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Responses of Seagrass *Amphibolis antarctica* Roots to Nutrient Additions Along a Salinity Gradient in Shark Bay, Western Australia

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ABSTRACT

Seagrass meadows in oligotrophic environments are particularly susceptible to nutrient enrichment, yet morphological and architectural seagrass root responses in these ecosystems are poorly understood. This study aimed to investigate the response of *Amphibolis antarctica*, one of dominant seagrass species in Shark Bay, roots to nutrient additions along a salinity gradient in the oligotrophic ecosystem of Shark Bay, Western Australia. A fully factorial nutrient additional experiment with four treatments (Control, N, P and N+P) was conducted at each of five sites along a salinity gradient (between ~38ppt in site 1 and ~50ppt in site 5) in Shark Bay across a three-year period (2012-2015). In the laboratory, the roots morphology and architecture *A. antarctica* were investigated using a software (WinRhizo). Then, a two-way analysis of variance (ANOVA) was performed to investigate if there was a significant change in the morphology and architecture of the roots after the nutrient inputs and along five sites with salinity gradient. There was no significant impact of nutrient addition on the root's morphology and architecture of *A. antarctica* species. However, the effect of site factor with salinity gradient was significant to all morphological aspects (total root length, root surface area and root diameter) of *A. antarctica* roots. These findings highlight the more ecological function of *A. antarctica* roots being in anchoring of the plant into the seafloor rather than to absorb nutrient from the sediment.

Keywords: Nutrient addition, Oligotrophic habitats, *Amphibolis antarctica*, Shark Bay

ABSTRAK

Padang lamun di daerah oligotropik memiliki kerentanan yang tinggi terhadap pengayaan nutrient, tetapi respon akar lamun baik secara morfologi maupun arsitektur di ekosistem ini jarang diketahui. Penelitian ini bertujuan untuk mengetahui respon akar lamun *Amphibolis antarctica*, salah satu spesies lamun yang dominan di Shark Bay, terhadap penambahan nutrient pada daerah dengan gradien salinitas di Shark Bay, Australia Barat yang memiliki ekosistem bersifat oligotropik. Sebuah eksperimen penambahan nutrient dengan empat perlakuan (kontrol, N, P dan N+P) telah dilakukan di lima stasiun pada daerah yang memiliki gradien salinitas (~38 ppt di stasiun 1 hingga ~50 ppt di stasiun 5) di Shark Bay selama tiga tahun (2012-2015). Di laboratorium, morfologi dan arsitektur akar dari *A. antarctica* diamati menggunakan program WinRhizo. Kemudian, analisis ANOVA dua arah dilakukan untuk melihat apakah penambahan nutrient dan perbedaan tingkat salinitis berpengaruh secara signifikan terhadap morfologi dan arsitektur akar spesies tersebut. Hasil penelitian ini menunjukan bahwa penambahan nutrien tidak berdampak signifikan terhadap morfologi maupun arsitektur akar *A. antarctica*. Tetapi, perbedaan tingkat salinitas berpengaruh signifikan terhadap semua aspek morfologi akar (panjang akar, area permukaan akar dan diameter akar) pada *A. antarctica*. Dilihat dari fungsi ekologi, hasil penelitian ini menunjukan bahwa akar dari spesies *A. antarctica* lebih berfungsi untuk menancapkan tanaman ke dasar laut daripada untuk menyerap nutrient dari sedimen.

Kata kunci: Penambahan nutrient, Daerah oligotropik, *Amphibolis antarctica*, Shark Bay

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1. Introduction

Spatial dispersion (architecture) and morphology of root system control the capability of plant roots to utilize soil nutrients in natural habitats where their nutrients are unevenly distributed (Lynch, 1995; Hodge, 2004). In order to absorb nutrients more efficiently, a plant will alter the morphological characteristics of its roots by raising the number of thin laterals and root length to enhance the total absorptive area of its roots (Hodge, 2004). Longer and thinner lateral roots have a higher nutrient absorption per unit root mass than thicker primary roots (Yano & Kume, 2005). An increase in the total length of thinner roots is often correlated with the rise in specific root length (SRL: root length per unit mass (cm mg^{-1})) (Hodge, 2004; Hovey et al., 2012). As the relative availability of nutrients increases, plants tend to change their roots architecture from a ‘herringbone’ root system to a ‘dichotomous’ root system (Figure 1) (Fitter et al., 1991; Robinson, 1994; Hodge, 2004). Herringbone root system is often indicative of nutrient-poor sediments since it is more efficient in utilizing sediment nutrients. The characteristic of herringbone root system is it has thicker main axis with side branches but few or no further orders of branching (Fitter & Stickland ,1991; Fitter et al., 1991). Conversely, dichotomous branching patterns are often indicative of nutrient-rich habitats, with a higher number of branches that increases the absorption of available nutrients (Fitter, 1991; Fitter & Stickland, 1991).

Architectural and morphological responses of plant roots to nitrogen and phosphorus addition have been widely studied in terrestrial plant species (Hovey et al., 2012). However, the responses of seagrass roots to changes in environmental conditions are relatively poorly understood (though see Kiswara et al., 2009; Hovey et al., 2012). Seagrass is the only underwater marine plant with underground rhizome and root systems (Short et al., 2007), that form large beds through a network of interconnected rhizomes in coastal marine habitats (Hemminga & Duarte, 2000; Mckenzie & Yoshida, 2016). Seagrasses often have higher below-ground biomass than above-ground biomass (Duarte & Chiscano, 1999), suggesting ecologically important role of below-ground biomass. Seagrass roots and rhizomes are important to anchor the plant in its habitat (Koch et al., 2006). In addition, seagrasses are also unique in that they can absorb nutrients from sediment porewaters

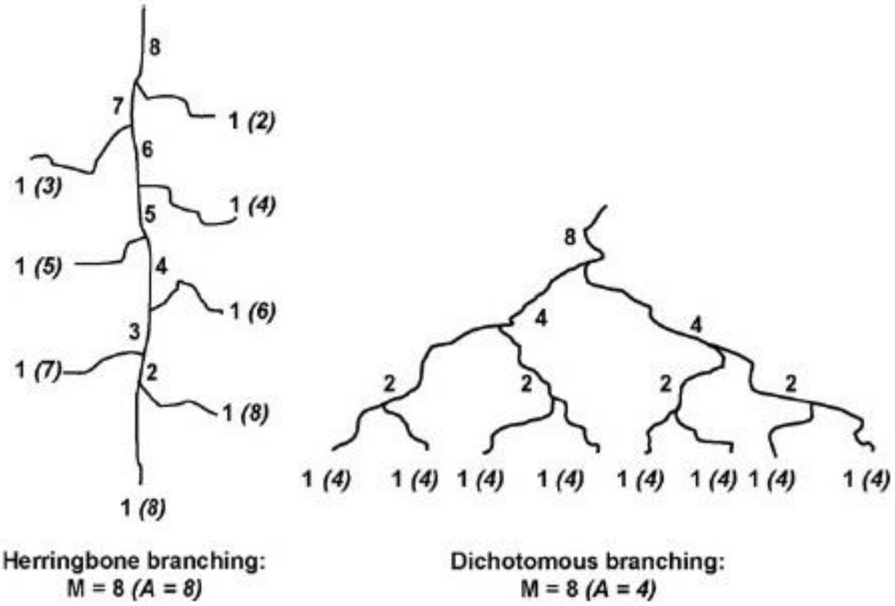

Figure 1. Plant root systems. A piece of root between two branching points (interior link) or between a branch and a meristem (exterior link) is called a link. The total number of root segments connected to the shoot through that specific link (characterized by numbers outside parentheses) are represented by the magnitude (M). The number of links in the longest path from an exterior link to the most basal link of the root system (i.e., where the roots connect to the shoot) are represented by the altitude (A) of the overall root system. The topological index of root system is described as log altitude/log magnitude (Kiswara et al. 2009).

Figure 2. The morphological characteristics of *Amphibolis antarctica* (Photo credit: Husen Rifai)

through roots uptake and from water column through leaves cuticles (Evrard et al., 2005; Kilminster et al., 2006).

Seagrasses act as foundation species and provide important ecosystem functions in coastal ecosystems including stabilizing sediments (Hemminga & Duarte, 2000), improving water quality (Hemminga & Duarte, 2000; Moore, 2004), providing habitat for many commercial marine creatures (Hemminga & Duarte, 2000, Nagelkerken et al., 2002, Heck et al., 2003), providing food source for grazing animals such as green turtles and dugongs (Mckenzie & Yoshida, 2016) and playing a role

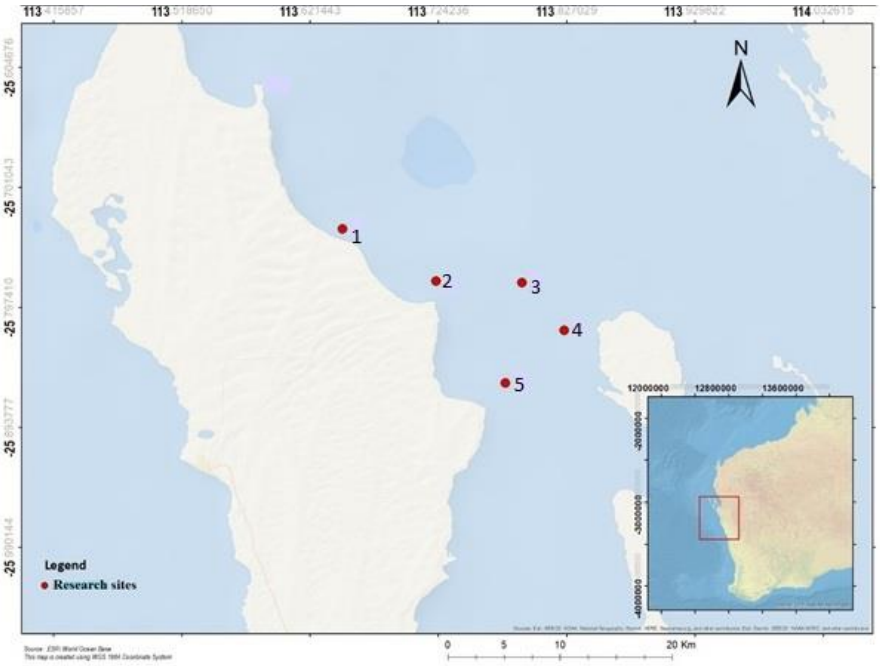

Figure 3. Map of 5 fertilization sites for *A. antarctica* in Shark Bay, Western Australia.

as carbon sinks in the ocean (Duarte et al., 2005, Fourqurean et al., 2012). With those essential values, the total benefit of seagrass ecosystems in the world is estimated $ 1.9 trillion per year (Waycott et al., 2009). However, seagrasses have been disappearing at a rate of 110 km^2 per year since 1980 mainly due to coastal development and eutrophication (Waycott et al., 2009; Mckenzie & Yoshida, 2016).

The Shark Bay World Heritage Area has one of the most extensive and diverse seagrass ecosystems in the world (Kendrick et al., 2012). There are twelve seagrass species present in Shark Bay, with *Amphibolis antarctica* is one of dominant species to form large, monospecific meadows (Walker et al., 1988). Seagrasses provide significant contribution to environmental, economic and cultural values of the Bay and are central to its status as a World Heritage Area (Fraser et al., 2014). Shark Bay has several unique environmental conditions such as high salinity gradient, hot and dry climate and very low anthropogenic pressure (Logan & Cebulski, 1970; Kendrick et al., 2012). An oligotrophic seagrass habitat like Shark Bay tend to respond more to nutrient additions than the mesotrophic and eutrophic ecosystems (Armitage et al., 2011). In an oligotrophic marine ecosystem like Shark Bay, increased nutrient inputs may represent a threat to seagrass health and have subsequent impacts on ecosystem functions these seagrasses provide (Fraser et al., 2014). Continued coastal development in Shark Bay could lead to increased localized nutrient inputs, while it is estimated that hydrological patterns in the Mid-West Australian will change significantly in the next century, with severe flood events becoming more frequent as the effect of climate change (Easterling et al., 2000; Fraser et al., 2014). Such flood events would be predicted to increase nutrient fluxes into Shark Bay, potentially impacting adjacent seagrass communities. The excess of nutrient in the seagrass environment would stimulate algal bloom and thus provide an adverse effect on seagrass resilience. Therefore, understanding how seagrasses (in particular, their belowground responses) will respond to nutrients inputs will provide important information as to potential trajectories of these meadows under future environmental change.

There are several previous studies on the responses of seagrass roots to nutrient enrichments. Kiswara et al. (2009) reveal that there only a minor variation in root systems of six tropical seagrass species placed in three sites which have different sediment type and nutrient availability. Another experiment involves two temperate seagrass species, *Posidonia australis* and *Posidonia sinuosa,* in Oyster Harbor, Western Australia, shows that there is a shift in branching patterns of *P.*

Figure 4. Experimental design along five sites with salinity gradient from site 1 to site 5.

Table 1. Two-way ANOVA results of *A. antarctica* roots analysis. Significant differences at * P < 0.05, ** P < 0.01

Source of variation	Total length (m)	Surface area (m^2)	Root diameter (mm)
Site	0.001 **	0.001 **	0.006 **
Treatment	0.397	0.449	0.811
Site x treatment	0.463	0.309	0.917

australis and *P. sinuosa* from herringbone to dichotomous patterns after the addition of nutrients (Hovey et al., 2012). While those two studies reveal the responses of seagrass roots to nutrient inputs in relatively higher N and P concentrations areas, the experiments to explore the impact of nutrient additions on seagrass roots in extremely low nutrients seagrass habitats like Shark Bay are lacking. In addition, most other nutrient addition studies only focus on above-ground responses of seagrass (e.g., shoot density, percent cover and leaf biomass). Thus, this study focuses on below-ground measurements (roots morphology and architecture) of *A. antarctica,* one of the most common species at all study sites in Shark Bay. This species has roots characteristics of thin rhizome with 1-2 roots at each node and the roots are branched (Figure 2) (den Hartog & Kuo, 2006).

This research aims to investigate the responses *A. antarctica* roots to inputs of nitrogen (N) and phosphorus (P) along a salinity and nutrient availability gradient in Shark Bay, Western Australia. This study focuses on responses in root morphology (i.e., root length, diameter and root surface area) and architecture (i.e., branching patterns) of *A. antarctica* after nutrient addition. We hypothesized that: 1) there will be an increase in root length and root surface area and at the same time a decrease in root diameter after the addition of nutrient; 2) there will be a shift in roots architecture from herringbone to dichotomous pattern after nutrient enrichments at each site.

2. Materials and Methods

2.1. Site description

Shark Bay is a 13,000-km^2 marine embayment situated ~800 km north of Perth, Western Australia. This Bay is divided by Peron Peninsula into a western and eastern

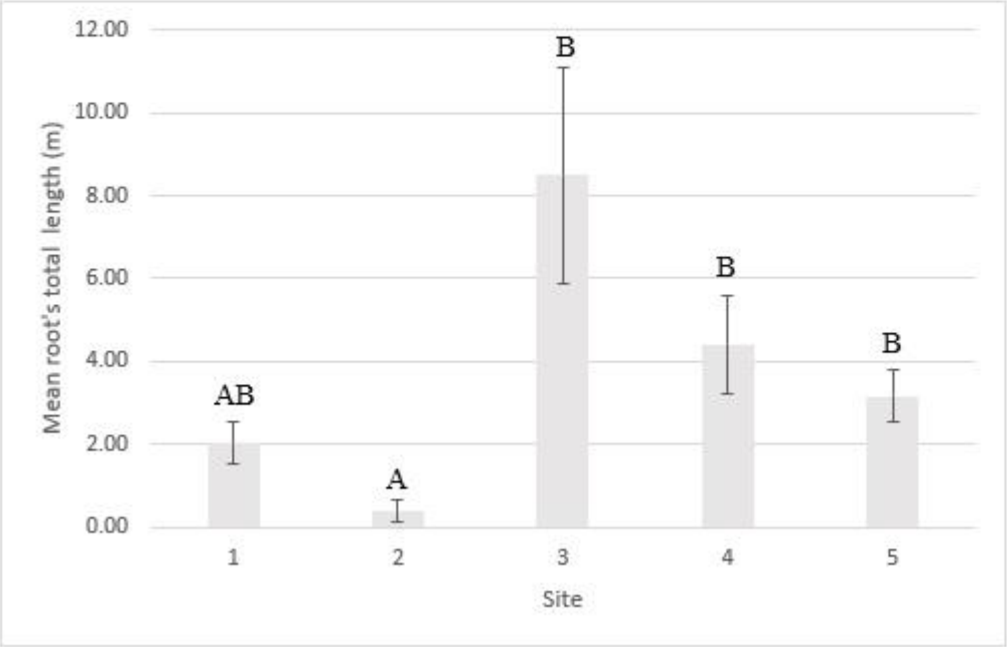

Figure 5. Response in total length of *A. antarctica* root system to site with salinity gradients from site 1 to site 5 (means ± SE, n = 100). Columns with the same letters are not significantly different from one another (P > 0.05).

embayment (Figure 3). In most years, Shark Bay only receives insignificant land inputs of water and this area is characterized by calcareous sediments. The hot and dry climate at Shark Bay is an impact of high annual evaporation rate (2000mm) that exceeds precipitation rate (200mm) by an order of magnitude, leading to a strong salinity gradient in this reverse estuary. The gradient of salinity at Shark Bay is further increased by the limited exchange of ocean waters across seagrass banks in the eastern embayment of Shark Bay that restrict water flow. Salinity increases with increasing distance from the open ocean (Logan & Cebulski, 1970). There are three different zones across the eastern embayment of Shark Bay as the effect of salinity gradient (36 ppt to > 65 ppt) namely: an oceanic region, a metahaline region, and a hypersaline region (Logan & Cebulski, 1970; Atkinson, 1987). The Faure Sill (a bank composed of calcareous sediment) that runs from the mainland to the eastern coast of the Peron Peninsula has divided the metahaline and hypersaline areas of the eastern embayment of Shark Bay (Walker, 1989).

2.2. *Experimental design*

Field work for this experiment was conducted between 2012 and 2015 in Shark Bay (25^{o}55'60^{o}S, 113^{o}32'32^{o}E). To summarize, five fertilization sites for *A. antarctica* were established off the eastern coast of the Monkey Mia peninsula, along a salinity gradient from ~38ppt in site 1 to ~50ppt in site 5 (Figure 3 & 4). 48 x 0.25m^2 study plots were established at each site and each study plot was marked out using wooden stakes driven into the sediment. To minimize mixing of treatments, all plots were separated by at least 1m from any adjacent plots. Then, one of four-treatments (Control, N, P, N+P) was randomly assigned to twelve plots per site (Figure 4). Nitrogen was added in the form of slow release urea (88g N m^{-2}, N:P;K - 33:0:0), and phosphorus in the form of superphosphate /soft-rock (23g P m^{-2}, N:P:K - 0:9:0). These concentrations were chosen to allow comparisons to other nutrient experiments carried out along Western Australia coastline (Cambridge & Kendrick, 2009; Hovey et al., 2011). All fertilizers were injected into sediments using modified 30 ml syringes with the tip ends removed. Control sediments were treated in a similar way to the other treatments. Fertilization activities were carried out quarterly in all plots from 2012 to 2015. Macrophyte percent cover was recorded before each fertilization. Eventually, seagrasses were harvested in March 2015, then frozen and brought back to the laboratory at University of Western Australia.

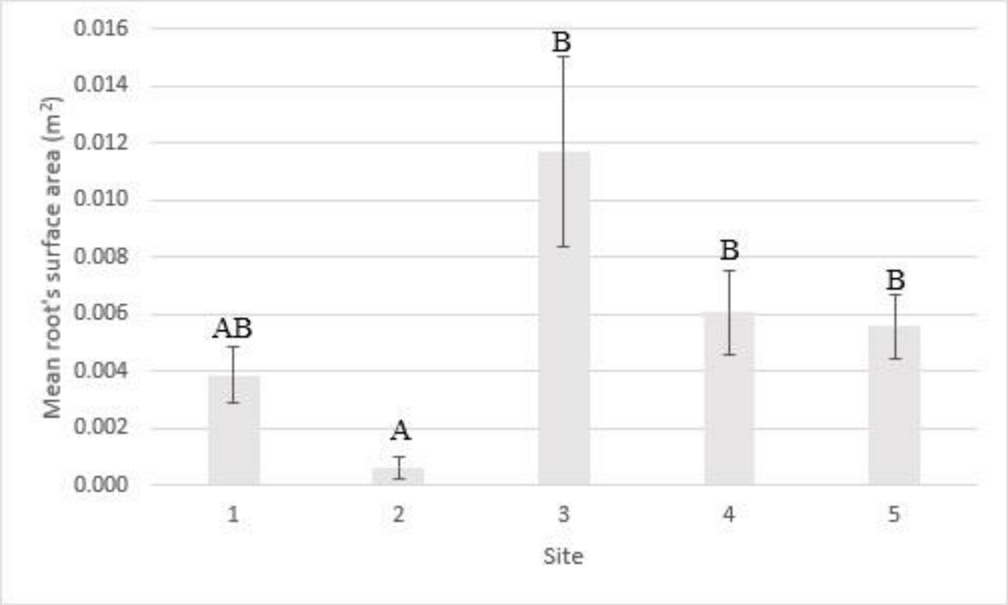

Figure 6. Response in surface area of *A. antarctica* root system to site with salinity gradients from site 1 to site 5 (means ± SE, n = 100). Columns with the same letters are not significantly different from one another (P > 0.05).

2.3. *Laboratory work*

Laboratory work of this experiment was conducted from May to September 2018. There were two steps in collecting the data. First, the roots of *A. antarctica* from Shark Bay were carefully spread out on a perspex tray and scanned using root scanner (Epson perfection v700 photo). Second, WinRHIZO software was used to measure the root length, diameter and surface area of scanned images of root samples per plant. Roots attached to the rhizome were called primary roots and roots branching from primary roots were called lateral roots, including first, second and third order branches (Hovey et al., 2011).

2.4. *Data analysis*

Raw data of the roots' total length, diameter and surface area of two seagrass species were pooled first into Microsoft Excel worksheet. Then, R software version 3.4.3 was used to analyze and visualize all data and graphs. Two-way analysis of variance (ANOVA) was performed to investigate direct and interactive effects of sites (5 levels: site 1 to 5) and nutrient additions (4 levels: control, N, P, N+P) as fixed factors on the morphological and architectural parameters of *A. antarctica* roots. If there was at least one significant main effect or interaction, a Tukey post hoc test was then be implemented to reveal significant differences in treatment means. Before conducting the analysis, all data were tested for homogeneity of variance using the Bartlett test, and data were transformed first to meet the assumptions of variances homogeneity (Underwood, 1997).

3. Results

Site was the only factor that had significant impact on the root morphology (total length, surface area and diameter) of *A. antarctica*. The addition of nutrients did not significantly affect the root morphology and there was no interaction between site and nutrient factors for *A. Antarctica* roots (see Table 1). The highest total length of *A. antarctica* root was occurred in site 3 and the lowest total length was occurred in site 2. Furthermore, the results of Tukey post hoc test revealed that the significant differences ($P < 0.05$) of root total length were occurred between site 2 and 3, site 2 and 4 and site 2 and 5 (Figure 5). For the root surface area analysis, site 2 had the lowest root surface area and site 3had the highest root surface area. The results of Tukey test for roots surface area of *A. antarctica* was the same with the results of Tukey test for total length where significant differences ($P < 0.05$) of roots surface area were occurred between site 2 and 3, site 2 and

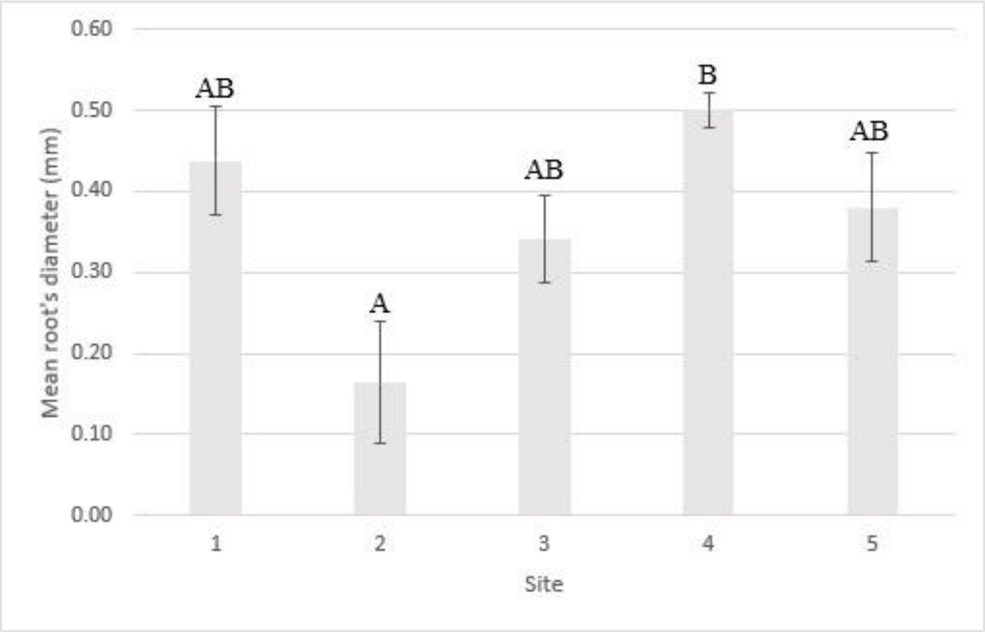

Figure 7. Response in diameter of *A. antarctica* root system to site with salinity gradients from site 1 to site 5 (means ± SE, n = 100). Columns with the same letters are not significantly different from one another ($P > 0.05$).

4and site 2 and 5 (Figure 6)

Regarding the results of diameter analysis of *A. antarctica* roots, the highest root diameter was occurred in site 4 and the lowest root diameter was occurred in site 2. Significant differences ($P < 0.05$) of roots diameter were only occurred between site 2 and 4 (Figure 7). In terms of roots architecture, treatment factors did not significantly affect the architecture of *A. antarctica* roots in all five-sites ($P>0.05$), and no shift from herringbone to dichotomous pattern after the nutrient enrichment was recorded (Figure 8).

4. Discussion

Nutrient additions to seagrass sediments in Shark Bay, an oligotrophic (low-level nutrient availability) ecosystem, did not significantly affect the root morphology and branching patterns of *A. Antarctica,* contrary to the first and second hypothesis. However, a similar nutrient addition study conducted in seagrass meadows in the mesotrophic (medium-level nutrient availability) habitat of Oyster Harbor, Western Australia showed a similar trend, with root morphology of *P. australis* and *P. sinuosa* was not significantly changed by nutrient addition (Hovey et al., 2012). Nevertheless, in terms of roots branching patterns, the results of this research were inconsistent with the study by Hovey et al. (2012) since they found that the addition of combined nitrogen and phosphorus to seagrass habitats has altered the roots branching patterns of *P. australis* and *P. sinuosa* from herringbone to dichotomous. The results of this study were also not in line with the study by Fitter & Stickland (1991) which found that root branching patterns would alter towards a dichotomous branching pattern with an increase in the availability of nitrogen and phosphorus in a particular habitat.

In terrestrial areas, an increase in nutrient availability in a certain habitat can trigger the formation and elongation of thinner and longer lateral roots to increase nutrient absorption per unit root mass (Charlton, 1996; Fitter & Stickland, 1991). However, the roots of *A. antarctica* did not show any consistent response in the morphology (total root length, root surface area and root diameter) of the root system with the enrichment of nutrients. This may suggest a more dominant ecological role of seagrass roots being in anchoring of the plant to the seafloor (Carruthers et al., 2007) rather than to uptake the nutrients from the sediment since seagrass has cuticle layers on its leaves which functioned to absorb the nutrients from the water column (Mckenzie & Yoshida, 2016). Jansen et al. (2005) also revealed that flooding-tolerant plants such *as Achillea ptarmica, Rumex palustris* and *Ranunculus repens* had the same lack of response in morphological aspects of root systems to the enrichment of nutrients when they were grown in water-saturated sediments, suggesting that aquatic plant roots often do not respond quickly to nutrient addition.

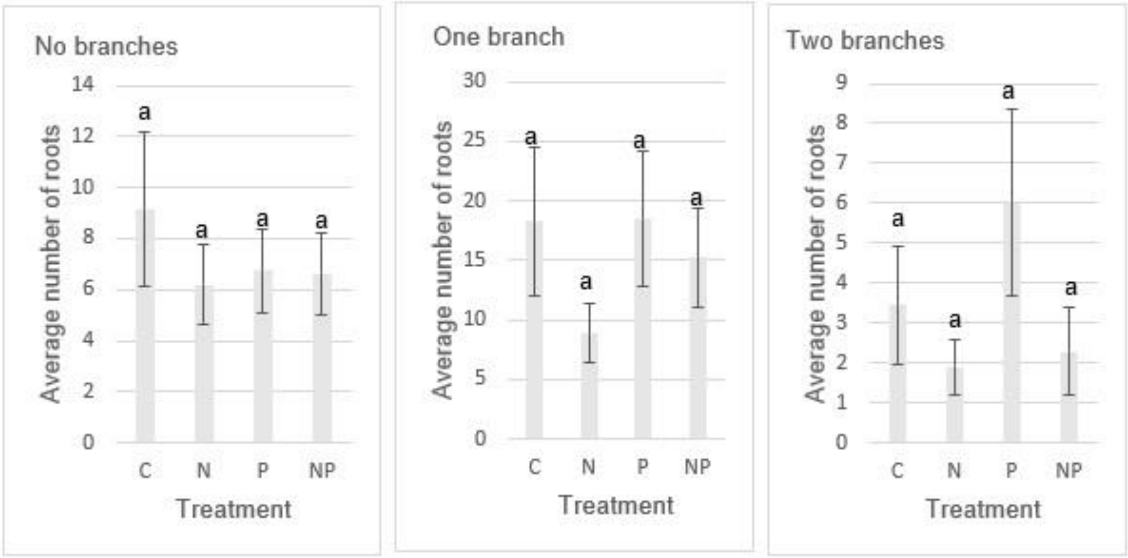

Figure 8. The impact of nutrient (control (C), nitrogen (N), phosphorus (P) and combined nitrogen and phosphorus (NP)) addition on root's branching pattern of *A. antarctica* (means ± SE, n = 20). Columns with the same letters are not significantly different from one another ($P > 0.05$).

Regarding whether or not site factor with gradient salinity provided significant impact to the morphology of *A. antarctica*, the results of the research revealed that this factor has significantly affected all morphological aspects of *A. antarctica’s* roots. Therefore, the results were consistent with the hypothesis for *A. antarctica* roots. This phenomenon indicated that *A. antarctica* roots had great plasticity to respond to the salinity gradient. This might be because *A. antarctica* had a greater range of salinity tolerant (35 - 62.4 $^{0}/_{00}$) to live (Walker et al., 1988).

The difference in root morphology of *A. antartica* along five sites in Shark Bay might be also affected by two extreme climatic events namely marine heat wave and Gascoyne floods. Those events were occurred between December 2010 and April 2011. During that austral summer, the sea temperatures of Western Australia coast increased 3^{o}C above average, and for fourteen days peaked at 5^{o}C above the normal temperatures and at the same time, there was floods delivered over 500 gigalitres of floodwater containing sediment and thus block the sun light came into the water (Fraser et al., 2014). It was estimated that there was 90% loss of the *A. antarctica* population in Shark Bay during the heat-wave and flood period. Site 2 at Monkey Mia was the most impacted site compare to the other sites. Two years after the extreme climatic events, there was a recovery of leaf biomass, however, below-ground biomass decreased by an order of magnitude. Since below-ground reserves support the tolerance of *A. antarctica* to disturbances, the decreasing trajectory of under-ground biomass would likely lower the resilience in *A. antarctica* to future disruptions. This explained why the root morphology (total root length, root diameter and root surface area) of *A. antarctica* in site 2 was the lowest compare to the other sites.

5. Conclusion

In conclusion, nutrient inputs did not significantly affect the root’s morphology and architecture of *A. antarctica* which live in oligotrophic habitats in Shark Bay, Western Australia. However, the site factor with a gradient of salinity had significant impact on all aspects of root’s morphology of *A. antarctica.* These findings highlight the more ecological role of *A. antarctica* roots being in anchoring of the plant into the seafloor rather than to uptake nutrient from the sediment.

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