

Carbon Sequestration and the Enzymic Latch Mechanism in Red, Black and White Mangrove Soils of Florida USA

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ABSTRACT

Mangrove swamps are important habitat types providing vital ecological services, such as protection of coastlines from erosion and extreme weather conditions including hurricanes, recycling of nutrients and sequestration of carbon. Mangrove swamps support a wide range of biodiversity, improve water quality, provide fish for local communities. They are also used as a source of wood fuel, medication as well as for harvesting honey for the local population. Soil samples for laboratory analyses were collected from red (*Rhizophora mangle*), black (*Avicennia germinans*) and white (*Laguncularia racemose*) mangroves in Florida, USA to determine the biogeochemistry processes. Results of analyses indicated that the red mangrove soil is the most efficient for carbon sequestration. It had the lowest phenol oxidase activity ($206.15 \text{ nmol dicq g}^{-1} \text{ h}^{-1}$), highest phenolic concentration ($262.33 \text{ } \mu\text{g g}^{-1}$) and lowest hydrolase enzyme activity (β -glucosidase) ($3.04 \text{ nmol g}^{-1} \text{ min}^{-1}$) and, as a result, the highest concentration of soil organic matter (SOM) (57.9%). It is believed that the high soil water content (84.2%) of the red mangrove, due to its proximity to the sea, is a key driver of these observations. The 'enzymic latch' mechanism appears to be prevalent in the red mangrove soil, in particular, allowing these ecosystems to be effective at carbon storage hence, could serve as an important natural tool in mitigating the effect of climate change. Preservation and conservation of mangrove swamps is vital in balancing the effect of global warming.

Keywords: Mangroves, Carbon, Sequestration, Enzymic latch, Enzymes, Decomposition

INTRODUCTION

Mangroves swamps are considered biologically active wetland ecosystems with high potentials to sequester and store huge quantities of carbon and other greenhouse gases (GHGs) as soil biomass [1, 2]. Mangroves are found between latitudes 30° North and South of the equator in several countries [3, 4]. From a global standpoint, mangroves inhabit a total coastal area of 157-160,000 km² [4]. Consequently, the world's mangroves are predominantly found along the coasts of Indonesia, Australia, Brazil, and Nigeria [5]. Mangroves forests provide vital coastal ecosystem services including water filtration, support biodiversity, protection for coastal communities against heavy storms including hurricanes, wood production, among many others [6, 7].

Donato *et al.* & Alongi [4 & 5] opined that mangrove swamps play a central role in carbon sequestration globally capturing about 18.4 Tg C yr⁻¹ to 23.2 Tg C yr⁻¹ [1]. Therefore,

mangrove ecosystems are an efficient natural tool for mitigating the effect of climate change [8, 9]. Saraswati *et al.*, Bridgham *et al.*, & Wiener *et al.* [10, 11, 12] posited that mangrove swamps could hold about 45-98% of organic carbon and up to 5metres of peat as soil biomass. Furthermore, Murdiyarso & Donato *et al.* [13, 4] revealed that mangrove swamps have sequestered an average of 1023 Mg ha⁻¹ of carbon which could be attributed to the high rates of leaf litter input from mangrove trees. Furthermore, Donato *et al.* [4] noted that mangroves soils have an average of three to four times the quantity of carbon in storage per unit area when compared to upland tropical forests.

The anoxic conditions in wetland soils due to limited atmospheric oxygen supply and low nutrient availability impairs microbial decomposition thereby encouraging the accumulation of vast organic matter in such soil environments. Consequently, Marx *et al.* [14] stated that in soils, extracellular hydrolytic enzymes activity is considered to be the key driver of organic matter breakdown and nutrient cycling. Thus, such anoxic conditions place a constraint on enzyme activities which boosts the build-up of inhibitory phenolics in wetland soils, as a result, the rate of organic matter decomposition is slowed down resulting in the accumulation of organic material as peat. Freeman *et al.* [15] opined that the entire process is controlled by oxygen limitations on a single enzyme, phenoloxidase ensuing in the phenolic build up and as a result placing a constraint on the activities of hydrolases which are the main enzymes implicated with decomposition, a process known as the 'enzymic latch' mechanism. As a result of the above scenario, mangrove wetlands are considered as significant global sinks of carbon. Saraswati *et al.* [10] investigated the influence of the 'enzymic latch mechanism' in red mangrove soil from Florida, USA, and found the mechanism to be active.

Anthropogenically induced activities such as harmful agricultural practices and land reclamation, oil spills, overexploitation of forest resources by local communities among others pose a serious threat to mangroves [16, 17]. Accordingly, the aforementioned alongside natural causes account for the loss of almost one-third of the world's mangrove forest in the last 50 years [18, 19, 10, & 20]. Similarly, Pendleton *et al.* [21] reported a 50% loss of sediment carbon within 8 years after clearing mangrove swamps in Panama. Such losses of vegetation alongside centuries of buried carbon could have the undesired impact of converting the mangrove wetlands from net sinks into net sources of GHGs with dire consequences on the global climate, which may include a rise in atmospheric temperatures and an increase in sea levels [18].

Valiela *et al.* & FAO, [22, 23] posited that without a good and sustained conservation program in place, mangrove forest could be lost at even a greater rate than tropical forest ecosystems. So also, Duke *et al.* [24] stated that 100% of mangrove forests, as well as 30-40% of coastal wetlands, is likely to be lost in the next 100 years if urgent steps are not taken to curtail the current rate of losses. Therefore, Onyena and Sam [7] suggested the establishment of effective or enabling conditions for the protection and conservation of mangrove swamps in Nigerias' Niger delta which would involve local communities to participate in a robust conservation framework aimed at preservation and conservation of the mangrove ecosystem such as is practised in India, where the government engaged rural counties in implementing preservation and conservation programs of mangrove forest reserves.

There remains much to be understood about the carbon sequestration dynamics of different mangrove forest species. This investigation is built-up on the work of Saraswati *et al.* [10] by determining the rate of microbial decomposition of organic matter on one hand and examining the impact of the 'enzymic latch' mechanism in the soils of red, black, and white mangroves in Florida, USA. It is, therefore, hypothesised that white mangrove soil has the highest rate of decomposition, whereas soils from the red mangrove have the lowest, due to their closeness to the sea and resultant period of inundation.

METHODOLOGY

A sampling of soils was done in southern Florida, the USA, close to Barefoot Beach County, Bonita Springs, in an area comprising all three mangrove tree species; red (*Rhizophora mangle*), black (*Avicennia germinans*) and white (*Laguncularia racemosa*). The red mangrove is situated closest to the sea, frequently flooded by tidal action, and closely followed by the black mangrove. The white mangrove is located inland at a higher gradient than the red and black mangroves and as a result, less frequently flooded. The three different areas had dense vegetation dominated by species peculiar to their area. The mean annual temperature range of the site is 18-29°C, and rainfall 1318 mm [25]. Soils were randomly sampled from the following locations in five replicates at a distance of about three meters apart: Red: Latitude: 26.29553, Longitude: -81.83155, Black: Latitude: 26.29600, Longitude: -81.83200, White: Latitude: 26.29465, Longitude: -81.83157.

Sample Collection

About 500g of the soil sample from a depth of 10-12 cm using a trowel was collected in five locations randomly and placed in labelled plastic bags and sealed. Samples were further packaged in cooler boxes containing ice packs and sent back to the UK and maintained at 4°C until analyses within 2 weeks of sampling.

Laboratory Analyses

Before commencement of analyses all soil samples, water and reagents were placed in an incubator at field temperature for 24 hours.

Water Extraction

Unwanted debris from soil samples were removed and hand homogenised, followed by placing a 5gram sub-sample into accordingly labelled 50 ml falcon tube, followed by the addition of 40 ml deionised water and placed on a shaker (KIKA®-Werke, GmbH & CO.KG, Germany) at 300 rpm for 24 hours. This was followed by the determination of pH and conductivity on an aliquot of the samples using SevenEasy and FiveGo (Mettler-Toledo, Leicester, UK) bench-top meters. After which, the remaining samples were centrifuged at 5000 rpm using a Sorvall ST-16R centrifuge (Thermo Scientific, UK) and 20 ml of sample filtered through 0.45 µm cellulose nitrate filters (Cole Palmer, St. Neots, UK).

Soil Water and Organic Contents

The determination of soil water and organic matter weights were carried as detailed by Frogbrook *et al.* [26]. Briefly, 10g of soil were placed in pre-weighed crucibles, and placed in an oven at 105°C for 24 hours to ensure thorough evaporation of water content. Thereafter, they were placed in a muffle furnace for 120 minutes at 550°C weighing at each point. The

weights were used to calculate the water and organic contents as a percentage of the original sample.

Phenol Oxidase Enzyme Assay

This was done by preparing a 10 mM solution of phenolic amino acid L-3, 4-dihydroxyphenylalanine (L-DOPA) (Sigma Aldrich Ltd, UK) substrate by dissolving 0.986g of powder and transferring into a 500ml capacity Duran bottle and making up the volume with deionised water as described by Dunn *et al.* [27].

Two 1g homogenised soil sub-samples were placed into two separate stomacher bags, one labelled as blank (B) and the other as substrate (S) followed by the addition of 9 ml deionised water to each bag and homogenised in stomacher equipment. This was followed by the addition of 10 ml L-DOPA solution and 10ml deionized water into the S and B bags respectively, homogenised and then placed in the incubator for 10 minutes. After the period of incubation, three 1.5 ml microcentrifuge tubes were filled with solution from each bag and centrifuged at 10000 rpm for 5 minutes. 300 μ L of the supernatant was then pipetted from each microcentrifuge tube into separate wells of a clear 96 well microplate and the absorbance at 475nm read using a SpectrMax M2e (Molecular Devices, Wokingham, UK) plate reader. The activity of the enzyme was calculated by subtracting the average blank absorbance value from the average substrate absorbance value and correcting for the dry weight of soil, to give an activity expressed as nmol of product formed (dopachrome or 2-carboxy-2,3-dihydroindole-5,6-quinone,) per minute (min^{-1}) per gram (g^{-1}) of soil (dry weight).

Hydrolase Enzyme Assay

Methylumbelliferone-based enzyme-substrate solutions were prepared for all 5 enzymes (400 μ M for β -glucosidase, β -xylosidase, sulphatase and chitinase; 200 μ M for phosphatase) were prepared according to Dunn *et al.* [27]. For each sample and each enzyme, 1 g of soil was placed in labelled stomacher bags and 7 ml of the relevant substrate was added. The bag was then homogenised and incubated for 1 hour (45 minutes for phosphatase) at field temperature. Following incubation, soil slurries were dispensed into 1.5 ml microcentrifuge tubes and centrifuged at 10,000 rpm for 5 minutes. 250 μ l supernatant was extracted from each and added to separate wells of a black 96 well microplate, to which 50 μ l of deionised water had been previously added. A similar procedure was adopted for the standard solutions, but instead using deionised water rather than enzyme substrate in the stomacher bags and 50 μ l of varying concentrations of MUF-free acid solution in the microplate wells. The concentration of the samples and standards was then measured using the SpectraMax M2e plate reader and converted into a value of activity following Dunn *et al.* [27].

Gas Fluxes

Soil respiration was performed by placing 10g of homogenized soil into a 50 ml falcon tube fitted with rubber septa in the lids and incubated at field temperature for 60 minutes. After the allotted 60-minute period of incubation, gases were collected from the tubes using a 10 cm³ syringe fitted with a short bevel hypodermic needle (Sigma Aldrich Ltd, Dorset, UK) and transferred into labelled (Time 2; T2), pre-evacuated 10 ml Exetainers (Labco Ltd, Lampeter, UK) fitted with screw caps with rubber septa. An air sample from above the centrifuge tubes

containing the samples at the start of the experiment was collected into five exetainers labelled as Time 1 (T1).

Gas samples were analyzed on a Varian model 450 gas chromatograph (GC) instrument, fitted with a flame ionization detector (FID) and a catalytic converter (methaniser) to measure CO₂ and CH₄ concentrations, and an electron capture detector (ECD) for N₂O. Oxygen-free nitrogen is used as the carrier gas. CH₄, CO₂, and N₂O (retention times 1.08, 1.87 and 2.25 minutes respectively) were quantified by comparison of peak area with that of the three standards of known concentrations, prepared by Scientific and Technical Gases Ltd (Newcastle under Lyme, Staffordshire, UK), used in the preparation of a standard curve

STATISTICAL ANALYSIS

Data were analysed by one-way ANOVA to test for the effect of one factor on the measured parameters; site (three levels, white, and black, red). Relationships between the enzyme activities and physico-chemical factors across the three mangrove zones were determined by correlation analysis. SPSS v22 (IBM Corporation, New York, USA) was used for all analyses. A p-value of <0.05 was used to denote significance for the ANOVA analysis, but <0.01 for the correlation analysis.

RESULTS

The red mangrove soil had a greater water content (84.2%) than soils in the black mangrove stands (73.1%), but this difference was not significant ($p>0.05$; figure 1). The soil beneath white mangroves had a much lower soil water content (44.1%), which is significantly different to the red and black ($p<0.05$). This trend was mirrored for the SOM (Figure 1), with the red mangrove having the highest SOM (57.9%), followed by the black mangrove (36.5%) and the white (9.9%), however, only the red and white mangroves sites were significantly different ($p<0.05$).

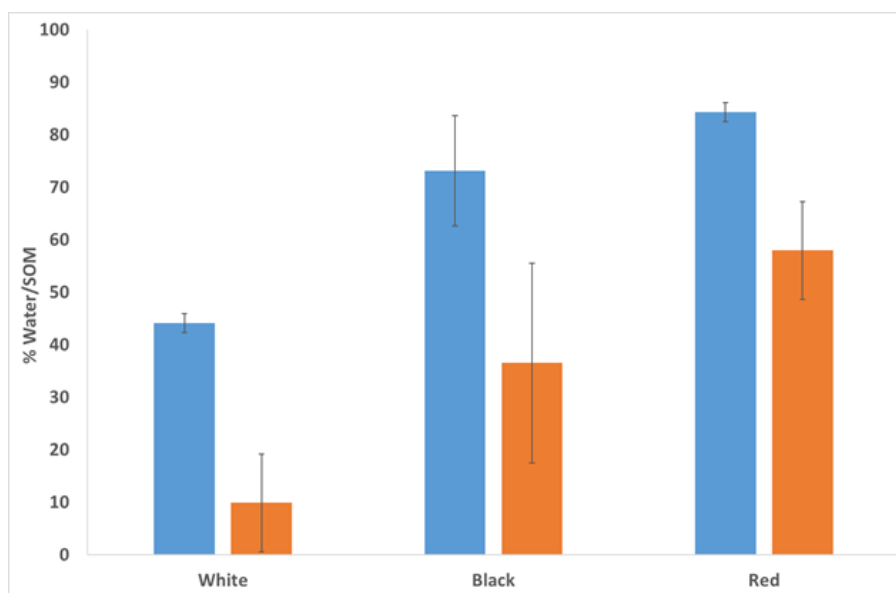


Figure 1: Bar chart showing mean soil water and soil organic matter contents in each mangrove zone (n=5, error bars + SD).

The mean soil pH differed substantially between the three zones (Figure 2), with ANOVA analysis demonstrating significant differences for all comparisons ($p < 0.05$). The white was the most alkaline (mean pH 8.09), followed by black (7.40) and red (6.32).

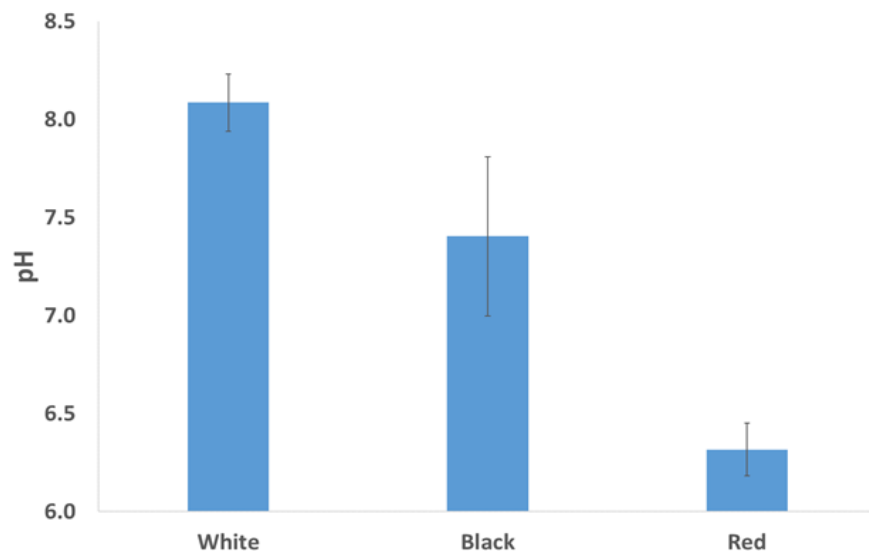


Figure 2: Bar chart showing mean soil pH in each mangrove zone (n=5, error bars + SD)

The white mangrove soil had a more than threefold greater activity of phenol oxidase (853.74 nmol dicq g^{-g} h^{-h}) in comparison to the red mangrove soil (206.15 nmol dicq g^{-g} h^{-h}), which was a significant difference ($p < 0.05$) while, black mangrove had more than twice the activity (439.48 nmol dicq g^{-g} h^{-h}) compared to the red soil, but this was not statistically significant (Figure 3).

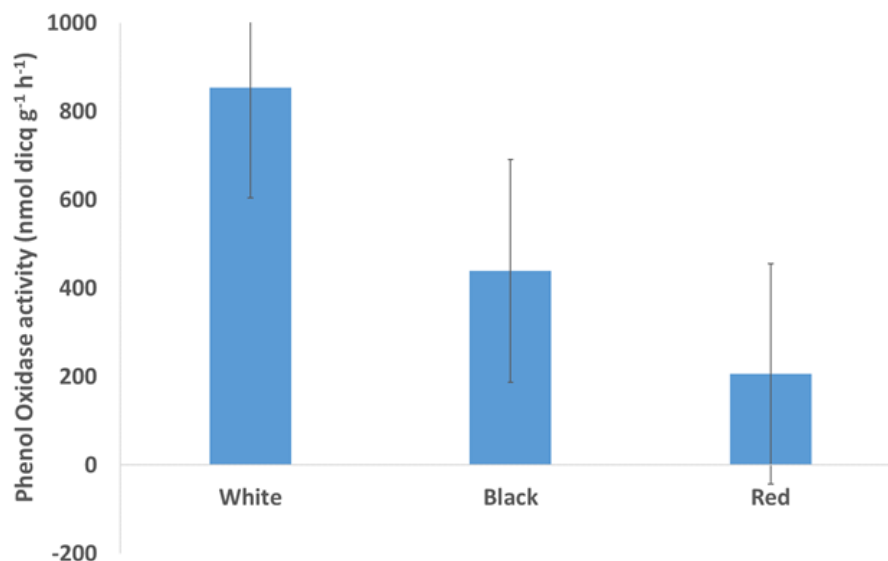


Figure 3: Bar chart showing mean activity of phenol oxidase in each mangrove zone (n=5, error bars + SD)

The concentration of soil phenolics (Figure 4) was similar in the black ($282.06 \mu\text{g g}^{-1}$) and red ($262.33 \mu\text{g g}^{-1}$) mangrove soils but for the white was significantly lower than both ($45.03 \mu\text{g g}^{-1}$) ($p < 0.05$).

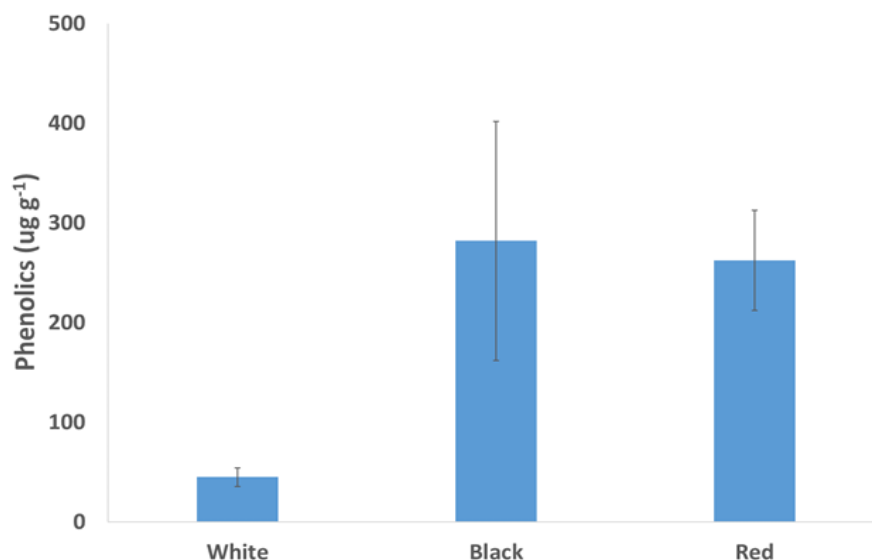


Figure 4: Bar chart showing mean concentration of soil phenolics in each mangrove zone (n=5, error bars + SD)

Similarly, the activity of β -glucosidase a hydrolase enzyme (Figure 5) does not differ much between the black ($4.41 \text{ nmol g}^{-1} \text{ min}^{-1}$) and red ($3.04 \text{ nmol g}^{-1} \text{ min}^{-1}$) mangrove soils but there was a significantly higher rate of activity in the white soil ($9.42 \text{ nmol g}^{-1} \text{ min}^{-1}$) ($p < 0.05$). The other four hydrolase enzymes showed similar trends, with the white mangrove soil always having the highest activity and the lowest activities usually being in the red mangrove.

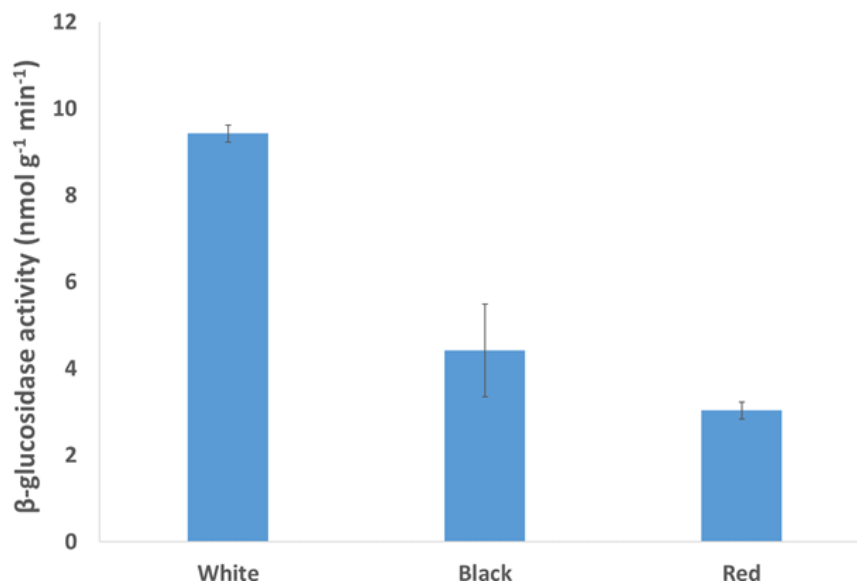


Figure 5: Bar chart showing mean activity of the enzyme β -glucosidase in each mangrove zone (n=5, error bars + SD)

The flux of CO₂ (Figure 6) does not show the same pattern as the previous parameters, with the highest flux measured from the red mangrove soils (9.33 $\mu\text{g g}^{-1}\text{s}^{-1}$) and the lowest from the black (4.39 $\mu\text{g g}^{-1}\text{s}^{-1}$), but these differences are not statistically significant ($p>0.05$).

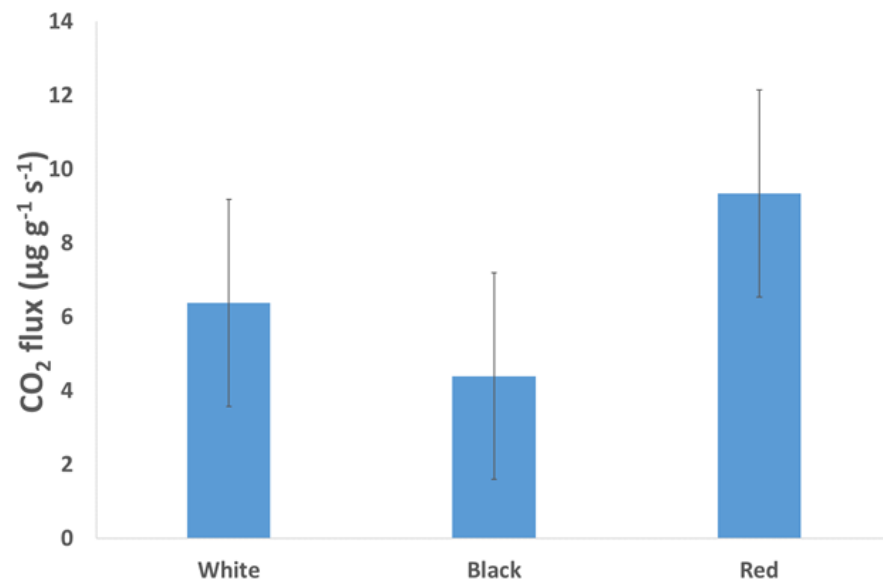


Figure 6: Bar chart showing mean CO₂ flux in each mangrove zone (n=5, error bars + SD)

A nonlinear ($r=0.953$, $p<0.001$); strong positive relationship between water percentage and SOM contents was observed (Figure 7). While no measured parameter correlated significantly with the CO₂ flux.

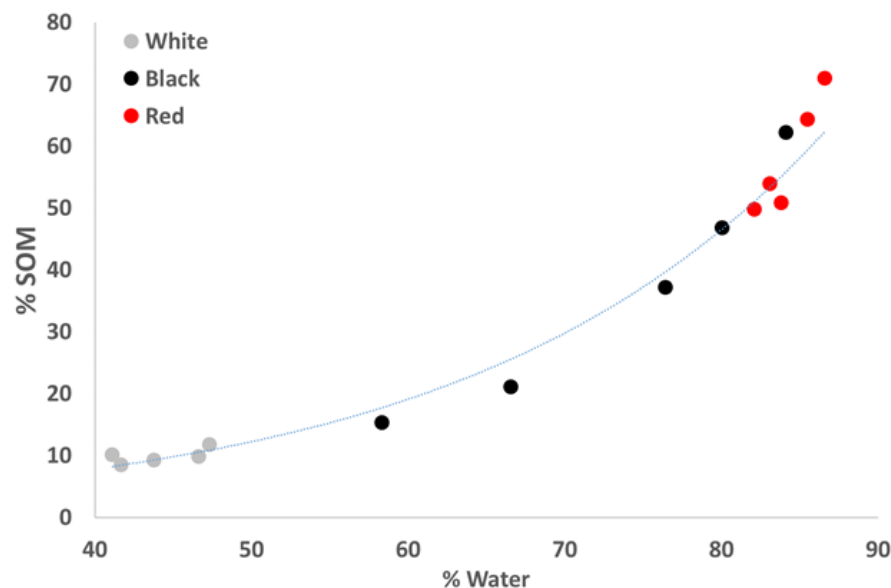


Figure 7: Scatterplot showing the relationship between % water and % soil organic matter across the 3 mangrove zones. The trend line shows an exponential relationship

DISCUSSION

A clear trend in the measured parameters was observed along the mangrove species gradient, with the white mangrove soil having high enzyme activity and low soil organic matter, the red mangrove soil having low enzyme activity and high soil organic matter and the black mangrove soil occupying a mid-point in between.

The mean height of the water table and resulting inundation is likely to be the key driver of these observations, with the red mangrove being closest to the sea and therefore having much more saturated soils. The black mangrove soils show some similarity by having higher organic matter and soil water contents with low hydrolase activity than the white mangrove soils, suggesting a low rate of decomposition. The white mangrove soil will be less frequently subject to flooding because of its location further away from the water's edge at a higher gradient. Soil water content influences the extent of oxygenation in soils and therefore exerts a strong influence on decomposition processes, with low soil oxygen availability implying low rates of decomposition [28] encouraging net sequestration of organic matter [4,10]. Friesen *et al.* [29] investigated the rate of decomposition as a factor of carbon accretion in mangroves and identified tidal inundation, vegetation types, faunal community and microbial processes as factors that could influence organic matter accretion in mangrove ecosystems.

Measurement of the activities of extracellular enzymes was a key component of this investigation, as it allows for the examination of the 'enzymic latch' mechanism in the ecosystem. The mechanism by which wetland soils can sequester globally significant amounts of organic matter in soil sediments [15].

The white mangrove soils exhibited some higher level of activities in all parameters measured except gas fluxes suggesting that the enzymic latch mechanism could not be as strong as it is in the red and black mangrove soils. Usually, the activity of phenol oxidase is perceived to be inversely correlated with phenolic compound concentrations, and this was the case in this study; the greater the activity of phenol oxidase the more phenolic compounds are broken down into smaller compounds [30,15]. This is why the highest phenolic content was found in the red mangrove soil compared to the white mangrove soil. Freeman *et al.* [28]) demonstrated that an abundance of inhibitory phenolics strengthens the enzymic latch mechanism in peatlands because phenolics are known to possess anti enzyme properties. The data obtained fits the mechanism that phenolic compounds are inhibitory to hydrolase enzymes [15]. The lowest activity of hydrolases (β -glucosidases) was observed in the red mangrove soils, followed by soils under the black mangrove stand while soils analysed from the white mangrove sites had higher enzymes activity. There was also a strong and significant negative correlation between phenolics and β -glucosidase activity (and for other hydrolase enzymes).

A strong variation in pH, by almost two-fold units, was also observed along the mangrove gradient, with the white mangrove soil having the highest followed by the black mangrove soil and then soils from the red mangrove areas. The impact of pH on decomposition processes is complex because of the range of pH optima that different microorganisms and enzymes can have (Lynch, Turner, [31, 32]. Soil pH correlated negatively with all but one of the assayed

enzymes, suggesting that it may be an additional factor as to why the red mangrove soil had the lowest rate of decomposition.

Soil samples were analysed for carbon dioxide (CO₂) emissions, which as the end-point of decomposition provide additional information alongside rates of enzyme activities. The CO₂ flux data did not conform to the pattern shown by the rest of the measured parameters. There were no significant differences recorded between the three sites. This suggests several things; either that soil decomposition processes are more complex than can be interpreted by only measuring enzyme activities, or there may have been some experimental error during the analysis. The large error bars suggest the latter may have been a contributing effect. Given the importance of CO₂ emissions in effecting climate change [33, 34], it would be worth investigating the CO₂ emissions from mangrove soils under these three species in more detail. Kristensen [35] evaluated CO₂ flux in pristine and anthropogenically-impacted mangrove forests in Tanzania, demonstrating that the pristine forest is a sink of greenhouse gases and the anthropogenically-impacted forest has reduced capacity to absorb CO₂ (although is still a net sink of carbon).

CONCLUSION

The outcome from this investigation was the discovery that the red mangrove soil had a higher capacity for water retention and build-up of organic matter than that beneath the black and white mangrove species, making it the most effective carbon sink out of the three dominant mangrove species found in much of the southern USA. The reasons for this appear to be due to the 'enzymic latch' mechanism and related to the greater soil water content of the red mangrove soil, which is the key driver of the biogeochemical differences observed. The mechanism is present in the black mangrove soils, but to a lesser extent this species, alongside the red, is a vital natural ecosystem for carbon sequestration and important in helping the fight against climate change [36].

This investigation agrees with the hypothesis that the white mangrove soil has the highest enzyme activities while soils from the red have the lowest base on proximity to the water edge. The key conclusions are:

Waterlogging is a key driver of the biogeochemical observations between the three-mangrove species.

The enzymic latch mechanism is prevalent in the red mangrove soils, due to the low phenol oxidase activity, high phenolic compound concentrations, low hydrolase enzyme activities and high content of organic matter.

The importance of mangrove ecosystems as a globally significant store of carbon cannot be understated. Mangrove swamp conservation and restoration will greatly improve the ecosystem services derived from mangroves and will allow for improved sequestration of carbon [37]. This study suggests that the red mangrove should be prioritised if the main goal of restoration is carbon sequestration.

ACKNOWLEDGEMENTS

The assistance and good guidance of Bob Wasno of the Florida Gulf Coast University, USA was very instrumental in identifying the sites for sample collection and is highly appreciated. The Funding from TETFund Nigeria is highly appreciated which made this work a success. The assistance rendered in soil sampling by the 2017 MSc Wetland conservation class of Bangor University, UK is highly appreciated.

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