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Tripartite Symbiosis of Soybean-Rhizobium-AMF in Riparian Peat under different Water Depths Gradients

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ABSTRACT

Soybean root-peat interface is a dynamic zone where numerous bio-geochemical processes occur. This study investigated the effects of water depth gradients on tripartite symbiosis of soybean-rhizobium-AM fungi. Peat blocks measuring 30-cm x 30-cm x 55-cm (L x W x H) were collected from riparian wetlands at the Arboretum of Universitas Sriwijaya and subjected to four different Water Depths (WD), designated as WD1 = -20cm, WD2 = -30cm, WD3 = -40cm, and WD4 = -50cm, which was kept constant throughout the study. Soybean was subjected to either single inoculation with Rhizobium japonicum (R) or dual inoculation with Rhizobium japonicum and AMF (RF), then grown for 60d. Despite the narrow range of pH, a significantly negative linear relationship between available Pi and pH was detected, confirming that pH is an essential factor determining the availability of Pi in the peat soils. Soybeans subjected to the RF treatment had more total nodules and more active nodules compared to those subjected to the R treatment, thereby confirming the synergistic effect of Rhizobium and AMF in soybeans. The findings also indicated that the colonization by the AMF was independent of the inoculation and the WD. Soybeans subjected to the RF treatment exhibited higher shoot N and P contents, as well as higher shoot dry weight compared to those treated with the R treatment. The colonization of soybeans inoculated with the R treatment by the AMF indicated the presence of indigenous AMF inoculum in the peat soils of the current study.

Keywords: **Peat; riparian wetland; water depth; Tripartite symbiosis; soybean**

INTRODUCTION

Managing peatlands for agricultural purposes is meant to uphold Indonesia's growing population and food demand. However, converting peatlands into agricultural fields has also been increasingly debated over the last century (McCarter *et al*., 2020; Putra *et al*., 2019; Wong *et al*., 2025). The problems stem mainly from the fact that conversion of natural peatlands into techno ecosystems, such as agricultural fields, require drainage to remove excessive water from the root zone. Because hydrology is the most critical factor controlling the C balance of peatlands, drainage through canalization, for example, exposes the peat to an aerobic condition, which leads to peat oxidation, turns the peat into a net C emitter, and has also been associated with severe and uncontrolled peat fires (Lastuti *et al*., 2016; Putra *et al*., 2019; Wong *et al*., 2025; Zhang *et al*., 2023).

Despite the controversy, peatlands in Indonesia are still undergoing a rapid transformation from natural forests to agriculture land (Basuki *et al*., 2019; Dohong *et al*., 2018; Uda *et al*., 2020). The driving factors are the increasing need for arable land, particularly for agriculture, the scarcity of appropriate unused uplands, and the attractiveness of peatlands' availability and flat topography (Hergoualc'h *et al*., 2018; Widyatmanti *et al*., 2022). Therefore, large-scale canalization for agriculture or plantations has been identified as the most influential interference for the water table decline in peatlands (Leifeld and Menichetti, 2018; Zhong *et al*., 2024; Evans *et al*., 2021; Strack *et al*., 2022).

Peatlands are in fact intricate ecosystems defined by various interactions among their essential components. Plants and microorganisms have been found as a strong regulator of the peatland ecosystem. The intricate web of interactions occurring within the rhizosphere, the

narrow zone of soil surrounding plant roots, plays a crucial role in plant health and nutrient acquisition (Hamard *et al*., 2021; Korn *et al*., 2024; Robroek *et al.*, 2015; Rintsona *et al*., 2021; Vishwakarma *et al*., 2020). Two important groups of microorganisms in the rhizosphere are Rhizobium, which form symbiotic relationships with legumes like soybean, and arbuscular mycorrhizal fungi (AMF), which establish mutualistic associations with plant roots. The interaction between these microorganisms can have significant impacts on plant nutrient acquisition, stress tolerance, and overall productivity (Liu *et al*., 2020; Rintsona *et al*., 2021). The Rhizobia are responsible for fixing atmospheric nitrogen, which is then made available to the soybean plant. Similarly, the AMF have been found to play a crucial role in enhancing plant adaptation to abiotic stresses. The AMF establish mutualistic associations with plant roots, expanding the root system's ability to access water and nutrients, thereby improving the overall nutrient status and stress tolerance of the plant. Even under certain circumstances, soybeans highly depend on the AMF (Cofré *et al*., 2020; Liu *et al*., 2020; Sefrila *et al*., 2023; Takács *et al*., 2018; Wen *et al*., 2023).

Despite numerous beneficial effects of dual inoculation of soybeans with Rhizobium and AMF have been reported, the actual outcome of the tripartite symbiosis is also influenced by soil environmental conditions (Cofré *et al.*, 2020; Goss *et al*, 2017; Liu *et al.*, 2020; Sefrila *et al.*, 2023; Takács *et al.*, 2018; Wen *et al.*, 2023). Studies have shown that changes in water table depth can affect the diversity and abundance of Rhizobium and mycorrhizae, as well as their interactions in the soybean rhizosphere (Guo *et al.*, 2022; Liu *et al*., 2020; Runnel *et al.*, 2023; Xu *et al.*, 2021). Imbalances in soil moisture and oxygen levels can disrupt the optimal functioning of these microbial partnerships, potentially leading to sub-optimal plant growth and productivity (McCarter *et al*., 2020; Guo *et al.*, 2022; Zhong *et al.*, 2024).

Peat soils are unique ecosystems characterized by high water table, which can influence the dynamics of rhizospheric microorganisms. The interplay between water table, Rhizobium, and AMF in peat soils can have significant implications for soybean production. Fluctuations in water table depth can affect the composition and activity of these microorganisms, potentially impacting nutrient acquisition, plant growth, and overall yield. The soybean root-peat interface is a dynamic zone where numerous biogeochemical processes occur. Modifying the water table can also affect the performance of the tripartite symbiosis, soybean-Rhizobium-AMF. The objective of this study was to evaluate the effect of water table gradients on the Rhizobium-AMF interaction in soybean grown in peat soils.

MATERIALS AND METHODS

Sampling site description

Peat soils used in the current study were collected from riparian wetlands of the Arboretum of the Faculty of Agriculture, *Universitas Sriwijaya* in Indralaya, South Sumatra, Indonesia. The climate of Indralaya belongs to Type A with a ratio of dry month to wet month of <1.5. Despite the seasonal shift, the rainy season usually starts from November to April with an average annual precipitation of >2,500mm, while the dry season starts from May to October. Air temperature is relatively similar all year long, with a mean annual temperature of 25°C. The sampling site covers a plot of 10.0ha, consisting of upland (±3.0ha) and riparian wetland (±7.0ha). Peat depths range from <50cm (1.6 ha), 50 to 75cm (2.8 ha), and >75cm (2.6 ha). Amongst crucial native tree species include *Alstonia scholaris*, *Peronema canescens*, *Schima wallichii, Fagraea fragrans, Melaleuca leucadendra*, *Parkia speciose*, *Shorea leprosula*, *Michelia champaca* L., and *Swietenia macrophylla*.

Peat sampling and characterization

Sampling points were carefully determined based on the degree of peat decomposition. The degree of peat decomposition was assessed using the von Post Humification Scale (Von Post, 1924). Precise assessment was crucial as both horizontal and vertical variability of peat humification degree was discovered in the study area.

Peat blocks of sapric peats measuring 30-cm x 30-cm x 55-cm (LxWxH) were collected from three sub-plots measuring 1m x 1m. All peat blocks were placed in air-tight plastic pouches and kept wet for transport to the plastic house. A small portion of disturbed peat samples were also collected for physical and chemical characterization. Water from the sampling site was also collected for watering the peat blocks during the experiment. Upon arriving at the plastic house, the peat blocks were immediately transferred to a polybag measuring 30-cm x 50-cm (DxH), while the small portions of peat samples were air-dried at room temperature (25°C), ground and sieved through for physical and chemical characterization. The peat soil was characterized by very low bulk density (0.16 g cm^{-3}), high acidity (pH 4.20), very high content of organic C and total N (631.30 g kg^{-1} and 14.29 g kg^{-1}, consecutively), low content of available inorganic phosphorus (Pi) (16.5 mg kg^{-1}), and very low to intermediate content of exchangeable bases (exch. K = 0.38 cmol (+) kg^{-1}, exch. Na = 0.33 cmol (+) kg^{-1}, exch. Ca = 0.50 cmol(+) kg^{-1}, and exch. Mg = 0.13 cmol (+) kg^{-1}, consecutively).

Preparation of planting media

Current experiment was to investigate the tripartite symbiosis of soybean-*Rhizobium japonicum*-AMF in riparian peat soil with constantly different water depths. The present study employed soybeans (*Glycine max* L. Merrill Cult. Mutiara), Rhizobium inoculant (*Rhizobium japonicum*), and AMF inoculant (*Glomus* sp.) commercially available and registered in the Ministry of Agriculture of Indonesia. The experiment used a factorial randomized complete block design with 2 (two) factors and 3 (three) replicates. The first factor was the microbial inoculation - single inoculation with *Rhizobium japonicum* (R) and dual inoculation with *Rhizobium japonicum* and AMF (RF). The second factor was the water depths (WD) - WD_1= -20cm, WD_2 = -30cm, WD_3= -40cm, and WD_4 = -50cm. In total, there were 24 experimental units.

The planting medium was put into a prepared planting container (**Figure 1**). This container consisted of plastic bucket (height, h_1 = 55 cm, upper diameter, d_1 = 50cm, and lower diameter, d_2 = 30cm), black polybag (height, h_1 = 55cm and diameter, d_2 = 30cm), and peat height in the polybag (h_2 = 50cm). The polybags were perforated (diameter, d_3 = 3mm) along the wall to enable water to flow constantly from the plastic bucket into the peat block.

Peat blocks, equivalent to 5.0kg of peat, were placed in the polybags. Liming material (dolomite) was added at 12.5g per 5.0kg of peat. The liming rate was determined based on a preliminary study. Four levels of liming (0; 0.5; 1.0; 1.5; and 2.0g of dolomite) were added to 100g of peat soils, mixed thoroughly, watered with deionized water, and incubated for 14d. During the incubation, water was added daily based on daily weight loss. After 14d, pH was measured in a peat-to-water ratio of 1:1 (10g of peat in 10mL of deionized water). The results of this preliminary study, as presented in **Figure 2**, were used to determine the liming rate. Dolomite was diluted in 100mL of water and sprayed carefully and evenly at a depth of 5mm from the peat surface. After liming, the peat soils were incubated for 14d. Watering was carried out daily using water from the sampling site.

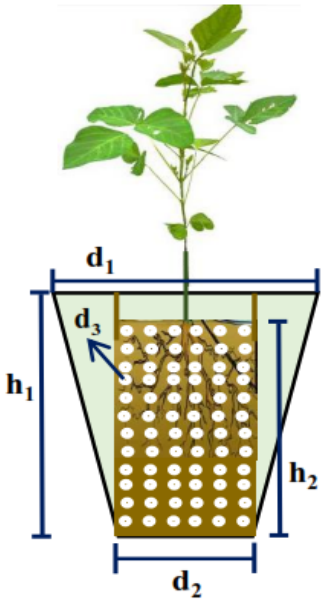

Figure 1. Planting container.

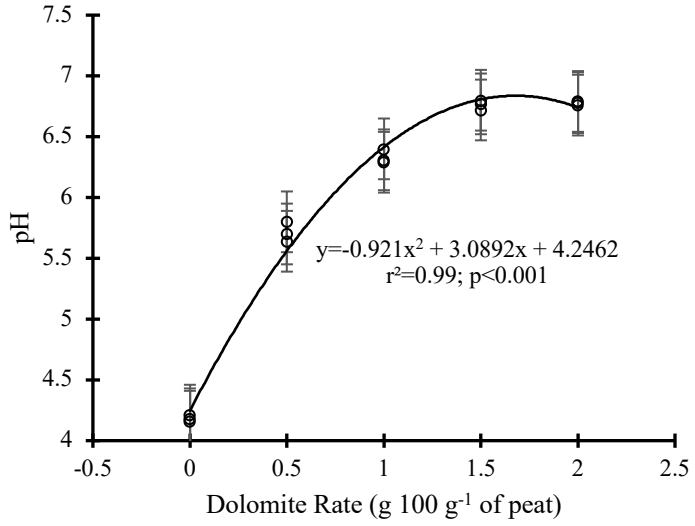

Figure 2. Relationship between dolomite rates and pH of peat in the simulation trial.

After 14d, the WD in the planting media were adjusted to four different levels, WD_1= -20cm, WD_2 = -30cm, WD_3= -40cm, and WD_4 = -50cm from peat surface (**Figure 3**). The WD was kept constant during the experiment. A water gauge mark was printed on the inner walls of each bucket. The WD was checked daily in the morning (at 9.00 AM). Once the WD subsided, water from the sampling site was added as needed to keep the WD consistent with each treatment. To avoid disturbance to the peat block in the polybag, especially physical compaction, water was added carefully by spilling water from the left or right side of the polybag in the bucket.

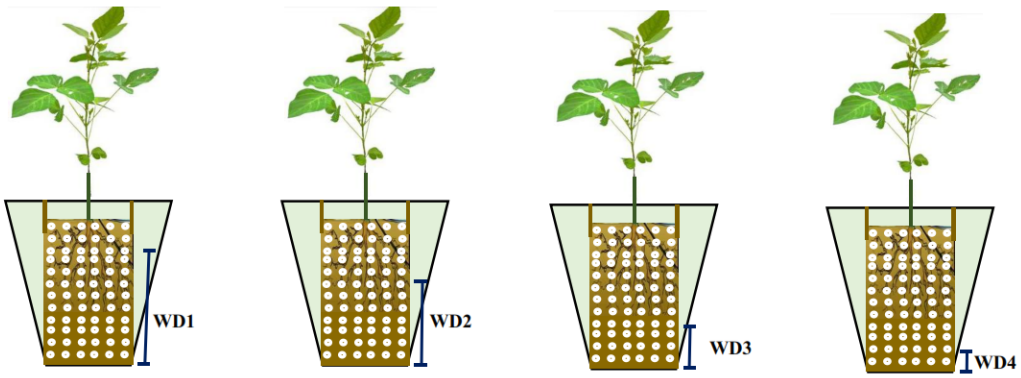

Figure 3. Water depth adjustment.

Fertilization

Fertilizers consisting of 320mg of N (Urea), 240mg of P_2O_5 (SP36), and 200mg of K_2O (KCl) per 5kg of peat were applied at planting time. The three fertilizers were mixed thoroughly with 200g of dry peat, then placed in four holes around planting holes at about 5-cm depth. The holes were eventually covered with peat soils to avoid volatilization.

Surface sterilization of soybean seed, microbial inoculation, and seeding

Soybean seeds were surfaced-sterilized in 10% H_2O_2 for 5 minutes, followed by three rinses with sterile distilled water. After disinfestation, soybean seeds were subjected to either R or RF treatment. Those subjected to the R treatment were mixed uniformly with Rhizobial inoculant and directly sown into planting holes (about 3cm below the surface). As for those subjected to the RF treatment, 9g of AMF inoculant was introduced into the planting holes, followed by the sowing of soybean seeds that had been pre-inoculated with Rhizobium on top of the AMF inoculant, which were then covered with peat. When the seeds germinated, the seedlings were thinned to two plants per polybag, subsequently reduced to one plant for further growth. The initial and subsequent thinning procedures were conducted successively, three and four days post-germination.

Plant harvest

Soybeans were harvested at the R2 stage, corresponding to 60% flowering. The whole plant and peat were removed from the polybag and subsequently immersed in water for 10 minutes, with gentle shaking to loose the peat. The whole plants were placed on a sieve with 1-mm openings, and the roots were rinsed with running tap water to collect the nodules. All fresh nodules (including those removed from the soil) were enumerated and recorded, then immersed in 70% alcohol for preservation.

Each nodule was bisected with a razor blade, and the cross-sections were examined under a magnifying glass to ascertain whether they were active. Active nodules contained leghemoglobin, a pigmented protein that resulted in a red coloration of the interior of nodules, signifying the vitality of the rhizobia. On the other hand, the inside of aged, dead, and inactive nodules was yellowish green or brown (Somasegaran and Hoben, 1994).

The assessment of AMF colonization was conducted following the methodology by Brundrett *et al.* (1984) and McGonigle *et al.* (1990). The fresh roots were dissected into approximately 1cm segments, mixed thoroughly, and sub-sampled. Subsequently, the entire root fragments were immersed in 8L of water and stirred thoroughly. Sub-sampling procedures were replicated in triplicate, amounting to a total of ten grams of fresh root fragments. The root specimens were preserved in a FAA solution (Formalin-Acetic-Alcohol) composed of a mixture of 95% ethyl alcohol, glacial acetic acid, and 37% formaldehyde in an 18:1:1 ratio,

before undergoing further processing for the assessment of AMF colonization. Root pieces previously stored in the FAA solution were transferred to a sieve of 1-mm openings, rinsed under running distilled water, placed in glass containers with 15mL of 10% KOH, and autoclaved at 121ºC for 15mins for bleaching.

After the root pieces had cooled down, they were carefully transferred to a sieve with 1-mm openings, thoroughly rinsed with running distilled water, and placed in a refrigerator for 45 minutes. Subsequently, the root pieces underwent another round of bleaching using an NH_4OH : H_2O_2 solution (3mL NH_4OH : 30mL H_2O_2 : 567mL H_2O), manually shaken for approximately 2 minutes, sieved, and then stained with Chlorazol Black E (100mL glycerin : 100mL 80% lactic acid : 100mL distilled water : 0.3g Chlorazol Black E) in an oven at 90ºC for 2 hrs.

The stained root pieces were rinsed with water and subsequently preserved in glycerin. These stained root pieces were mounted onto microscope slides and examined using a light microscope at a magnification of 200x. The graticule was accurately aligned with the roots, and intersections with the root were counted. Scoring was conducted based on the observed structures of arbuscules (A), vesicles (V), a combination of AV, mycorrhizal hyphae (MH), hyphae without arbuscules or vesicles (H), or the absence of fungal structures (NS). The total number of intersections was then calculated accordingly.

$$G = A+V+AV+MH+H+NS \quad \text{(Equation 1)}$$

A minimum of 150 intersections from one sample was necessary to acquire a representative count. The percentage of root length colonized by each structure was computed as follows:

$$\text{Arbuscular Colonization (AC)} = (A \div G) \times 100\% \quad \text{(Equation 2)}$$

$$\text{Vesicular Colonization (VC)} = (V \div G) \times 100\% \quad \text{(Equation 3)}$$

$$\text{Hyphal Colonization (HC)} = (G - NS) \div G) \times 100\% \quad \text{(Equation 4)}$$

Data analysis

The means of three replicates were calculated using WPS Spreadsheet 2019 (WPS Office 2019, Kingsoft Office Software) and JASP statistical software, which is an open-source graphical program for statistical analysis developed at the University of Amsterdam. Significant differences among treatments were assessed using a t-test ($P \leq 0.05$) performed in JASP. Additionally, regression and correlation analyses were conducted to examine the relationship between two quantitative variables.

RESULTS AND DISCUSSION

Peat acidity and available Pi

The WD significantly affected the pH and the available Pi of the peat soils (**Figure 4**). The decline in pH from 4.77 to 4.44 showed a significant correlation (r^2=0.99; p=0.017) with the decreasing WD from -20 to -50cm (**Figure 4a**). Peat soil used in the present study were naturally acidic as a result of the accumulation of organic acids generated during the gradual decomposition of plant material. As the WD decreased from -20cm to -50cm, the previously anaerobic peat altered into an aerobic state. Such a condition accelerated microbial decomposition releasing more of phenolic-OH and COOH groups and eventually decreased the peat pH (Amesbury *et al.*, 2019; Niu *et al.*, 2024). The decline of the WD also triggered oxidation reactions, transforming reduced ferrous iron (Fe^{2+}) and sulfide (S^{2-}) into oxidized forms - ferric iron and sulfate, respectively. This oxidation process led to the release of H^+ and SO_4^{2-} ions. In contrast, the utilization of bicarbonate (HCO_3^-) ions, which typically functioned

as a natural buffer against acidification, was increased, thereby contributing to further decreases in the pH of the peat soils (Amesbury *et al.*, 2019; Neina, 2019; Wei *et al.*, 2019).

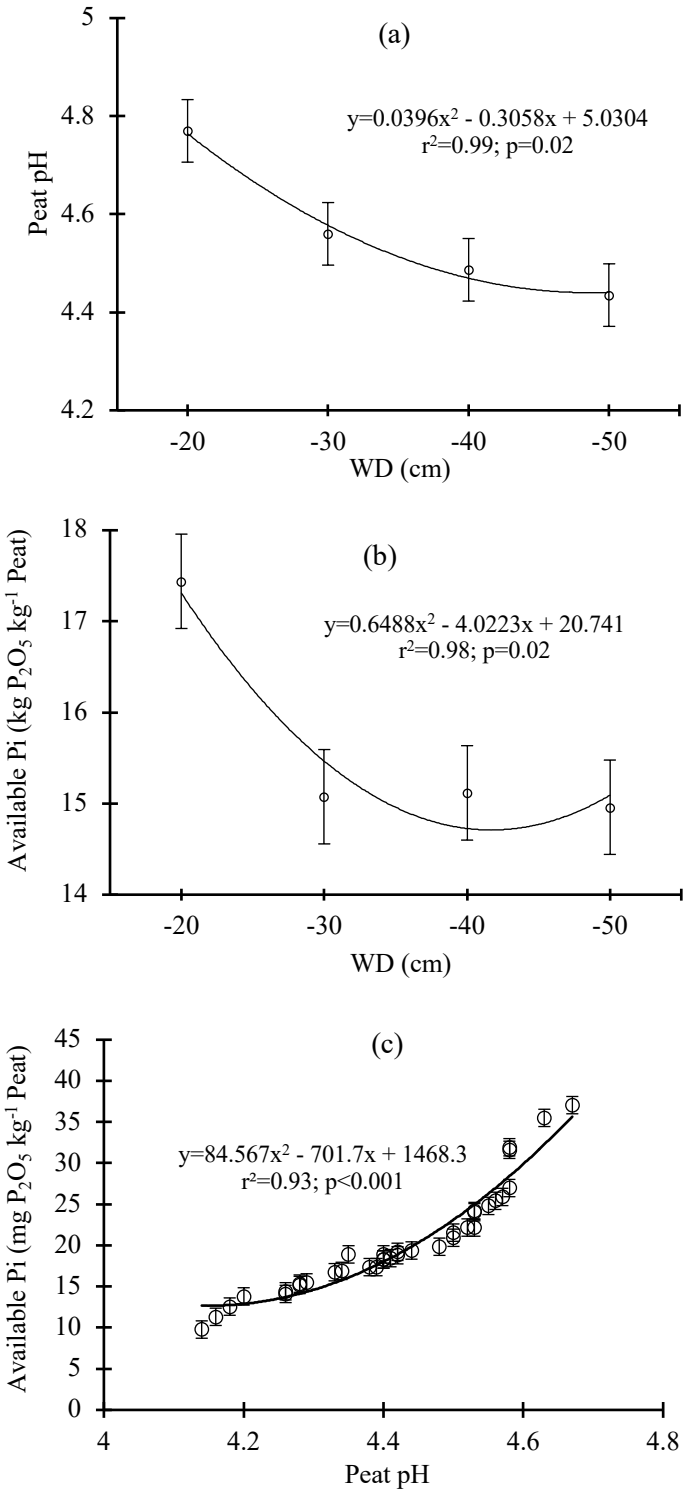

Figure 4. Correlation analysis of the WD with (a) pH, (b) available Pi, and (c) pH with available Pi in the peat soils.

A significant relationship (r^2=0.98; p=0.02) was also found between the available Pi and the WD (Figure 4b). A significant decrease in Pi availability was detected as the WD

decreased from -20 cm to -30cm. Further decreases in the WD to -50cm did not significantly change the available Pi (Figure 4b). The two main sources of Pi in our experiment were P fertilizer and peat decomposition. Both sources were applicable only to the upper layer. In contrast, the main source of Pi in the lower layer was only peat decomposition.

All treatments in our experiment received an equal quantity of P fertilizers upon planting, specifically 240mg P_2O_5 polybag^{-1}, which was applied at a depth of 5cm beneath the peat surface. Therefore, it resulted in a P-enrichment layer only in the first 5 to 20cm. Furthermore, since no overhead watering was applied during the experiment, the accumulated Pi within the peat upper layer (5 to 20 cm) did not percolate into the deeper layer (>20 cm). Additionally, the high macroporosity within the upper 20cm layer likely restricted vertical solute exchanges between this layer and the underlying layers of the peat in our study (Dom *et al*., 2021; Kiuru *et al.*, 2022; Mrotzek *et al.*, 2020).

The acidic condition in the peat soils (Figure 4a) could significantly restrict the bio-availability of the Pi. The natural Pi availability in the peat soils used in the current study was notably low, only 16.50mg P_2O_5 kg^{-1}. Although the peat pH in the current study was within a narrow range (from 4.44 to 4.77), it appeared to be a crucial factor in determining the availability of the Pi. The current study demonstrated a significant correlation (r^2=0.93; $p<0.001$) between the available Pi and the pH; the available Pi increased from 9.77mg P_2O_5 kg^{-1} to 37.05mg P_2O_5 kg^{-1} as the peat pH increased from 4.14 to 5.67 (Figure 4c). Previous studies demonstrated that in acidic environments, the Pi sorption index, a parameter showing the sorptive capacity of soils for Pi, increased with decreasing pH and increasing concentrations of Fe, thereby increasing the formation of insoluble Fe complexes (Maru *et al.*, 2020; Gondal *et al.*, 2021). It was likely that peat pH co-varying with the WD in our study controlled the abundance of Fe-oxyhydroxide, mainly Fe(III) oxyhydroxide (Maru *et al.*, 2020; Gondal *et al.*, 2021).

In fact, the study on the microbial Pi cycle and acquisition in peat soils is still lacking compared to that of other terrestrial ecosystems such as forests or agricultural soils (Hamdan *et al.*, 2012; Lin *et al.*, 2014; Weedon *et al.*, 2013). This knowledge gap is partly due to the fact that research on peatlands over the past two decades has focused on peat degradation and CO_2 emissions resulting from deforestation, land use and land use change (LULUC), fire, and canalization in peatlands. The findings of the current study confirm that the availability Pi remains one of the important issues in the management of peat soils for soybean cultivation.

Nodulation and AM colonization

Among all the treatments, only the WD showed a significant effect on both the total number of nodules (p=0.005) and the number of active nodules (p=0.007). This study indicated a significant correlation between the total number of nodules (r^2=0.94; p=0.06) and the number of active nodules (r^2=0.99; p=0.04) with the WD. These results indicated that the WD exerted significant effect on nodulation in soybeans. While the soybeans in this study did not experience hypoxia, the swallow WD (-20cm) restricted the aerobic zone, which hindered root growth and functionality in water and nutrient absorption, and inhibiting the formation of root hairs. Consequently, this led to a decrease in the number of nodulation sites. Increasing the WD to -50cm resulted in an expansion of the oxidative zone, which enhanced oxygen availability, root respiration, root development, and the formation of nodulation sites. As a result, the total number of nodules per plant increased to 52, with 34 of those nodules being active, as shown in **Figure 5**.

The lack of a significant effect of microbial inoculation on nodulation indicates that there was no competition between the Rhizobia and the AMF for root infection. Instead, these symbionts could coexist and provide complementary benefits to the soybeans. Our study

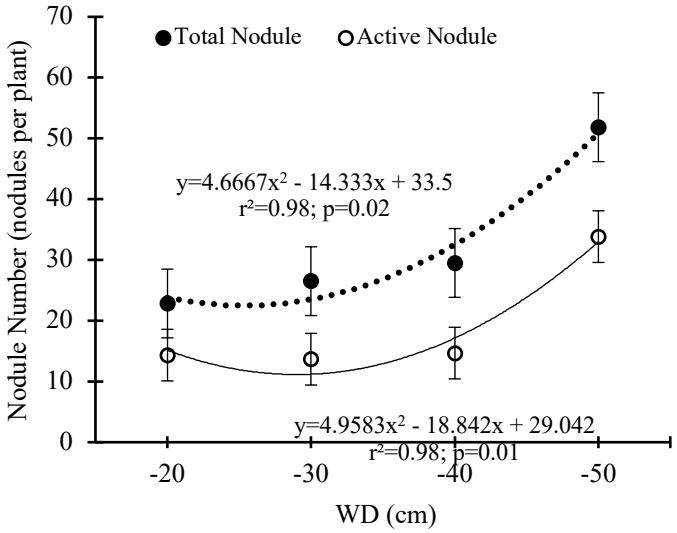

Figure 5. Correlation analysis of the WD with the nodule number at the R2 stage.

found that soybeans treated with RF showed a 17% increase in total nodules and a 31% increase in active nodules compared to those treated with R (**Figure 6**). This improvement could be attributed to several factors due to the AMF colonization, including enhanced acquisition Pi, mineralization of organic P (Po) by extracellular phosphatase (Liu *et al.*, 2021; Vieira *et al.*, 2020) and other essential nutrients (Jou *et al.*, 2018; Hao *et al.*, 2019; Machiani *et al.*, 2021), improved delivery of Pi to the nodules (Hu *et al.*, 2022; Liu *et al.*, 2020), and increased resilience against various abiotic stresses in soybeans (Ashwin *et al.*, 2022; Machiani *et al.*, 2021). Meanwhile the Rhizobia are responsible for fixing atmospheric N (Ashwin *et al.*, 2022; Igiehon and Babalola, 2021; Khaliq *et al.*, 2022; Liu *et al.*, 2021).

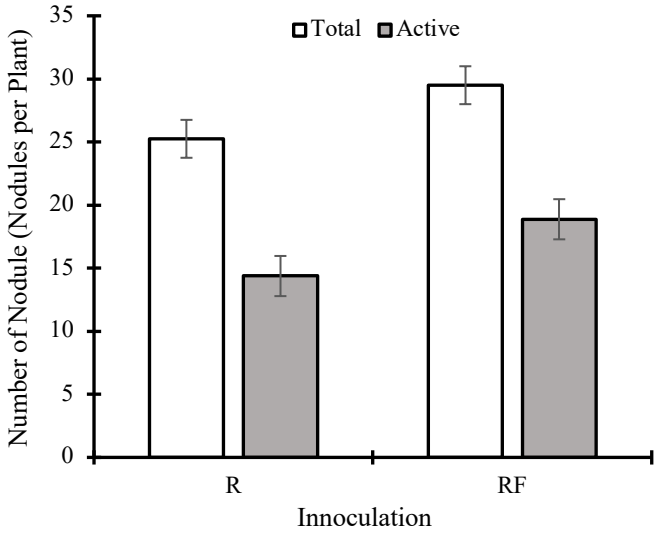

Figure 6. Effect of inoculation on the number of nodules in soybeans at the R2 stage.

The extensive network of hyphae formed by the AMF increases the depletion zone of Pi around plant roots. This expansion allows the soybeans to access Pi that would otherwise be unavailable (Shao *et al.,* 2023; Van't Padje *et al.*, 2021). Furthermore, it has been observed that

rhizobia and AMF interact in the soil before colonizing the roots of the host plant. The extra-radical mycelia produced by the AMF play a crucial role in facilitating the movement and migration of rhizobia toward the host roots (de Novais *et al.*, 2020; Gorgia and Tsikou, 2025).

The current results indicate that soybean roots were successfully infected and colonized by the AMF across the inoculation treatments and the WD, as presented in **Table 1**. The extensive root colonization, primarily by hyphae (>90%) and arbuscules (≥30%), demonstrates that soybeans grown in peat soils responded favorably to the AMF infection and colonization. In contrast, colonization by vesicles was relatively low, ranging from 1% to 2%, suggesting that the AMF were still actively growing and developing within the soybean roots.

Table 1: AMF colonization in soybeans at the R2 stage

WD (cm)	AMF Colonization (% of root length)					
	Hyphae		Arbuscule		Vesicle	
	R	RF	R	RF	R	RF
-20	98.1	99.7	30.9	31.9	2.1	2.1
-30	100.0	100.0	39.1	29.7	1.9	2.1
-40	99.4	98.6	35.2	33.7	1.5	1.5
-50	99.4	97.2	42.7	37.2	1.2	0.9

Current results also show that soybean roots subjected to the R treatment were effectively colonized by the AMF across all levels of the WD. The extent of colonization was similar to the soybeans subjected to the RF treatment as indicated in Table 1. These findings indicate the presence of native AMF inoculum in the peat soils. The significant colonization by native AMF - with over 90% hyphae and at least 30% arbuscules - suggests their crucial role in establishing a tripartite symbiosis between the soybean, rhizobium, and AMF in the peat soils examined in this study. Our findings confirm that the prevalence of native AMF has increased over the years due to their high adaptability to the physico-chemical characteristics of local soils. The native AMF persist because the sampling site from which the peat originated experiences regular drought periods, allowing native plants, such as wild grasses and herbs, to grow and serve as hosts for the native AMF.

N and P content, and soybean growth

Our findings indicate that inoculation had a significant effect ($p = 0.01$) on N and P content at the pod-filling stage, as well as on the growth of soybeans. Soybeans that received the RF treatment showed a significantly higher N content of 103.8 mg per plant, compared to 81.99 mg per plant for those that receiving the R treatment. This results in a 21% increase in nitrogen content (**Figure 7**).

It is widely recognized that the acquisition and accumulation of N by soybeans depend on two primary sources: biological nitrogen fixation (BNF) and the uptake of soil N. Previous studies have shown that BNF can satisfy nearly all of the N requirements of soybeans (Maluk *et al.*, 2023; Peoples *et al.*, 2021). While the current study did not quantify the proportion of N derived from BNF, the number of active nodule was used as a proxy indicator of BNF activity. As illustrated earlier in Figure 6, soybeans subjected to the RF treatment had a higher number of active nodules compared to those subjected to the R treatment. Recent research by Zhong *et al.* (2024) revealed that enhanced nodulation can optimize N fixation, and eventually increase the yield of soybeans.

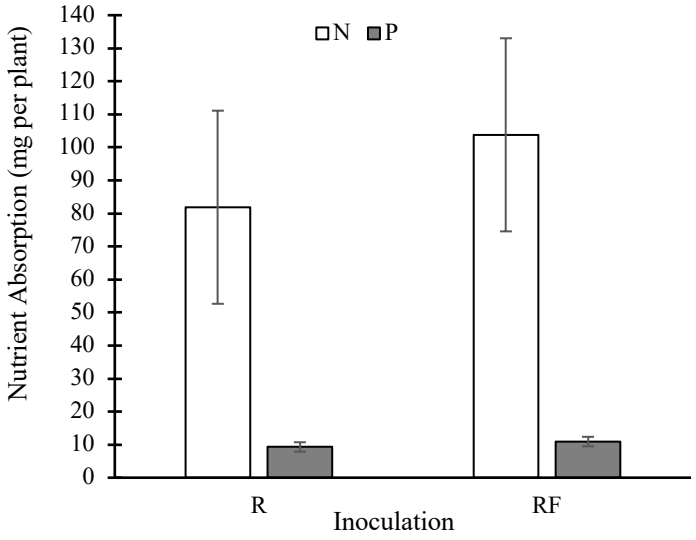

Figure 7. Effect of inoculation on the N and P content of soybeans at the R2 stage.

The effectiveness of BNF can be influenced by several factors, including the availability of Pi in the soil. As mentioned earlier, the peat soils used in this study had inherently low available Pi. As a result, the RF treatment played a crucial role in enhancing the Pi-scavenging ability of the soybeans, allowing them to meet their high P requirements for nodulation and N fixation. Present study demonstrates that P uptake of soybeans subjected to the RF treatment was higher (10.93mg plant^{-1}) compared to those treated with the R treatment (9.29mg plant^{-1}), resulting in a notable increase of 15% (**Figure 7**). Such enhancement illustrates that the coexistence of Rhizobia and AMF in the RF treatment could provide biological advantages to soybeans by enhancing Pi uptake from the peat soils. The intensive mycorrhization allowed the soybeans to access and absorb Pi beyond the root depletion zone, thereby increasing nitrogenase activity and alleviating metabolic limitations of photosynthesis under low Pi availability (Khaliq *et al.*, 2022; Liu *et al.*, 2021).

Despite the significant improvement in the nodulation brought about by the RF treatment (**Figure 6**), the draw-down of the WD was followed by declines in both N and P contents of soybeans the pod-filling stage. A significant correlation was observed between the N content (r^2=0.88; p=0.01) and P content (r^2=0.96; p=0.02) with the WD (**Figure 8**). These results underscores the strong impact of the WD on the capacity of soybean roots to access N pools in the soils and to optimize the function of the BNF, as well as on the ability of the AMF to access Pi pools in the peat soils. In spite of the fact that soybeans did not exhibit water stress symptoms throughout the experiment, even as the WD draw-downed from -20 to -50cm, it might have limited water acquisition and absorption, which is eventually hindering N and P absorption.

The findings of this study show that N and P contents, along with soybean growth during the pod-filling stage, significantly decreased as the WD levels declined, particularly in the range of -30 to -50 cm. This trend was observed regardless of the inoculation treatment applied (**Figure 9**). Notably, there was a significant correlation between the WD and both N (**Figure 9a**) and P (**Figure 9b**) contents, as well as the dry weight of soybeans (**Figure 9c**), independent of the microbial inoculation treatments used. These results emphasize the negative effects of the WD on the nutrient absorption and accumulation, the efficacy of BNF, and overall soybean growth in peat soils. Additionally, it suggests that the WD of -30 cm is a critical

threshold for optimal soybean growth in this study. These adverse effects can be attributed to several

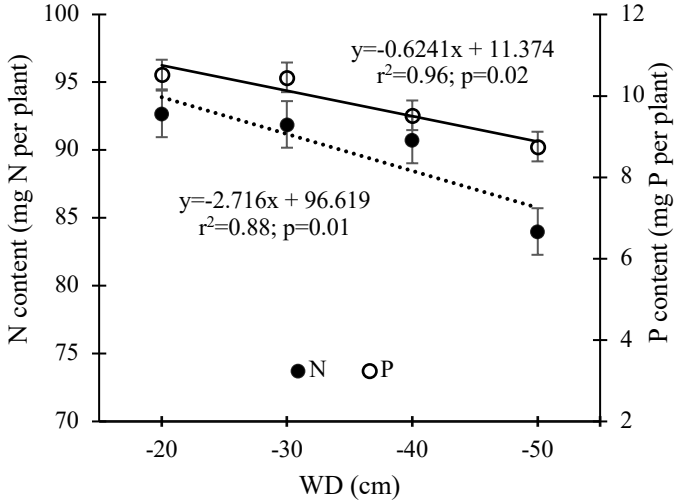

Figure 8. Correlation analysis of the WD with N and P content of soybean at the R2 stage.

factors, including impaired access to and utilization of N and P for biomass accumulation, impaired nutrient transport, reduced photosynthetic activity, and accelerated senescence. Collectively, these factors indicate that the impact of the WD outweighs the effects of microbial interactions in the rhizosphere.

A tripartite symbiosis involving soybeans, Rhizobium, and AMF has long been recognized as beneficial for growth and productivity, particularly under unfavorable conditions (Ashwin *et al.*, 2022; Liu *et al.*, 2021; Wang *et al.*, 2021). Our results indicate that the RF treatment had a positive synergistic effect on N and P contents, as well as the dry weight of soybeans at the pod-filling stage, regardless of the WD levels. Soybeans subjected to the RF treatment exhibited higher N and P contents, and greater dry weight at the pod-filling stage compared to those that received only the R treatment (**Figures 9a** to **c**). These findings highlight the synergistic benefits of the symbiotic interaction between Rhizobium and AMF in the rhizosphere. In conditions of limited P availability, such as those found in the peat soils examined in this study, soybeans tend to allocate more P to their nodules. This allocation strategy helps maintain optimal P levels, thereby supporting BNF and promoting soybean growth (Cabeza *et al.*, 2024; Liu *et al.*, 2021; Machiani *et al.*, 2021; Zhong *et al.*, 2023).

Furthermore, previous studies have demonstrated that AMF significantly enhance plant resilience against various abiotic stressors, such as limited water availability (Gorgia and Tsikou, 2025; Igiehon and Babalola, 2021; Wang *et al.*, 2024). In the current study, as the WD decreased from -30 to -50 cm, the AMF mycelia were able to explore a larger volume of peat soil compared to soybean roots. This capability improved water absorption, which subsequently enhanced osmotic regulation, cellular functions, and physiological metabolism in soybeans.

CONCLUSION

In summary, the WD significantly affected Pi availability and the soybean-rhizobium-AMF symbiosis. Shallow WD (-20 cm) restricted root growth, root hair development, and nodulation in soybeans, while deeper WD enhanced nodulation. Soybeans inoculated with both Rhizobium and AMF exhibited greater nodulation compared to those inoculated with Rhizobium alone, highlighting the benefits of this symbiotic relationship. The colonization of

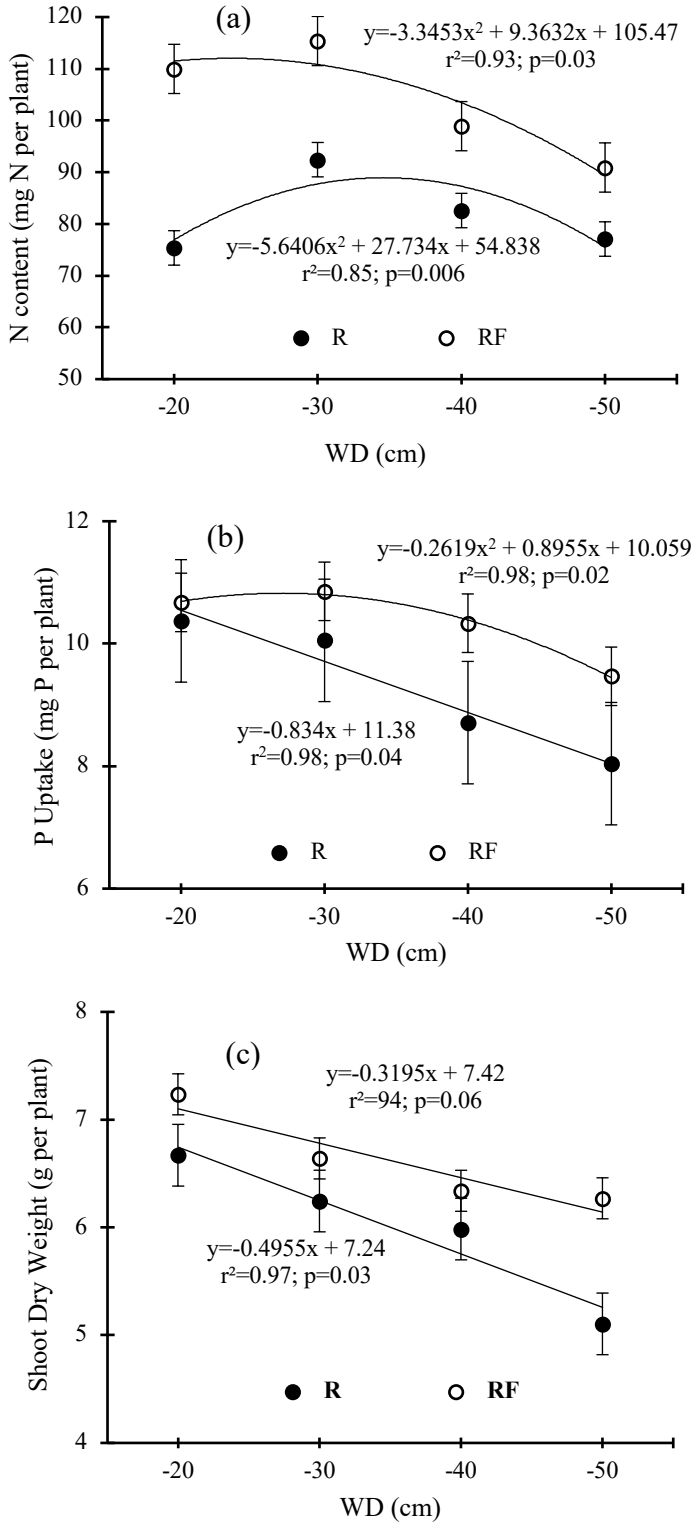

Figure 9. Correlation analysis of the WD with (a) N content, (b) P content, (c) shoot dry weight of soybean at the R2 stage under different inoculation treatments.

arbuscular mycorrhizal fungi (AMF) was uniform across all treatments, with high colonization rates (hyphae over 90%, arbuscules at least 30%), highlighting the crucial role of AMF in peat soils.The RF treatment improved N and P uptake and soybean growth across all WD levels. This improvement demonstrates that the co-inoculation of rhizobium and AMF in the RF

treatment provides biological advantages to soybeans by enhancing nutrient acquisition and overall plant performance. The similar extent of AMF colonization on soybeans inoculated with Rhizobium alone indicates the significance of native AMF in establishing a tripartite symbiosis among soybean, rhizobium, and AMF in the peat soils. Investigating the potential use of native AMF as a natural method to enhance soil fertility, promote carbon sequestration, and improve overall ecosystem health and resilience in peatlands could represent an important area for further research.

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REFERENCES

Amesbury, M.J., A. Gallego-Sala & J. Loisel. 2019. Peatlands as prolific carbon sinks. *Nature Geoscience* 12(11): 880-881. http://dx.doi.org/10.1038/s41561-019-0455-y.

Ashwin, R., D.J. Bagyaraj & B.M. Raju. 2022. Dual inoculation with rhizobia and arbuscular mycorrhizal fungus improves water stress tolerance and productivity in soybean. *Plant Stress* 4:100084. https://doi.org/10.1016/j.stress.2022.100084.

Basuki, I., J.B. Kauffman, J. Peterson, G. Anshari & D. Murdiyarso. 2019. Land cover changes reduce net primary production in tropical coastal peatlands of West Kalimantan, Indonesia. *Mitig. Adapt. Strateg. Glob. Change* 24 (4): 557-573.

Brundrett, M.C., Y. Piché, & R.L. Peterson. 1984. A new method for observing the morphology of vesicular arbuscular mycorrhizae. *Can. J. Bot.* 62:2128-2134. https://doi.org/10.1139/b84-290.

Cabezaa, R.A., J. Schulze, S. Salinas-Roco, A. Morales-González, R. Amigo, R. Pérez-Díaz, B. Carrasco, R. Contreras-Soto, C. Maldonado, R. Pedreschi, S. Espinoza, & A. del Pozo. 2024. The inhibition of N_2 fixation by nitrogen is attenuated by the P supply, altering the plant metabolism. *Environ. and Exper. Bot.* 222:105762. https://doi.org/10.1016/j.envexpbot.2024.105762.

Cofré, N., A.G. Becerra, N. Marro, L. Domínguez & C. Urcelay. 2020. Soybean growth and foliar phosphorus concentration mediated by arbuscular mycorrhizal fungi from soils under different no-till cropping systems. *Rhizosphere* 16: 100254. https://doi.org/10.1016/j.rhisph.2020.100254.

de Novais, C.B., C. Sbrana, E. da Conceição Jesus, L.F.M. Rouws, M. Giovannetti, L. Avio, J.O. Siqueira, O.J. Saggin Júnior, E.M.R. da Silva & S.M. de Faria. 2020. Mycorrhizal networks facilitate the colonization of legume roots by a symbiotic nitrogen-fixing bacterium. *Mycorrhiza* 30(2-3):389-396. https://doi.org/10.1007/s00572-020-00948-w.

Dohong, A., A. Aziz & P. Dargusch. 2018. A review of techniques for effective tropical peatland restoration. *Wetlands* 38: 275-292.

Dom, S. P., M. Ikenaga, S.Y.L. Lau, S. Radu, F. Midot, M.L. Yap, M.Y. Chin, M.L. Lo, M.S. Jee,N. Maie & L. Melling. 2021. Linking prokaryotic community composition to carbon biogeochemical cycling across a tropical peat dome in Sarawak, Malaysia. *Sci. Rep.* 11: 6416. https://doi.org/10.1038/s41598-021-81865-6.

Evans, C.D., M. Peacock, A.J. Baird, R.R.E. Artz, A. Burden, N. Callaghan, P.J. Chapman, H.M. Cooper, M. Coyle, E. Craig, A. Cumming, S. Dixon, V. Gauci, R.P. Grayson, C. Helfter, C.M. Heppell, J. Holden, Davey, J.L., J. Kaduk, P. Levy, R. Matthews, N.P. McNamara, T. Misselbrook, S. Oakley, S.E. Page, Rayment, M. Ridley, L., K.M. Stanley, J.L. Williamson, F. Worrall & R. Morrison. 2021. Overriding water table control on managed peatland greenhouse gas emissions. *Nature* 593: 548-552. https://doi.org/10.1038/s41586-021-03523-1.

Gondal, A.H., Q. Farooq, S. Sohail, S.S. Kumar, M.D. Toor, A. Zafar & B. Rehman. 2021. Adaptability of soil pH through innovative microbial approach. *Curr. Res. in Agric. Sci.* 8(2): 71-79. https://doi.org/10.18488/journal.68.2021.82.71.79.

Gorgia, P. & D. Tsikou. 2025. Tripartite symbiosis between legumes, arbuscular mycorrhizal fungi and nitrogen fixing rhizobia: Interactions and regulation. *Plant, Cell & Environ.* 1-19. https://doi.org/10.1111/pce.15341.

Goss, M.J., M. Carvalho, I. Brito, L. Alho & S. Kadir. 2017. Impacts on host plants of interactions between AMF and other soil organisms in the rhizosphere. *In* Goss, M.J., M. Carvalho, I. Brito: Functional diversity of mycorrhiza and sustainable agriculture: Management to overcome biotic and abiotic stresses. *Academic Press* pp. 81-109

Guo, J., C. Zhao, L. Zhang, Y. Han, R. Cao, Y. Liu & S. Sun. 2022. Water table decline alters arthropod community structure by shifting plant communities and leaf nutrients in a Tibetan peatland. *Sci. of the Tot. Enviro.* 814:151944. http://dx.doi.org/10.1016/j.scitotenv.2021.151944.

Hamard, S., M. Küttim, R. Céréghino & V.E. Jassey. 2021. Peat-land microhabitat heterogeneity drives phototrophic microbe distribution and photosynthetic activity. *Environ. Microbi.* 23: 6811-6827.

Hamdan, R., H.M. El-Rifai, A.W. Cheesman, B.L. Turner, K.R. Reddy & W.T Cooper. 2012. Linking phosphorus sequestration to carbon humification in wetland soils by P-31 and C-13 NMR spectroscopy. *Environ. Sci. Technol.* 46:4775-4782. https://doi.org/10.1021/es204072k.

Hao, Z., W. Xie, X. Jiang, Z. Wu, X. Zhang & B. Chen. 2019. Arbuscular mycorrhizal fungus improves Rhizobium-Glycyrrhiza seedling symbiosis under drought stress. *Agronomy* 9(10): 572. http://doi.org/10.3390/agronomy9100572.

Hergoualc'h, K., S. Atmadja, R. Carmenta, C. Martius, D. Murdiyarso & H. Purnomo. 2018. Managing peatlands in Indonesia: Challenges and opportunities for local and global communities. *CIFOR Infobriefs* No 205. https://doi.org/10.17528/cifor/006449.

Hu, Y., A.K. Pandey, X. Wu, P. Fang & P. Xu. 2022. The role of arbuscular mycorrhiza fungi in drought tolerance in legume crops: a review. *Legume Res.* 45(1): 1–9. http://dx.doi.org/10.18805/LRF-660.

Igiehon, O. & O.O. Babalola. 2021. Rhizobium and mycorrhizal fungal species improved soybean yield under drought stress conditions. *Curr. Microbiol.* 78:1615-1627. https://doi.org/10.1007/s00284-021-02432-w.

Jou, M.H.H. & A.A. Besalatpour. 2018. Interactive effects of co-inoculation of *Bradyrhizobium japonicum* strains and mycorrhiza species on soybean growth and nutrient contents in plant. *J. Plant Nutr.* 41:10-18. https://doi.org/10.1080/01904167.2017.1346666.

Khaliq, A., S. Perveen, K.H. Alamer, M. Zia Ul Haq, Z. Rafique, I.M. Alsudays, A.T. Althobaiti, M.A. Saleh, S. Hussain & H. Attia. 2022. Arbuscular mycorrhizal fungi symbiosis to enhance plant-soil interaction. *Sustainability* 14(13): 7840. https://doi.org/10.3390/su14137840.

Kiuru, P., M. Palviainen, A. Marchionne, T. Grönholm, M. Raivonen, L. Kohl & A. Laurén. 2022. Pore network modeling as a new tool for determining gas diffusivity in peat. *Biogeosciences* 19: 5041–5058. https://doi.org/10.5194/bg-19-5041-2022.

Korn, R., C. Berg, L.F. Bersier, S.M. Gray & G.G. Thallinger. 2024. Habitat conditions and not moss composition mediate microbial community structure in Swiss peatlands. *Brief Report Environ. Microbiol.* 26:e16631. https://doi.org/10.1111/1462-2920.16631.

Lastuti, D., S. Kadir & D. Budianta. 2016. Microcosmic study on heterotrophic CO_2 emission from tropical peat as related to water table modification. *Sriwijaya J. of Environ.* 1(1): 5-9. http://dx.doi.org/10.22135/sje.2016.1.1.5-9.

Leifeld, J. & L. Menichetti. 2018. The underappreciated potential of peatlands in global climate change mitigation strategies. *Nature Comm.* 9: 1-. https://doi.org/10.1038/s41467-018-03406-6.

Lin, X., M.M. Tfaily, S.J. Green, J.M. Steinweg, P. Chanton, A. Imvittaya, J.P. Chanton, W. Cooper, C. Schadt, & J.E. Kostka. 2014. Microbial metabolic potential for carbon degradation and nutrient (Nitrogen and Phosphorus) acquisition in an Ombrotrophic Peatland. *Appl. and Environ. Microbiol.* 80(11):3531-3540. https://doi.org/10.1128/AEM.00206-14.

Liu, A., Y.S. Ku, C.A. Contador & H.M. Lam. 2020. The impacts of domestication and agricultural practices on legume nutrient acquisition through symbiosis with rhizobia and arbuscular mycorrhizal fungi. Front Genet. 11:583954. https://doi.org/10.3389/fgene.2020.583954.

Liu, Y., G. Zhang, X. Luo, E. Hou, M. Zheng, L. Zhang, X. He, W. Shen & D. Wen. 2021. Mycorrhizal fungi and phosphatase involvement in rhizosphere phosphorus transformations improves plant nutrition during subtropical forest succession. *Soil Biol. and Biochem.* 153:108099. https://doi.org/10.1016/j.soilbio.2020.108099.

Machiani, M.A., A. Javanmard, M.R. Morshedloo, A. Aghaee & F. Maggi. 2021. *Funneliformis mosseae* inoculation under water deficit stress improves the yield and phytochemical characteristics of thyme in intercropping with soybean. *Sci. Rep.* 11:15279. https://doi.org/10.1038/s41598-021-94681-9.

Maluk, M., M. Giles, G.E. Wardell, A.T. Akramin, F. Ferrando-Molina, A. Murdoch, M. Barros, C. Beukes, M. Vasconcelos, E. Harrison, T.J. Daniell, R.S. Quilliam, P.P.M. Iannetta & E.K. James. 2023. Biological nitrogen fixation by soybean (*Glycine max* [L.] Merr.), a novel, high protein crop in Scotland, requires inoculation with non-native bradyrhizobia. *Front. Agron.* 5:1196873. http://doi.org/10.3389/fagro.2023.1196873.

Maru, A., A.O. Haruna, A. Asap, N.M.Abd. Majid, N. Maikol & A.V. Jeffary. 2020. Reducing acidity of tropical acid soil to improve phosphorus availability and *Zea mays* L. productivity through efficient use of chicken litter biochar and triple superphosphate. *Appl. Sci.* 10(6): 2127. https://doi.org/10.3390/app10062127.

McCarter, C.P.R., F. Rezanezhad, W.L. Quinton, B. Gharedaghloo, B. Lennartz, R. Connon, & P. Van Cappellen. 2020. Pore-scale controls on hydrological and geochemical processes in peat: Implications on interacting processes. *Earth-Sci. Rev.* 207: 103227. https://doi.org/10.1016/j.earscirev.2020.103227.

McGonigle, T.P., M.H. Miller, D.G. Evans, G.L. Fairchild & J.A. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular arbuscular mycorrhizal fungi. *New Phytol.* 115:495-501. https://doi.org/10.1111/j.1469-8137.1990.tb00476.x.

Mrotzek, A., D. Michaelis, A. Günther, N. Wrage-Mönnig & J. Couwenberg. 2020. Mass balances of a drained and a rewetted peatland: On former losses and recent gains. *Soil Syst.* 4(1): 16. https://doi.org/10.3390/soilsystems4010016.

Neina, D. 2019. The role of soil pH in plant nutrition and soil remediation. In Applied and Environmental Soil Science. *Hindawi Publishing Corporation*. https://doi.org/10.1155/2019/5794869.

Niu, Y, E. Kang, Y. Li, X. Zhang, Z. Yan, M. Li, L. Yan, K. Zhang, X. Wang, A. Yang, X. Yu, X. Kang & X. Cui. 2024. Non-flooding conditions caused by water table drawdown alter microbial network complexity and decrease multifunctionality in alpine wetland soils. *Environ Res.* 254:119152. https://doi.org/10.1016/j.envres.2024.119152.

Peoples, M.B., K.E. Giller, E.S. Jensen & D.F. Herridge. 2021. Quantifying country-to-global scale nitrogen fixation for grain legumes: I. Reliance on nitrogen fixation of soybean, groundnut and pulses. *Plant Soil* 469(1): 1-14. http://doi.org/10.1007/s11104-021-05167-6.

Putra, R., E. Sutriyono, S. Kadir, I. Iskandar, & D.O. Letari. 2019. Dynamical link of peat fires in South Sumatra and the climate modes in the Indo-Pacific region. *Indonesian J. of Geography* 51(1): 18-22. https://doi.org/10.22146/ijg.35667.

Ritsona, J.P., D.M. Aldersona, C.H. Robinson, A.E. Burkittc, A. Heinemeyer, A.G. Stimsone, A. Gallego-Salaf, A. Harris, A. Quilleth, A.A.Malik, B. Cole, B.J.M. Robroek, C.M. Heppell, D.W. Rivett, D.M. Chandler, D.R. Elliott, E. Shuttleworth, E. Lilleskov, F. Cox, G.D. Clay, I. Diack, J. Rowson, J. Pratscher, J.R. Lloyd, J.S.Walker, L.R. Belyea, M.G. Dumont, M. Longden, N.G.A. Bell, R.R.E. Artz, R.D. Bardgett, R.I. Griffiths, R. Andersen, S.E. Chadburn, S.M. Hutchinson, S.E. Page, T. Thom, W. Burn & M.G. Evans. 2021. Towards a microbial process-based understanding of the resilience of peatland ecosystem service provisioning - A research agenda. *Sci. of the Tot. Enviro.* 759:143467. https://doi.org/10.1016/j.scitotenv.2020.143467.

Robroek, B.J.M., V.E.J. Jassey, M.A.R. Kox, R.L. Berendsen, R.T.E. Mills, L. Cécillon, J. Puissant, M. Meima-Franke, P.A.H.M. Bakker & P.L.E. Bodelier. 2015. Peatland vascular plant functional types affect methane dynamics by altering microbial community structure. *J. Ecol.* 103: 925-934. https://doi.org/10.1111/1365-2745.12413.

Runnel, K., H. Tamm, M. Kohv, M.Pent, K. Vellak, J. Lodjak & A. Lõhmus. 2023. Short-term responses of the soil microbiome and its environment indicate an uncertain future of restored peatland forests. *J. of Enviro. Manag.* 345:118879. https://doi.org/10.1016/j.jenvman.2023.118879.

Sefrila, M., M. Ghulamahdi, P. Purwono, M. Melati & I. Mansur. 2023. Growth and production of soybean on different inoculant sources of arbuscular mycorrhizal fungi and water saturation periods. *Indonesian J. of Agron.* 51(1): 45-53. https://dx.doi.org/10.24831/ija.v51i1.46041.

Shao, Y., S. Jiang, H. Peng, H. Li, P. Li, R. Jiang, W. Fang, T. Chen, G. Jiang, T. Yang, S.U. Nambeesan, Y. Xu & C. Dong. 2023. Indigenous and commercial isolates of arbuscular mycorrhizal fungi display differential effects in *Pyrus betulaefolia* roots and elicit divergent transcriptomic and metabolomic responses. *Front. Plant Sci.* 13:1040134. https://doi.org/10.3389/fpls.2022.1040134.

Somasegaran, P. & H.J. Hoben. 1994. Handbook for Rhizobia: Methods in Legumes-Rhizobium technology. Springer-Verlag, New York, Inc., 450. https://doi.org/10.1007/978-1-4613-8375-8.

Strack, M., S.J. Davidson, T. Hirano & C. Dunn. 2022. The potential of peatlands as nature-based climate solutions. *Curr. Clim. Change. Rep.* 8: 71–82. https://doi.org/10.1007/s40641-022-00183-9.

Takács, T., I. Cseresnyés, R. Kovács, I. Parádi, B. Kelemen, T. Szili-Kovács & A. Füzy. 2018. Symbiotic effectivity of dual and tripartite associations on soybean (*Glycine max* L. Merr.) cultivars inoculated with *Bradyrhizobium japonicum* and AM fungi. *Front. Plant Sci.* 9:163. https://doi.org/10.3389/fpls.2018.01631.

Uda, S.K., L. Hein & A. Adventa. 2020. Towards better use of Indonesian peatlands with paludiculture and low-drainage food crops. *Wetland Ecol.* Manag. 28; 509-526. https://link.springer.com/article/10.1007/s11273-020-09728-x.

Van't Padje, A., L.O. Galvez, M. Klein, M.A. Hink, M. Postma, T. Shimizu & E.T. Kiers. 2021. Temporal tracking of quantum-dot apatite across in vitro mycorrhizal networks shows how host demand can influence fungal nutrient transfer strategies. *The ISME Journal* 15: 435-449. https://doi.org/10.1038/s41396-020-00786-w.

Vieira, L., D.K.A. da Silva, I.E.C. Escobar, J.M. da Silva, I.A. de Moura, F. Oehl & G.A. da Silva. 2020. Changes in an arbuscular mycorrhizal fungi community along an environmental gradient. *Plants* 9(1): 52. https://doi.org/10.3390/plants9010052.

Vishwakarma, K., N. Kumar, C. Shandilya, S. Mohapatra, S. Bhayana & A. Varma. 2020. Revisiting plant-microbe interactions and microbial consortia application for enhancing sustainable agriculture: A review. *Front. Microbiol.* 11:560406. https://doi.org/10.3389/fmicb.2020.560406.

Von Post, L. 1924. Das genetische System der organogenen Bildungen Schwedens. Memoires sur la nomenclature et la classification des sols. International Committee of Soil Science, Helsinki: 287-304.

Wang, Q., J. Sheng, Y. Wang, K. Chen, H. Lambers & X. Wang. 2021. The relative contribution of indigenous and introduced arbuscular mycorrhizal fungi and rhizobia to plant nutrient acquisition in soybean/maize intercropping in unsterilized soils. *Appl. Soil Ecol.* 168:104124. https://doi.org/10.1016/j.apsoil.2021.104124.

Wang, Q., M. Liu, Z. Wang, J. Li, K. Liu & D. Huang. 2024. The role of Arbuscular mycorrhizal symbiosis in plant abiotic stress. *Front. in Microbiol.* 14: 1323881. https://doi.org/10.3389/fmicb.2023.1323881.

Weedon, J.T., R. Aerts, G.A. Kowalchuk, R. van Logtestijn, D. Andringa & P.M. van Bodegom. 2013. Temperature sensitivity of peatland C and N cycling: Does substrate supply play a role? *Soil Biol. Biochem.* 61:109-120. https://doi.org/10.1016/j.soilbio.2013.02.019.

Wei, H., Y.Liu, H. Xiang, J. Zhang, S. Li & J. Yang. 2019. Soil pH responses to simulated acid rain leaching in three agricultural soils. *Sustainability* 12(1): 280. https://doi.org/10.3390/su12010280.

Wen, Z., M. Yang, H. Han, A. Fazal, Y. Liao, R. Ren, T. Yin, J. Qi, S. Sun, G. Lu, S. Hu & Y. Yang. 2023. Mycorrhizae enhance soybean plant growth and Aluminum stress tolerance by shaping the microbiome assembly in an acidic soil. *Microbio. Spectrum* 11(2): e03310-22. https://doi.org/10.1128/spectrum.03310-22.

Widyatmanti, W., B. Minasny, D. Awanda, D.A. Umarhadi, Z.S.N. Fatma, W.K. Mahendra & D.J. Field. 2022. Codification to secure Indonesian peatlands: From policy to practices as revealed by remote sensing analysis. Soil Security 9: 100080. https://doi.org/10.1016/j.soisec.2022.100080.

Wong, G.X., R. Hiratab, T. Hiranoc, F. Kiewa, J.W. Wailia, Ü. Manderd, K. Soosaard, & L. Melling. 2025. Impact of land conversion on environmental conditions and methane emissions from a tropical peatland. *Sci. of the Tot. Env.* 962: 178466. https://doi.org/10.1016/j.scitotenv.2025.178466.

Xu, Z., S.Wang, Z. Wang, Y. Dong, Y. Zhang, S. Liu & J. Li. 2021. Effect of drainage on microbial enzyme activities and communities dependent on depth in peatland soil. *Biogeochemistry* 155: 323-341. https://doi.org/10.1007/s10533-021-00828-1.

Zhang, Z., B. Poulter, A.F. Feldman, Q. Ying, P. Ciais, S. Peng & X. Li. 2023. Recent intensification of wetland methane feedback. *Nat. Clim. Change* 13: 430-433. https://doi.org/10.1038/s41558-023-01629-0.

Zhong, Y., J. Tian, X. Li & H. Liao. 2023. Cooperative interactions between nitrogen fixation and phosphorus nutrition in legumes. *New Phytol.* 237: 734-745. https://doi.org/10.1111/nph.18593.

Zhong, P., Y. Chen, Q. Sun, L.J. Lamit, J. Liu, H. Tian & Z. Wang. 2024. Drainage induced carbon nitrogen loss and microbial community change were closely related and hard to be restored in subsurface peat. *Appl. Soil Ecol.* 202: 105582. https://doi.org/10.1016/j.apsoil.2024.105582.