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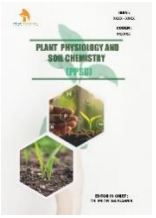

RESEARCH ARTICLE

EFFECTS OF PLANT INVASION ON PHYSICOCHEMICAL PROPERTIES, SOIL MICROBIAL COMPOSITION, AND MYCORRHIZAL COLONIZATION IN A TROPICAL FOREST OF GHANA

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ABSTRACT

Plant-soil interactions play crucial roles in facilitating invasion success, although their underlying mechanisms remain unclear particularly in tropical forest ecosystems. In this study, microbial composition, soil physicochemical properties and arbuscular mycorrhiza colonization in the root zones of two invasive species (Broussonetia papyrifera and Cedrela odorata) and two co-occurring native species (Celtis mildbraedii and Trichilia prieuriana) were compared to elucidate their roles in the spread of these invaders in the Opro River Forest Reserve in Ghana. A total of 80 plants, 80 soil cores (0-10 cm depth) and 80 fine lateral root samples were collected from 20 randomly distributed plots (50 m ×50 m each) established within the reserve for analysis. Microbial composition and arbuscular mycorrhizal colonization of the fine root samples were determined using culturing technique and microscopic examination of root fragment respectively. Results revealed no significant differences in soil microbial composition and bacteria biomass among the plant species except Aspergillus ochraceous which was found only under B. papyrifera. However, fungal load in the root zone of C. odorata was higher than those of T. prieuriana and C. mildbraedii, but comparable to that of B. papyrifera. There were no consistent effects of plant invasion on soil physicochemical properties and frequency of mycorrhizal colonization. B. papyrifera had the highest ammonification rate and intensity of arbuscular mycorrhizal colonization. These findings suggest B. papyrifera alter the soil environment differently from co-occurring plants to invade, impact and dominate in a tropical forest ecosystem.

KEYWORDS

Belowground interaction; species invasion; Opro Forest; plant - soil feedback; Alien plants; Rhizosphere

1. INTRODUCTION

Invasive alien plant species (IAPS) is a pervasive problem throughout the world and largely human driven phenomena (Bartz and Kowarik, 2019). Through transportation and commerce, many invasive plants have become established and continue to increase in their distribution in many ecosystems (Seebens et al., 2021). Report of IPBES (2019) indicates that, about one fifth of the Earth's surface including the global biodiversity hotspots are at risk due to species invasion. Understanding the key mechanism driving the success of these plant invaders is critical to maintaining local biodiversity, environmental sustainability and human wellbeing (Rai and Singh, 2020). IAPS refers to plants that are introduced intentionally or unintentionally into areas outside their native range and causing some degree of harm to humans and the environment (Essl et al., 2020). The forest ecosystems are among the common recipients of many IAPS due to their inclusion in forest rehabilitation and other silvicultural practices (Peter and Harrington, 2018). While acknowledging the roles of IAPS as biological tools for carbon sequestration and in some cases, ecological indicators of environmental quality, they can pose significant environmental, economic and health threats to humans (Souza et al., 2018). These include reduction in local biodiversity and its associated ecosystem services, modification of soil characteristics, nutrient cycling dynamics, hydrology and response to fire regimes (Rai and Singh, 2020; Kumar et al., 2021). The nature of economic impacts and responses associated with these changes differ across sectors and in many countries For instance, in Canada, annual revenue loss for 16 worst invasive species in the agriculture and forestry sectors alone was estimated as CAD$7.5 billion (Canadian Council on Invasive Species, 2023). The United State of America is reported to spend US$700 million per year to compensate for damages caused by invasive plants in forest operations (Fantle-Lepczyk et al., 2022). In Ghana and other low income countries where data on IAPS are scanty, the economic impacts are usually linked with the quality of public health, food security and other livelihood supports (Souza et al., 2018).These impacts alongside with the global climate change are reducing the resilience of native biodiversity to favourably compete with the IAPS for survival and productivity in many forest communities.

Multiple factors influence the success of plant invasion in new communities. These include propagule pressure, allelopathic effects, susceptibility of native communities to invasion as well as the functional traits of invasive species (Shephard et al., 2022). For many decades, ecologists have mostly focused on traits related to reproduction and other aboveground processes to measure invasive success and invisibility (Pearson et al., 2018). However, in recent times, belowground interactions such as plant-soil feedback (PSF) has received increased attention as an important mechanism for explaining the success of plant invasion and coexistence (Thakur et al., 2021). PSF describes the ability of the plant to

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influence plant growth by changing the biotic and abiotic structure of the soil in which they grow (Klironomos, 2019). The effects of PSF can vary between individuals of the same species (i.e., conspecific feedback) or between species (i.e. heterospecific feedback).There is growing body of evidence that, most negative PSF promotes species coexistence and maintain local biodiversity whereas positive PSF facilitates invasion success through resource acquisition and suppression of native symbiont communities (Crawford et al., 2019). The direction of the feedback has the potential to shape the patterns of plant growth and community composition in the tropics.

Ghana has a long history of plant invasion although the exact date and mode of introduction of alien plant species are unclear (Anning and Yeboah-Gyan, 2007). Ghana's diverse climatic and environmental conditions make the country highly vulnerable to biotic invasion (Ansong et al., 2019). The Opro River Forest Reserve, is a dry-semi deciduous protected forest in Ghana. This reserve has experienced past and recent disturbances in the form of illegal logging, wildfires, bushfires, and farming activities, which coupled with climate change, has resulted in extensive invasions by Broussonetia papyrifera (L.) L'Hér. ex Vent. (paper mulberry; family Moraceae) and Cedrela odorata L. (cedar wood; family Meliaceae).These invasive plants like others, grow fast, cope with diverse conditions and are aided by mutualists (Bosu et al., 2013). However, much of the research on B. papyrifera and C. odorata invasions in Ghana has focused on their impacts on aboveground communities, particularly those that describe patterns (Agyeman et al., 2016). To date, little is known about the impacts of B. papyrifera and C. odorata on soil communities and how these in turn mediate their spread into native plant communities. The purpose of this study was to evaluate belowground impacts of plant invasion in a dry semi-deciduous forest of Ghana (i.e., Opro River Forest Reserve) by comparing microbial composition and activity in the rhizophere and arbuscular mycorrhiza colonization of two invasive plants (B. papyrifera and C. odorata) with two competitive co-occurring native plants (Celtis mildbraedii Engl. (family: Cannabaceae) and Trichilia prieuriana A. Juss (family: Meliaceae). These invasive species were expected to influence the soil physicochemical properties, microbial activity and biomass in the rhizosphere as well as mycorrhizal colonization intensity and frequency than the native plants.

2. Materials And Methods

2.1 Description of study area

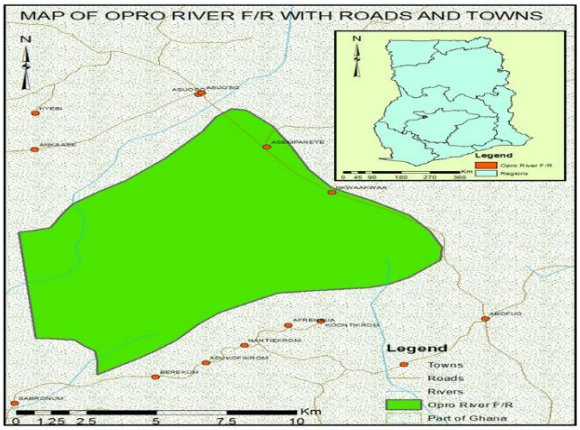

Figure 1: Map showing the Opro River Forest Reserve

The study was carried out in the Opro River Forest Reserve, located at Abofour, in the Offinso District, Ashanti Region, Ghana (Figure 1) with total area of 129.29 km2. This forest forms the boundary between the Tropical High Forest Zone of the south and the Guinea Savanna to the north of Ghana. The estimated terrain elevation above sea level is 315 m (latitude 7°10' 60' N and longitude 1°48'0'W). The forest has two rainfall seasons per year; the first season starts from April to June while the second period is from September to October. The mean annual rainfall is between 125 cm and 180 cm. The dry season is quite severe and occurs between November and March. Relative humidity is generally high ranging between 75 and 80 % in the rainy season and 70 and 72 % in the dry season. A maximum temperature of 30 °C is experienced between March and April. The Opro River Forest Reserve is one of many reserves established for their economic, ecological and ethical values and host diverse plant species including vulnerable timber species, lianas, ferns and palms.

2.2 Sampling design

Twenty (20) plots of dimension 50 m x 50 m, were established within the forest reserve. In each plot, one plant of each of the four species (B. papyrifera, C. odorata, C. mildbraedii and T. prieuriana) of similar sizes was identified and a 1m x 1m quadrat demarcated around it for sampling. A total of 80 soil samples, one under each plant, from the demarcated plots were collected for analysis. Soil that was attached to and immediately affected by the roots of the plant (rhizosphere soil) was collected after removal of all litter and organic matter. Soil samples were collected up to a depth of 10 cm from three randomly selected points within the rhizosphere with a soil corer and homogenized to form a composite sample. These samples were collected in Ziploc bag, appropriately labeled, and transported to the laboratory. The rest of each soil sample was air-dried for physicochemical analysis. In addition to the soil samples, very fine lateral roots of each of the studied plants were collected, washed and preserved in sampling bottles containing 65 % alcohol and appropriately labeled for mycorrhizal colonization determination.

2.3 Determination of soil physicochemical properties and microbial Activity

The soil physicochemical properties were determined using standard procedures. pH was determined using the pH meter, Total nitrogen (TN) by Kjeldahl method, potassium (K) and sodium (Na) followed Flame Photometery (Page et al., 1982). The Walkley and Black technique (1934) was used to determine organic carbon (OC) content. Soil organic matter (SOM) was computed by multiplying OC by the conventional "Van Bemmelen factor" of 1.724. Available phosphorus (P) was determined by Bray No.1 method (Bray and Kurtz, 1945). Steam distillation of ammonia (NH_3), using heavy MgO for NH+4 and Devarda's Alloy for NO-3 as catalyst, were performed to determine concentrations of NH+4-N and NO-3-N respectively (Bremner and Keeney, 1965). NH+4 and NO-3 were initially determined from part of the samples, with the rest of the samples kept in the dark at 25°C. NH+4 and NO-3 determination was repeated after four (4) weeks. Microbial activity was determined as rhizosphere nutrients and rates of nitrogen mineralization and ammonification. Net ammonification rate was calculated as the difference in NH+4 between the incubated and the un-incubated subsample and net N mineralization rate as the difference in NH+4 plus NO-3 and reported in µgNg-1 soil day-1 (Aguilera et al., 2010).

2.4 Microbiological Analysis

Soil samples (1g each) was diluted into 10 ml of sterilized distilled water so that 1 ml of the suspension would contain 0.1g of soil, and then shaken for 40 min. on a shaker (150 rev min-1). The suspension was used to make a four successive tenfold dilutions 10-1 to 10-4). To estimate bacteria and fungal abundance, 1 ml aliquots from each of the dilutions were cultured (by pour plating technique) using Plate Count Agar (PCA) and Potato Dextrose Agar (PDA), respectively. These plates were incubated at 25°C for 24 hours. The microbial biomass was estimated by counting the bacterial and fungal colonies (all white spot or spread) that grew in the inoculated petri plates as total viable count (TVC) using the colony counter. The results were transformed into colony forming units per gram dry weight of soil (cfu·g−1 DWs). Gram staining (using methylene blue) technique was done to identify bacteria and fungi present in the sampled soil. All specimens were observed at medium to high power under light microscope.

2.5 Assessment of Arbuscular Mycorrizal Fungi Colonization Frequency and Intensity

The lateral roots of each of the study plants were collected, washed and preserved in sampling bottles containing 65 % alcohol and appropriately labeled for mycorrhizal colonization determination. Thereafter, the root samples were stained according to (Derkowska et al., 2013). This procedure involves thoroughly rinsing the roots in water, cutting and incubating the fragments in NaOH (10 %) at 65°C for 30 minutes. After the incubation, the roots were washed with water for 5 minutes, acidified with 10 % lactic acid for 10 minutes. Following this, the root fragments were stained with carbol fuchsin for 10 minutes, rinsed with excess dye and stored in glycerol. Microscopic specimens were prepared for each plant by selecting the finest and the lightest root fragments. Thirty (30) fields were viewed per individual plant and the number of arbuscules and vesicles counted. The frequency and intensity of mycorrhizal colonization (arbuscules and vesicles) for each plant was determined using the method of (Trouvelot et al., 1986).

$$\text{Frequency (F \%)} = \frac{\text{number of views with mycorrhiza}}{\text{total number of views}} \times 100\% \qquad \text{Eqn.1}$$

$$\text{Intensity (AMM}_I\text{ \%)} = \sum_{i=1}^{N} = \frac{\text{proportion colonized by AMi}}{\text{total number of root fragments}} \times 100\% \qquad \text{Eqn.2}$$

2.6 Statistical Analysis

Differences in physicochemical properties, microbial biomass, as well as the frequency and intensity of Arbuscular Mycorrizal colonization (arbuscules and vesicles) among the plant species were tested using Analysis of Variance (ANOVA). Where a significant effect was observed, a post-hoc multiple comparison test (Tukey's Honest Significant Difference, HSD) was performed to tease out the differences among the four plant species. For the microbial biomass, data were log-transformed to normalize them before analysis of variance. The Pearson's product-moment correlation analysis was also performed to evaluate the relationship between the microbial biomass and activity under the plant species. All analyses were performed using R (R Core Team, 2024) and at $\alpha = 0.05$.

3. Results And Discussion

3.1 Variations in soil physicochemical properties

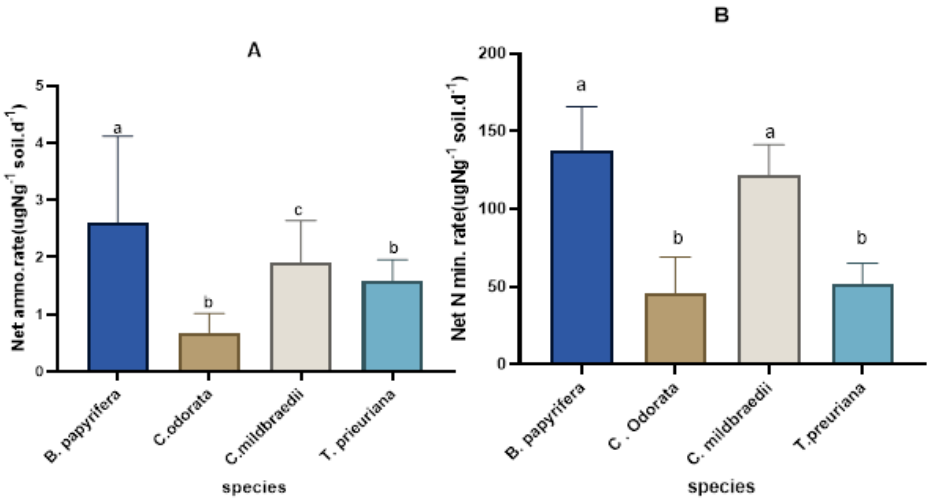

Figure 2: Net ammonification and N mineralization rates under the plant species. Bars represent standard errors (n = 20). Values with different letters differ significantly ($p < 0.05$)

The effects of plant invasion on physicochemical properties of soils and ecosystems structure are widely reported (eg.,Kumar et al., 2021;Shiferaw et al.,2021). Elsewhere, studies have demonstrated that invasive plants such as Lantana camara, Prosopis juliflora, Impatiens glandulifera and Leucanthemum vulgare improve soil nutrient pools in the invaded areas compared to uninvaded ones (Kumar et al., 2021). However, in the present study, plant invasion did not have any substantial effect on soil physicochemical properties (Table 1).The pH levels were within the acidic range of 5.64 - 5.97. TN in the soil samples ranged from 23.30 µgNg-1 soil under B. papyrifera to 28.33 µgNg-1 soil in the rhizosphere of C. mildbraedii. TN was comparable but higher for C. odorata (0.33%) and T. prieuriana (0.32 %) relative to B. papyrifera (0.20%) and C. mildbraedii (0.25 %). P concentration was higher under C. mildbraedii (4.56 mg/kg) than the other studied plants, whose recorded mean values ranging from 0.69 to 1.97 mg / kg. Like P, sodium differed between the invasive and native species, ranging from 0.42 Cmol/kg under B. papyrifera to 0.51 Cmol/kg in the rhizosphere of C. mildbraedii. However, mean concentration of K varied between T. prieuriana (0.39 Cmol / kg) and C. mildbraedii (0.53 Cmol / kg) only, with both B. papyrifera and C. odorata recording 0.47 Cmol /kg. Mean values of OC (4.71, 5.68) recorded in the root zone varied between C. odorata and C. mildbraedii. Ammonium nitrogen was higher in B. papyrifera (117.45µgNg-1 soil) and C. mildbraedii (106.97µgNg-1 soil) than the other species. The four plant species showed differences in mean net ammonification and N mineralization rates (Figure 2). Both ammonification and N mineralization rates were higher under B. papyrifera (2.00 and 137.98 µgNg-1 soil day-1, respectively) and C. mildbraedii (1.51 and 132.12 µgNg-1 soil day-1) than under C. odorata (0.55 and 66.25 µgNg-1 soil day-1) and T. prieuriana (0.82 and 81.61 µgNg-1 soil day-1). The higher ammonification rate under B. papyrifera suggests its ability to enhance nitrogen transformation and available N pool over the native species (Liu et al., 2018)

Table 1: Comparison of physicochemical properties in the root zone of the four plant species under study. Means of parameters with the same letters within a row are not significantly different at $p < 0.05$.

	Mean Concentration ± SE				
Parameter	B. papyrifera	C. odorata	C. mildbraedii	T. prieuriana	P-value
pH	5.97 ± 0.08^{a}	5.64 ± 0.11^{a}	5.80 ± 0.15^{a}	5.75 ± 0.11^{a}	0.22
Available phosphorus (mg/kg)	1.97 ± 0.45^{a}	1.25 ± 0.38^{a}	4.56 ± 0.91^{b}	0.69 ± 0.12^{a}	0.01
Potassium (Cmol/kg)	0.47 ± 0.03^{ab}	0.47 ± 0.03^{ab}	0.53 ± 0.04^{a}	0.39 ± 0.01^{b}	0.01
Sodium (Cmol/kg)	0.42 ± 0.01^{a}	0.43 ± 0.01^{a}	0.51 ± 0.02^{b}	0.49 ± 0.01^{b}	0.01
Organic carbon (%)	3.09 ± 0.12^{ab}	2.73 ± 0.12^{a}	3.30 ± 0.10^{b}	2.92 ± 0.14^{ab}	0.01
Organic matter (%)	5.33 ± 0.20^{ab}	4.71 ± 0.21^{a}	5.68 ± 0.17^{b}	5.03 ± 0.24^{ab}	0.01
Total nitrogen (%)	0.20 ± 0.01^{a}	0.33 ± 0.01^{b}	0.25 ± 0.02^{a}	0.32 ± 0.02^{b}	0.01
Ammonium nitrogen (µgNg^{-1} soil)	117.45 ± 1.96^{a}	43.47 ± 2.52^{b}	106.97 ± 4.60^{a}	59.91 ± 6.30^{c}	0.01
Nitrate nitrogen (µgNg^{-1} soil)	23.30 ± 1.51^{a}	24.37 ± 1.47^{a}	28.33 ± 2.37^{a}	23.64 ± 2.14^{a}	0.23

3.2. Variations in soil microbe composition and abundance

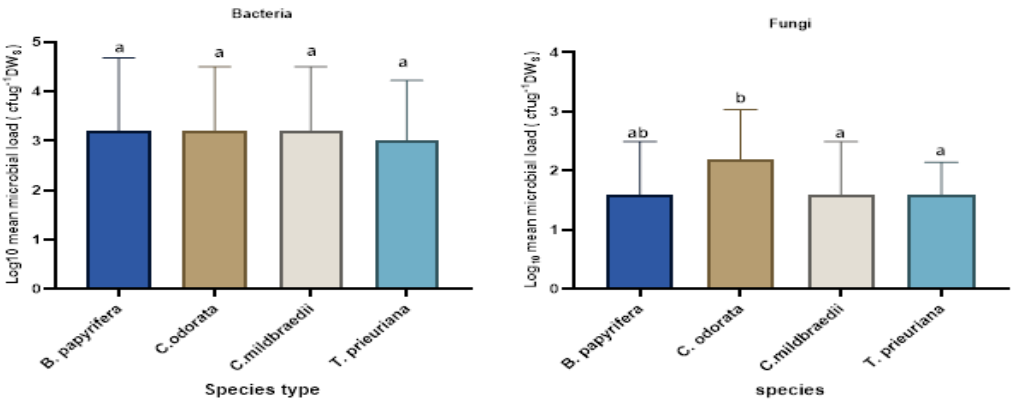

Figure 3 : Log10 mean microbial load in the rhizophere soil of plant species. Bars represent standard errors (n = 20). Values with different letters differ significantly ($p < 0.05$)

The four studied plant species recorded common soil microbes except Aspergillus ochraceous which was found under B. papyrifera only (Table 2). It is unclear if the presence of A. ochraceous play a role in the growth of B. papyrifera than the other concurring species. Fungal load in the root zone of C. odorata was higher (3.95 × 103 cfug-1 DWs) than those of T. prieuriana (2.74 ×103 cfug-1 DWs) and C. mildbraedii (2.79×103 cfug-1 DWs) but comparable to that of B. papyrifera (2.91 × 103 cfug-1 DWs, Figure 3). The relatively higher fungal load recorded affirms the ability of most plant species to form mutualistic relationships with fungi particularly Arbuscular mycorrhizal fungi (Brundrett and Tedersoo, 2018). This finding also indicates its contribution to the growth and invasion success over the native species (Yao et al., 2017). On the other hand, bacteria biomass did not vary among the studied species (range: 5.49 × 105 - 5.55 × 105 cfug-1 DWs). Most soils are known to contain 105-10^7 culturable, heterotrophic bacteria per g soil, representing only 0.1-1% of total cells (Portillo et al., 2013.). This statement is supported by the current study which found the soils sampled to contain 10^5 bacteria per g soil. Many important bacteria groups, in particular autotrophs such as nitrifiers and methane oxidisers, are very difficult to culture in laboratory conditions (Brewer et al., 2019). Thus, results from culturing approaches select a small subset of the total population. This, in part, may explain the smaller number of major types of microbes identified in the study.

Plate 1 Leaf morphology of studied plant species: C. odorata (A); B. papyrifera (B); C. mildbraedii (C); and T. prieuriana (D).

3.3 Relationship between Microbial biomass and Activity

Table 2 : List of major types/groups of microorganisms found under the plant species. Major type/group of microorganisms present in root zone of the plant species is indicated by + sign whereas – sign indicate major type/group of microorganisms absent

Type	B. papyrifera	C. odorata	C. mildbraedii	T. prieuriana
Bacteria				
Gram positive bacillus	+	+	+	+
Gram negative bacillus	+	+	+	+
E. coli	+	+	+	+
Fungi				
Aspergillus niger	+	+	+	+
Aspergillus flavus	+	+	+	+
Aspergillus ochraceous	+	-	-	-

Table 3: Pearson's product-moment correlation between microbial biomass and activity. Significant correlation is indicated by $p < 0.05$ and is bold. r values indicate coefficient of correlation.

Parameter	Bacteria		Fungi	
	R	p	R	p
pH	-0.07	0.55	-0.11	0.35
Available phosphorus	-0.03	0.76	0.02	0.89
Potassium	-0.06	0.60	0.07	0.56
Sodium	0.08	0.50	-0.05	0.64
Organic carbon	-0.18	0.11	**-0.26**	**0.02**
Organic matter	-0.18	0.11	**-0.26**	**0.02**
Total nitrogen	**0.30**	**0.01**	0.21	0.06

Table 3 (cont): Pearson's product-moment correlation between microbial biomass and activity. Significant correlation is indicated by p < 0.05 and is bold. r values indicate coefficient of correlation.				
Ammonium nitrogen	-0.03	0.76	**-0.23**	**0.04**
Nitrate nitrogen	-0.01	0.96	0.13	0.23
Ammonification rate	0.02	0.86	-0.21	0.06
N mineralization rate	-0.03	0.79	**-0.24**	**0.03**

Results of the Pearson's product-moment correlation analysis revealed variable relationships between microbial biomass and activity (Table 3). Bacteria load positively correlated (r = 0.30, p = 0.01) with total nitrogen. In contrast, fungal load correlated negatively with organic carbon and organic matter (r = -0.26, p = 0.02), ammonium nitrogen (r = -0.23, p = 0.04) and N mineralization rate (r = -0.24, p = 0.03). Fungal biomass was weakly associated with total nitrogen and ammonification rates. The positive relationship between bacteria and total N in this study is consistent with the observation that asymbiotic microorganisms mainly bacteria can fix significant amounts of nitrogen (Pang et al., 2023). On the other hand, the negative correlations exhibited by fungal load and physicochemical parameters underscores their regulatory role in litter decomposition, soil organic matter mineralization and soil nutrient dynamics (Li et al., 2021).

3.4 Arbuscular Mycorrhizal Colonization

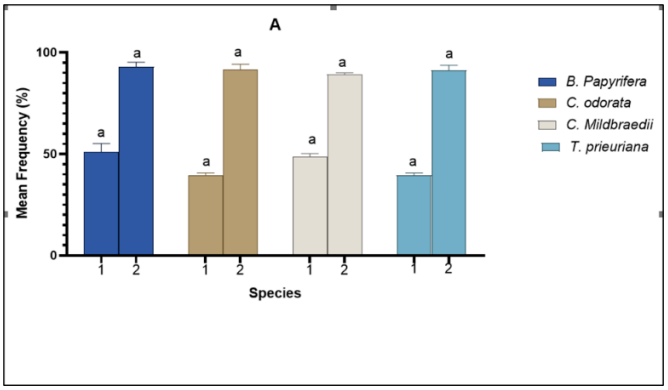

Figure 4: Mean frequency arbuscules and vesicles in the roots of plant species. Bars represent standard errors (n = 20), 1 and 2 refers to each type of mycorrhiza

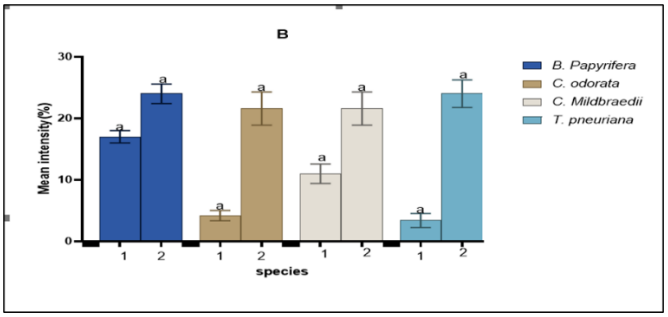

Figure 5: Mean intensity of arbuscules and vesicles in the roots of plant species. Bars represents standard errors (n = 20), 1 and 2 refers to Arbuscles and Vesicles of each type of mycorrhizal,

The frequency and intensity of vesicles were generally higher compared to the arbuscules (Figure 4 and 5). Frequency of vesicles ranged from 90.67 - 94.17% whereas that of arbuscules was 41.83 -50.33%.Vesicle intensity ranged from 21.16 – 24.1% and did not differ among species. B. papyrifera had the highest mean arbuscule intensity (17%) followed by C .mildbraedii (11%) T.prieuriana (4.2%). The least was associated with C. odorata (3.4 %). The higher intensity of arbuscules under B. papyrifera relative to the co-occurring plant species could be due to differences in colonizing fungal species (Weber et al., 2019). It has been demonstrated that co-existing plants can harbor different abuscular mycorrhizal fungi to cope with resource scarcity and environmental changes (Genre et al., 2020). Other factors such as differences in growth rate, seasons of sporulation and mineral composition of the environment may also explain the variation in fungal intensity among the studied species. The high intensity of arbuscules of B. papyrifera could be advantageous considering that, their presence can positively influence nutrient turnover, soil organic matter and other ecosystem functions (Neuenkamp et al., 2018).

4. Conclusion

The current study provides information to evaluate the impacts of belowground interactions by examining the microbial activities in the rhizophere and arbuscular mycorrhizal colonization of invasive plants with co-occurring native plants in a dry semi-deciduous forest of Ghana. Clearly, plant species invasion had little effect on belowground effects. However, the higher microbial activity, intensity of abuscular mycorrhizal colonization and nutrients in the root zone of B. papyrifera conditions the soil environment to enable it gain competitive advantage over co-occurring plants. This likely serves as a positive feedback mechanism to enhance its invasion and dominance in the reserve. Considering the importance of the Opro Forest Reserve and the extent of ongoing degradation, it would be important to institute effective restoration and mitigation measures to prevent further invasion and impacts on ecosystem processes and functioning. Such management measures should involve strategies to slow or inhibit this potential positive feedback mechanism used by the B. papyrifera in promoting its invasion.

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