant ($P > 0.05$) difference in the number of positive vials (AM observed) between the two-year CR and no-CR soils. However, the two-year CR soil consistently had more positive vials at various dilution levels, except for the 10^{-2} dilution. Specifically, the no-CR soil had 5 positive vials at undiluted soil, 4 at 10^{-1} dilution, 3 at 10^{-2} dilution, and none at 10^{-3} and 10^{-4} dilutions. In contrast, the two-year CR soil had 5 positive vials at undiluted soil, 4 at 10^{-1}, 4 at 10^{-2}, and none at 10^{-3} and 10^{-4} dilution levels. The MIP bioassay and subsequent calculations indicated that the no-CR soil had 0.8 propagule g soil^{-1}, while the two-year CR soil had 1.0 propagule g soil^{-1}, suggesting a 20% higher mycorrhizal inoculum potential**.**

3.3 Arbuscular Mycorrhizal Fungi (AMF) Biomass in Soil

In the field experiment, the biomarker fatty acid contents for the AMF in two-year CR were significantly ($P < 0.05$) greater compared to no-CR treatment. Barley had a higher concentration of AMF biomarker fatty acid (0.19 μg g soil^{-1}) after two-year CR use, while in the bean field there was no significant difference in AMF biomarker fatty acids between no-CR and two-year CR soils. These effects are shown in Table 4.

Table 4. Effects of CR on AMF biomarker fatty acids on bean and barley in the field experiment

Crop rotation	AMF biomarker (μg g soil^{-1})	
	Bean	Barley
No-rotation soil	0.13±0.05^{a}	0.12±0.06^{b}
2yr-rotation soil	0.9±0.06^{a}	0.19±0.07^{a}

Note. ± indicates the Standard deviation and values with different letters in it are significantly different at $P < 0.05$.

The greenhouse experimental results showed the effect of CR on AMF biomarker fatty acid contents for collected soil samples are shown in Table 5. Crop rotation significantly ($P < 0.05$) impacted the biomarker fatty acid contents for AMF. Specifically, the soil biomarkers for AMF were substantially greater in the two-year CR soil compared to that of soil without CR (Table 5). Concentration of AMF biomarker fatty acid was 86% higher in the two-year CR soil, indicating that the CR has a significant enhancement of AMF biomass production.

Table 5. Effect of CR on AMF biomarker fatty acids in the greenhouse soil experiment

Crop rotation	AMF biomarker (μg g soil^{-1})
No-rotation soil	0.12±0.01^{b}
2yr-rotation soil	0.32±0.17^{a}

Note. ± indicates the Standard deviation and values with different letters in it are significantly different at $P < 0.05$.

4. Discussion

Sustainable crop production depends on understanding how soil and agroecosystem management techniques, such as CR and irrigation, affect soil health and microorganisms, especially AMF. This study demonstrates the importance of CR for AMF activity. We hypothesized that CR would increase the AMF colonization in roots compared to treatment where CR was not used. In our field study, we found that AMF colonization in bean and barley roots was on average 15% and 17% higher after a two-year CR compared to no-CR fields. Also, in the barley field CR increased the AMF biomarker fatty acid contents after two-year of CR compared to no CR used. These findings are consistent with previous studies showing that CR was positively related to AMF colonization (Bakhshandeh et al., 2017) and had a greater percentage of AMF (Ambrosano et al., 2010).

The MIP bioassay (Powell, 1980) estimates the quantity of infective mycorrhizal propagules in soils. The measurement of the mycorrhizal inoculum potential revealed a 20% higher density of mycorrhizal inoculum in soil managed with a two-year CR soil compared to the soil without CR. Although, the two-year CR soil exhibited higher mycorrhizal infectivity, its AMF infectivity was relatively low compared to that of undisturbed non-agricultural native sage-grassland soils, which typically ranges from 10 to 25 propagules g soil^{-1} (Pfetffer & Bloss, 1988) which clearly shows the effects of agricultural practices on the soil microbial community.

Plants grown in undiluted soil under dry conditions (15% field capacity) exhibited a greater percentage of roots colonized by AMF in both soil treatments (No-CR and two-year CR) which may be due to AMF increase host plant water uptake under drought conditions and improve host plant water relations by increasing AMF root colonization. The two-year CR soil had a higher density of AMF propagules and biomass compared to that of soil with no-CR. Crop rotation significantly increased AM root colonization potential compared to soils managed with no CR (Hu et al., 2015; Mäder et al., 2000), likely due to increased carbon substrate resources (Stromberger, 2005) varied root structure, and altered abiotic soil conditions (Liu et al., 2013), leading to root colonization by different portions of the fungal community (Bazghaleh et al., 2015; Borrell et al., 2017; Esmaeili Taheri et al., 2011). Rotation positively affects AMF root colonization within two-years, aligning with Marro et al. (2020) who showed that rotation increased AMF propagule density. Higher AMF root colonization was observed in the two-year CR soil, indicating greater AMF propagule density and activity (Higo et al., 2015). Soil AMF

propagule density increased within a given range after two-years of CR, corroborating with the findings of (Bakhshandeh et al., 2017) and (Castillo et al., 2006). AMF colonization was greater in plants under rotation and dry conditions, likely because indigenous AMFs are adapted to dry soil environments (Pfetffer and Bloss, 1988; Tsang and Maun, 1999). Consequently, high water availability adversely affected the AMF root colonization, as the AMF in the soil from Powell, WY, are adapted to semiarid conditions. A study by Mäder et al. (2000) also reported similar results regarding AMF root colonization. No AMF root colonization was observed at high dilution levels (10^{-3} and 10^{-4}) under both water availability conditions (15 and 60% Field Capacity), in both the two-year CR, and no-CR soils.

The results showed that CR increased the AMF content in soil compared with soil no CR used. Our results from this study showed significantly greater amount of the AMF biomarker fatty acids (16:1w5c and 20:1w9c) in soil in the two-year of CR treatment. The distribution of AMF species varies with land use, climate, and edaphic conditions, and can be influenced by management practices like fertilization and tillage, leading to low native AMF occurrence (Jansa et al., 2002; Oehl et al., 2003). The soil environment significantly impacts the development and vitality of mycorrhizal fungi. In such areas, plants face considerable environmental stress, including water stress. Results indicated higher AMF biomarker fatty acids in the two-year CR soil compared to no-CR soil (Tables 4 and 5). These results align with previous findings that diverse rotations increase AMF biomass in soil (Moitinho et al., 2020; Zhang et al., 2018). Crop rotation enhances plant diversity and available niches, influencing AMF biomass production through diverse root exudate profiles (Ellouze et al., 2013) varied root structure, and modified biotic and abiotic soil conditions (Gan et al., 2011; Liu et al., 2013) leading to root colonization by different subsets of the fungal community (Bainard et al., 2014; Bazghaleh et al., 2015; Borrell et al., 2017; Ellouze et al., 2013; Esmaeili Taheri et al., 2011).

5. Conclusion

Our findings indicated the importance of agriculture management practices like CR to the AMF community. The results of this study demonstrated that soil subjected to a two-year CR had higher AMF inoculum infectivity, greater root colonization, and more AMF biomarker fatty acids contents compared to that of soil without CR. The rotation significantly enhanced soil AMF community, likely due to increased diversity of carbon substrates and varied root structure of AMF host plants. The study also revealed that AMF colonization was more pronounced in plants under rotational and dry conditions, whereas high water availability negatively impacted AMF root colonization. Overall, our findings suggest that CR and low soil water availability significantly enhance AMF's ability to increase inoculum production in semiarid soils. By emphasizing the stronger role of AMF promoting crop growth, the results of our study provide an important perspective to improve agricultural practices in the face of increasing drought events. Consequently, future field research in agricultural systems are very important and should focus more on better understanding complex of interactions between crops and associated AMF communities.

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Authors Contributions

Dr. Alsunuse was responsible for the study design, data collection, writing original manuscript, data analysis and editing the manuscript. Dr. Al-Awwal was responsible for writing the original manuscript, editing, and data analysis. Mr. Budhathoki was responsible for soil analysis, data collection, and writing original manuscript. Dr. Thapa was responsible for writing original manuscript and data curation. Dr. Baidoo was responsible for writing and editing the manuscript. Dr. Zaid was responsible for writing and editing the manuscript. Dr. Stahl was responsible for supervision and reviewing the manuscript. All authors read and approved the final manuscript.

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Data Sharing Statement

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