Carbon and nutrient storage of the Swartkops Estuary salt marsh and seagrass habitats

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Abstract

Coastal wetlands play an important role in filtering nutrient contaminants from water bodies and are also effective carbon sinks. These systems are known as blue carbon ecosystems. Blue carbon is defined as the carbon stored and sequestered by coastal vegetated habitats such as seagrasses, salt marsh and mangroves. These habitats are being lost on a global scale due to climate change and other anthropogenic pressures. Quantifying ecosystem services provided by these habitats may lead to better conservation and restoration strategies. Research on this topic has escalated over the past decade but there are no published studies in South Africa. The aim of this study was to quantify the carbon, nitrogen, and phosphorus stocks in the above and below ground tissues of *Zostera capensis, Spartina maritima*, and *Salicornia tegetaria* — a seagrass, salt marsh grass, and salt marsh succulent. This was done in both summer and winter to understand the variability of carbon and nutrient storage. The organic carbon stock of the sediment beneath these three species was also quantified. Results showed that *S. maritima*, *S. tegetaria*, and *Z. capensis* stored 16 ± 2.9 Mg C. ha^{-1}, 4.3 ± 0.7 Mg C. ha^{-1}, and 2.1 ± 0.5 Mg C. ha^{-1} in their respective biomass, and 247 ± 48 Mg C. ha^{-1}, 212 ± 44 Mg C. ha^{-1}, and 224 ± 38 Mg C. ha^{-1} respectively in the sediment beneath these habitats. This was determined by elemental analysis and the loss on ignition method (LOI). The sediment made up the dominant carbon pool in the estuary and there was very little seasonal variation, however spatial variation was evident. The sediment carbon stocks were similar to the global mean for salt marsh (255 Mg C. ha^{-1}) and greater than the global mean for seagrass (108 Mg C. ha^{-1}). The Swartkops Estuary stored a total (biomass and sediment carbon combined) of 14 094 Mg C in the *Z. capensis* area of 62 ha, 25 286 Mg C in the *S. maritima* area of 96 ha, and 5 916 Mg C in the *S. tegetaria*, covering an area of 27 ha. This is significantly less than what has been found globally in estuaries, but this is largely due to the smaller area cover of these macrophytes. The amount of carbon stored per hectare is much larger in this South African system than in many international studies — possibly due to the high levels of pollution coming into the system. Nitrogen and phosphorus stocks in the plants fluctuated seasonally in relation to the nutrient input to the estuary, with the greatest stocks found in winter in *Z. capensis, S. maritima,* and *S. tegetaria* (0.42 ± 0.03 Mg N. ha^{-1}, 1.6 ± 0.13 Mg N. ha^{-1}, and 0.37 ± 0.02 Mg N. ha^{-1}, respectively; and 0.4 ± 0.03 Mg P. ha^{-1}, 1.2 ± 0.10 Mg P. ha^{-1} in *Z. capensis* and *S. maritima* respectively) because nutrient inputs to the system were highest in winter, however the P stocks in *S. tegetaria* were greatest in summer (0.35 ± 0.04 Mg P. ha^{-1}). The reason for this difference is because of their ability to store phosphorus better than nitrogen and for longer periods of time due to luxury uptake. *Salicornia tegetaria* N and P stocks were also lower than the other two species, possibly due to its placement along the intertidal gradient, as it is not tidally inundated for as long as the other two species. The *Z.*

capensis and *S. maritima* at Site 1 showed extremely high amounts of nitrogen in their tissues (105.3 ± 1.6 g kg^{-1} and 74.91 ± 4.1 g kg^{-1} respectively). This is due to the area being a depositional site as it was an old oyster farm and experiences little tidal flushing from the sea despite its proximity to the mouth. Nutrient ratios and N: biomass were determined as an indication of nutrient pollution. The N: biomass was low in both seasons in *Z. capensis, S. maritima*, and *S. tegetaria* (0.08, 0.02, 0.04 respectively) indicating consistant eutrophic conditions in the estuary. Plant biomass was a better indicator of nutrient pollution than epiphytes which were very low in the Swartkops Estuary and did not prove as a useful indicator of nutrient enrichment. These results can inform local management plans of the ecosystem service potential of these species and how they should be protected for future and current sustainable use as filters for nutrient pollution to keep the water quality in a better state. It also outlines the current state of blue carbon and nutrient stocks in an urban South African estuary.

Table of Contents

List of Figures

List of Tables

Terminology and Acronyms

AB	Aboveground biomass
BB	Belowground biomass
C	Carbon
C_{org}	Organic carbon
DBD	Dry bulk density
g cm^{-3}	Grams per centimetre cubed
g. kg^{-1}	Grams per kilogram
g m^{-2}	Grams per meter squared
LOI	Loss on ignition
Mg ha^{-1}	Megagrams per hectare
mg l^{-1}	Milligrams per litre
N	Nitrogen
P	Phosphorus
SAV	Submerged aquatic vegetation

1. Introduction

Salt marshes and seagrasses are known as the most productive ecosystems on earth despite the salinity and inundation stressors they face (Boorman and Ashton, 1997). These vegetated coastal habitats, along with mangroves, are known as blue carbon ecosystems and are some of the most effective carbon sinks that play important roles in mitigating climate change (Mcleod *et al*., 2011). Salt marsh and seagrass facilitate the uptake and storage of carbon and nutrients through their above- and belowground biomass (Howard *et al*., 2014), however, the sediment carbon pool beneath the coastal vegetation makes up the bulk of the carbon stocks in estuaries (Howard *et al*., 2014). Carbon and nutrient stock, in this dissertation, refers to the amount of an element (C, N, P) present in a certain plant biomass at a certain time, or at a specific sediment depth and is measured in g m^{-2} or Mg ha^{-1} (Sousa *et al*., 2017). Globally salt marshes are estimated to cover an area between 22 000 km^2 and 400 000 km^2, however this is ambiguous because of how understudied salt marshes are around the world (Duarte *et a*l., 2013). This in turn has a major influence on the global carbon estimates and the role they play in nutrient cycling. These systems provide many other -important ecosystem services, defined as, the benefits people obtain from ecosystems that contribute to the direct or indirect well-being of human populations (MEA, 2005; Barbier, 2011). These ecosystem services include; erosion and storm surge protection, water quality maintenance by assimilating waste and pollution, coastal biodiversity and commercial and recreational value (Barbier, 2017). Despite being ecologically, socially, and economically valuable, salt marsh and seagrass habitats are being lost at a rapid rate globally — 50 % of seagrasses (Waycott, *et al*., 2009) and 25% of salt marsh (Duarte *et al*., 2008) have been lost since the early 1990's and this number continues to climb. In South Africa approximately 30% of salt marsh areas have been lost due to poor land use practices (Adams *et al*., 2019; Van Niekerk *et al.,* 2019).

Human activities have had major negative impacts on these ecosystems and their services. One such service that has been affected is the cycling of nutrients because of the nutrient pollution from waste water treatment works (WWTW) and urban runoff (de Jonge *et al*., 2002). This results in eutrophication — one of the primary stressors to estuarine systems, as it promotes micro- and macroalgal growth which limits the amount of light available to the submerged macrophytes such as seagrass (Govers *et al.,* 2014). Eutrophication can have a variety of effects on submerged aquatic vegetation (SAV) such as changing plant community composition which in turn effects the faunal communities that depend on these plants for their habitat (Flindt *et al*.,1999). For this reason, both submerged aquatic vegetation and salt marsh macrophytes are vital for regulating nutrients as they form the link for nutrients between the sediment and water column (Flindt *et al*., 1999; Penk *et al*., 2019). Excess nutrient input to estuaries often results in increased plant productivity, but it also alters community structure, decreases biodiversity, and changes the ecosystem functioning (Johnson *et al*., 2016). This is mainly based on short term studies while long term affects may lead to entire ecosystems changing. The results from this study are compared to previous studies by Pierce (1979), and Talbot and Bate (1987) who assessed the biomass of *Spartina maritima* (Curtis) Fernald and *Zostera capensis* Setch. respectively in the Swartkops Estuary. The changes in biomass from 1979 to 2019 may give good estimates of how estuarine macrophytes are affected by increased nutrient inputs. We are inclined to expect that the more nutrients available, the greater the increase in biomass will be, however this is largely dependent on the specific macrophyte. Seagrasses are known to be predictors of nutrient enrichment however more research is being put into finding ways in which they can sooner predict nutrient enrichment. The ratio of nitrogen to leaf biomass has shown promise of a nutrient pollution indicator, but this has only been tested on *Zostera marina* and the results were not as promising as what had been hoped for (Burkholder *et al*., 2007). Lee *et al.* (2004) on the other hand found the nitrogen to biomass ratio to be quite promising and called it the nutrient pollution indicator (NPI). Literature has shown that seagrasses are not as good at surviving in high nutrient conditions in comparison to intertidal grass *Spartina* spp. for example. Expected intertidal salt marsh responses to eutrophication are that biomass would increase, accrete more sediment and overall marsh size would increase, but instead root density and biomass have been found to decrease leading to marsh collapse and erosion at the edges (Deegan *et al.*, 2007; Johnson *et al.*, 2016; Kearns *et al.*, 2016). Thus, using salt marsh macrophytes leaf nitrogen to biomass ratio may be better indicators of enrichment.

Swartkops Estuary is a heavily polluted estuary and it is eutrophic which makes it the perfect site to study the effect of nutrient enrichment on plant biomass and their nutrient stocks. Swartkops Estuary has a present ecological status of a “D” which means that it is largely modified (Van Niekerk and Turpie, 2012). The present ecological status of an estuary is determined by the estuarine health index (EHI) that considers a number of biotic and abiotic factors within the estuary including; hydrodynamics, mouth condition, water chemistry, sediment processes, microalgae, macrophytes, invertibrates, fish, and birds. Each is assigned a score based on the similarity to natural conditons. The change in health from natural is rated as a percentage for each variable and an overall score is determined which indicates the present health status of the estuary. The overall percentage will determine the category (A - F) within the estuary will fall, ranging from extremely degraded (F) to pristine conditions (A) (Van Niekerk *et al*., 2019). To move the Swartkops Estuary to category “C” (moderately modified), there would need to be major improvements in the water quality (Adams *et al.*,

2014) and salt marsh and seagrass have proven to be effective filters for nitrogen (Nelson and Zavaleta, 2012). There are many factors effecting the rate at which eutrophication occurs in estuaries such as; nutrient levels, turbidity, residence time, tidal exchange, and freshwater inflow (Hilton *et al*., 2006). Focussing specifically on nutrients, dissolved values of > 400 µg TN l^{-1} and > 30 µg TP l^{-1} have been found to result in eutrophication in coastal ecosystems (de Villiers and Thiart, 2007; Lemley, 2015). De Villiers and Thiart (2007) suggested that in freshwater systems, values < 40 µg TN l^{-1} and < 5 µg TP l^{-1} indicate natural or near pristine conditions. A similar study conducted in China found that eutrophication occurs when concentrations reach 300 µg TN l^{-1} and 20 µg TP l^{-1} (Yang *et al*., 2008). The nutrient input to the Swartkops Estuary has increased significantly over the past 40 years (Adams *et al*., 2014; Adams *et al*., 2019). DWAF and SKR consulting (Pty) Ltd (2011) noted significant increases in the nitrogen input to the estuary between 2009 and 2013, increased inputs were also recorded at Perseverance (DWAF, 2012; Adams *et al*., 2014), however the nitrogen loads at the mouth (Settlers bridge) have shown a large decrease from a mean of 240 µg l^{-1} to 60 µg l^{-1} (Emmerson, 1985; Adams *et al*., 2014). Similarly, in this study and in other international studies, the phosphorus also decreases from the upper reaches of the estuary to the mouth (Jiménez-Cárceles *et al*., 2010; Nelson and Zavaleta, 2012; Adams *et al*., 2014). Swartkops is known to often exceed the threshold 400 µg TN l^{-1} for acceptable nitrogen levels, indicating eutrophic conditions (de Villiers and Thiart, 2007).

Spartina maritima, Salicornia tegetaria (S. Steffen, Mucina & G. Kadereit) Piirainen & G. Kadereit (previously known as *Sarcocornia tegetaria*)*,* and *Zostera capensis* were the species investigated in the current study. These are the dominant lower intertidal species in South African estuaries that are open to the sea. *Zostera capensis* is also endemic to Africa and it covers less than 2000 km^2 and is classified as an endangered species (Adams, 2016; Adams and Van der Colff, 2016). This is the most common submerged macrophyte in estuaries from the southern cape to St Lucia (Veldkornet, 2012), however it is easily outcompeted when there are changes in salinity or light penetration, and algal blooms (Berglund *et al.,* 2003; Burkholder *et al*., 2007; Pillay *et al*., 2010; Human *et al*., 2015). Nutrient loading is a cause for concern because it results in the loss of submerged aquatic vegetation (SAV), but seagrasses (and salt marsh) release oxygen and organic content into the surrounding environment which results in denitrification in eutrophic systems where nitrate is abundant which limits the growth of algal blooms and improves the conditions for the submerged aquatic vegetation (SAV) (McGlathery *et al*., 2007; Gurbisz *et al*., 2017). This means that if denitrifying bacteria is present in abundance, submerged aquatic vegetation like seagrass can play a role in "rehabilitating" their surroundings to create optimum conditions. This is one of the important ecosystem services of seagrasses — improving water clarity and quality. However, when nutrient concentrations are too high, macroalgae and microalgae take up nutrients a lot faster than seagrass making it difficult for them to be outcompeted (Gurbisz *et al*., 2017). Talbot and Bate (1987) did an in-depth study on seasonal changes in *Z. capensis* biomass in the Swartkops Estuary. *Spartina maritima* has a wide distribution and in South Africa it is found in the Eastern and Western Cape (Fish *et al*., 2006; Adams, 2016) and in the Swartkops Estuary it covers 60 ha which is 22.7% of the lower intertidal salt marsh (Bornman *et al*., 2016) and they are one of the few salt marsh species found there that have monospecifc stands across the whole estuary (Adams and Bate, 1995). This makes *S. maritima* the dominant macrophyte in the Swartkops Estuary having the third largest salt marsh in South Africa which was comprehensively studied in the 1970's (Pierce, 1979). Both Pierce (1979) and Talbot and Bate (1987) studies provide good comparisons for the change in biomass over time as biomass changes with increased nutrient inputs and carbon accumulation (Ondiviela *et al.*, 2014). Little historical literature exists on *S. tegetaria* changes in biomass, however, it was included in the study because it is one of the dominant lower intertidal succulent salt marsh species. *Salicornia tegetara* is endemic to Southern Africa (Steffen *et al*., 2009). Studies have found that *S. tegetaria* habitat has a low sediment organic content (Davy *et al*., 2006), however, in the Swartkops Estuary it was associated with high sediment organic content (Bornman *et al*., 2016). Sediment organic content relationship with nutrient availability and macrophyte biomass can be complex. Vegetated habitats have higher sediment organic content which results in increased surface stability (Reef *et al*., 2018) so it is important when sea-level rise and climate change threatens salt marsh. This highlights the importance of the belowground biomass of salt marsh plants, especially those in the lower intertidal zone.

Many studies on the above- and belowground biomass of salt marsh and their nutrient cycling potential have been done in the past however these were mainly international studies. Chaudhary *et al.* (2018) found that most of these focussed on *Atriplex, Spergularia, Artemisia, Limoniastrum, Spartina, Scurpis, Juncus, Salicornia* (Boorman and Ashton, 1997; Karaer *et al.*, 2007; Neves *et al.,* 2007, 2010; Negrin *et al.,* 2012; Shao *et al*., 2013). South African studies that have focussed on the biomass and nutrients of salt marsh include; *Spartina maritima*, *Salicornia meyeriana* biomass, the biomass of the invasive *Spartina alterniflora*, (Pierce, 1979; Schmidt, 2013; Adams *et al*., 2016) while the seagrass *Zostera capensis* biomass has been quite well studied in South African estuaries (Adams, 2016). The relationship between nutrients and reeds — *Phragmites australis* (Human and Adams, 2011)— as well as macroalgae — *Ulva lactuca, Cladophora glomerata* (Human *et al.,* 2015, Human *et al*., 2016), have been studied more recently in South Africa. Shortle and Horan (2016) suggested that nutrient pollution is one of the most important problems facing aquatic systems globally because they come from several sources and interact in complex ways over space and time. This could result in negative ecological and economic challenges

1.1 Purpose of the research

This study has global relevance as it speaks directly to the 2030 sustainability development goal of “life below water” and indirectly to “clean water and sanitation”, “economic growth”, and “climate action”. The Paris agreement was signed by South Africa indicating a commitment towards mitigating climate change and as part of this, developing an increased understanding of our blue carbon ecosystems, their functions, and how we can restore them. Quantifying the ecosystem services, which can be extrapolated for other South African estuaries is directly in line with the Paris agreement within the United Nations Framework Convention on Climate Change (UNFCCC) outline. Further, this study is a step towards standardizing research methodologies and techniques for the analysis of parameters so that these systems can be assessed globally, and that blue carbon and nutrient storage results may be comparable. This will then allow greater information sharing to find the best management and restoration plans and outcomes for each country. This study is important in managing the Swartkops Estuary salt marsh and seagrass habitats to benefit the local people who depend on the estuary for their livelihoods. This research will help management and decision-making authorities better understand the ecosystem service potential of the estuary. Due to the increasing pressures on seagrass and salt marsh ecosystems from both environmental influences and human induced factors, more data are needed on their ecology, distribution, and functional traits so that attention can be drawn to the importance of the ecosystem services they provide. This study fills some of these gaps in knowledge and the data will be able to support resource management and conservation decisions as well as reduce the global uncertainties around carbon and nutrient storage.

1.2 Hypotheses

- Salt marsh and seagrass area cover and biomass have increased in the Swartkops Estuary due to increased nutrient input.
- Organic carbon will be highest in the sediment beneath the vegetated beds in the creeks and lower in the main channel.
- The organic carbon stored in the aboveground biomass will be greater than that stored in the belowground biomass

1.3 Aims and Objectives

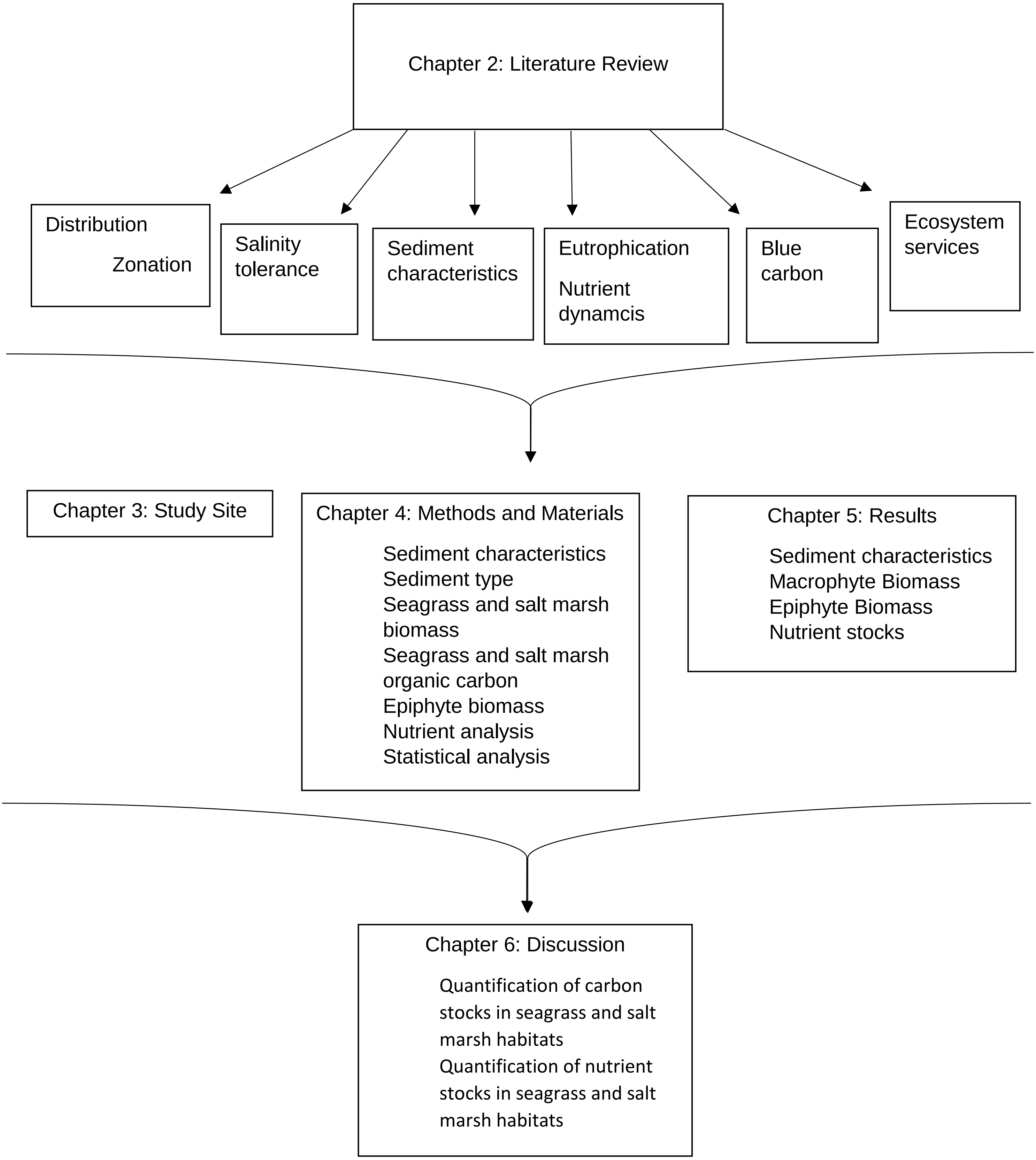
The overall aim of this research is:

- To quantify the carbon, nitrogen, and phosphorus stocks in *Zostera capensis, Spartina maritima*, and *Salicornia tegetaria* as a step towards the quantification of ecosystem services.

The overall aim was addressed through the following objectives:

- Determine the change in salt marsh and seagrass area cover in the Swartkops Estuary to understand the variability in carbon storage.
- Measure the organic carbon stored in the sediment below each of the three species.
- Determine the organic carbon stored in the above- and belowground biomass of the seagrass (*Zostera capensis)* as well as the dominant salt marsh species *Spartina maritima* and *Salicornia tegetaria*.
- Determine the effect of eutrophication on the salt marsh and seagrass by measuring tissue N and P and by comparing biomass, including epiphyte biomass with previous studies.

1.4 Chapter structure



2. Literature Review

2.1 Salt marsh and seagrass emergent macrophytes

Salt marshes are defined as the transitional zones between aquatic and terrestrial ecosystems that are regularly influence by inundation due to the tidal cycle and are therefore susceptible to physiochemical variations (Adam *et al*., 1990; Lubke and van Wijk, 1998; Adams *et al*., 1999; Ryan *et al*., 2003; Keith, 2004; Best *et al*., 2007; Butler and Weiss, 2009). Seagrass is often included in salt marsh definitions and studies; however, it can be defined separately as a submerged monocotyledonous vascular plant with narrow grass-like blades and are often referred to as eelgrass, turtle grass or tape grass (Phillips and Milchakova, 2003).

Salt marshes are made up of halophytic macrophytes found in the intertidal zone of estuaries. These habitats are low in oxygen, high in salts, and waterlogged (Butler and Weiss, 2009). The dominant species making up these habitats tend to be grasses such as *Spartina* spp., rushes, and salt worts (Butler and Weiss, 2009). *Spartina maritima* has a broad distribution and occurs across the world from Western Europe to north, east, and southern Africa. In the Swartkops Estuary *S. maritima* covers 82.33 ha which is 22.7% of the total intertidal salt marsh (Bornman *et al.,* 2016). Bornman *et al*. (2016) also found that *S. maritima* sediment is characterized by high organic content and soil moisture. *Sarcocornia tegetaria* is endemic to Africa and is found in Namibia, South Africa, and Mozambique (Steffen *et al*., 2009). Bornman *et al*. (2016) found that in the Swartkops Estuary *S. tegetaria* sediment is characterized by high organic content.

Most seagrasses have strap-like leaves except for *Halophila* species and *Syringodium* species which have rounded leaves and cylindrical shaped leaves respectively (Hemminga and Duarte, 2000). They also vary in size with some seagrasses such as *Posidonia* and *Thalassodendron* growing leaves of longer than 1m and having roots reaching up to 40cm in some species (Larkum *et al*., 2006) while others such as *Halophila* species are approximately 4 – 6mm long (McDermida *et al.,* 2002). The longest seagrass reported was *Zostera caulescens* in north-eastern Japan measuring 7m in length while their average height is 4.8m (Aioi, *et al*., 1998). Seagrass is prone to die back over different seasons and therefore they will differ in lengths at different times of the year with higher biomass in summer and less biomass in winter (Nienhuis and De-bree, 1980). From this, seagrasses are very versatile plants which come in many different shapes and sizes. The main characteristic of *Zostera* species is that it is both vegetative and reproductive. This means that the stems are perennial vegetative, and the rhizomes are annual reproductive; however, in most species both are present. The leaves have a sheath base which is open or split (Setchell, 1933). *Zostera capensis* is a species of eelgrass which has a wide distribution along the coast of South Africa ranging from the Oliphant's Estuary on the west coast to Kosi Bay on the east coast (Whitfield et al., 1989; Adams, 2016). This is also the most common submerged macrophyte in estuaries from the southern cape to St Lucia (Veldkornet, 2012). *Halophila ovalis* generally occurs with *Zostera capensis* but only in low abundances and is said to be more opportunistic so it is found most abundantly post-floods in estuaries (Day, 1981). *Zostera capensis* generally occurs on the lower intertidal zone and according to Adams (2016) and Duarte, *et al*. (2013) the seagrass found in the deeper calmer waters had longer and broader leaves than those found at shallower more exposed sites. This plant is endemic to Africa and covers less than 2000 km^2 and is therefore listed as an endangered species according to the IUCN (Adams, 2016; Adams and Van der Colff, 2016).

Salt marshes and seagrasses are known as the most productive ecosystems on earth despite the salinity and inundation stressors they face (Boorman and Ashton, 1997). These vegetated coastal habitats, along with mangroves, are known as blue carbon ecosystems (McLeod *et al*., 2011).

2.2 Distribution

Salt marshes occur worldwide, particularly in sheltered areas in temperate regions from 30° to 80° latitudes (Chapman, 1977). The most recent estimate of their global cover is 54 951 km^2 (Mcowen *et al.,* 2017) which expands throughout 43 countries (Figure 2.1). That study focussed mainly on the USA, Europe and Australia acknowledging that there are still gaps in spatial data for marshes in Canada, Africa, South America and Northern Russia. Although mapping has taken place internationally and nationally, a method and effort needs to be made to map the distribution of salt marshes globally. They cover the sedimentary banks of all continents except Antarctica, especially in estuaries and deltas (Gu *et al.,* 2018). They make up the transition zone between submerged aquatic vegetation and terrestrial vegetation. Over the last 50 years however, 50% of salt marshes have been lost and degraded worldwide (Barbier, 2012). These losses can be attributed to both natural phenomena and anthropogenic influences — some examples are provided in Table 2.1. Mangrove encroachment is a big factor effecting the change in distribution of salt marshes, a cause related to climate change (Kelleway *et al*., 2017). This has resulted in a loss of many important functions of salt marshes such as being a specialized habitat for some fauna and recreational activities such as swimming, fishing, and boating are affected. There are some changes that are potentially seen as pros as this shift arises, namely that mangroves store higher amounts of nutrients and carbon dioxide and they provide better protection to coastal communities from storm surges (Barbier *et al*., 2008; Koch *et al.,* 2009). The largest salt marshes are found in the USA and Australia, and these are generally monospecific stands (Mcowen *et al*., 2017). Seagrasses on the other hand are often found as mixed beds (Wittington *et al*., 1997).

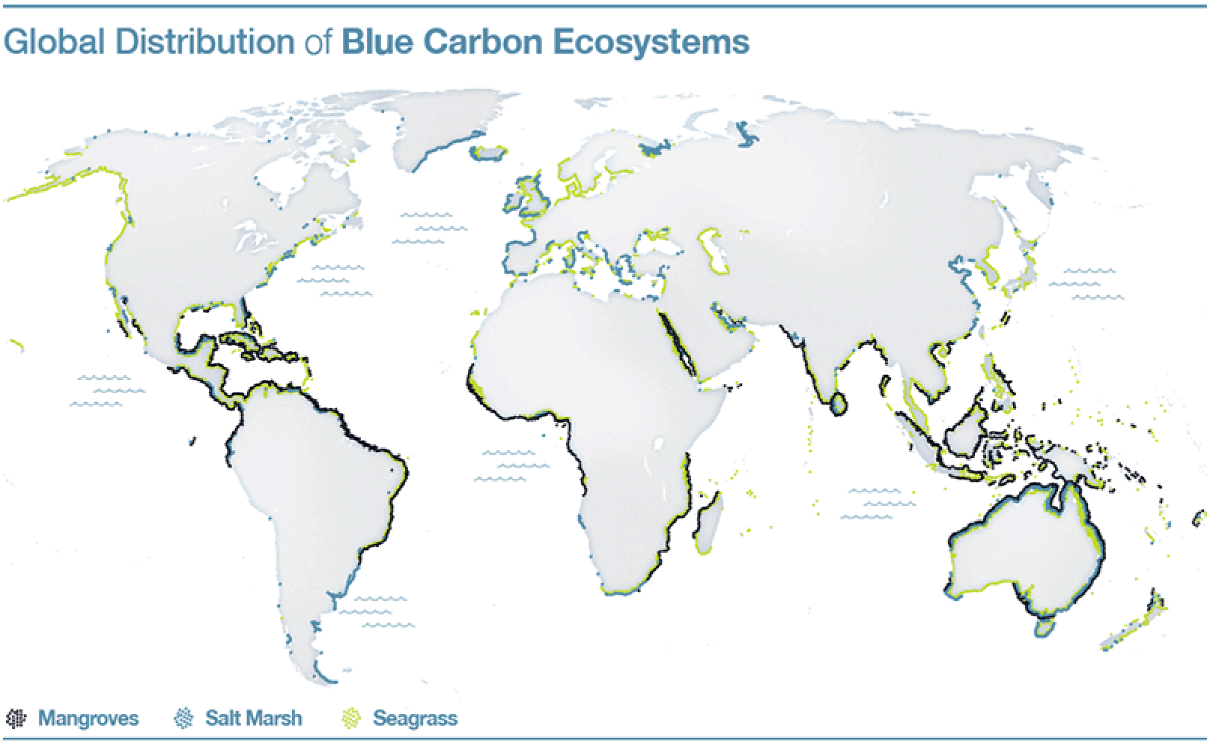


Figure 2.1: Global distribution of seagrass and salt marsh habitats (http://thebluecarboninitiative.org).

Seagrasses are a small group of marine angiosperms — only fifty species (Bandeira and Bjork, 2001) which cover approximately only 0.1% of the ocean floor (Mcleod, *et al*., 2011; Kennedy *et al*., 2010). In his book “World Atlas of Seagrasses” Green (2003) indicated that there were sixty species of seagrass across the world. Short *et al*., (2007) suggested that there is a low diversity globally because there are less than sixty species. There have also been a few discrepancies in whether certain species should be considered seagrasses (Setchell, 1933). They are found along the coast of all continents except for Antarctica and up to depths of 50m depending on the clarity of the water (Hemminga and Duarte, 2000) — 11% clarity (Duarte, 1995). They are specially adapted to living in seawater because of their roots and rhizomes that keep them firmly anchored to the substrate. Their air lacunae supply the roots with oxygen and pollination via the water make them well adapted to life in the water (Den-Hartog, 1970). Figure 2.1 shows the global distribution of seagrasses. Seagrasses are divided into different biogeographic regions. Short *et al*. (2007) defines these regions as follows: The

Temperate North Atlantic is a low diversity region dominated by *Zostera marina*, while the Temperate North Pacific is rich in seagrass diversity with a number of *Zostera* species occurring in estuaries and lagoons and *Phyllospadix* species occurring in the intertidal zone. The Mediterranean contains both temperate and tropical seagrasses but is dominated by *Posidonia oceanica* which grows fairly deep while the Temperate Southern Ocean which includes Africa, Australia and South America has a range of low to high diversity meadows which are dominated by *Posidonia* and *Zostera* (Short *et al*., 2007). Lastly, the Tropical Atlantic bioregion has a high diversity and is dominated by *Thelassia testudinum* and in the Tropical Indo-Pacific region up to fourteen species of seagrass can be found growing together therefore making it the area with the richest seagrass diversity in the world (Short *et al*., 2007). The *Zostera* genus in made up of eelgrass and is well distributed across the world. There is a total of seven species; two of which are found in the North Atlantic, two in the North Pacific, one in the Southwestern Indian Ocean coastlines, and three along the coast of the South Pacific Ocean. Another three species were later added from Australia.

South Africa's estuarine habitats are made up of a number of components such as the water column, mud flats, macroalgae, submerged macrophytes, salt marsh, reeds and sedges, mangroves and floodplains (Adams *et al.,* 1999) that all contribute in part to the effective functioning of an estuary. In South Africa, estuaries cover a total area of 95 675 ha and this can be broken down into the reeds and sedges which are dominant and cover 14 732.60 ha, intertidal salt marsh covering 5 868.72 ha, supratidal salt marsh 6 189.78 ha, submerged macrophytes covering 2 564.78 ha, swamp forests covering 2 852.65 ha, and mangroves covering a much smaller area of 1 631.03 ha (Adams *et al*., 2016). This means that just the intertidal salt marsh and supratidal salt marsh cover an area of approximately 12 058.5 ha which is much larger than the remote sensing estimate by Mcowen *et al.* (2017). These habitat types are distributed across the warm and cool temperate regions with supratidal salt marsh dominating the cool temperate region and intertidal salt marsh dominating the warm temperate region (Adams *et al.*, 2016). Intertidal salt marshes occur in permanently open estuaries and only 18% of South Africa's estuaries are permanently open. Of South Africa's nearly 300 estuaries, less than 70% of them are smaller than 50 ha (Van Niekerk *et al*., 2013). Adams *et al*., (1999) found that salt marshes only occurred in 70 of the estuaries in South Africa. This is potentially due to temporarily open/ closed (TOC) estuaries fluctuating conditions and periodic high salinity in comparison to permanently open (PO) estuaries. This was shown in a study on some TOC (Seekoei and Kabeljous) and PO (Gamtoos and Kromme) estuaries in the Eastern Cape (Adams, *et al.,* 1992). In 2019 the National Biodiversity Assessment classified estuaries into nine different types rather than the previously nown five estuarine types due to their dynamic nature and structure. These estuarine types are; estuarine lake, estuarine bay, estuarine lagoon, predominantly open, large temporarily closed, small temporarily closed, large fluvially dominanted, small fluvially dominated, and arid predominantly closed (Van Niekerk *et al*., 2019). Knysna, Swartkops, Langebaan, Berg, and the Olifants estuaries have the largest salt marsh areas (Schmidt, 2013; Veldkornet *et al.,* 2015; Adams *et al*., 2016). South Africa has four biogeographic regions — cool temperate, warm temperate, subtropical, and tropical (Van Niekerk *et al.,* 2019) — which results in our estuaries being vastly different from one another. Structural and functional differences are attributed to the temperature, salinity (van Niekerk *et al*., 2013) and rainfall patterns which vary significantly across the three regions (Lynch, 2004; Schulze and Lynch, 2007). This is likely the reason for the diversity observed in South African estuaries. Apart from this, South African estuaries within specific regions also differ slightly in their physiochemical make up (Harrison, 2004). Australian estuaries have also shown distinct differences around the coast — largely due to climatic differences (Kench, 1999).

Of these fifty species, East Africa has fourteen species making it a highly diverse region with regards to its seagrasses (Duarte *et al*., 2012, 2014; Browne *et al.,* 2013). These fourteen species are spread out across Mozambique and the coast of Southeastern Africa, Seychelles, Comoros, and Mauritius (Green and Short, 2003). Mauritius is dominated by *Thalassodendron ciliatum, Halodule uninervis*, and *Syringodium isoetifolium* but they experienced great losses in the aerial cover in the most populated areas (Green and Short, 2003). The seagrasses such as *Thalassodendron ciliatum,* in Seychelles are found from the intertidal zone to depths of 30m. The densities of these seagrasses in this area also vary with *Thalassia hemprichi* having low densities per squared meter to *Syringodium isoetifolium* having much higher shoot densities per meter square (Green and Short, 2003). In Mozambique the seagrasses play a big role in their economic sustainability and food security for the local people especially in the Quirimba Archipelago where the main fishery is between the mainland and one of the main islands of the archipelago (Gell, 1999). This area has mixed seagrass meadows of ten species which grow in the intertidal zone and the subtidal zone, these species are; *Enhalus acroides*, *Thalassodendron ciliatum, Cymodocea rotundata, Cymodocea serrulata, Syringodium isoetifolium, Halodule uninervis, Halodule wrightii, Halophila ovalis, Halophila stipulacea, Thalassia hemprichi* (Wittington *et al*., 1997). Maputo is dominated by *Zostera capensis* which has decreased in cover from 60% to 10% in the last ten years mainly due to the collection of bivalves which requires this seagrass to be dug up (Green and Short, 2003). In Maputo Bay alone the total area covered by seagrass is 3 875 ha (Bandeira *et al*., 2014). In South Africa there are a few species (*Cymodocea rotundata, Cymodocea serrulate, Thalassodendron* *leptocaule, Halophila ovalis*, and *Thalassia hemprichii*), but they do not have extensive distributions apart from *Z. capensis.* There are a large number of discrepences in the global data sets and local data sets — for example, submerged macrophytes in South Africa cover 2 565 ha while globally seagrasses alone are said to cover 40 557 ha (Adams, 2016). This is likely because the seagrass cover in South Africa only refers to that found in estuaries while globally the near shore environment is also considered. Seagrasses are important because of the numerous ecosystem services they provide, both in South Africa and across the world.

2.3 Zonation

A typical characteristic of salt marshes is zonation. This occurs between plant communities along an elevation gradient from the subtidal zone to the supratidal zone. Salt marsh zonation has been heavily studied, however it is still difficult to differentiate between their land and seaward boundaries (Tagliapietra *et al*., 2009). The landward boundaries are dynamic transition zones between the coastal and terrestrial environments and often experience physical changes (Rasser *et al*., 2013; Attrill and Rundle, 2002). The zonation of species is generally dependent on the physiochemical properties that occur along the elevation gradient. A South African study found that abiotic factors effected the seaward distribution of terrestrial vegetation because those species are generally not as well adapted to salinity and inundation while salt marsh landward distribution is not affected by abiotic factors (Veldkornet *et al*., 2015a). Physiochemical characteristics and the interaction with one another in salt marsh species beds may allow them to be used as bioindicators (Veldkornet *et al.,* 2016). The conclusion of the particular study was that rare salt marsh species are important for ecological assessments, but species that occur over a wider range of conditions (for example, *Salicornia tegetaria, Sporobolus virginicus)* may respond better to the changing climate. Landward distribution is generally affected by competition resulting in shading (Purer, 1942; Veldkornet *et al*., 2015a). This means that salt marshes can respond to the effects of climate change such as sea-level rise by migrating landward, however this can only occur where no land use changes have occurred at the interface between salt marsh and terrestrial habitats (Veldkornet *et al*., 2015a). The different salt marsh zones have been found to occur in parallel bands to the banks of the estuary (Adam, 1981). International literature refers to these zones as the upper, middle, and lower marsh habitats, while South African literature refers to the distinct zones as subtidal, intertidal, and supratidal zones (Bornman, 2002). Despite these site-specific variations the general species pattern is the same between all salt marshes (Schmidt, 2013). This zonation and changes due to the tidal cycle make salt marsh ecosystems good indicators of sea-level rise and change (Horton and Edwards, 2006; Stratchan, 2016). International salt marsh zonation is similar internationally to what is found in South Africa, but some are seen as “inverted salt marshes” (Adam, 1990), but this is not the regular pattern. The south-west Atlantic coast salt marshes have shown sedges and grasses to dominate the lower, tidally inundated intertidal zone while the upper zones are occupied by halophytic species (West, 1977). Freshwater inflow from seepage and runoff into the estuary often results in reeds and sedges, but this is generally a result of anthropogenic influences (Lubke and Van Wijk, 1988; Bart *et al.,* 2004). Permanently open and temporary open closed estuaries with larger tidal cycles result in more definitive zonation patterns, example the Knysna, Great Brak, and Swartkops estuaries, while those that experience little tidal action generally have a more mosaic appearance than zoned (Adams, 2002). In South Africa the subtidal zone is normally occupied by *Zostera capensis* and it is classified as occurring below the mean sea-level which is only partially exposed during low tide (O’Callaghan., 1994). The intertidal zone is divided into two sections, the upper and the lower intertidal zone. The lower intertidal zone occurs between the mean spring high tide mark and the mean neap high water mark where *Spartina maritima* occurs adjacent to *Z. capensis* and adjacent to *S. maritima* is *Salicornia tegetaria* (Schmidt, 2013). O’Callaghan (1987) described the upper intertidal by the presence of *Bassia diffusa, Sarcocornia decumbens*, and on occasions when the salinity is less than 35 (winter), *Cotula coronopifolia*. Above the upper intertidal zone is the supratidal zone that only experiences inundation in extremely rare conditions. This zone is characterised by grasses (*Sporobolus and Stenotaphrum*) and succulents (*Sarcocornia, Disphyma*, and *Plantago*) (O’Callaghan, 1994).

The estuarine functional zone (EFZ) incorporates these zones of distribution of salt marsh plants. Tidal flushing of the EFZ is important to maintain nutrient exchange and removal of salt accumulation resulting in the overall maintenance and diversity of the salt marsh (Van Niekerk *et al.,* 2019). Salt marsh zonation is important to understand in the context of blue carbon, nitrogen, and phosphorus stocks because of the changes in the physiochemical properties, especially of the sediment. Sediment organic content, moisture content, electrical conductivity, and redox potential increase with elevation while pH decrease (Veldkornet *et al.*, 2015). Literature has agreed that the lower limits of the zones are set by physical tolerance while the upper limit is set by competition (Gonzalez – Alcaraz *et al*., 2014; Hasanuzzaman *et al*., 2019). Salinity, along with inundation are two of the main driving forces of salt marsh zonation and they may have the largest effect in the response of these macrophytes to sea-level rise (Noto *et al*., 2017).

2.4 Salinity tolerance

Salinity is the product of the rainfall and evaporation regimes (Schmidt, 2013). Adam (1990) found that salinity in the soil was higher in the supratidal zone compared to that of the lower areas of zonation because those areas are not frequently inundated which results in the salt staying behind once the water is evaporated, increasing the salt concentration. For this reason, the plant species growing in these dynamic zones need to be able to tolerate salt stress. These plants are known as halophytes. Halophytes are salt tolerant plants that grow in waters with high salinity. They are specially adapted to cope with the high saline conditions as well as the inundation that occurs in these habitats (Reaper, 1995; Mishra and Tanna, 2017). These plants survive well in these habitats because they are specially adapted. Halophytes can be facultative or obligate which means that they can be classified on their tolerance to salt (Mishra and Tanna, 2017). Facultative halophytes can grow even if there is no salt present, but obligate halophytes require salt for their growth (Braun-Blanquet, 1962). Salt tolerance mechanisms have been well studied for many decades. The mechanisms for dealing with high salinity are salt elimination, succulence, restricted uptake, compatible solutes, and ion compartmentalization (Gulzar *et al*., 2003). These mechanisms are extremely useful because plants that suffer from excess salt are usually water deficit, have ionic imbalances and ion toxicity (Marschner and Rimmington, 1996). *Spartina* grass has many salt mechanisms to deal with excess salts such as; salt exclusion in the leaves through salt glands, ion exclusion through the roots (Bradley *et al.,* 1991), accumulating compatible solutes to maintain the reduced osmotic potential (Drake and Gallagher, 1982), and maintaining photosynthesis (Longstreth and Strain, 1977). *Spartina maritima* was studied in the lab and growth was reduced at salinity greater than 35, but particularly at salinity between 55 and 75 (Adams and Bate, 1995). One of the most important features for *S. maritima* growth and production is tidal flushing which is why it only occurs in permanently open estuaries in South Africa (Reddering, 1988).

Salicornia spp. make use of their succulence to tolerate extreme saline conditions in estuaries (Mishra and Tanna, 2017) and they have also been highlighted as one of the plants that has salt tolerant genes (Singh *et al.,* 2016; Udawat *et al*., 2017). A South African study found that *Sarcocornia perennis* (Mill.) A.J. Scott, an intertidal succulent salt marsh plant, experiences reduced growth at conditions where salinity is above 35 and completely submerged but grew well when the sediment was saturated (Adams and Bate, 1994). *Sarcocornia* grew best at salinity between 0 and 15 (Adams and Bate, 1994). The same study suggested that where salinity was greater than 35, flowering and seed production was reduced resulting in little recruitment of new plants. Most salt marsh plants grow best at salinity below 35 (Breen *et al*., 1977; Adams and Bate, 1994; Adams and Bate, 1995). *Bassia diffusa* is another example of a plant found in South African salt marshes which decreased in productivity with an increase in salinity (>18) (Tabot and Adams, 2013). This study was done in order to understand the effects of climate change on salt marsh macrophytes. Sea-level rise (increased salinity and inundation) will likely have a negative effect on salt marsh diversity and cover unless they can migrate landward (Tabot and Adams, 2013). *Triglochin buchenaui* was more tolerant to higher salinity and survived in saline conditions of up to 45 but thrived at salinity between 0 and 18 (Tabot and Adams, 2012). This study showed that proline accumulation and the response of photosynthetic pigments were important for osmotic membrane regulation so that *T. buchenaui* could respond to increases in salinity. The less saline the conditions the more succulent *T. buchenaui* was. Although halophytes can withstand salinity stresses, these coupled with other stress can sometimes be detrimental to the plant. Nutrient loading in saline environments has been a topic of keen interest to the research community and there are many positive and negative impacts on salt marsh plants in the studies done to date (Alldred *et al.*, 2017). Salinity specifically influences plant nitrogen assimilation in the roots so together salinity and nitrogen may influence the belowground biomass of the plants (Turner *et al*., 2009; Deegan *et al.,* 2012) which is the most important part of the plant for bank stabilization. A study done on *Spartina alterniflora* in New York found that the belowground biomass of the plant decreased by 60 to 70% in high nitrogen conditions and increased by 70% in high salinity conditions indicating that eutrophication and increased salinity from sea-level rise may have opposing effects on salt marsh stability going forward (Alldred *et al*., 2017). Understanding how marshes respond to stresses is vital for coastal communities and their sustainable economic development worldwide (Millennium Ecosystem Assessment 2005), because if it is not well understood, critical ecosystem services may be lost.

2.5 Sediment characteristics

A large part of any blue carbon and nutrient stocks project is the sediment characteristics because this influences the overall health of the plant. Organic matter is formed from *in situ* break down of plant and animal detritus because of die back (Adams and Bate, 1994; Adams *et al.,* 1999). Organic matter in the sediment is an important sediment characteristic because it plays a role in the accretion of sediments enabling salt marsh habitats to keep up with sea-level rise. Salt marsh is one of the ecosystems that is heavily impacted by rising sea levels. The relative sea level has been rising by 1.82 mm yr^{-1} for the past 36 years (Bornman *et al*., 2016). A study done on the Swartkops Estuary salt marshes suggested that the marshes are keeping up with the sea level rise (SLR) by accreting at an approximate rate of 2.98 mm yr^{-1}

(Bornman *et al*., 2016). This is good for now but due to increases and changes in the ocean temperature distribution and the rate at which glaciers are being lost, the salt marshes may not be able to equal the rate of sea level rise (SLR) (Church *et al*., 2013). Jamaican salt marshes on the other hand have shown negative results with regards to them keeping pace with sea level rise which may lead to a loss of these critically important habitats (Hartig *et al*., 2002). Organic matter production adds to soil building so that salt marshes can accrete to keep up with sea level rise, but denser vegetation canopies are also advantageous to reduce the loses of sediment and in turn reduce erosion (Moller *et al*., 2014; Temmerman *et al.,* 2012). Many view salt marshes as extremely vulnerable to sea level rise, however studies have shown that salt marshes are keeping up by accreting at rates greater than sea level rise (SLR) (French, 2006). This does not take away from the fact that salt marshes are showing resistance in the vertical direction but are still fragile in the lateral directions (Gunnell *et al*., 2006; Mariotti, and Fagherazzi., 2013). Supratidal salt marshes may especially show a high affinity as organic carbon sinks because during spring high tides detritus and other organic materials are deposited on the upper marsh area and have time to decompose before the next spring high tide (Vromans, 2010). This was seen in a South African estuary where the study found that the supratidal salt marsh had significantly higher organic content than the intertidal and subtidal marsh areas (Veldkornet *et al*., 2015). Fourqurean *et al*. (2012) found that organic matter can be a proxy for organic carbon. Kirwin *et al.* (2016) suggested that organic matter resulted in increased sedimentation. This together with increased temperatures and carbon dioxide from climate change would result in greater salt marsh vertical accretion which would have a positive effect on marshes (Kirwin *et al.,* 2016). Bulk density also plays a role in the sediment budget of marshes responding to sea-level rise (Gunju *et al*., 2017) so it is important to take all necessary factors into consideration.

Soil organic carbon is usually negatively correlated to bulk density (Ellsion and Beasy, 2018; Serrano *et al*., 2018) which is a key component in understanding the organic carbon content of the sediment as it gives a measure of carbon density when multiplied by the percentage of organic carbon (Howard *et al*., 2014). We want to know what the carbon density is because it indicates how much carbon is stored in a specific section of the sediment (Howard *et al*., 2014). Avnimelech *et al*. (2001) also found that as the organic carbon in the sediment increased, bulk density decreased and vice versa. Sediments that have high bulk density and low organic carbon indicate mineral rich substrates while low bulk density and high organic carbon content indicates peat soils that are rich in organic matter (Stringer *et al.,* 2015). This is because bulk density is the weight of a soil in a given volume and it usually is an indication of compaction. If the bulk density is greater than 1.6 g cm^{-3}, the sediment will restrict root growth, so this tends to increase with depth. Sandy sediments are prone to higher bulk density than finer grained soils (Dadey *et al*., 1992; Ellison and Beasy, 2018). Bulk density is not easily altered by disturbances except changes in water flow as this affects the sediment water holding capacity (Avnimelech *et al*., 2001). Macreadie *et al.* (2013) studied the effect of wrack disturbance on *Spartina* salt marsh sediments and found that there was no difference between the disturbed and undisturbed sediments. These sediments tend to have lower bulk density beneath *Spartina* stands (Vu *et al.,* 2017). It has been noted in numerous studies that sediment properties interact with one another and impacts can result in shifts in more than one feature of the sediment. One of the main factors influencing the sediment dynamics are particle size. The carbon stored by salt marsh habitats is generally greater than the organic carbon stored beneath seagrasses (Howard *et al.,* 2014).

Particle size analysis is used to characterise the size distribution of particles within the sediment (Bouyoucos, 1962). Sediment particles consist of sand (0.05 to 2.0 mm), silt (0.05 to 0.002 mm), and clay (less than 0.002 mm). Sediment particle size is especially important in the drainage and water holding capacity of the sediment — larger particles result in increased drainage, whereas smaller silt and clay particles hold more water, draining poorly (Syvitski, 2007). As much as this is the case for water movement, it is also the case for the movement of nutrients through the sediment, so nutrient retention is longer in fine grained silt or clay sediments (Barko and Smart, 1978; Prasad and Ramanathan, 2008). The sediment particle size distribution of a typical salt marsh is 47 % sand, 27 % silt and clay and 26 % organic matter (Greenwood, 2008). Seagrass sediments have similar sediment grain size distribution as salt marsh sediment, but they are known to be dominated by sandy sediments (Cole, 2016; Potouroglou, 2017). Bezuidenhout (2011) found that the Kromme, Olifants, Mngazi, Great Brak, East Kleinemonde and Seekoei estuaries salt marshes had large ranges of grain sizes — clay ranged between 2.8 and 79.5%, silt between 0 and 84.2% and sand between 12.6 and 97.2%. Byrd and Kelly (2006) found in a study in California that sand deposition to estuarine habitats resulted in a decrease in soil nitrogen, salinity, and moisture content and in turn altered the species composition. This shows how sediment particle size can affect the distribution and zonation of salt marsh species (Traut, 2005). Fine textured sediment accumulates more phosphorus and nitrogen due to the higher surface area and this resulted in greater growth rates in *Spartina* (Barko and Smart, 1978). Many studies have taken place on *Spartina* spp. (Barko and Smart, 1978; Ganju *et al*., 2017; Vu *et al.,* 2017; Matzke and Elsey-Quirk, 2018) but there is still a necessity for these kinds of studies to take place on succulent salt marsh and seagrass species.

Particle size influences soil nutrients, which the plants then take up via their roots and rhizomes. The belowground biomass, once it dies contributes to the organic content in the sediment which releases nutrients into the ecosystem (Matzke and Elsey-Quirk, 2018). The same study looked at the response of added nutrients to the plant and sediment and found that there was a huge influence on the plant, but sediment properties were unaffected by the nutrient enrichment.

2.6 Eutrophication

Eutrophication is a globally rife issue for many estuaries and communities living off estuaries. This is largely due to nutrient enrichment from humans. Eutrophication was originally defined as "an increase in the rate of supply of organic matter to an ecosystem" (Nixon, 1995). A modern definition may be from Ferreira *et al*. (2011), where cultural eutrophication is defined as the "the enrichment of water by nutrients causing an accelerated growth of algae and higher forms of plant life to produce an undesirable disturbance to the balance of organisms present in the water and to the quality of the water concerned". The two main anthropogenic threats to seagrasses worldwide are eutrophication and sediment loading (Björk *et al*., 2008). Eutrophication is usually more of a problem in highly developed areas. Swartkops Estuary has a substantial amount of development surrounding it. Sedimentation occurs to a large extent when terrestrial vegetation is removed resulting in erosion and transport of sediment into estuaries. The water clarity then decreases because of the suspended particles and increased turbidity. Increased nutrients entering the system on the other hand stimulates excessive growth of phytoplankton and macrophytes which then outcompete the seagrass. Both Western Australia (Cambridge *et al*., 1986) and Florida Bay (Hall *et al.*, 1999) have experienced large scale seagrass losses due to epiphyte fouling and light reductions respectively which occurred because of eutrophication. Although eutrophication is often associated with negative impacts, if minimal extra nutrients are added to a system it can result in increased growth and productivity, however if productivity decreases due to nutrient enrichment, oxygen in the sediment decreases, sulphides form which kill the roots and ultimately the entire seagrass bed dies (Perez *et al*., 2007). Salt marsh plants have been found to be effective filters of nutrient pollution (Yoon *et al.,* 2006; Rathore *et al*., 2016; Chaudhary *et al.,* 2018), however more local research is necessary.

2.6.1 Nutrients

Nitrogen (N) and phosphorus (P) are limiting nutrients in coastal ecosystems. This means that nitrogen and phosphorus are usually in short supply because plants require these nutrients in large amounts for growth daily. Macrophytes act as sources or sinks for nitrogen and phosphorus (Human, 2013). Goeck (2005) found that in the Swartkops Estuary the sediment act as a sink for nitrogen and phosphorus, but a source of ammonium to the water column. She also stated that temperature was the main reason that nutrient fluxes within the system varied (Goeck, 2005). Plants require both micro and macronutrients in various quantities for optimal growth and survival — deficiencies of these will lead to deterioration in plant quality while over supply can either lead to luxury uptake or detrimental effects (Jones *et al*., 2013).

Nitrogen is a key nutrient for coastal ecosystems especially in salt marshes because it plays a role in the structure and function of the system – increased nitrogen results in increased primary productivity especially in marsh grasses (Valiela and Teal, 1979). Large amounts of nitrogen are dissolved in the oceans and only 0.002% of nitrogen occurs in organic matter (Potgieter, 2008). Increased nitrogen has also shown to result in *Spartina alternifolia* changing from short to tall growth forms (Valiela *et al*., 1978). Valiela and Teal (1979) found that 64% of the nitrogen entering the Great Sippewissett Marsh as nitrate was captured by the marsh. Old marshes such as this one is suggested to be in a long-term steady state, however, young marshes may be traps for sediment and particulate nutrients, but this changes as the marsh develops and starts exporting particulates (Valiela and Teal, 1979). Fourqurean *et al*. (1997) found that nitrogen in the tissues of seagrass, *Z. marina*, had a strong spatial pattern in estuaries, but phosphorus did not. Nitrogen increased in plants that were furthest away from the mouth of the estuary (Fourqurean *et al.,* 1997). Nitrogen gas makes up 79% of the atmosphere but this is not directly available to plants and animals. Nitrogen cycling is a complicated process because nitrogen occurs in many oxidation states (Goeck 2005). Figure 2.2 gives more insight to the nitrogen cycle and its associated processes (Herbert *et al.*, 1999). Nitrogen fixation is an important process as it results in nitrogen gas being transformed into a usable form of nitrogen for plants (ammonia, nitrates, and nitrites) by microbial activity which make up the total nitrogen.

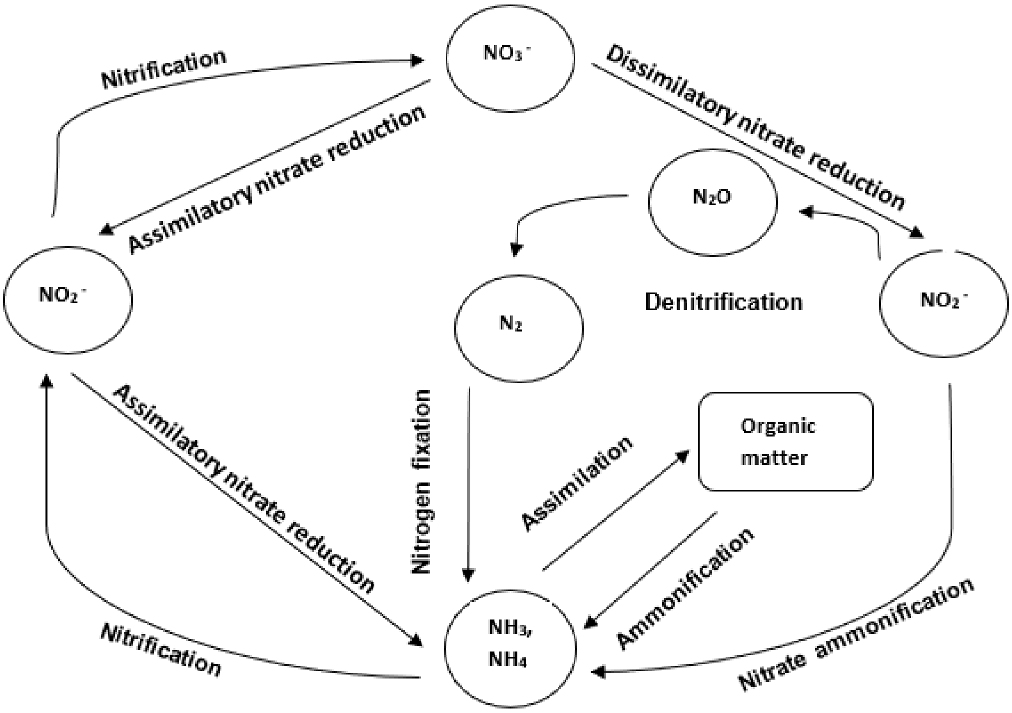


Figure 2.2: Biogeochmical cycling of nitrogen (Herbert et al. 1999).

Phosphorus is naturally available for biological consumption through the weathering of rocks however, only 5 to 10% of this is available in the ocean in a dissolved form (Froelich 1988). The phosphorus cycle is simple compared to the carbon and nitrogen cycles and has been described as “one-way traffic” from rock deposits to the sediment and water columns. The impact of human activity on the phosphorus cycle is not clear but phosphorus to the oceans has doubled because of it. Commercially it is found in fertilizers but also in products such as; fireworks, pesticides and detergents to mention a few (Smith *et al.* 2005; Le Tissier *et al.* 2006). Phosphorus has no volatile forms and it is usually measured as dissolved inorganic phosphorus (Holtan *et al*. 1988). Slomp (2012) suggested that phosphorus enrichment results in eutrophication and hypoxia and hypoxia results in the increased availability of phosphorus to the water column because it can no longer bind with organic matter (Ingall *et al*. 1993). Many studies regarding this have occurred in the Baltic Sea (Conley *et al*., 2002; Vahtera *et al*., 2007). Figure 2.3 explains the phosphorus cycle in a diagrammatic way.

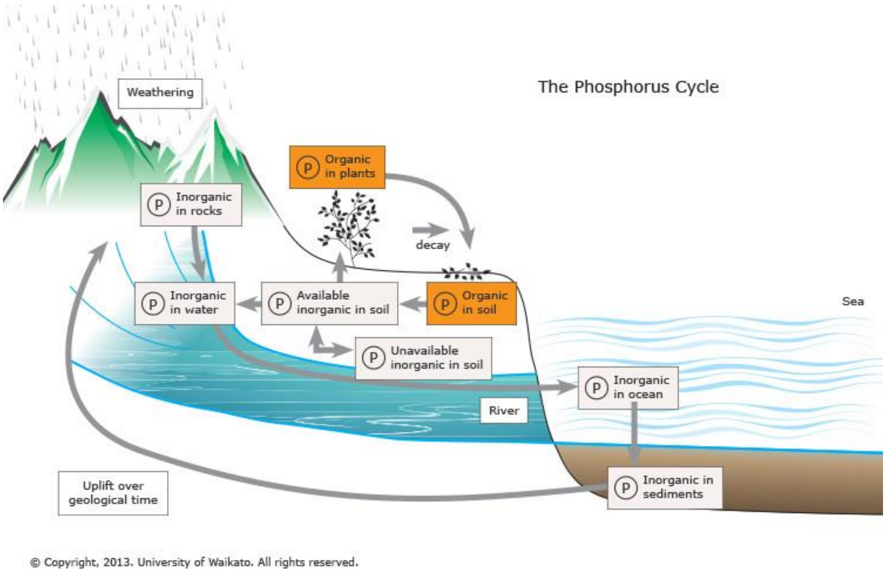


Figure 2.3: Phosphorus biogeochemical cycle (Monaghan, 2019, University of Waikato).

2.6.2 Nutrient storage

Seagrasses and salt marsh play an important role in assimilating and cycling nutrients and other chemicals from the sediment and the water column which is beneficial to both estuarine health and the plant as nitrogen and phosphorus are key nutrients for growth (Björk *et al*., 2008). This is important in the Swartkops Estuary because effluent is released from the surrounding industrial and urbanized areas. Long-term storage of nutrients in plant tissues is generally a result of luxury uptake. Luxury uptake is defined as the excess uptake of nutrients by a plant from an enriched environment even though it has all the essential nutrients for growth in the right quantities (Eixler *et al.,* 2006). This basically means that the plant takes up more nutrients than what it needs for growth. This is quite an understudied area of research but Shardendu *et al.* (2012) suggests that it will be a good field of research with the aim of cleaning up polluted, nutrient enriched water bodies. Once the initial increase in plant growth has occurred from excess nutrients being available, the plant will reach a plateau in its growth during the optimal growth stage, but once the biomass starts to be adversely affected the plant has reached the nutrient toxicity stage. Any extra nutrients taken up during the optimal growth and toxicity stages are considered luxury uptake (Kadlec *et al*., 1996). Luxury uptake is to the plants advantage because it acts as a safety net in case the nutrients in the system are depleted at a later stage. The plant however, needs to balance the ability to use the nutrients for rapid growth and to extract and retain nutrients and this is largely dependent on the plants physiological traits (Garbey *et al.,* 2004). Thiebaut (2005) indicated that plants with high storage capacities for nutrients occur over a broader ecological range than those with lower storage capacities. By this statement, *S. maritima* should have the highest nutrient storage capacity followed by *Z. capensis* and *S. tegetaria* due to their various distributions. Salt marsh halophytes that are well adapted to salinity tolerance are generally also more effective at nitrogen assimilation and should be considered for the removal of/or mitigation strategy for nutrient loading rather than *Typha* and *Phragmites* which are not effective at assimilating phosphorus (Shardendu *et al*., 2012).

Nitrogen and phosphorus uptake mechanisms are not well understood for aquatic species, but it is known that roots (and root hairs) are the primary organ that plants use to take up nutrients because they generally exceed the surface area of the shoots, but many plants are also able to acquire nutrients through other organs like the leaves (Salisbury and Ross, 1985; Thiebaut, 2008). This is an active process. Submerged aquatic vegetation are different in that their nutrient uptake is dominantly via the leaves from the water column although it can be via the roots as well thereby making the sediment the main storage "facility" or sink for excess nutrients (Short *et al*., 1987; Baldy *et al*., 2007). Seagrasses have air channels and are able to take up nutrients from the water column easier than more rigid plants. Studies have found that seagrass biomass and productivity increase in shallower waters due to the light availability, but in waters that are too shallow their growth is inhibited because the seagrass is exposed to greater light intensity and higher water temperatures (Paynter *et al*., 2001). Nutrient concentrations in the sediment and the water column are considered to be the primary reason for seagrass growth (Fong and Harwell, 1994) although other studies have found that it is nutrient concentrations that limit the growth of some seagrasses (Tussenbroek *et al.,* 1996). This was tested by Paynter *et al.* (2001) who studied the growth of *Thalassia testudinum* at different sites in Costa Rica and they found that the three sites had very different growth rates and levels of productivity supposedly from the different concentrations of nutrients from the river outflow at some sites. This suggests that the growth depends on the amount and the main types of nutrients in the sediment. The nutrient status of the sediment plays a big role in the above and belowground biomass, increasing the belowground biomass when the sediment nutrient content is low and visa versa (Barko *et al*., 1991; Flindt *et al.,* 1999).

The algae, *Cladophora glomerate* acted as a sink for nitrogen and phosphorus during closed mouth conditions when nutrients were assimilated by the alga in the Great Brak Estuary (Human, 2013). *Ulva* has also shown to act as a sink for nitrogen and phosphorus when there are increases in nutrients entering systems (Zertuche-González *et al*., 2009; Human *et al*., 2016). When these algae become "sinks", they are effectively blooming and result in the loss of seagrass. In the Meditteranean, *Zostera noltii* stored more nitrogen in its aboveground biomass than in its belowground biomass throughout the year (Kramaer, 1999). The mean total nitrogen stored in *Z. noltii* was 0.01 Mg N ha^{-1}. This was significantly less than what was stored in *Cymodea nodosa* (0.04 Mg N ha^{-1}) which falls within the same size class as *Zostera* species (Cancemi *et al*., 2002). *Zostera marina* tissues stored 34.5 g N m^{-2} in Oresund near Copenhagen which equates to 0.35 Mg N ha^{-1} (Pederson and Borum, 1993). The Oresund channel has a lot of urban development around it and the famous Oresund bridge going across the sound. Phosphorus levels are generally lower in both plant tissues and the water column and is usually the more limiting nutrient (Brix and Lyngby, 1985). In the case of Swartkops Estuary neither nitrogen or phosphorus was a limiting nutrient. The total nitrogen and phospohorus stored in *Z. capensis* in a South African system found that there were no changes in nitrogen storage in the tissues during the open and closed mouth states in the estuary but there were differences in phosphorus storage (Human, 2013). An average of 2132.8 kg of nitrogen and 1494.4 kg phosphorus was stored in *Z. capensis* in the estuary. This is equivalent to 2.13 Mg N and 1.49 Mg P. *Zostera noltii* in the Palmones River estuary in Spain also showed seasonal variations in the phosphorus strorage — the highest stocks were seen in winter and the lowest in summer (Perez-Llorenz and Niell, 1993). The mean total phosphorus stored in *Z. noltii* in the Palmones Estuary was 0.01 Mg P ha^{-1}. This estuary experiences oil spills and is prone to waste from boats in the harbour (Perez-Llorenz and Niell, 1993). The nutrient content differs spatially in plant biomass largely depending on the factors acting on the estuary, such as the levels of pollution it experiences and the flow dynamics (Govers *et al*., 2014). Using seagrass species tissue nutrient content as indicators of eutrophication has been tested using Thalassia in the USA and surrounding islands, China, and Indonesia (Van Katwijk *et al*., 2011; Campbell *et al.,* 2012; Zhang *et al*., 2014). Summarizing all these studies Govers *et al.* (2014) found that plants consisting of 0.14 – 0.7% phosphorus indicated eutrophic conditions while those containing between 0.07 and 0.18 indicated pristine conditions. Although overlap occurred there was still a significant difference between values indicating pristine and eutrophic conditions.

Sousa *et al*. (2017) found that salt marsh habitats were effective at storing nitrogen and phosphorus and this is essential as we face a changing climate. This is because salt marshes buffer estuarine and coastal waters from nitrogen loading (Nelson and Zavaleta, 2012). Sousa *et al.* (2017) also determined that 90% of the nitrogen and phosphorus stocks were in the upper marsh. Spatial and temporal variation is evident between salt marshes of the same species as was seen in the Mondego Estuary depending on the biotic and abiotic variables of the estuary (Sousa *et al.,* 2008). In the same estuary, more nitrogen was stored in the aboveground biomass (0.7 Mg N ha^{-1}) than in the belowground biomass (0.2 Mg N ha^{-1}).
A previous study found that *Spartina maritima* was more effective in retaining nitrogen than *Sarcocornia* spp. due to its higher affinity to store nutrients long term (Sousa *et al*., 2010).

A study on the biomass nutrient pools of *Salicornia brachiata* in Indian salt marshes found that the maximum nitrogen and phosphorus content in the plant tissues were in winter (0.048 Mg N ha^{-1}; 0.004 Mg P ha^{-1}) (Chaudhary *et al*., 2018). This study found significant spatial and temporal differences which were attributed to different sediment characteristics, but the aboveground biomass always stored more nitrogen and phosphorus. Both nitrogen and phosphorus have been seen to decrease in salt marsh plants as they mature due to increased carbon fixation (Stribling and Cornwell, 2001; Zhao *et al*., 2014). Many halophytes use large amounts of nitrogen to produce compatible solutes for osmoregulation (Donnovan *et al*., 1997). *Salicornia brachiata* has been identified as a suitable species for phytoremediation in India because of its ability to take up and store nutrients (Chaudhary *et al*., 2018). *Salicornia virginica* stored significantly more nitrogen and phosphorus in winter in the protected Mugu Lagoon salt marsh in Southern California (Boyer *et al*., 2001). This study measured the total nitrogen in the tissues as a percentage of the biomass — approximately 3.5% of the total biomass (succulent and woody parts of the plant). This results in an approximate nitrogen storage of 0.7 Mg N ha^{-1} in *S. virginica*.

Nutrient ratios are important for understanding whether systems are nutrient limited or if they are enriched. Macrophytes found in low nutrient habitats usually have high C:N and C:P ratios and those growing in nutrient poor habitats have low ratios (Atkinson and Smith, 1984; Duarte, 1990; Yang *et al*., 2018). Nitrogen: Phosphorus is predominantly used as an indicator of phosphorus limitation in a system (Walker *et al*., 2004). This is common in many estuaries where although excess nitrogen is coming into the system, there is not enough P for plant survival, growth, and reproduction (Atkinson and Smith, 1983; Fourqurean *et al*., 1992; Walker *et al.,* 2004). A study on the nutrient content in seagrasses in Japan found that there was large variation in the nitrogen leaf tissue content for seagrass species at a specific location (Yamamuro *et al.,* 2003). They suggested that δ15N is a better indicator to measure increase and decrease in nitrogen content. It is worth noting that although C:N:P ratios in seagrasses reflect nutrient conditions, growth may affect the changes in the seagrass nutrients (Yamamuro *et al.,* 2003). Carbon: nitrogen ratios have been used as a food quality measure as well and a value of 17 is acceptable for animal food (Russell-Hunter, 1970; Wahbeh, 1988). A higher value would be necessary for human consumption. Since there are many people who depend on these macrophytes and environments for their livelihood, the low C:N ratios are a cause for concern and may result in decreased physical health for these individuals. This brings into perspective why it is important for the nutrient status of estuarine macrophytes to be understood. Yang *et al*. (2018) determined a benchmark value differentiating between eutrophic and low-nitrogen values. This value was determined to be 18 and anything below this was considered eutrophic. The nitrogen to biomass ratio is most commonly used as this indicator of nutrient enrichment (Lee *et al*., 2004; Burkholder *et al.,* 2007). Kennish and Haag (2014) studied *Z. marina* as an indicator of pollution using the same index at Barnegat Estuary in the northern hemisphere and noted distinct temporal changes in the NPI values. This may be because of the various flow rates and possibly nutrient input at different times of year. *Zostera marina* in Tomales Bay — lower C:N ratios were noted in winter, but no seasonal changes were apparent for C:P (Fourqurean *et al.*, 1997). A study in three estuaries on *Zostera* species that experience nutrient enrichment (Great Bay, Narragansett Bay, and Waquoit Bay) reported N: biomass ratios between 0.3 and 2.5 (Lee *et al*., 2004; Burkholder *et al*., 2007). This is indicative of a eutrophic estuary. Perez-Llourens and Niell (1993) found a N: biomass value of 0.02 for *Z. noltii* which indicated that the estuary was highly enriched with nutrients. This was true as it experienced severe *Ulva* blooms due to eutrophication (Hernandez *et al.,* 1997). *Thalassia testudinum* on the other hand has N:P values of 30 which is high indicating low P contents in the tissues leading to phosphorus limitation, but not N-limitation (Patriquin, 1972; Fourqurean *et al*., 2002). Nutrient ratios are important for understanding both nutrients limiting in a system as well as indicating areas of enrichment, however, the right combinations of ratios should be used for understanding nutrient enrichment and deficit. Unlike seagrasses, salt marsh plants have not been as readily used as indicators of nutrient enrichment, but they may still be effective and there is still a lot of room for research. Literature shows that nutrient inputs can shift species composition resulting in succulent salt marsh species such as *Salicornia* becoming the dominant salt marsh species (Covin and Zedler, 1988; Boyer and Zedler, 1999; Boyer *et al.,* 2001). This is as a result of nitrogen input as phosphorus does not result in biomass changes as was seen in a study on *Salicornia virginica* in a Southern California salt marsh (Boyer *et al*., 2001). This study was done in the Mugu Lagoon that experiences toxic waste and pesticide pollution. Its N: biomass ratio was calculated as 0.002 indicating severely polluted waters.

During the literature search for this study it was apparent that studies used different measures for nutrient storage. Some used milligrams per plant (Zhang and Liu, 2011), other's grams per square meter (Hill *et al.,* 2018), milligrams per litre (Jesus *et al*., 2017) and others megagrams for the total area (Sousa *et al*., 2017), or percentage of the plant (Pierce, 1979; Alldred *et al.,* 2017). This study used megagrams per hectare as for the carbon storage as recent studies are looking at the nutrients and components (C, N, and P) of the ecosystem together and not in isolation (Sousa *et al*., 2017). Standardization for this would be a good start for simplified local and international comparison studies and reviews. It may be beneficial to work with N:P, C:N, C:P, and N: biomass ratios as a universal method of understanding and quantifying nutrient storage in estuarine macrophytes (Lee *et al.,* 2004; Burkholder *et al.,* 2007). These kinds of studies indicate that halophytic macrophytes are essential for reducing eutrophication in estuaries and that they play an important role in maintaining ecosystem functions and health (Sousa *et al*., 2010).

2.7 Blue carbon storage

Blue carbon is defined as the carbon stored and sequestered in coastal ecosystems such as mangroves, salt marsh, and seagrasses (Mcleod *et al*., 2011). This is because the soil is permanently saturated keeping it in an anaerobic state which results in a continual build-up of carbon over time (Chmura *et al.,* 2003). The global average estimates for carbon stocks (to 1 m depth) are 386 Mg ha^{-1} for mangroves, 255 Mg ha^{-1} for salt marsh and 108 Mg ha^{-1} for seagrasses (IPCC, 2013). These ecosystems capture up to 70% of the organic carbon in the marine environment which makes carbon sequestration an important ecosystem service (Nelleman, 2009). Blue carbon studies have increased since the 2009 Rapid Response Assessment by the United Nations Environment Programme (UNEP) that indicated that these habitats are extremely efficient carbon sinks. The UNFCCC Paris Agreement also stipulated that the countries who signed the agreement should give attention to understanding and conserving these blue carbon ecosystems as they have the potential to play a role in climate change mitigation. These ecosystems are under threat globally, despite their significance and this is a huge problem because instead of acting as carbon sinks they can become sources of carbon dioxide releasing emissions into the atmosphere. This is then recognized as a source of greenhouse gases by the Intergovernmental Panel on Climate Change and the United Nations Framework Convention on Climate Change. These greenhouse gases released are approximately 45 billion tons annually. Because of this the Blue Carbon Initiative was formed. It is a program focused at mitigating climate change through conservation and protection of these habitats, which is of utmost importance. There are three tiers of assessment that describe the various levels of detail for carbon inventories and this is generally determined by the purpose of the carbon inventory and the resources available to determine the carbon stocks (IPCC, 2013). A tier one assessment is the most basic and cost effective and are not known for accuracy. This is based on published default values and can encounter up to 50% error in the biomass pool and up to 90% variability in the sediment carbon pool. Tier two assessments will reduce this variability by including some site-specific data, such as there may be mean carbon stock values for the different ecosystem types in the country. IPCC (2013) recommends that tier three assessments are aimed for as they are the most accurate, although they are rather costly to implement. This assessment requires specific data on the carbon stock of all the components making up the ecosystem as well as repeated measures over time to assess change or flux (GOFC-GOLD, 2009).

An important part of blue carbon studies that needs to be clarified is the terminology. A carbon sink refers to either a natural or artificial habitat which accumulates and stores carbon over either long or short periods of time. Carbon sources are habitats that release carbon back into the atmosphere or ocean — this can be due to habitat degradation or natural processes like respiration by plants. Carbon sinks are often associated with carbon stocks. The carbon stock is the current amount of carbon stored within a particular habitat, specific plant species, or area and it is usually reported as megagrams of carbon per hectare (Mg C ha^{-1}). The carbon stock is usually determined by adding the relevant carbon pools together. Within an ecosystem there are a number of carbon pools that store and release carbon. These reservoirs for carbon include the vegetation, sediment, ocean and atmosphere (Howard *et al*., 2014). The various carbon pools in an ecosystem are the biomass, dead organic matter and the sediment. The aboveground biomass is usually the herbaceous part of the plant mass for seagrass and salt marsh, while the belowground biomass includes the roots and rhizomes, however any roots smaller than 2 mm in diameter are excluded from this carbon pool and are included in the sediment. The dead organic litter is all the non-living biomass that is greater in size than the sediment organic matter. The sediment is the greatest carbon pool and it includes all the organic carbon in the mineral soils. Blue carbon habitats can act as both a sink and a source of carbon dioxide (Howard *et al*., 2014). The benefit of these systems is that they generally store more carbon than what they release. According to the IPCC (2007), carbon pools can be further broken down into short- and long-term carbon pools, but long-term carbon pool are the more important of the two for climate change mitigation potential.

The carbon cycle (Figure 2.4) is a biogeochemical cycle where carbon is exchanged between the biosphere and the atmosphere of the earth (Prentice *et al*., 2001). Carbon is one of the basic building blocks of life and is present in all living and non-living things. It cannot be broken down into smaller substances because it is an element. Simply, the carbon cycle is when plants take up carbon dioxide from the atmosphere that is released from the burning of fossil fuels, and plant and animal respiration (Solomon *et al.,* 2007). The plant then uses the carbon dioxide along with water and sunlight to photosynthesize. The animal then eats the plant and it releases carbon dioxide back into the atmosphere through respiration. Some plants, however, can store carbon for longer periods of time and these are the ones useful for carbon storage as an ecosystem service. It is important to note that the carbon cycle is more detailed than this brief explanation. Figure 2.4 represents the carbon pools (Blue) in the global carbon cycle and the carbon fluxes (red) (Verlinden, 2013). Carbon fluxes are the movement of carbon between the various carbon pools, but it can be between both natural and anthropogenic systems (Chapin, 2002). The sources of carbon to the macrophyte can either be autochthonous or allochthonous (Middelburg *et al*. 1997; Kennedy *et al*. 2010). Autochthonous carbon is carbon that was produced and deposited in the same area, so this generally means that it comes from photosynthesis. The plant then stores the carbon in the roots where it decomposes slowly and eventually adds to the sediment carbon pool beneath the plant itself (Middelburg *et al*. 1997; Kennedy *et al*. 2010). Allochthonous means that the carbon is from an external source, it was produced in a different place to where it is deposited (Middelburg *et al*. 1997; Kennedy *et al*. 2010). Due to the nature of blue carbon ecosystems and the vegetation growing within them, the plants are effective at trapping particles containing carbon such as algae, debris, or sediment as it moves through the plant habitat (Githaiga *et al.,* 2016). Kennedy *et al*. (2010) suggested that autochthonous and allochthonous carbon studies should be assessed separately because the processes are so different.

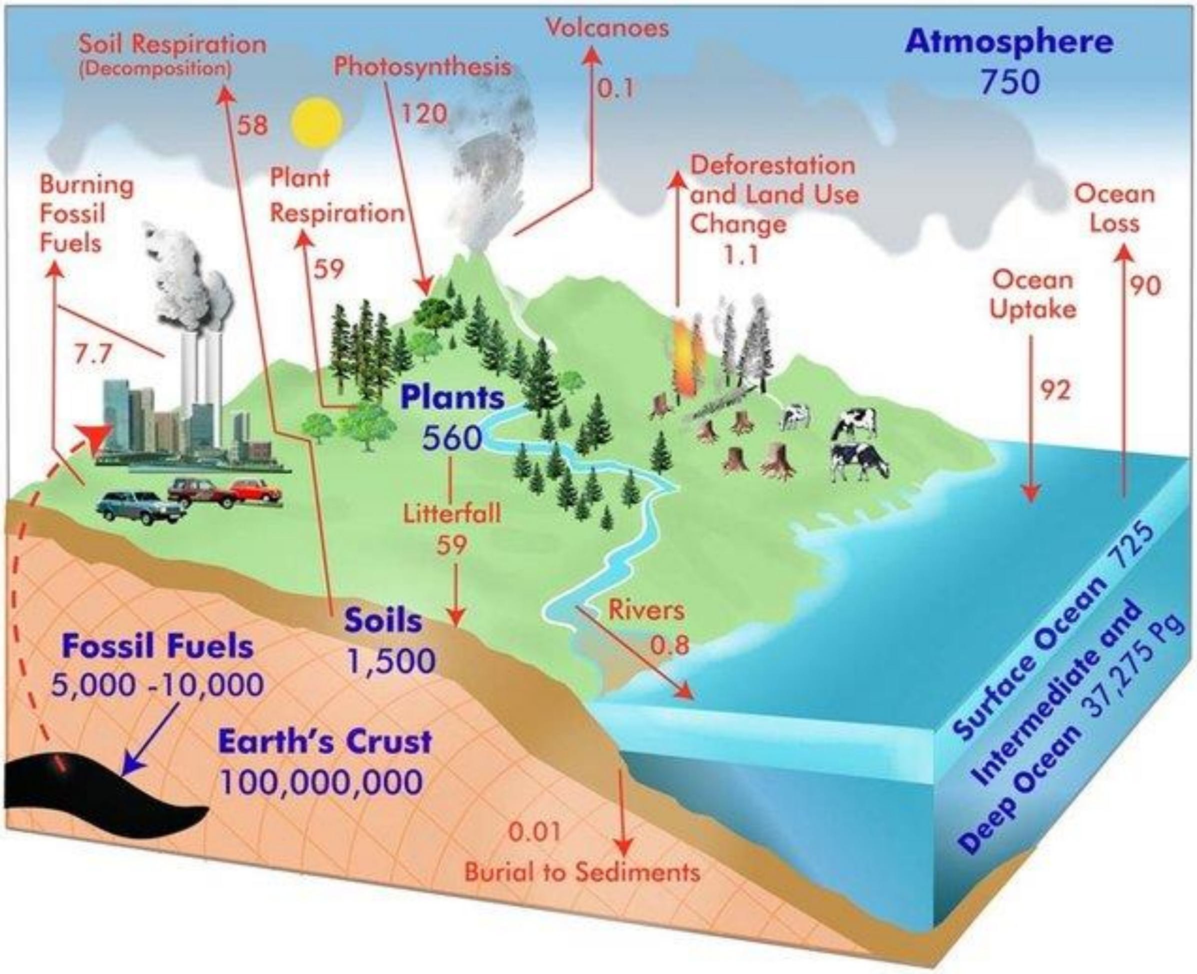


Figure 2.4: The global carbon cycle (Verlindin, 2013)

Over the past decade there has been a substantial amount of research quantifying blue carbon sequestration and storage. Despite these ecosystems being almost two times smaller than terrestrial forests, their long-term carbon sequestration capacity is much greater because of their efficiency in trapping suspended matter that contains organic carbon during tidal inundation (Duarte *et al.,* 2005). These habitats accumulate carbon in their sediment up to 55 times faster than tropical rainforests (McLeod *et al*., 2011; Macreadie *et al*., 2017). The number of studies around the globe on blue carbon stocks are increasing, however, most have taken place in North America, Europe, and Australia. Many areas still lack blue carbon data, including Africa, South America, and South-east Asia (Duarte *et al.,* 2017). Many studies on salt marshes have occurred in areas such as eastern and north eastern United States of America (Drake *et al.,* 2015; Tripathee and Schafër, 2015), in the United Kingdom (Beaumont *et al.,* 2014), and many detailed studies have been done in Australia (Saintilan *et al*., 2013; Rogers *et al.,* 2014, Macreadie *et al*., 2013; Macreadie *et al*., 2017; Kelleway *et al*., 2016, 2017). Seagrasses have a large extent in the west African region that may contribute globally to carbon sequestration and storage, but even so, studies have been few and far between (Duarte *et al*., 2011; Dahl *et al*., 2016). Most studies have taken place in the USA, Europe, and Australia (Lavery *et al.,* 2013; Serrano *et al.,* 2014; Armitage and Fourqurean, 2016; Dahl *et al.,* 2016 and Gullström *et al*., 2017).

Salt marshes play a large role in the storage and sequestration of carbon because they are one of the most productive ecosystems worldwide — storing up to 3900 g C m^{-2} yr^{-1} (Mitsch and Gosselink, 2008). What makes salt marshes unique in their carbon storage capabilities is that in most of the world's ecosystems the turnover of carbon is quick, and it does not often reach the long-term stages of the carbon cycle. Because of the anaerobic soils of salt marshes, the carbon captured for photosynthesis is often shifted from the short-term carbon cycle (10 – 100 years) to the long-term carbon cycle where it is buried as slowly decaying biomass (1000 years) (Mayor and Hicks, 2009). The position of the plant on the salt marsh also influences the amount of carbon stored. In the Tagus salt marsh, the lower *S. maritima* in the younger part of the estuary stored 3.32 Mg C ha^{-1} in the biomass while *Halimione portulacoides,* a shrub, which is higher on the intertidal marsh stored more carbon (20.22 Mg C ha^{-2}) (Cacador et al., 2003). In the same study the smaller and more industrialized and polluted part of the estuary stored more carbon in the intertidal *S. maritima* (27.24 Mg C ha^{-1}), while *H. portulacoides* stored 24.91 Mg C ha^{-1}. These values are quite high compared to what has been found elsewhere in the world. *Spartina alterniflora* only stored 4.46 Mg C ha^{-1} in its biomass in the Yangtze Estuary in China (Liu *et al.,* 2013). A South-eastern Australian study found that salt marsh grasses stored 7.51 ± 0.91 Mg C ha^{-1} in the estuary (Owers *et al.,* 2018). Literature has shown that the C_4 *Spartina* generally stores more carbon than the C_3 succulent halophytes like *Sarcocornia* and *Salicornia* (Liu *et al.,* 2013; Schile *et al.,* 2017; Chastain *et al*., 2018; Owers *et al.,* 2018). Wang *et al*. (2012) found that most C4 plants are more effective at carbon fixation which increases photosynthesis and plant yields. Photosynthesis in C_3 plants is increasing with increases in carbon dioxide and this may result in increased carbon assimilation by the plant (Koch *et al.*, 2013). *Sarcocornia* salt marshes in South-east Australia stored 6.88 ± 1.38 Mg ha^{-1} (Owers *et al*., 2018) which falls within the range of salt marsh carbon storage in arid areas (1.9 to 7.2 Mg C ha^{-1}) (Schile *et al*., 2017).

The carbon stored by seagrasses is determined by specific growth characteristics. For example, pioneer species such as, *Halodule* and *Halophila*, that expand rapidly and produce shoots quickly store less carbon while species such as, *Thalassia* and *Posidonia,* that spread slowly and develop extensive rhizome mats tend to build up large carbon reserves in the sediments (Björk et al., 2008). Seagrasses also decompose slowly which adds to the carbon that is stored. The thick rhizome mats that form over thousands of years play a huge role in the carbon fixation in the ocean which results in seagrasses storing 12% of the ocean carbon (Duarte and Cebrian, 1996). When these seagrass beds die back however, large amounts of carbon are released into the ocean. *Zostera marina* is likely the most similar seagrass species to *Z. capensis*. *Zostera marina* beds in Studland Bay in the UK were found to store 2.51 ± 0.49 Mg C ha^{-1} (Green *et al*., 2018). Other *Z. marina* beds along the Pacific coast of Canada stored 0.17 ± 0.01 Mg C ha^{-1} (Postlethwaite *et al.,* 2018). *Posidonia oceanica* is thought to be the most effective seagrass species at long term carbon storage, storing 7.29 ± 1.52 Mg C ha^{-1} (Serrano, *et al*., 2016). On average seagrasses store 138 ± 38 g C m^{-2} yr^{-1} (Mcleod *et al*., 2011). This indicates the variability of carbon storage in seagrass meadows globally between seagrass species. In Africa studies on carbon storage are still in their initial stages with the first study being published in 2017 from Gazi Bay in Kenya on seagrass (Githaiga *et al.,* 2017). This study also confirmed the variability finding significant differences between seagrass species in the same estuary. The average carbon stored was 5.9 ± 0.9 Mg C ha^{-1} (Githaiga *et al*., 2017). In all these ecosystems the largest carbon stocks were found in the sediment (Howard *et al*., 2014).

2.8 Ecosystem services

Seagrass and salt marshes have numerous important ecosystem services, such as reducing the impact of erosion and flooding, increasing water quality, and sequestering nutrients (McLuskey and Elliot, 2004). However, eutrophication has become common within estuarine systems especially where there are extensive urban pressures and nutrient input is dominated by industrial waste water, urban drainage, and agricultural effluent (Kemp *et al*., 2005; Sousa *et al*., 2011). Ecosystem services can be grouped into four major categories (Table 2.1) according to the Millennium Ecosystem Assessment — firstly, provisioning services which are goods from the environment that provide material or nutritional output that can either be used directly by the person catching or collecting the good, or the goods can be traded and used for manufacturing. Regulating services are the benefits that arise from the managing and maintaining of ecosystem processes by the various components of the ecosystem while the supporting ecosystem services are the services required for the production of all other ecosystem services. Lastly, cultural services are the benefits obtained from the non-material aspects of the ecosystem, such as spiritual and aesthetic wellness. (Millennium Ecosystem Assessment, 2005). Minimal studies have been done on salt marsh ecosystem services and the valuating of them in comparison to mangroves and seagrasses (Himes-Cornell *et al*., 2018). These ecosystem services need to be in a good state for human consumption without the resources becoming depleted or in a state where they are no longer fit for human consumption. These ecosystems are under threat globally (Macreadie *et al.,* 2013). There are various numbers of threats and they have varying impacts on estuarine ecosystem health and function (Table 2.1). The ecosystem services provided by seagrass are not equal in their provision because larger seagrasses for example may provide habitats for species such as the duogong in Mozambique while smaller seagrass species still provide important services in nutrient regulation for example (Nordlund *et al*., 2016). Nordlund *et al.* (2016) therefore advised that caution be taken when giving ecosystem services economic value and comparing across global boundaries.

Table 2.1: Ecosystem services and threats to these services

Ecosystem Service	**Threat**	**Reference**
Provisioning Services		
Food	Urbanisation, Overfishing	Egoh *et al.* (2012)
Wood/ plant materials	Climate change	Hughes (2004)
Biomedical	Biological invasion	Gedan *et al*. (2009)
Energy	Overgrazing	Muenzel and Martino (2018)
Regulating Services		
Flood prevention	Jetties/ Docks	Logan *et al*. (2018)
Climate regulation	Coastal development	Heckbert *et al.* (2011)
Erosion control	Sea-level rise	Kirwan *et al*. (2016)
Pest/ Invasive control	Climate change	Thorne *et al.* (2012)
Carbon sequestration	Sediment toxicity, grazing	Disney *et al*. (2014), Muenzel and Martino (2018)
Water purification	Invasive species	Hansen *et al.* (2015)
Supporting Services		
Nutrient recycling	Eutrophication	Valiela *et al*. (1976)
Primary production	Hydrologic alterations	Gedan *et al*. (2009)
Biodiversity maintenance	Dredging	Baptist *et al*. (2016)
Soil formation	Sea-level rise	Weis *et al*. (2016)
Cultural Services		
Recreational activities	Decreased air/ water quality/ pollution	Banerjee *et al.* (2017)
Aesthetic value	Habitat degradation	Banerjee *et al.* (2017)
Heritage	Natural disasters	Rojas *et al.* (2017)

Spiritual value	Giving salt marshes monetary value	Cooper *et al*. (2016)
Tourism	Industrial development	Thornes (1999)
Commercial	Heavy metal pollution	Conesa and Jimenez-Carceles, (2007)
Educational	Mangrove encroachment	Kelleway *et al.* (2017)

3. Study site

The Swartkops Estuary is located close to Port Elizabeth at 33°51'54"S; 25°38'00"E and is permanently open to the sea. This estuary is defined by its tidal range of 16.4 km (Baird *et al.*, 1986). The estuary is wide in the lower reaches (350 m width) and starts to narrow slightly in the middle reaches (90 m width) and narrows even more in the upper reaches. The main channel was reported to be deepest in the upper reaches and approximately 1.5 m shallower at the mouth (Reddering and Esterhuysen, 1981). This is a nationally important estuary because of the variety of ecosystem services it has to offer the surrounding communities. It has an importance ranking of 5th amongst temperate estuaries in South Africa. With regards to its biodiversity and conservation importance, the estuary is ranked as 11th in the country. The estuary is ranked as 4th overall in terms of its botanical importance and of the various community types, intertidal salt marsh was said to be the most important (Colloty *et al*., 2001). Swartkops Estuary has the third largest salt marsh areas in the country which makes it a vital habitat for biodiversity.

The Swartkops Estuary has one of the largest *Z. capensis* area cover in South Africa after Langebaan lagoon, Knysna, Berg, and Keurbooms estuaries (Adams, 2016). Combining all the contributing biotic and abiotic factors to the structure and functioning of the estuary a Present Ecological State (PES) was determined. The Swartkops Estuary has a PES of a D which means that it is largely modified (Van Niekerk and Turpie, 2012). This estuary is in an urbanised area — residential areas that occur along the estuarine banks include Amsterdamhoek, Bluewater Bay, Redhouse, and the Swartkops Village. Kwazakele and Motherwell are also located in the area although not directly on the estuary. There is also a large industrial area bordering the estuary, including the brickworks, Fishwater Flats sewage works, abandoned salt pans, sand and clay mining and motor vehicle industries. Freshwater inflow may come from Groendal Dam, sewage and storm water effluents, and urbanisation (Scharler and Baird, 2003). It is a well-known fact that the Swartkops Estuary is heavily polluted by nutrients, toxins, microalgae, and faecal matter because of the high wastewater and storm water runoff. The main sources of these pollutants are from the Perseverance river inflow, as well as Motherwell canal, Markman canal, and the Chatty River (Adams *et al.,* 2014, 2019). The Swartkops river main catchment covers an area of 1354 km^2. This originates from the Groot Winterhoek mountains to the west of Uitenhauge (Reddering and Esterhuysen, 1981).

The climate of the Swartkops Estuary area is moderate. It has a mean annual rainfall of 636 mm with slight peaks in Spring and Autumn, but it is evenly distributed throughout the year. Temperature shows more variation through the year than rainfall with an average high of 26°C and 19°C in January and July respectively. There are extreme conditions where the temperatures may reach up to 42°C and 32°C in the respective months. The average minimum temperatures are 15°C and 7°C for summer and winter months respectively. Berg winds tend to occur mainly in late winter, however, wind is frequent and strong along the coast (Reddering and Esterhuysen, 1981).

The sites were selected based on the sites used by Talbot and Bate (1987) for the measurement of *Z. capensis* biomass and the sites used by Pierce (1979) for *S. maritima.* Six sites were selected along the length of the estuary (Figure 3.1). Since the study by Talbot and Bate (1987) the seagrass distribution has changed, and it is no longer found beyond Site 6. Sampling took place in late summer (February 2018) as this is when biomass is usually at its peak growth and again in winter (June 2018) (Howard *et al*., 2014). This is sufficient for an assessment of the current nutrient and carbon stocks in the macrophyte biomass and sediment beneath the various species. Most blue carbon studies do once off assessments or take measurements on an annual basis to assess long-term changes.

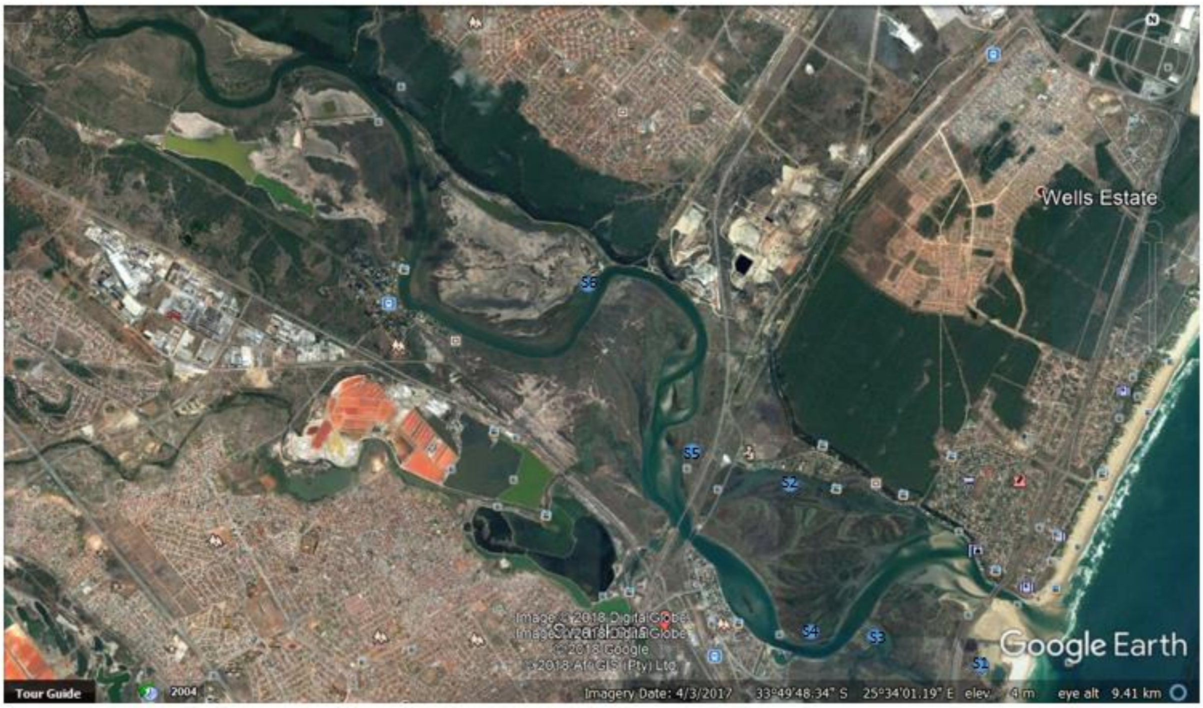


Figure 3.1: Swartkops Estuary sampling sites (●) for the seagrass, Zostera capensis, and salt marsh species, Spartina maritima and Salicornia tegetaria.

4. Methods and materials

4.1 Aerial cover of the dominant macrophytes

Orthorectified RGB images were obtained for the Swartkops Estuary. These images were used together with Google Earth images to map the seagrass beds, *S. maritima* stands, and remaining intertidal salt marsh using ArcMap 10.3 for Desktop (ESRI®). The projected coordinate system used for mapping was AEA_WGS84, Projection Albers, with central meridian 25. The geographic coordinate system was GCS_WGS_1984, with D_WGS_1984 datum. This information together with the biomass allowed for the calculation of the total carbon within the dominant intertidal macrophytes for the entire estuary. *Salicornia tegetaria* could not be mapped as it is mixed with other salt marsh species and the 100% cover stands were patchy making mapping a difficult activity. The estimated total carbon for *Salicornia tegetaria* was therefore calculated as 30% of the intertidal salt marsh based on site specific observations of abundance.

4.2 Sediment characteristics

Three important parameters were considered namely; the depth, dry bulk density and organic carbon content in the sediment. Six soil cores of 1 m were taken in the summer season at each of the six sites and six cores of 0.5 m were taken in the winter season at each of the six sites. There was no change in the organic content below 0.5 m for the summer sampling, so it was unnecessary to sample to 1 m in winter. Samples were collected using a Russian peat corer (Stainless steel 5 cm diameter X 50 cm length with extensions to core deeper). Subsamples were collected at four appropriate intervals where sediment colour changes were observed in each core so that variation with depth could be analysed. During the laboratory analysis, the dry bulk density (DBD) was calculated by drying the sediment at 60°C for 48 to 72 hours. The organic carbon content was calculated using the loss on ignition (LOI) method — half of each sample was put in the ashing oven. The equations used for these calculations are:

Equation 1: Dry bulk density (g/cm^3) = Mass of dry soil (g) / Original volume sampled (cm^3)

Equation 2: % Loss on Ignition (OC) = [(dry mass before combustion (mg) – dry mass after combustion (mg))/ dry mass before combustion (mg)] * 100

Figure 4.1: Russian peat corer with a sediment core beneath Salicornia tegetaria.

4.2.1 Acidification

Further elemental analysis was done to make this a Tier 3 assessment which is more accurate. To prepare the samples for elemental analysis carbonates were removed. Once the samples were dried, they were homogenized into a fine powder followed by acidification. Each sample was acidified using 1N hydrochloric acid which just covered the entirety of the sample (the remaining half of the sediment sample that was not ashed). The samples were then mixed for 15 minutes on a Labcon micro-processor controlled platform shaker (SPL 15) and left to stand overnight. The acid was then removed with a syringe or pipette and more acid was added to see if the sample continued to effervesce. If gases were no longer being released, the sample was rinsed three times with distilled water, mixed and left to stand between each rinse so that the sediment could settle. The samples were then placed in the oven at 60°C for 48 hours, weighed again and the initial weight before acidification was subtracted to determine the carbonate in the sample. The inorganic carbon in the sample could then be determined (Equation 4). The carbon is multiplied by 12% because this accounts for the weight difference in the carbon that makes up 12% of the molecular weight of calcium carbonate (Howard, et al., 2014).

Equation 4: Inorganic carbon = Mass of carbonate * 0.12

4.2.2 Elemental analysis

Samples were sent to Louisiana State University Wetland Biogeochemistry Analytical Services Laboratory for elemental analysis of carbon in the sediment. Preparing the samples was delicate and time-consuming work. A clean work space was prepared, and all equipment was cleaned with ethanol between each sample that was weighed (Howard, *et al*., 2014). For each sample the tin capsule was weighed and tared and if the organic content of the sample as previously determined was between 0.5 and 1%, 25-30 mg of sample was weighed out to be sent. If the samples organic content was between 2 and 11%, 9 to 10 mg of sample were weighed into the tin capsule which was then folded into a tiny ball and placed in a tray to be sent to the analytical laboratory for analysis. The amounts of sample sent for analysis were prescribed by the laboratory. Most of the samples measured were in the range of 2 to 11% organic content.

4.2.3 Carbon density and total blue carbon for seagrass and salt marsh sediments

It was necessary to calculate carbon density so that the total carbon in the sediment could be determined. This was done using the organic carbon and the dry bulk density for each depth interval. Using the soil carbon density, the total carbon per core could be calculated and determined in the globally accepted carbon assessment units (Megagrams per hectare). The equations are below (Howard, *et al*., 2014):

Soil carbon density (g/cm^3) = dry bulk density (g/cm^3) * (%C$_{org}$ /100)

Amount of carbon in core section (g/cm^3) = Soil carbon density (g/cm^3) * thickness interval (cm)

Total core carbon (MgC/hectare-cm) = Total carbon for all cores (g/cm^3) * 1Mg/1000000g) *(100000000cm^2/1 hectare)

4.3 Sediment type

Additional sediment was collected using a PVC core (Ø=0.1m). One 0.5 m core was collected from the sediment beneath *Z. capensis, S. maritima*, and *S. tegetaria* at each of the six sites. Each core (18 total) was sub-divided into three replicates which were then analysed. The sediment type was determined by means of particle size analysis using the hydrometer method (Bouyoucos, 1962). The collected soil was dried at 105°C for 24 hours. Once dried and weighed the sediment was homogenized and sieved until it was less than 2 mm, all large particles were removed. Fifty grams of soil was weighed out. A sodium hexametaphosphate (HMP) solution was prepared and added to the sediment which helped suspend the soil particles. Fifty grams of Na HMP was mixed with 1L deionized water while it was stirred on a stir plate and this was left to mix for a few hours until it was thoroughly mixed, and the solution was transparent. One hundred millilitres were added to the 50 g of sediment which was thoroughly mixed for 30 to 60 seconds. It was then placed in a 1000 ml cylinder and topped up with 900 ml deionized water at room temperature. The solution was mixed with a plunger for 30 seconds until a uniform suspension was obtained. This was followed by waiting forty seconds before taking the temperature reading and the hydrometer reading. This was repeated to obtain three replicates. Another thermometer reading, and hydrometer reading were taken after 1.5 hours. This time period represented the amount of suspended silt, clay, and sand that had settled. The hydrometer was rinsed between readings. After 24 hours another hydrometer and temperature reading was taken as this was the amount of clay suspended and the silt that has settled. For every degree celcius above 20°C, 0.2 was added to the hydrometer readings and 0.2 was subtracted for every 1°C below 20°C. Below are the equations that were used to calculate the percent sand, silt and clay. Rsand was the 1.5-hour hydrometer reading, Rclay was the 24-hour reading and RC1 and RC2 were the values of the blank at 1.5 hours and 24 hours.

1. Sand % = ((oven dry soil mass) – (Rsand – RC1))/ (oven dry soil mass) x 100
2. Clay % = (Rclay – RC2) / (oven dry soil mass) x 100
3. Silt % = 100 – (Sand % + Clay %)

4.4 Seagrass and salt marsh biomass

Zostera capensis was collected in the Swartkops Estuary using a PVC corer (Ø=0.1m). Samples were taken up to a 20 cm depth in the rhizosphere. Summer and winter sampling took place to represent the temperature extremes of the seasons. Six replicates were taken of each macrophyte species at the six sites (in winter) and five sites (in summer) along the length of the estuary so that it was comparable to the study by Talbot and Bate (1987) and Pierce (1979). Samples were only collected at five sites in summer due to restricted access to the one site. The samples were stored in a cool place while in transit. In the laboratory the epiphytes were removed manually from the leaves by scraping them with a blade for later biomass analysis. The leaf length was then measured. The samples were separated into above and belowground biomass. The wet weight was measured using an electronic balance and the above and belowground biomass were placed in separate beakers and dried in the oven at 60̊ C for 72 hours so that the biomass could be determined, expressed as g DW m^{-2}. The salt marsh plants were sampled and processed in the same way as the seagrass. This study focussed on the two dominant lower intertidal species *Spartina maritima* and *Salicornia* *tegetaria* and samples were collected in areas of 100 % cover. While leaf length was measured for the seagrass, stem height was measured for *S. maritima* as it grows upright, and stem length was measured for *S. tegetaria* which grows along the ground. These variables were measured so that a relationship could be determined between biomass and plant height or leaf length. A strong correlation between the two variables would allow for leaf length or stem height to be used to estimate biomass and reduce destructive sampling measures.

4.5 Seagrass and salt marsh blue carbon

The calculated biomass was used with a carbon conversion factor specific to seagrass to determine the organic carbon stored in the plant (Equation 3). This is a Tier 1 assessment as it only makes use of an allometric equation. The conversion factor of 0.34 assumes that 34% of the biomass consists of organic carbon in seagrass (Githaiga, et al., 2017). According to Howard, et al. (2014) salt marsh have a conversion factor of between 0.4 and 0.46.

Equation 3: Carbon in the living component (g C m^{-2}) = (Estimated biomass of the plant * Carbon conversion factor (0.34)) / area of the plot

A Tier 3 assessment was also done so that the results could be compared. The same steps were followed as stipulated in Section 4.2.1 “Acidification” to remove any inorganic carbon from the samples. The same process followed for the sediment in Section 4.2.2 “elemental analysis” was followed to package the samples. The only exception is that for plant material, 4.0 – 4.5 mg was weighed and placed in the tin capsule for elemental analysis. A carbon conversion factor specific to *Z. capensis, S. maritima*, and *S. tegetaria* biomass was calculated based on the results from the elemental analyser by finding the mean of the results returned from analysis. The table below displays the carbon conversion factors for the above and belowground carbon content of the three species.

Table 4.1: Species specific carbon conversion factor for plant biomass (Determined from elemental analysis of the specific plant species in this study)

	Aboveground	Belowground
Zostera capensis	0.35	0.33
Spartina maritima	0.40	0.25
Salicornia tegetaria	0.32	0.38

4.6 Epiphyte biomass (Chlorophyll a)

The chlorophyll *a* (biomass) was determined by scraping the epiphytes off the seagrass leaves into filtered seawater and then filtering that water again so that the epiphytes were caught on the filter paper. The filter paper was then placed in 10 ml of 95% ethanol in a glass vial and left to extract for 24 h in a cold, dark room. Spectrophotometric determinations of chlorophyll *a* were then made. Absorbance at 665 nm wavelength was measured before and after acidification with 1N HCL (Nusch, 1980). The chlorophyll *a* was measured per unit area (mg m^{-2}).

4.7 Nutrient analysis

Total nitrogen and phosphorus were determined in the plant samples and water samples by the SAEON biogeochemical laboratory situated at Nelson Mandela University's Ocean Science Campus. Six samples of aboveground biomass and six samples of belowground biomass were analysed for total N and P at each site for each plant species. 0.05 g of plant material were weighed into autoclave safe bottles and 50 ml of oxidizing agent (made up of 11.25 g potassium persulphate, 4.75 g sodium hydroxide, and 6.75 g boric acid to make one litre) was added to them. This was then placed in an autoclave at 120° C for 1.5 hours. Once cooled the liquid was then filtered through a gravity filter to remove all pieces of plant material. The samples were then frozen and analysed within three weeks on the Seal AA3 autoanalyzer (Grasshooff, et al., 1983). Once total N and P were determined, molar nutrient ratios were calculated. Nitrogen: biomass was also determined as this has been found to be an effective nutrient pollution indicator (NPI) in estuaries (Lee*, et al*., 2004; Burkholder*, et al.,* 2007).

4.8 Statistical analysis

Sediment variables such as bulk density, organic content, organic carbon, and carbon density were analysed using analysis of variance (ANOVA) where data was normal, and a Kruskal-Wallis test was used for the non-parametric data to test for significant differences between seasons and sites. Normality was tested for by making use of a Shapiro-Wilks test. Changes in depth and changes across sites were fixed factors using R version 3.5.1 (Copyright © 2018, The R Foundation for Statistical Computing), Rcmdr package (Fox and Bouchet-Valat, 2018). The same package was used to analyse significant changes in the biomass across sites and between seasons. A Spearman’s rank correlation was applied to the data to determine whether biomass was correlated to leaf length and stem height. Correlation analysis was also done between sediment organic carbon content and the organic content to determine allometric equations for future carbon analysis if elemental analysis is not a possibility.

5. Results

5.1 Aerial cover of dominant macrophytes

The total area for the seagrass *Z. capensis* was 62.3 ha (Figure 5.1) and 96 ha of *S. maritima* was mapped in the Swartkops Estuary. Significant losses in area cover have been observed in the upper reaches since the study by Talbot and Bate (1987) (Figure 5.2). The yellow circle represents the new uppermost extent of where seagrass occurs currently. Although *Z. capensis* is no longer found in the upper reaches, the area of seagrass beds has increased in the lower reaches. Table 5.1 displays consistency in the seagrass cover, between 1939 and 1982, but since 1996 until the current study the seagrass area has increased significantly. *Spartina maritima* has shown a similar trend to *Z. capensis* since the 1930's — increasing in area cover. This is an estimation looking at data from the 1970's (Table 5.2) because the *S. maritima* aerial cover from google earth images were not clear which is why only intertidal salt marsh could be mapped. *Salicornia tegetaria* stands are patchy and relatively small, making them difficult to map. Due to this, 30% of the intertidal salt marsh was estimated to be *S. tegetaria* giving it an areal cover of 27.32 ha.

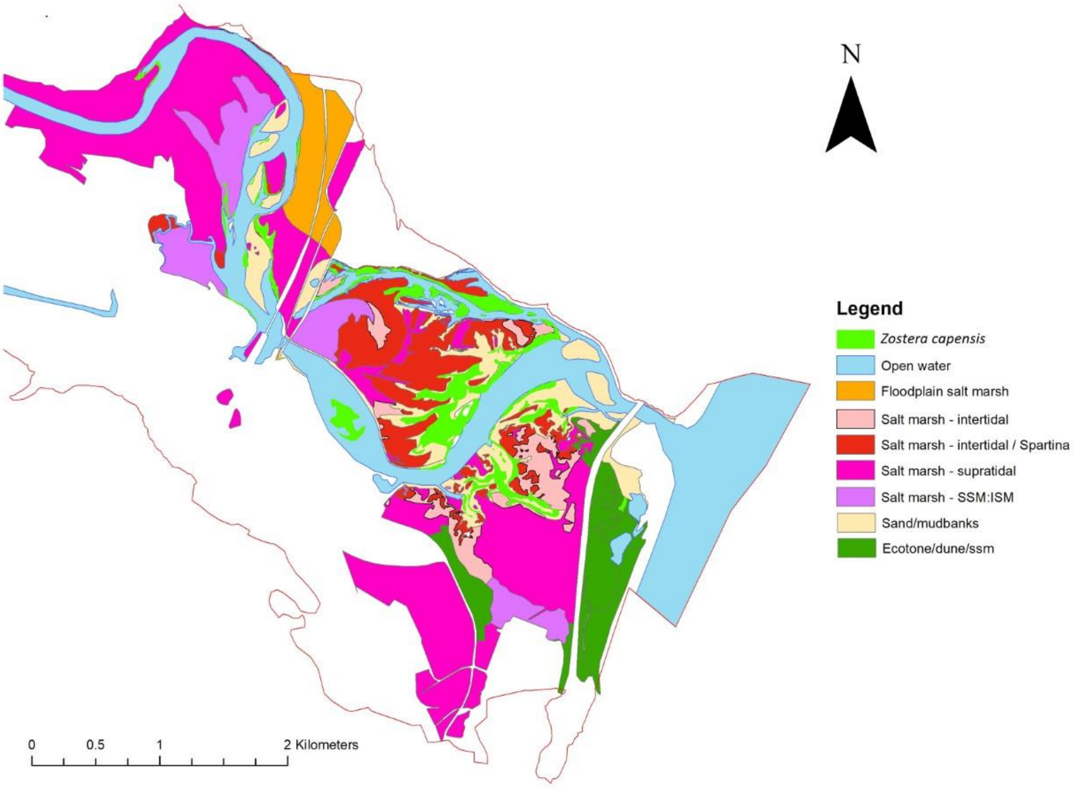


Figure 5.1: Distribution of Z. capensis and S. maritima in the Swartkops Estuary (2019).

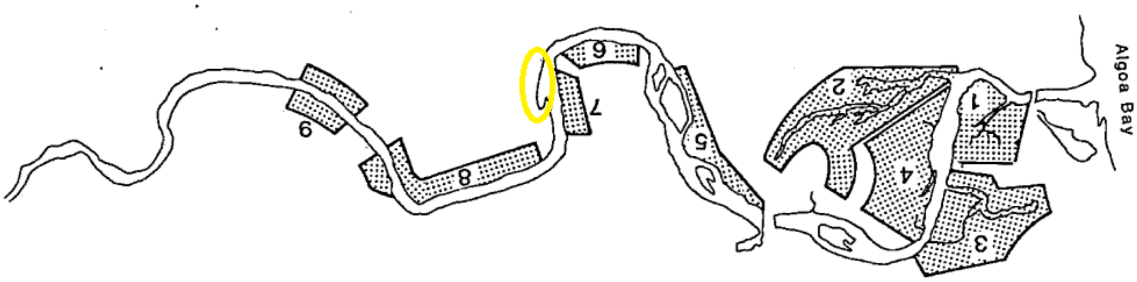


Figure 5.2: Distribution of Z. capensis biomass from Talbot and Bate (1987).

Table 5.1: Zostera capensis area cover changes from 1939 to 2019.

Area cover (ha)	**Year**	**Reference**
24.8	1939	Schmidt (2013)
15.0	1957	Macnae (1957)
16.1	1982	Talbot and Bate (1987)
12.5	1996	Colloty, *et al.* (2000)
44.7	2013	Bornman, *et al*. (2016)
62.3	2019	This study (2019)

Table 5.2: Spartina maritima area cover from 1939 to 2019.

Area cover (ha)	**Year**	**Reference**
143.4 (Intertidal marsh)	1939	Schmidt (2013)
82.3	1979	Pierce (1979)
68.5	2008	Schmidt (2013)
60.1	2012	Bornman, *et al.* (2016)
96.0	2019	This study

5.2 Sediment characteristics

5.2.1 Bulk density

Overall the sediment bulk density within the estuary ranged between 0.74 to 1.6 g. cm^{-3} so that root growth was not restricted (Bulk density > 1.6 g. cm^{-3}). The bulk density was consistent across seasons and depth ($F = 0.06$; $df = 1$; $p > 0.05$) for all three species (Figure 5.3), however there was significant spatial variability ($F = 9.57$; $df = 5$; $p < 0.0001$). In summer and winter Site 1 had the highest bulk density ($H= 24.64$; $df= 4$; $P < 0.001$) beneath *Z. capensis, S. maritima*, and *S. tegetaria* stands. In summer the bulk density was similar at 0.5 m and 1 m depths for all sites and species. In winter cores were only taken to 0.5 m and the changes with depth were also not significant.

Figure 5.3: Bulk density of the sediment beneath Z. capensis, S. maritima, and S. tegetaria in summer and winter.

5.2.2 Carbon density

Carbon density is the amount of carbon in a given volume of sediment. The carbon density ranged between 0.064 g. cm^{-3} and 0.009 g. cm^{-3}. There was minimal difference in the carbon density determined in summer and in winter ($H = 0.27$; $df = 1$; $p > 0.05$) and there were no significant changes with depth ($H = 16.27$; $df = 3$; $p > 0.01$), but spatially there were significant diferences ($H = 22.26$; $df = 5$, $p < 0.0005$) for *Z. capensis, S. maritima*, and *S. tegetaria*. The spatial variation was more evident in winter than in summer ($H = 15.62$; $df = 5$; $p < 0.01$, Figure 5.4) for *Z. capensis* and *S. maritima*. The sediment carbon density beneath *Z. capensis* was significantly higher at Site 4 in summer and even more so in winter ($F = 7.70$; $df = 5$; $p < 0.0005$) and did not differ significantly between the other sites in either season. In the *S. maritima* stands in summer Site 1 (0.02 ± 0.002 g C cm^{-3}) had significantly lower carbon density than the other sites ($H = 13.96$; $df = 4$; $p < 0.01$). This was also the case in winter where the mean carbon density was 0.05 g C cm^{-3} compared to a higher range of mean values (0.15 g C cm^{-3} to 0.29 g C cm^{-3}) at the other sites. *Salicornia tegetaria* also differed between sites — Site 3 (0.06 ± 0.007 g. cm^{-3}) and 4 (0.06 ± 0.017 g. cm^{-3}) had significantly higher carbon density than the other sites in summer ($H = 15.814$; $df = 4$; $p < 0.005$). In the winter season, Sites 2 (0.06 ± 0.005 g. cm^{-3}) and 3 (0.06 ± 0.009 g. cm^{-3}) had a higher carbon density ($H = 14.97$; $df = 5$; $p < 0.05$) than the other sites.

Figure 5.4: Carbon density of the sediment beneath the dominant lower intertidal species in the Swartkops Estuary.

5.2.3 Organic content

Organic content beneath *Z. capensis* and *S. maritima* in the Swartkops Estuary was greater in the summer than in winter (F = 5.89; df = 1; $p < 0.05$), but no significant difference occurred between the organic content of the sediment beneath *S. tegetaria* in the two seasons. Similar trends were observed between *Z. capensis* and *S. maritima*. The organic matter beneath both *Z. capensis* and *S. maritima* differed significantly between sites in summer and winter (H = 31; df = 5; $p < 0.00001$). In summer Site 1 (1.8 ± 0.1 %) and 5 (3.2 ± 0.2 %) had lower organic content than the other sites (F = 38.74; df = 4; $p < 0.001$). In winter, only Site 1 had significantly lower sediment organic content (F = 4.86; df = 5; $p < 0.005$). *Spartina maritima* sediment organic content was significantly higher at Site 2 (7.5 ± 0.9 %) than at any of the other sites (F = 4.74; df =5; $p < 0.001$).

Salicornia tegetaria sediment organic content had different trends to *Z. capensis* and *S. maritima*. In summer and winter Site 3 had the highest organic content (4 ± 0.7 % and 4.1 ± 0.6 %, respectively) compared to the remaining sites (H= 24.64; df= 4; $P < 0.001$). In winter specifically, Site 1 had lower sediment organic content (H = 15.61; df = 5; $p < 0.01$).

Overall the organic content appeared to decrease with depth across all sites (Figure 5.5), but this relationship was only significant at Site 4 for *Z. capensis* and *S. maritima* (F = 4.35, df = 3, $P < 0.01$). This was most apparent at the 0 to 30 cm depth interval which was significantly higher in organic content than the other depths ($p < 0.01$). Sediment organic content of *S. tegetaria* decreased significantly with depth at Site 3 in the summer (F = 4.85, df = 8, $P < 0.005$), but in winter, only Site 2 differed significantly between depths (F = 5.64, df = 3, $P < 0.001$). The little variation observed overall between depths in the summer season and the slightly lower organic content at deeper depths resulted in it not being necessary to collect 1 m cores in the winter season as the 0 – 0.5 m depth intervals are where the greatest variation occur.

Figure 5.5: Organic content of the sediment beneath Z. capensis, S. maritima, and S. tegetaria stands in summer and winter.

5.2.4 Organic carbon

Sediment organic carbon results from the elemental analyser were plotted against the organic content results from the loss on ignition (LOI) method to determine whether there was a relationship between the two variables. The averages for both seasons resulted in a stronger relationship between the two variables (Figure 5.6). From this formula and r^2-value, an equation was determined which could aid future studies in determining the organic carbon content in the sediments if samples could not be sent for elemental analysis. Organic content has been used as a proxy for organic carbon where elemental analysis was not possible because as organic content increases so does the organic carbon (Howard, et al., 2014). For the sediment beneath *Z. capensis* stands the linear regression resulted in an r^2 - value of 0.64 ($p < 0.001$). *Spartina maritima* stands had a stronger relationship between sediment organic content and organic carbon ($r^2 = 0.73$, $p < 0.001$) and *S. tegetaria* stands had the strongest relationship between the two sediment variables ($r^2 = 0.82$, $p < 0.001$). The equations below were then used along with the sediment organic content values to determine the site-specific organic carbon in the sediment beneath the various macrophyte stands. These equations will result in a more accurate representation of sediment organic carbon in the future for the specific species.

Zostera capensis zone*:* C_{org} (%) = 0.9026 (% LOI) + 0,1199
Spartina maritima zone*:* C_{org} (%) = 1.1345 (% LOI) – 0.8806
Salicornia tegetaria zone*:* C_{org} (%) = 0.8559 (% LOI) + 0.1953

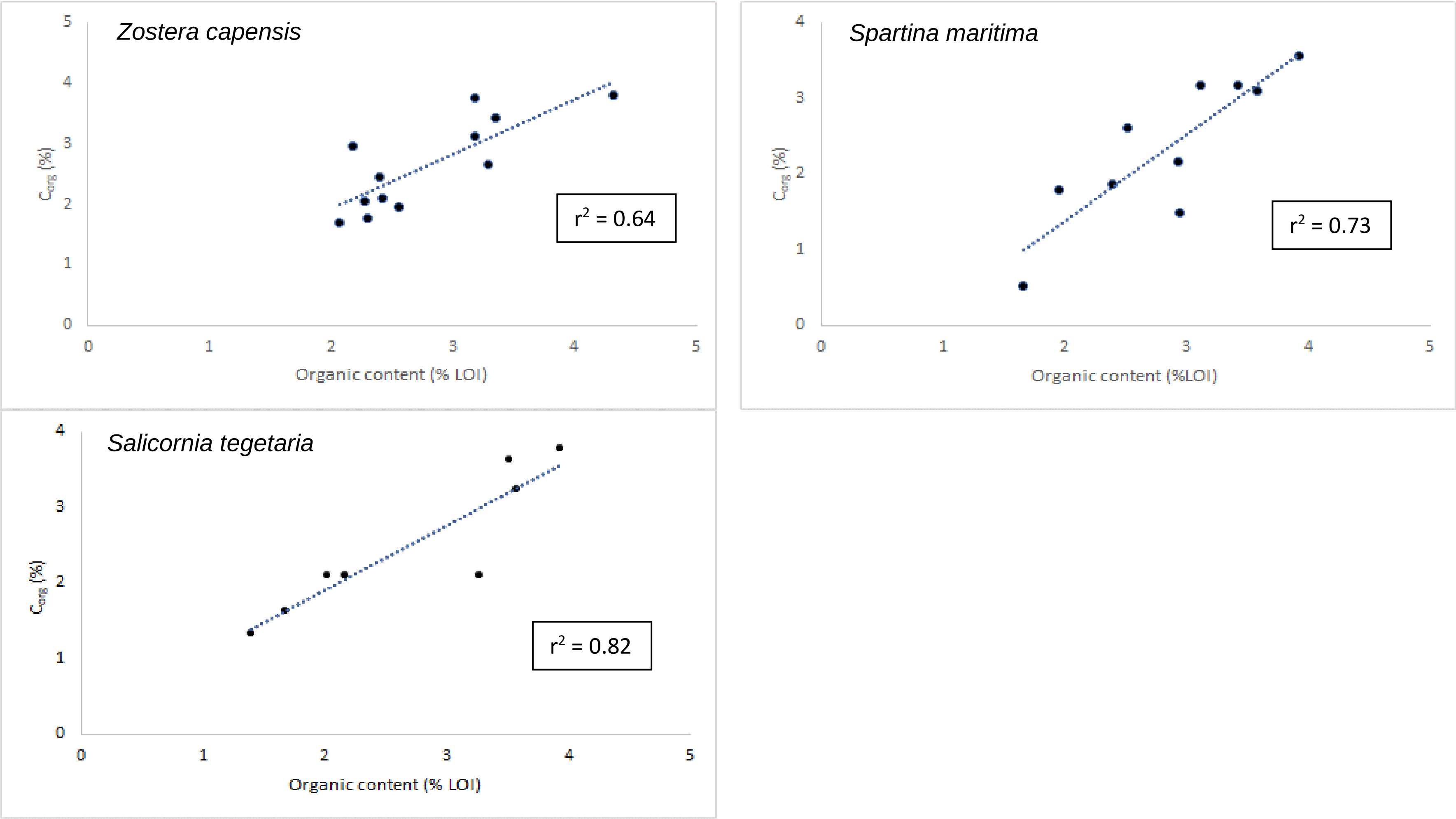


Figure 5.6: Correlation between the sediment organic matter (%LOI) and sediment organic carbon (%) of the seasonal average between sites for Z. capensis, S. maritima, and S. tegetaria.

The organic carbon in the estuary did not differ significantly between summer and winter for all three species. Overall spatial variation was significant in the estuary in the sediment beneath each macrophyte (F = 7.28; df = 5; p < 0.0001, Figure 5.7). In both summer and winter beneath *Z. capensis* and *S. maritima*, Site 1 had the lowest organic carbon making it significantly different from the other sites (F = 3.559; df = 5; p < 0.05). The organic carbon beneath *S. tegetaria* at Site 1 was significantly lower than the other sites (H = 15.39; df = 5; p < 0.01) during winter. There were also no significant changes in depth, although there is a slight decrease in each season, with an overall range of 3.1% at 0.5 m to 5.2% at the surface (Figure 5.7).

Figure 5.7: Organic carbon as determined from the allometric equation for summer and winter in the sediment.

Figure 5.8 indicates the differences between the summer and winter sediment organic content (± SE) and organic carbon (± SE) at each site. The sediment oraganic content and organic carbon show similar trends at each site. These two paramaters were statistically insignificant from one another ($p < 0.05$). *Zostera capensis* had higher sediment organic content and carbon at themajority of the sites in summer (except Site 5), however these were not significant differences. In contrast to what was observed for *Z. capensis*, summer and winter organic content were very similar in both seasons with smaller standard errors. *Salicornia tegetaria* sediment organic content and organic carbon also had the same patterns when averaged per site (Figure 5.8). Both sediment organic content and sediment organic carbon did not differ significantly between seasons or between sites.

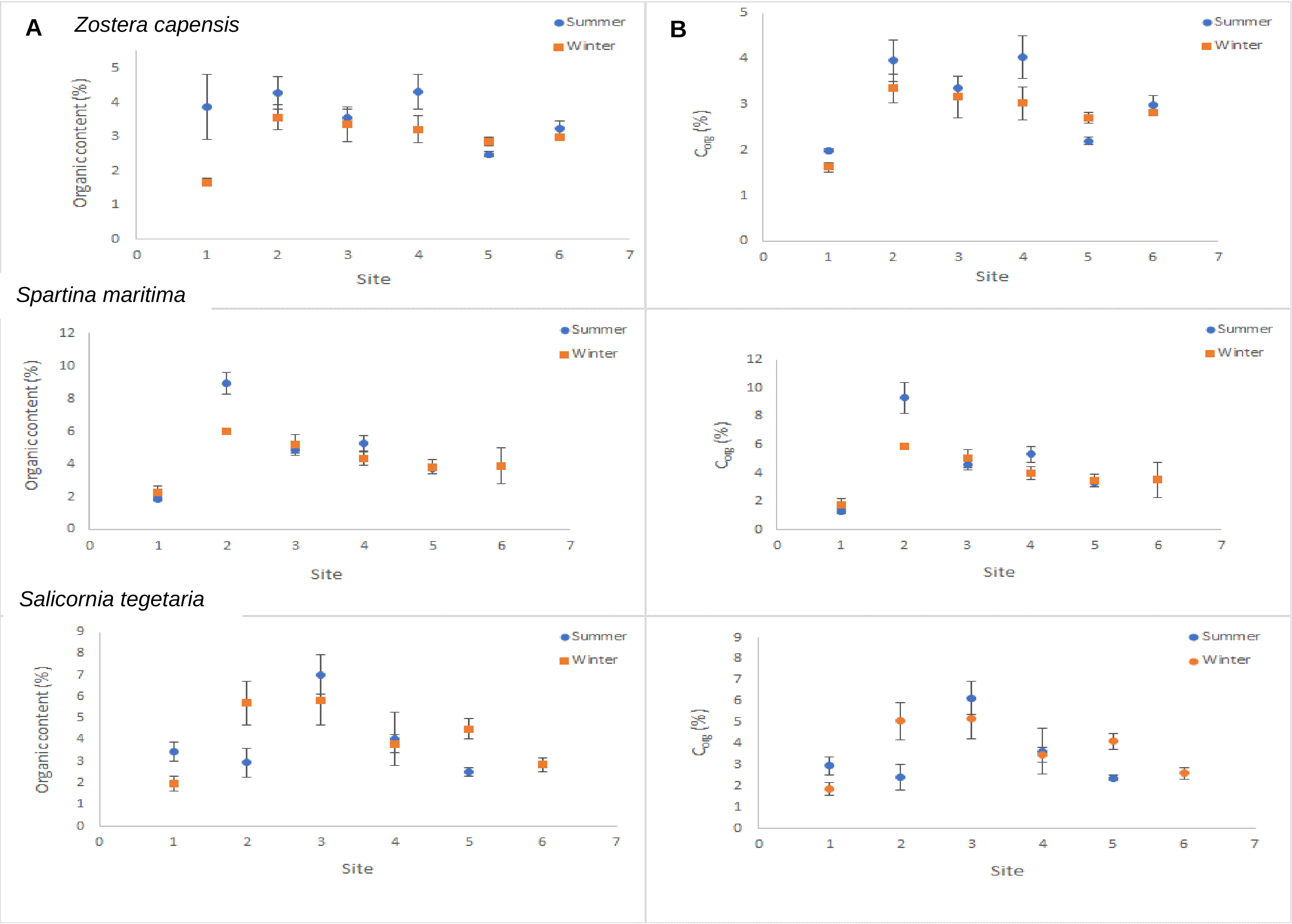


Figure 5.8: Average sediment organic content (%LOI) (A) and sediment organic carbon (%) (B) across sites beneath the Z. capensis beds, S. maritima, and S. tegetaria stands.

5.2.5 Sediment type

The percentage of sand made up the dominant sediment type throughout the estuary. The sediment beneath each macrophyte did not differ throughout the estuary or at each site, but significant differences were observed between the various types of sediment — sand, silt, and clay — (x^2 = 36, df = 2, $p < 0.0001$). The sediment types (% ± SE) beneath *Z. capensis* and *S. maritima,* and *S. tegetaria* were variable between sites. The sand content at Sites 1 (94.8 ± 0.6 %) and 4 (95 ± 1.2 %) were much higher than the other sites (H = 12.86, df = 4, $p < 0.02$), while Site 3 had the highest silt content (34.7 ± 1.2 %, H = 12.39, df = 4, $p < 0.01$). The clay content was significantly greater at Site 2 (19.3 ± 1.2 %) in comparison to the other sites (H = 11.75, df = 4, $p < 0.02$). Site 3 had a very small significant difference between sand and silt (H = 6, df = 2, $p < 0.05$, Figure 5.9)

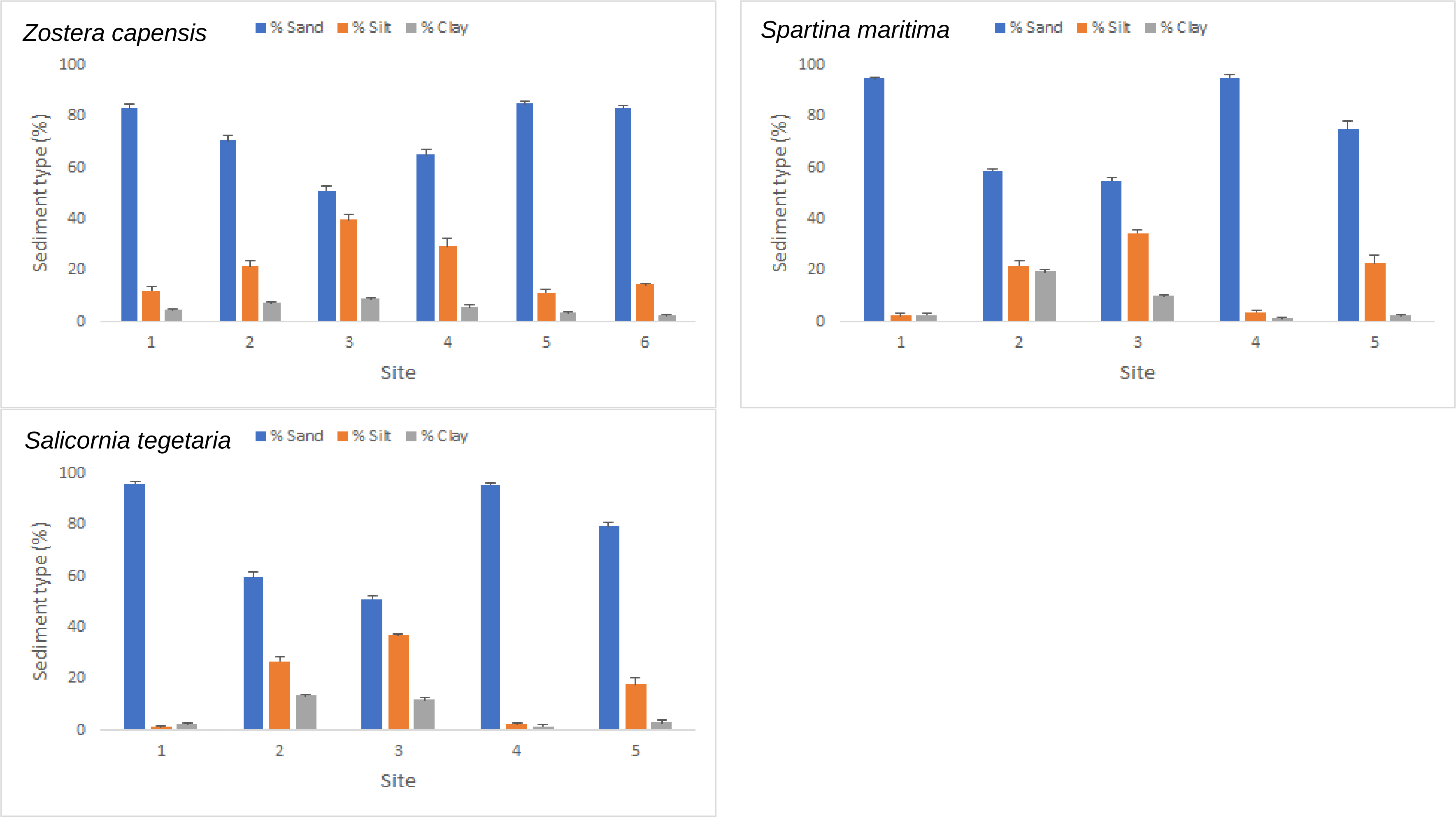


Figure 5.9: Sediment texture beneath each macrophyte stand (% ± SE).

5.2.6 Sediment results summary

Spartina maritima stands in the Swartkops Estuary were the most effective at storing carbon in their sediment (247.13 ± 47.71 Mg ha^{-1}), however significant differences were not noted between the respective species (Table 5.3). *Zostera capensis* (224.14 ± 37.93 Mg ha^{-1}) stored higher amounts of organic carbon in the sediment than *S. tegetaria* (212.26 ± 43.99 Mg ha^{-1}). These values did not differ significantly between summer and winter.

Table 5.3: Sediment organic matter and organic carbon for the various species

Species	**Season**	**% Sediment Organic matter**	**% Sediment Organic carbon**	**Sediment Organic carbon (Mg. ha^{-1})**	**Average sediment organic carbon (Mg. ha^{-1})**
Zostera capensis	Summer	3.63 ± 0.33	2.93 ± 0.31	209.96 ± 16.49	224.14 ± 37.93
	Winter	2.95 ± 0.21	2.78 ± 0.18	238.32 ± 59.36	
Spartina maritima	Summer	4.94 ± 0.37	4.16 ± 0.51	243.58 ± 61.93	247.13 ± 47.71
	Winter	4.26 ± 0.51	4.13 ± 0.31	250.67 ± 33.49	
Salicornia tegetaria	Summer	4.00 ± 0.69	3.42 ± 0.39	203.25 ± 35.03	212.26 ± 43.99
	Winter	4.12 ± 0.62	3.59 ± 0.25	221.27 ± 52.94	

5.3 Biomass of salt marsh and seagrass

5.3.1 Biomass

The total *Z. capensis* biomass in the estuary was significantly higher in winter than in summer (H = 26.26, df = 1, $p < 0.001$) (Figure 5.10). In summer there was significant spatial variability in the aboveground biomass (AB) (H = 18.78, df = 5, $p < 0.005$). This was especially evident at Site 6, the uppermost site, which had the lowest AB ($p < 0.001$). Similarly, to what was observed in summer, Site 6 and Site 3 had significantly lower AB in winter (H = 24.12, df = 5, $p < 0.001$), while the other sites AB did not differ significantly. The belowground biomass (BB) did not differ significantly between sites in summer (H = 10.54, df = 5, $p > 0.05$), but in winter the BB differed between sites (H = 13.81, df = 5, $p < 0.05$). Sites 1 ($p < 0.05$), 5 ($p < 0.01$), and 6 ($p < 0.05$) had significantly lower BB than the true creek sites (2, 3, and 4) (Figure 5.10). For Swartkops Estuary as a whole, *Z. capensis* AB is much higher than the BB ($p < 0.001$) as can be seen by the annual mean AB (483.7 ± 86.1 g DW m^{-2}) and BB (163.7 ± 26.9 g DW m^{-2}) biomass. The AB: BB ratio was 2.16, indicating that the AB was more than double the BB.

Spartina maritima biomass was more consistant throughout the estuary than *Z. capensis*. Total *S. maritima* biomass was significantly different between summer and winter (H = 27.34, df = 1, $p < 0.001$) (Figure 5.10). In summer the AB did not differ significantly between sites (H = 6.82, df = 4, $P < 0.05$). However, the BB did show significant spatial differences (H = 10.15, df = 4, $p < 0.05$). Site 1 had significantly lower BB than the other sites ($p < 0.01$). Overall for the summer season the AB and BB did not differ significantly except for Site 2 which had higher BB biomass ($p < 0.05$). Spatial variation in biomass had different trends in winter compared to that found in summer. The AB differed significantly between sites in summer (H =24.82, df = 5, $p < 0.001$). Site 2 and 5 have significantly lower AB than the other sites ($p < 0.05$), however they do not differ from one another ($p > 0.05$). The BB also varied spatially (H = 17.43, df = 5, $p < 0.005$), this was again evident in Site 2 and 5 having significantly lower BB than the other sites ($p < 0.005$) but not differing from one another. Overall for both seasons the AB and the BB did not differ significantly and the ratio of AB: BB was 0.9.

Salicornia tegetaria had an overall mean AB of 918.4 ± 154.3 g DW m^{-2} and BB of 250.8 ± 46.8 g DW m^{-2}. The total biomass was significantly greater in summer than in winter (H = 18.83, df = 1, $p < 0.0001$). The AB was significantly higher at Site 3 than at the other sites (H= 15.18, N= 30, $p < 0.05$), except Site 5 in summer. Only Site 1 had significantly higher BB than the other sites (H = 17.81, df = 4, $p < 0.005$). From field observations, Site 1 belowground biomass was a mat-like root network which did not occur at any of the other sites. There was also significant spatial variation in winter for the AB (H= 17.81, N= 30, $p < .005$), because Site 1 had lower AB than the remaining sites ($p < 0.05$). In winter there were no significant differences between sites (H = 3.71, df = 5, $p > 0.5$). *Salicornia tegetaria* had a ratio of AB to BB of 4.96 which indicates that overall there were large differences between the AB and BB (V = 631, $p < 0.0001$). This was evident at all sites in both summer and winter ($P < 0.05$), except Site 1 which had equal ratios of AB to BB (0.9 for summer and 1.2 for winter).

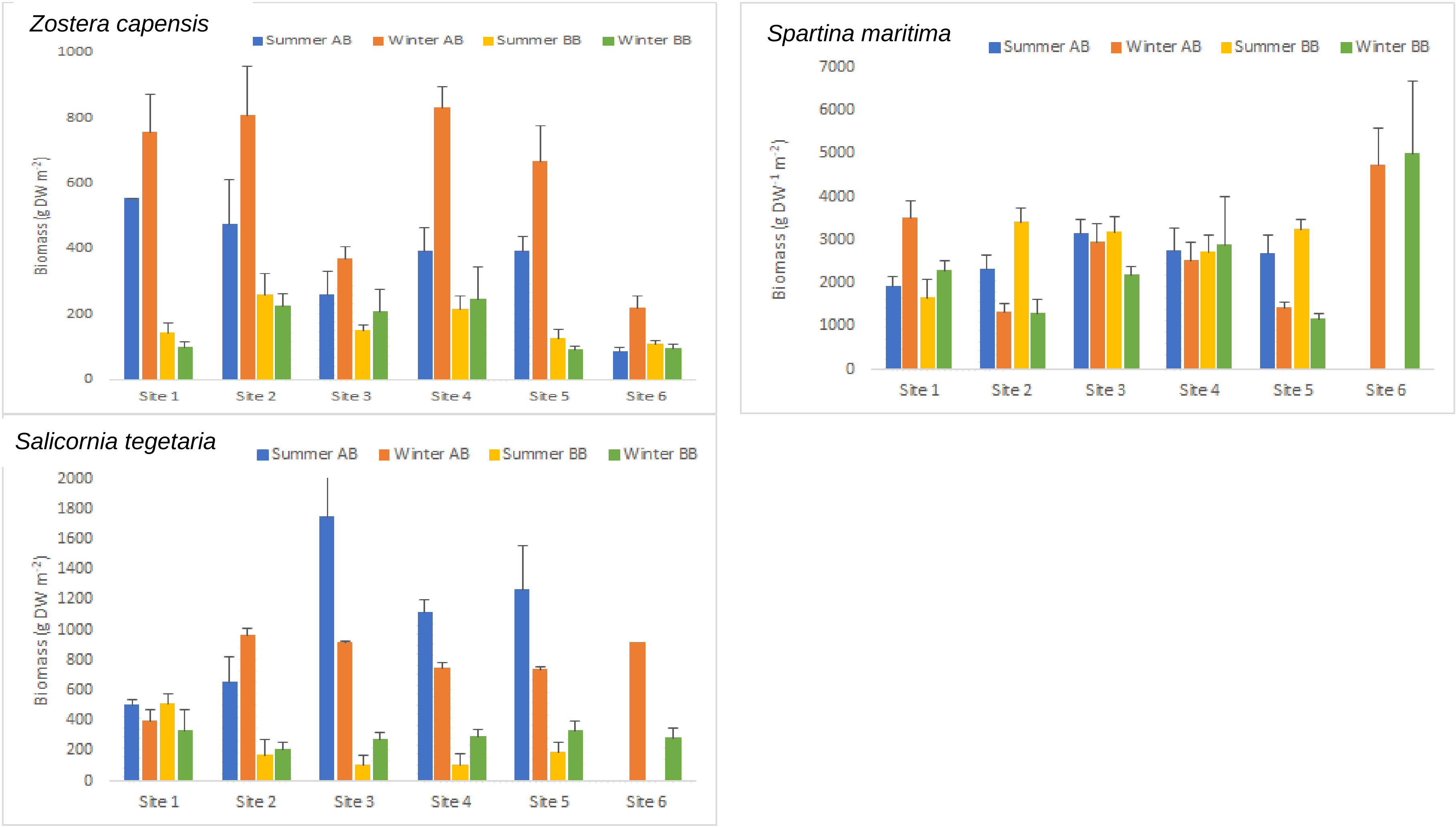


Figure 5.10: Above and belowground biomass (± SE) of Z. capensis, S. maritima, and S. tegetaria in the Swartkops Estuary

5.3.2 Leaf length and stem height

The leaf length of *Z. capensis* did not differ significantly between summer and winter (H = 3.58, df = 1, $p > 0.05$). There was a mean of 25.20 ± 3.80 cm in summer and 30.3 ± 1.8 cm in the winter season. There appeared to be an exception — at Site 3 the leaves were significantly longer in winter (48.6 cm) than in summer ($p < 0.01$) (Figure 5.11). The leaf length varied significantly throughout the estuary (H = 24.64, N = 36, $p < 0.001$). In summer and winter Site 6 had shorter leaves (17.2 cm and 14.1 cm respectively) than the other sites ($p < 0.05$) which was also the uppermost extent of the seagrass and it was more sparsely distributed. In winter, Site 3 had significantly longer leaves than the other sites ($p < 0.001$). Figure 5.11 shows a normal curve indicating that the leaf length in the estuary was longest in the lower-middle reaches of the estuary (Site 4) and decreases towards the upper reaches. Sites sampled in the lower-middle reaches consisted of creeks and backwater areas compared to the main channel sites in the upper reaches.

There were no significant differences in stem height in summer and winter for *S. maritima* either (F = 0.13, df = 1, $p > 0.5$). The mean stem height for the estuary was 35.9 ± 1.6 cm. Spatial differences were however significant in summer (F= 16.41, df= 4, $p < 0.001$), the stem height increased at sites further away from the mouth with Site 4 having longer stems than all the other sites ($p < 0.05$). In winter Sites 3 and 4 had significantly shorter stems than Site 2 (F = 6.56, df = 5, $p < 0.001$) and no consistent patten was identified. The average stem height throughout the estuary ranged from 32 to 42 cm.

Salicornia tegetaria had significantly longer stems in summer (H =10.70, df = 1, $p < 0.005$). This was evident at all sites (Figure 5.11), but only significant at Sites 3 ($p < 0.01$) and 5 ($p < 0.01$). Spatial variation was not apparent in winter (H = 8.25, df = 5, $p > 0.1$). However, in summer the stem length differed significantly between sites (H = 19.54, df = 4, $p < 0.001$). Sites 3 (25.9 ± 4.1 cm) and 5 (27.4 ± 4.8 cm) had longer stems than the other sites ($p < 0.001$) while the other sites did not differ from one another ($p > 0.05$).

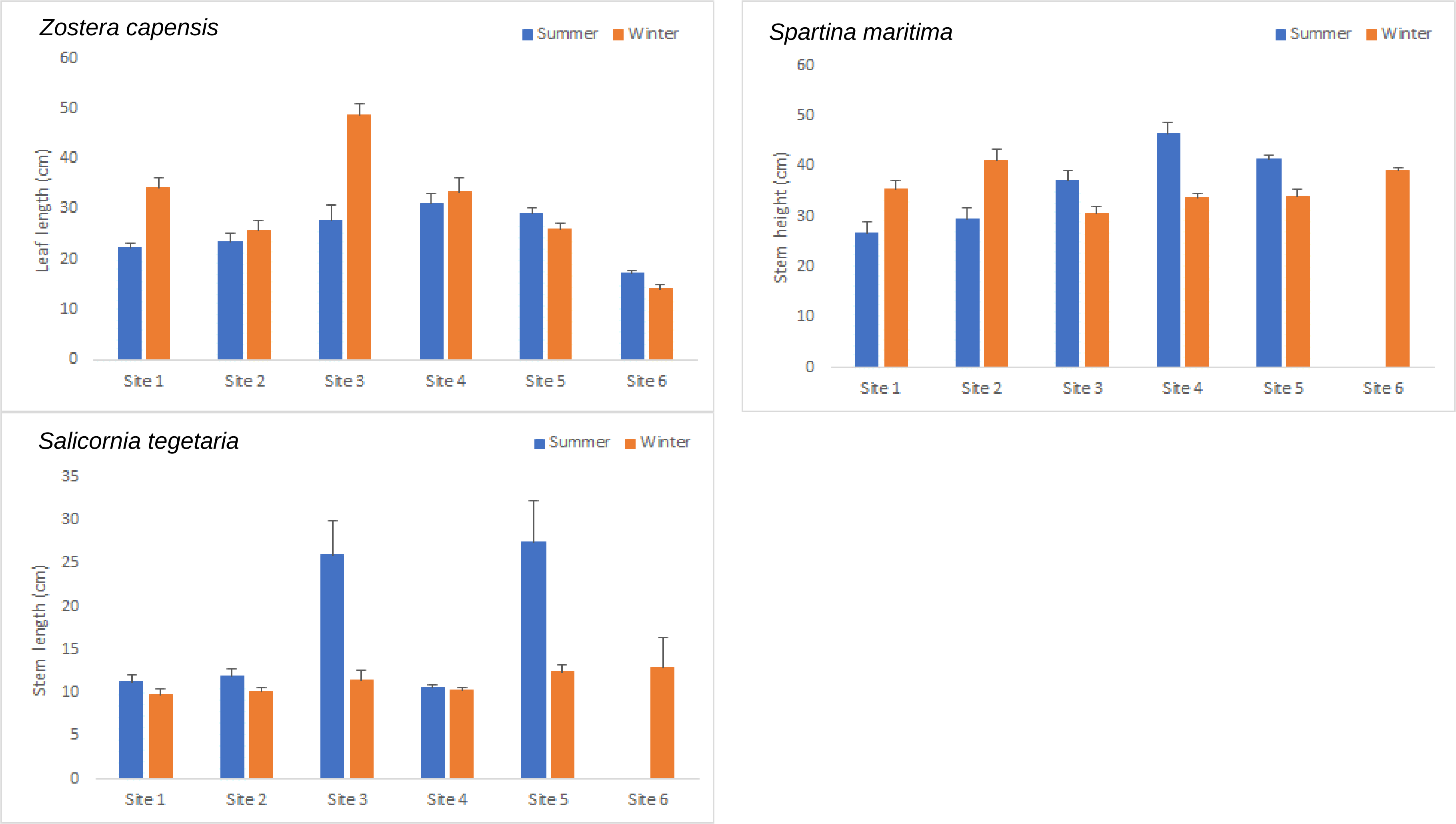


Figure 5.11: Leaf length and stem height of Z. capensis, S. maritima, and S. tegetaria in the Swartkops Estuary

The correlation between leaf length and biomass is presented in Figure 5.12. *Zostera capensis* leaf length increased as the biomass increased in both summer ($r^2 = 0.22$, $p < 0.01$) and winter ($r^2 = 0.25$, $p < 0.005$). *Spartina maritma* had a stronger relationship in summer ($r^2 = 0.34$; $p < 0.02$) than in winter ($r^2 = 0.03$, $p < 0.05$). Although *S. tegetaria* is a branching herbaceous shrub very different from the simple structured salt marsh species, it had the best relationship between the two variables in summer ($r^2 = 0.48$; $p < 0.01$), but this was still not a good fit. More replicates, however, would need to be collected for all the species to ensure a potentially greater r^2 value. Once a better trend is realized leaf length could be used as a proxy for biomass.

The aboveground biomass to belowground biomass values differed significantly between seasons for *Z. capensis* and *S. tegetaria* ($H = 9.54$, $df = 1$, $p < 0.01$) which is why determining a relationship between leaf/ stem length and biomass is not an accurate method for sampling in the future to avoid destructive measures.

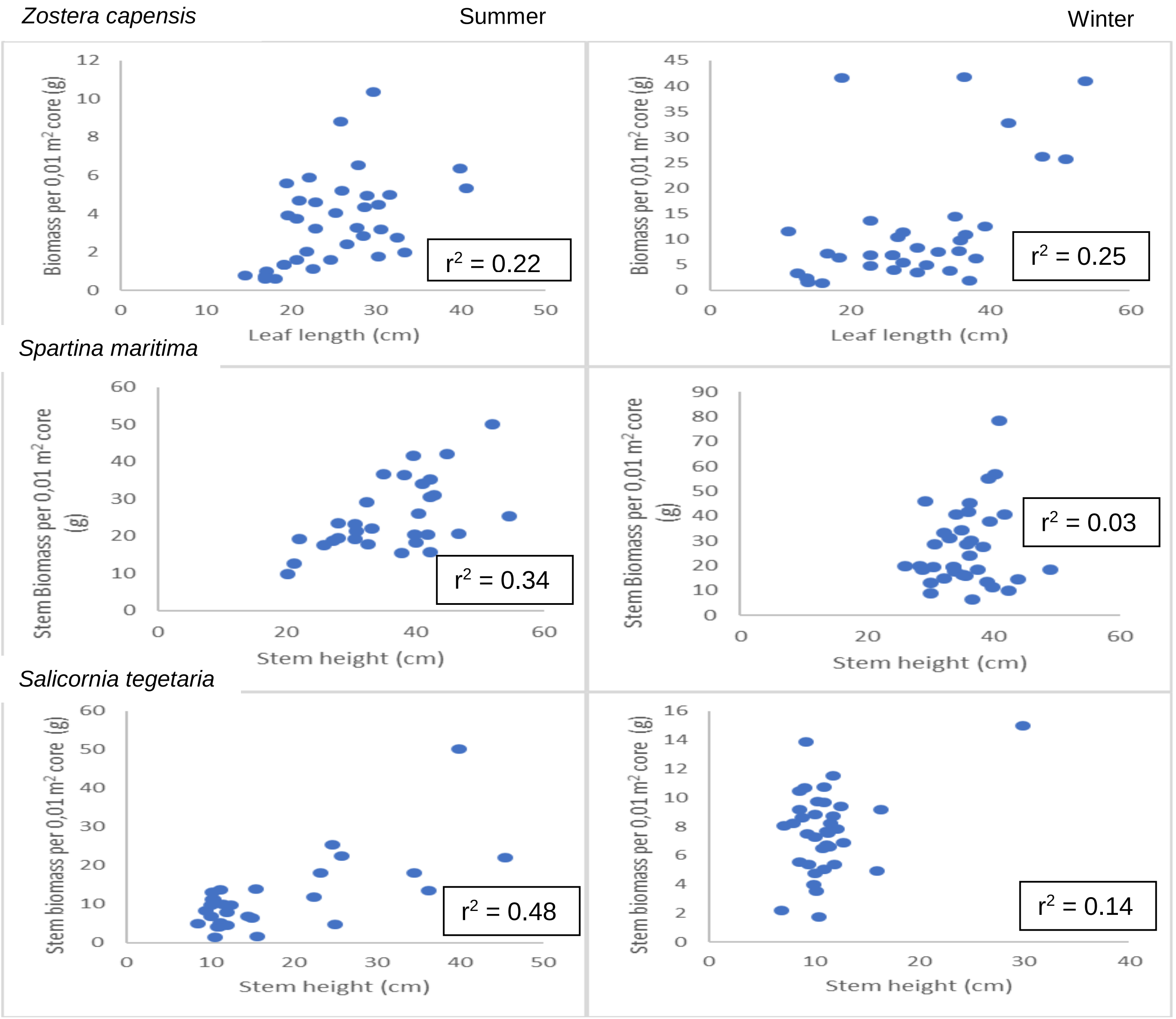


Figure 5.12: Relationship between leaf length (stem height) and biomass of each of the three respective species in the Swartkops Estuary in Summer and Winter.

Table 5. 4: Above to belowground biomass ratios for the Swartkops Estuary.

Species	**Summer**	**Winter**
Zostera capensis	2.16	7.17
Spartina maritima	0.90	1.11
Salicornia tegetaria	4.96	2.70

5.3.3 Carbon in the plant tissues

In Figure 5.13 the carbon stored in the biomass of each macrophyte is displayed. The carbon stored in the AB and BB of *Z. capensis* in the estuary overall did not differ significantly between summer and winter. There was one exception to this — Site 4 stored significantly more carbon in winter than in summer (H = 13.24, df = 1, $p < 0.001$). Carbon storage differed significantly at each site (H = 26.789, df = 5, $p < 0.01$). Spatially, in summer, Sites 1 (111.4 ± 11.7 g C m^{-2}; $p < 0.005$) and 4 (104.1 ± 16.3 g C m^{-2}; $p < 0.05$) had significantly higher AB carbon stocks than Site 6 (31.5 ± 3.7 g C m^{-2}). In winter Site 4 stored more carbon in the AB than the other sites (112.1 ± 11.4 g C m^{-2}; $p< 0.001$). Site 3 and Site 6 stored the least carbon during winter ($p < 0.01$, $p < 0.005$). The BB did not vary significantly between sites in either season ($p > 0.05$). The AB stored more carbon than the BB in both seasons and at each site (H = 11.21, df = 24, p-value < 0.0001) This is evident by the respective annual means (158 ± 21.5 g C m^{-2}; 50.1 ± 9.6 g C m^{-2}).

Spartina maritima stored significantly more carbon in the estuary in summer rather than winter (H = 6.6103, df = 109, $p < 0.05$). The mean carbon stock stored by *S. maritima* in summer was 1 754.4 ± 249.5 g C m^{-2} and in winter it was 1 589.9 ± 323 g C m^{-2}. This was related to the biomass. Spatial differences were apparent in both summer and winter (H = 11.911, df = 5, $p < 0.05$). In summer Site 3 (1455.84 ± 90.46 g C m^{-2}, $p < 0.01$) and Site 5 (1258.32 ± 194.35 g C m^{-2}, $p < 0.05$) stored significantly more carbon in the AB than Site 1 (745.73 ± 15.62 g C m^{-2}). In winter Sites 1 (2 099.8 ± 183 g C m^{-2}, $p < 0.005$) and 6 (2 765.7 ± 460.8 g C m^{-2}, $p < 0.001$) stored more carbon in the AB than the other sites. The BB carbon storage was greater at Sites 2 (970.23 ± 42.57 g C m^{-2}, $p < 0.01$) and 5 (807.07 ± 63.78 g C m^{-2}, $p < 0.05$) than at the other sites in summer. Figure 5.13 shows that more carbon was stored in the AB than the BB in summer (H = 12.02, df = 1, $p < 0.0005$) and in winter (H = 22.94, df = 1, $p < 0.0001$). Site 2 was the only site that showed greater carbon storage in the BB in summer, but this difference was not significant ($p > 0.05$).

Seasonal — summer and winter — variation in carbon storage by *S. tegetaria* in the estuary was minimal (H = 0.48, df = 1, $p > 0.10$). Overall carbon storage did not differ spatially either (H = 9.23, df = 5, $p > 0.10$), but in Figure 5.13 it appears that Site 3 is higher than all the other sites, especially Site 1. Significantly more carbon was stored in the AB in both seasons than that which was stored in the BB (H = 31.66, df = 1, $p < 0.0001$). In summer Site 3 stored the most carbon in the AB (646.9 ± 72.9 g C m^{-2}) and the least in its BB (44.9 ± 17.5 g C m^{-2}) (H = 31.66, df = 1, $p <0.0001$). Similar trends were seen in all the other sites in summer, except Site 1 which stored more carbon in its BB (192.15 ± 27.52 g C m^{-2}) than AB (159.53 ± 13.18

g C m^{-2}) but this difference was not significant. Site 6 stored significantly more carbon in its BB (435.08 ± 51.64 g C m^{-2}, $p < 0.01$) in winter than in its AB (254.58 ± 37.81 g C m^{-2}). All other sites stored significantly more carbon in their AB than BB in winter.

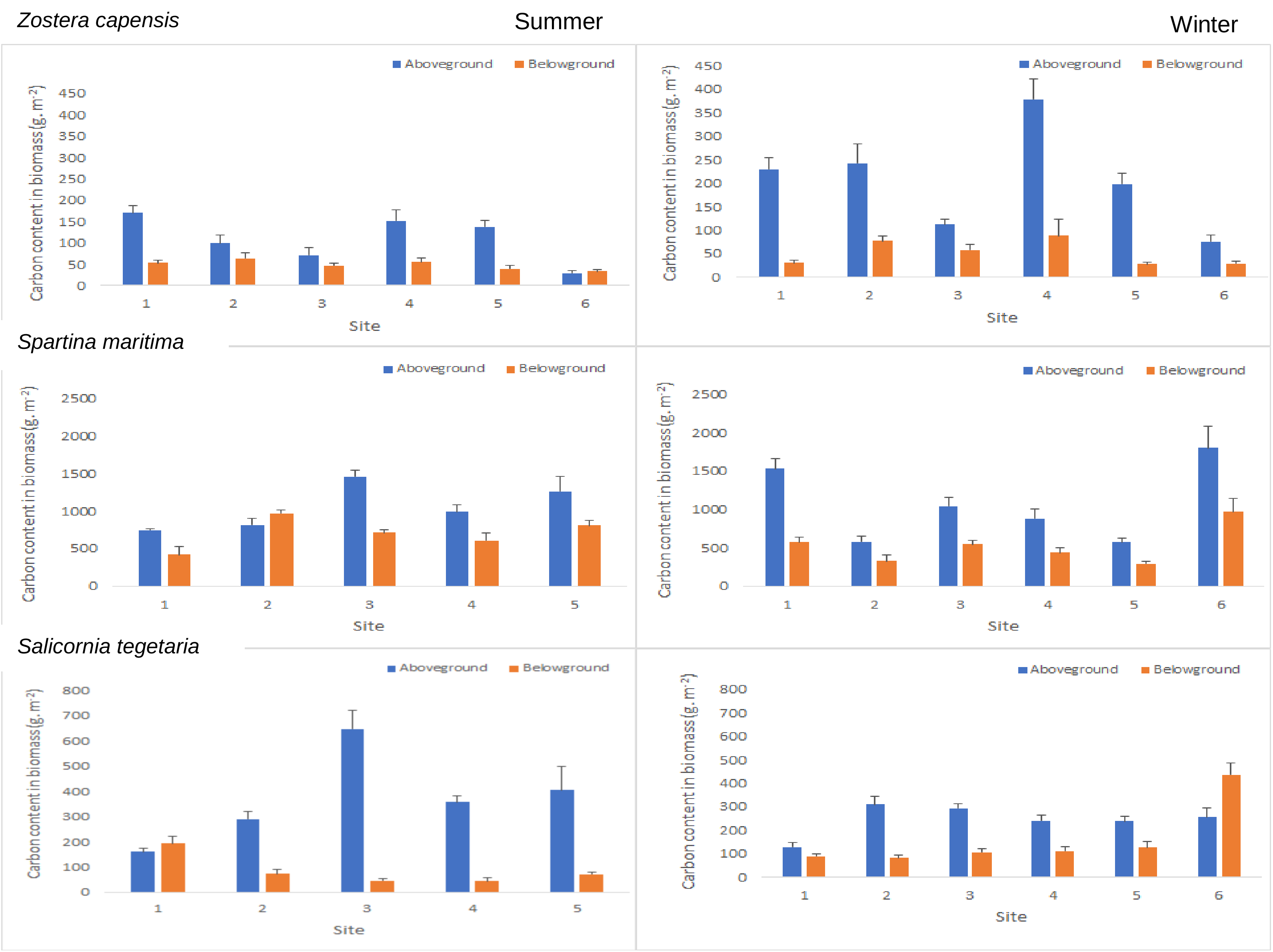


Figure 5.13: Carbon content (±SE) in summer and winter in Z. capensis, S. maritima, and S. tegetaria biomass of Swartkops Estuary making use of the allometric equation and a carbon conversion factor from elemental analysis

Spartina maritima beds were the most effective carbon sinks for storage in the plant biomass (16.27 ± 2.86 Mg ha^{-1}). Table 5.5 shows that organic carbon stocks in the biomass were greater in *S. tegetaria* (4.28 ± 0.72 Mg ha^{-1}) than in *Z. capensis* (2.08 ± 0.49 Mg ha^{-1}).

Table 5.5: Total carbon in the vegetative component

Species	**Season**	**Average Biomass (g.DW. m^{-2})**		**Area (ha)**	**Total biomass C (Mg. C. ha^{-1})**	**Total C (Mg. C)**
		Aboveground	**Belowground**			
Zostera capensis	Summer	360.38 ± 68.06	166.77 ± 23.84	62.30	2.08 ± 0.49	129.58 ± 30.53
	Winter	607.01 ± 104.08	160.54 ± 29.98			
Spartina maritima	Summer	2553.72 ± 207.54	2836.67 ± 317.40	96.00	16.27 ± 2.86	1561.92 ± 274.56
	Winter	2744.08 ± 482.04	2464.67 ± 519.62			
Salicornia tegetaria	Summer	1055.8 ± 223.12	212.85 ± 75.2	27.32	4.28 ± 0.72	116.93 ± 19.67
	Winter	780.93 ± 85.55	288.88 ± 18.34			

5.3.4 Nitrogen storage in the plant tissues

Zostera capensis nitrogen stocks were significantly higher in the winter than in the summer in both the above (59.9 ± 3.5 g N kg^{-1} and 5.6 ± 0.5 g N kg^{-1} respectively) and belowground (35 ± 3 g N kg^{-1} and 3 ± 1.6 g N kg^{-1}) biomass (H = 107.46; df = 1, $p < 0.0001$). Spatially changes in nitrogen storage were not significant in summer in the AB or the BB (H = 4.66, df = 5, $p > 0.1$), but nitrogen storage differed significantly between sites in winter (H = 18.19, df = 5, $p < 0.005$). Sites 1, 2, and 6 stored significantly more nitrogen in the AB than Sites 3, 4, and 5 ($p < 0.001$) (Figure 5.14). In winter spatial variation was also evident in the BB (H = 28.11, df = 5, $p < 0.0001$). The upper reaches (Sites 5 and 6) had greater nitrogen stocks than the other sites ($p < 0.01$). The nitrogen stored in the AB and BB differed significantly at all sites in summer (H = 34.78, df = 1, $p < 0.0001$) and in winter (H = 17.38, df = 1, $p < 0.0001$).

Spartina maritima stored significantly more N in winter than in summer in the BB (H = 17.41; df = 1; $p < 0.0001$), but AB storage did not differ significantly between the two seasons (Figure 5.14). The combined total nitrogen stocks for AB and BB in summer were 54.2 ± 1.9 g N m^{-2} and in winter the nitrogen stocks were slightly higher at 62.1 ± 1.3 g N m^{-2}. Nitrogen storage in the AB was greater at Site 1 in the summer than at the other sites (H = 10.92, df = 4, $p < 0.05$). In summer the N stored in the BB also differed spatially — Site 3 stored less N than the other sites ($p < 0.01$). In winter the N storage was more consistent between sites than in summer, but significant differences were still present as Site 3 stored less N in the AB than any of the other sites (H = 14.54, df = 5, $p < 0.05$). The N storage in the BB did not differ significantly spatially in winter ($p > 0.05$). *Spartina maritima* stored significantly more nitrogen in the AB than in the BB in both seasons at all sites (H = 72.742, df = 1, $p < 0.0001$).

Salicornia tegetaria N storage differed between summer and winter (H= 65.15; df = 1; $p < 0.0001$). More N was stored in winter (72.2 ± 2.5 g N kg^{-1}) than in summer (29.72 ± 1.93 g N kg^{-1}) as was seen in the other species. Spatial variation was evident in the BB storage in both seasons (H = 29.70; df = 5; $p < 0.0001$). The AB did not differ spatially ($p > 0.05$). Site 4 and 5 in summer had larger N storage in the BB compared to the other sites (H = 29.70, df = 5, $p < 0.0001$). The BB N storage in winter was lowest at Site 1 than in the other sites (H = 58.40, df = 5, $p < 0.001$). The N storage AB and BB did not differ significantly in either season (H = 3.44, df = 1, $p > 0.05$).

Table 5.6 indicates a summary of all three-plant species which acted as effective sinks for excess nutrients in the water column. Overall large fluctuations were observed in the amount of nitrogen stored seasonally by the macrophytes ($H = 203.25$; df = 1; $p < 0.001$). More N was stored in winter (Table 5.6). Overall nitrogen stored in the various species did not differ significantly ($H = 3.0716$; df = 2; $p > 0.05$). More N was stored in the AB than the BB for all three species (($H = 25.24$, df = 1, $p < 0.00001$)

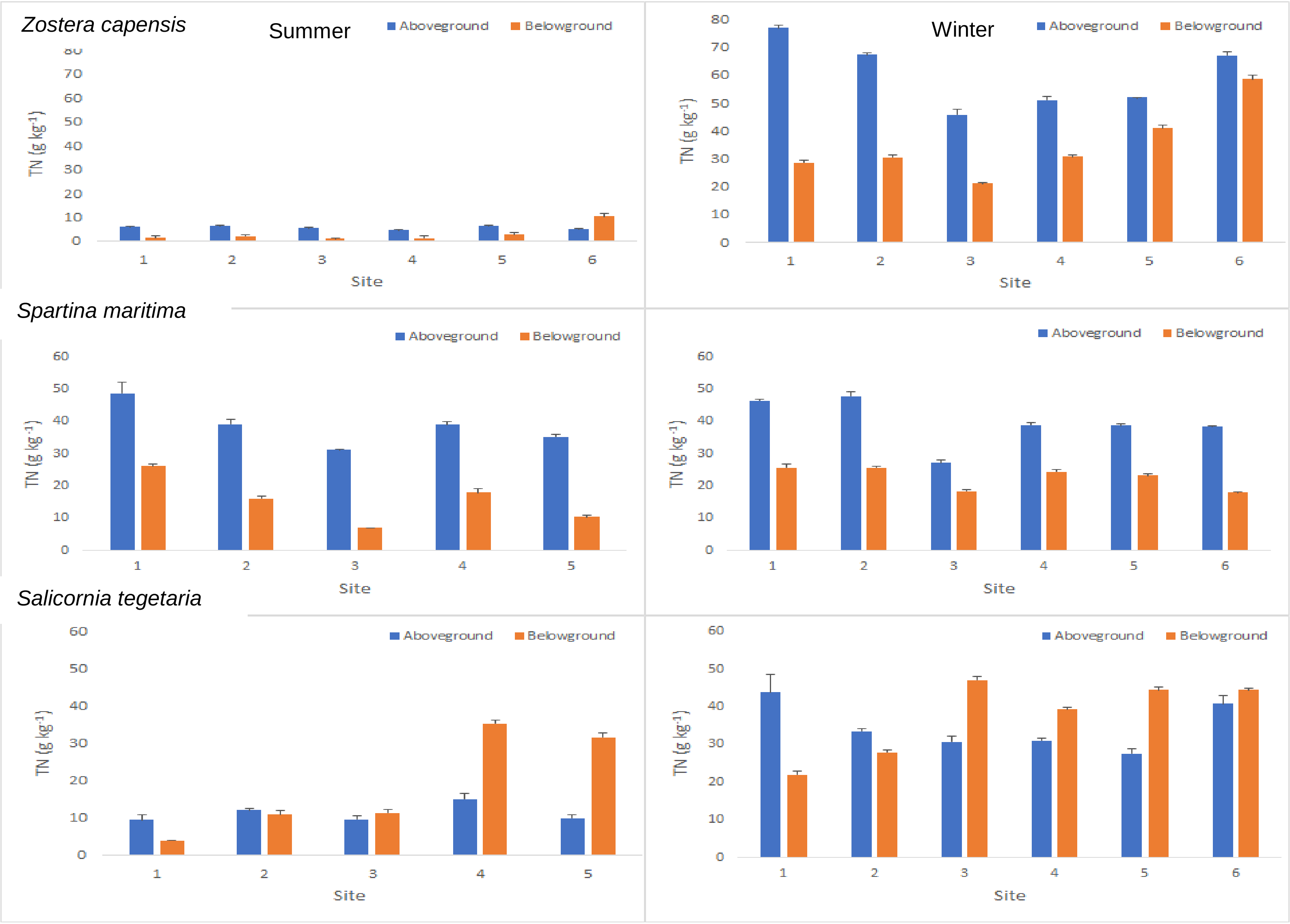


Figure 5.14: Total nitrogen (± SE) stored in the above and belowground biomass of Z. capensis, S. maritima, and S. tegetaria in summer and winter.

Table 5.6: Total nitrogen in the vegetative component

Species	**Season**	**Average Biomass N (Mg. ha^{-1})**		**Total Biomass N (Mg. ha^{-1})**	**Total N (Mg)**
		Aboveground	**Belowground**		
Zostera capensis	Summer	0.021 ± 0.002	0.004 ± 0.001	0.214 ± 0.003	13.27 ± 0.186
	Winter	0.367 ± 0.031	0.051 ± 0.003	0.418 ± 0.034	25.92 ± 2.11
Spartina maritima	Summer	0.965 ± 0.011	0.405 ± 0.021	1.370 ± 0.032	131.52 ± 3.07
	Winter	1.068 ± 0.089	0.533 ± 0.040	1.601 ± 0.129	153.70 ± 12.38
Salicornia tegetaria	Summer	0.117 ± 0.009	0.029 ± 0.019	0.146 ± 0.028	3.99 ± 0.65
	Winter	0.265 ± 0.013	0.109 ± 0.006	0.374 ± 0.019	10.18 ± 0.52

5.3.5 Phosphorus in the plant tissues

Zostera capensis stored less phosphorus than nitrogen in the macrophyte biomass. Phosphorus storage was greater in winter than in summer (H = 52.012, df = 1, $p < 0.0001$). In summer spatial variation was only significant in the BB (H = 28.42; df = 5; $p < 0.0001$) and not in the AB ($p > 0.05$). Sites 5 (97.3 ± 8.2 g P kg^{-1}) and 6 (104.5 ± 12.2 g P kg^{-1}) — closest to Motherwell and Markman canals —stored more P than the other sites. In winter the spatial variation was significantly different in the AB storage (H = 24.52, df = 5, $p < 0.001$) and in the BB storage (H = 27.67, df = 5, $p < 0.0001$). Site 3 stored the least P in the AB and the BB ($p < 0.01$). Significant differences were observed between the AB storage and the BB storage in both seasons (H = 9.20, df = 1, $p < 0.005$). In summer significantly, more P was stored in the BB than in the AB at Site 5 (0.005) and 6 ($p < 0.001$). In winter Site 5 was the only site where P storage did not differ between the AB and the BB ($p > 0.05$).

Phosphorus storage did not differ significantly between summer and winter (H = 0.26, df = 1, $p > 0.50$) for *S. maritima*. There was no significant spatial variation in AB and BB P storage in summer (H = 5.46, df = 4, $p > 0.1$), however, P storage varied significantly between sites in winter (H = 50.26, df = 5, $p < 0.0001$). Phosphorus was greater in the AB (30.45 ± 2.40 g P m^{-2}) and BB (26.75 ± 0.91 g P m^{-2}) at Site 4 compared to the other sites. The same pattern was seen in the phosphorus storage of the above and belowground biomass of the macrophyte (Figures 5.14). *Spartina maritima* stored significantly more P in the AB in both seasons and at all sites than the storage in the BB (H = 26.45, df = 1, $p < 0.001$).

Salicornia tegetaria phosphorus storage was greater in summer than in winter (H = 46.37, df = 1, $p < 0.001$). Total P in the AB and BB at Site 2 (72.3 ± 12.4 g kg^{-1}) and 4 (57.8 ± 6.2 g kg^{-1}) in summer were significantly higher than the other sites. In winter Site 6 stored significantly more P in the BB than the other sites ($p < 0.001$). In winter Site 1 stored more P in the AB than in any of the other sites ($p < 0.001$). The P storage did not differ significantly between the AB and the BB in summer (H = 0.03, df = 1, $p > 0.05$) or winter (H = 6.57, df = 1, $p > 0.05$).

Overall the P stored by the three species differed significantly (H = 35.383; df = 2; $p < 0.0001$) — *S. maritima* stored the most P. Phosphorus also fluctuated seasonally with more storage occurring in winter (H = 203.25; df = 1; $p < 0.0001$). More P was stored in the AB than in the BB (H = 15.57, df = 1, $p < 0.0001$). A Spearmans rank correlation showed that nitrogen and phosphorus had a significant correlation — nitrogen and phosphorus increased simultaneously for *Z. capensis* (r = 0.77, $p < 0.001$) and *S. maritima* (r = 0.51, $p < 0.001$), but not for *S. tegetaria* (r = 0.39; $p < 0.001$).

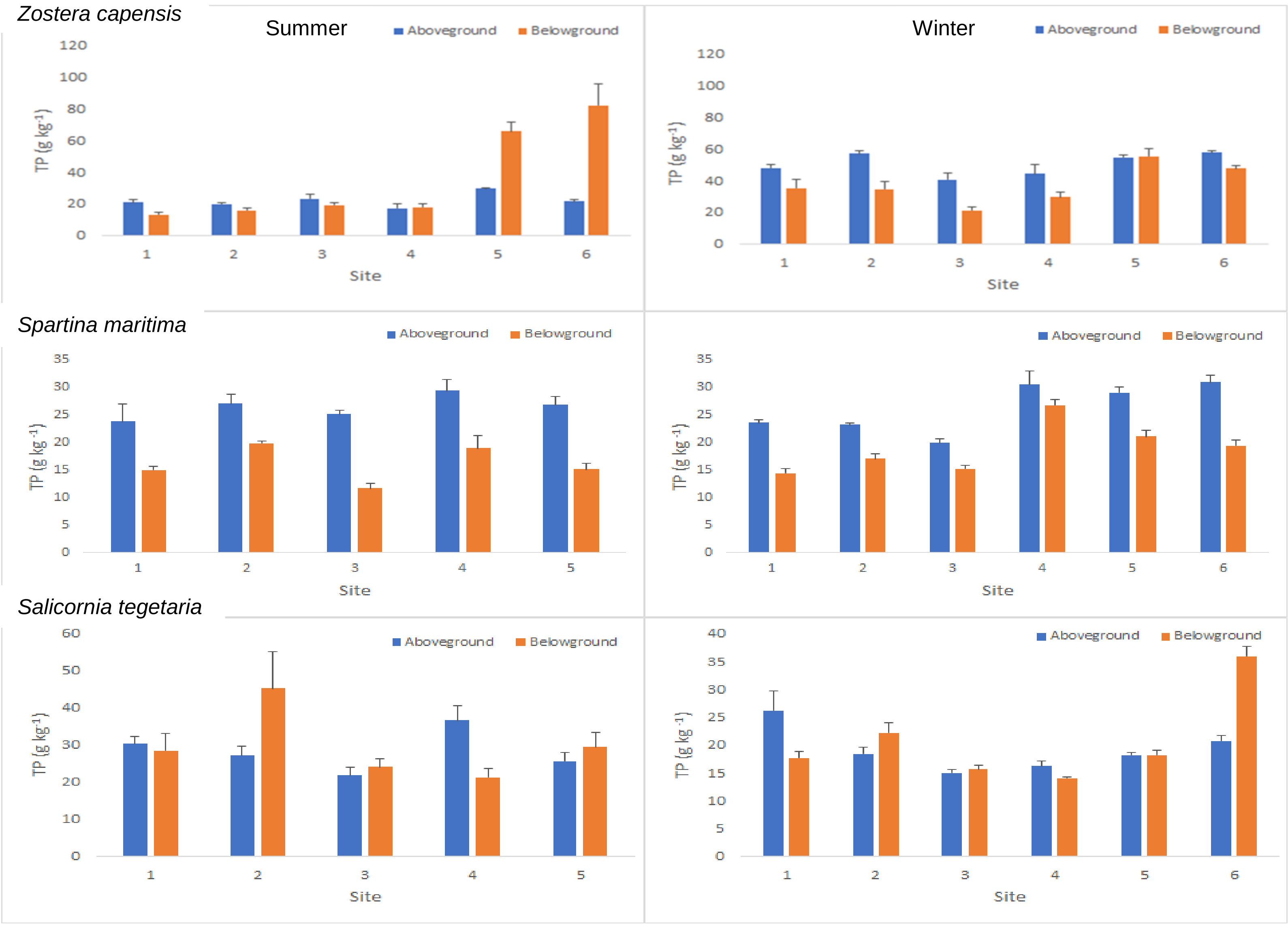


Figure 5.15: Total phosphorus stored in the above and belowground biomass of Z. capensis, S. maritima, and S. tegetaria in summer and winter.

Table 5.7: Total phosphorus in the vegetative component

Species	**Season**	**Average Biomass P (Mg. ha^{-1})**		**Total Biomass P (Mg. ha^{-1})**	**Total P (Mg)**
		Aboveground	**Belowground**		
Zostera capensis	Summer	0.078 ± 0.006	0.049 ± 0.005	0.127 ± 0.011	7.90 ± 0.68
	Winter	0.303 ± 0.022	0.054 ± 0.003	0.357 ± 0.025	22.13 ± 1.55
Spartina maritima	Summer	0.676 ± 0.024	0.458 ± 0.027	1.134 ± 0.051	108.86 ± 4.90
	Winter	0.727 ± 0.068	0.477 ± 0.052	1.204 ± 0.12	115.58 ± 11.52
Salicornia tegetaria	Summer	0.288 ± 0.019	0.064 ± 0.019	0.352 ± 0.038	9.58 ± 1.03
	Winter	0.144 ± 0.005	0.059 ± 0.004	0.203 ± 0.009	5.53 ± 0.25

5.4 Nutrient Ratios

The respective ratios represented in Tables 5.8 to 5.10 below indicate nutrient enrichment. Significant differences were noted between seasons for *Z. capensis* with winter having lower C: N and C: P values, a higher N:P ratio in winter ($H = 8.31$, $df = 1$, $p < 0.005$). The N: biomass ratio was significantly greater in winter ($H = 8.79$, $df = 1$, $p < 0.01$), while P: biomass values did not differ seasonally. The *Z. capensis* N: biomass and P: biomass did not differ significantly between sites in both summer ($H = 9.62$, $df = 5$, $p > 0.05$) and winter ($H = 2.15$, $df = 5$, $p > 0.8$).

Table 5.8: Nutrient ratios and nutrient to biomass ratios for Z. capensis as indicators of nutrient pollution.

Site	Season	C: N	C: P	N: P	N: Biomass	P: Biomass
1	Summer	43.16	12.47	0.29	0.01	0.04
	Winter	4.60	7.41	1.61	0.10	0.06
2	Summer	62.40	19.96	0.32	0.01	0.04
	Winter	4.36	5.16	1.18	0.08	0.07
3	Summer	59.41	14.49	0.24	0.02	0.09
	Winter	4.12	4.66	1.13	0.12	0.11
4	Summer	70.27	19.01	0.27	0.01	0.04
	Winter	7.06	8.19	1.16	0.06	0.05
5	Summer	50.09	10.58	0.21	0.02	0.07
	Winter	5.35	5.11	0.95	0.08	0.08
6	Summer	65.36	15.56	0.24	0.06	0.25
	Winter	5.78	6.72	1.16	0.31	0.27

Spartina maritima stored more C, N, and P than the other two species. None of the ratios differed significantly between seasons for *S. maritima* ($H = 0.03$, $df = 1$, $p > 0.1$). In summer no ratios differed significantly between sites ($H = 5.50$, $df = 5$, $p > 0.3$) and in winter Site 3 had significantly greater C:N and C:P values ($H = 6.94$, $df = 5$, $p < 0.05$), however, the N:P and nutrient: biomass ratios did not differ between sites ($p > 0.05$).

Table 5.9: Nutrient ratios and nutrient to biomass ratios for S. maritima as indicators of nutrient pollution.

Site	Season	C: N	C: P	N: P	N: Biomass	P: Biomass
1	Summer	7.86	16.15	2.05	0.03	0.01
	Winter	8.95	17.61	1.97	0.01	0.01
2	Summer	9.37	13.61	1.45	0.02	0.01
	Winter	7.02	14.49	2.06	0.04	0.02
3	Summer	11.97	14.84	1.24	0.01	0.01
	Winter	15.69	21.44	1.37	0.01	0.01
4	Summer	10.15	13.52	1.33	0.01	0.01
	Winter	9.53	12.14	1.27	0.02	0.01
5	Summer	11.13	14.68	1.32	0.01	0.01
	Winter	8.30	11.06	1.33	0.03	0.02
6	Summer	-	-	-	-	-
	Winter	8.81	10.97	1.25	0.01	0.01

Salicornia tegetaria C:N (higher in summer) and N:P (higher in winter) ratios differed significantly between seasons (H = 8.73, df = 1, $p < 0.05$), but C:P did not ($p > 0.05$). The N: biomass value was also higher in winter than in summer (H = 7.5, df = 1, $p < 0.01$) while P: biomass did not differ significantly between seasons ($p > 0.05$). Significant spatial variation was not seen overall in either season for any of the ratios (H = 7.45, df = 5, $p > 0.1$). More specifically, in winter N:P was greater at Site 3 than at any of the other sites (H = 10.30, df = 5, $p < 0.05$) and Site 1 had a significantly higher N: biomass ratio in winter (H = 17.56, df = 5, $p < 0.01$) than the other sites. Overall the phosphorus remained consistent in the biomass and the nitrogen in the biomass was consistent in summer, but less so in winter.

Table 5.10: Nutrient ratios and nutrient to biomass ratios for S. tegetaria as indicators of nutrient pollution.

Site	Season	C: N	C: P	N: P	N: Biomass	P: Biomass
1	Summer	36.97	11.43	0.31	0.02	0.06
	Winter	6.72	11.25	1.67	0.11	0.07
2	Summer	22.45	9.91	0.44	0.02	0.04
	Winter	8.51	15.50	1.82	0.03	0.02
3	Summer	29.20	12.83	0.44	0.01	0.01
	Winter	10.64	21.90	2.06	0.03	0.02
4	Summer	19.34	7.90	0.41	0.01	0.03
	Winter	8.88	16.98	1.91	0.04	0.02
5	Summer	32.50	12.60	0.39	0.01	0.02
	Winter	11.97	18.19	1.52	0.04	0.02
6	Summer	-	-	-	-	-
	Winter	7.39	14.60	1.98	0.04	0.02

5.5 Epiphyte biomass

The epiphyte biomass was significantly greater in winter (27.3 ± 9.1 mg m^{-2}) (H = 52.13, df = 1, $p < 0.001$) compared with summer. The epiphyte biomass did not differ between sites in summer (2.9 ± 1.1 mg m^{-2}), but significant spatial differences were found in winter (H= 29.39, N= 36, $p<0.001$). This was particularly evident at Site 2 (4.3 ± 1.1 mg m^{-2}; $p < 0.01$) and 4 (2.4 ± 0.6 mg m^{-2}; $p < 0.001$) which had the lowest epiphyte biomass (Figure 5.17). Site 3 and Site 6 had high epiphyte biomass that differed significantly from the other sites but not from one another (H = 25.1, df = 5, $p < 0.01$). Epiphyte biomass was not related to the *Z. capensis* biomass or leaf length in Figures 5.10 and 5.11. Due to the low chlorophyll *a* result, the load was not calculated.

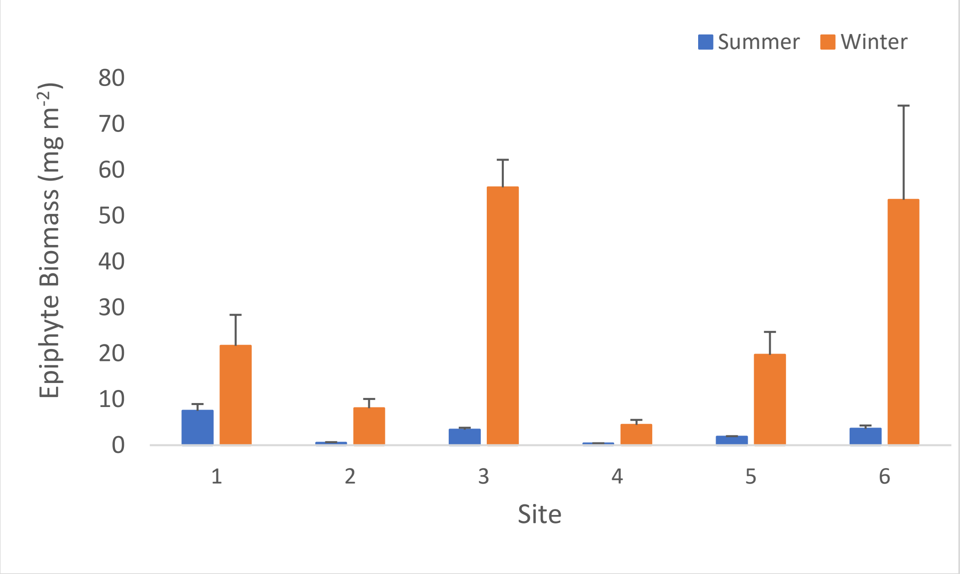


Figure 5.16: Epiphyte biomass (Chl a) (± SE) on the Z. capensis leaves at each site.

6. Discussion

The overall aim of the study was to quantify the carbon, nitrogen, and phosphorus stocks in *Zostera capensis, Spartina maritima*, and *Salicornia tegetaria* as a step towards the quantification of ecosystem services in the highly urbanised Swartkops Estuary. This was also a preliminary study towards understanding the effect of eutrophication on these macrophytes. This is one of the first studies on carbon in South African estuaries. Although blue carbon studies have increased over the past few years, there are still major gaps in knowledge, especially in South America, South-east Asia and African countries (Howard *et al*., 2014). Nutrient (Nitrogen and Phosphorus) storage is another aspect that is of vital importance for the effective functioning of the ecosystem and the ecosystem services it offers the surrounding communities. This work, therefore, gives an account of the blue carbon and nutrient stocks in the Swartkops Estuary. This is important for filling the gaps in global and local knowledge of these habitats. Not many studies have been done on the nutrient stocks in *Z. capensis, S. maritima*, and *S. tegetaria* biomass in South Africa thus providing important baseline data.

6.1 Aerial cover of dominant macrophytes

Determining the change in salt marsh and seagrass area cover is important to understand how carbon and nutrient storage is not fixed. This study hypothesized that the area cover of both seagrass and salt marsh have potentially increased due to the increased pollution input. The N: biomass ratio indicated that there was nutrient pollution evident in the estuary and it showed the link between the seagrass biomass and nutrients. This has been used in international studies as an indicator of nutrient pollution (Lee *et al*., 2004; Burkholder *et al.,* 2007). *Zostera capensis* cover can be variable because it is sensitive to flooding, drought and changes in salinity or nutrient enrichment as well as climate change and other anthropogenic influences (Arendse, 2011; Phair, 2016). It is then neccesary that these changes be interpreted in relation to the dynamic nature of the specific estuary (Adams *et al.,* 2016). There is also the potential that the area cover increased due to reduced floods in the Swartkops Estuary and greater sediment stability because of the drought the region has been experiencing. The current study mapped the *Z. capensis* cover in the Swartkops Estuary at 62.3 ha which is greater than the 44.7 ha that was mapped in a 2016 study (Bornman *et al*., 2016). Two studies done in the Knysna Estuary, also permanently open to the sea, mapped the seagrass cover and have very different results — Maree (2000) mapped 355 ha, while Schmidt (2013) mapped 254 ha. This indicates the importance of mapping the seagrass distribution within an estuary because of its dynamic nature (Adams, 2016), and even more so because it is an endangered species (Adams, 2016; Adams and Van der Colff, 2016). Table 5.2 indicates the changes in seagrass aerial cover in the Swartkops Estuary since 1939 until current. Aerial cover changes in the Swartkops Estuary are quite significant. Emmerson, *et al.* (1982) reported complete removal of *Z. capensis* from the estuary following severe flooding. The increased aerial cover may be a result of increased biomass in specific regions because of increased nutrient input into the system (US EPA, 2002; Johnson *et al*., 2016; Meza-lopez and Siemann, 2017).

Despite the increase in cover of the seagrass beds, this study noted a decrease in the longitudinal distribution of the seagrass throughout the estuary. Residents (from Zwartkops Conservancy) that have lived on the banks of the estuary for many years suggested that the *Z. capensis* beds in the lower reaches have increased. Talbot and Bate (1987) found that the seagrass beds were sparse and had smaller leaves in the upper reaches, above Redhouse, however, this study noted a drastic decrease in biomass at the new upper limit of *Z. capensis* — between Brickfields and Salmonspruit (Site 6). Figure 5.2 shows the Talbot and Bate (1987) distribution of *Z. capensis* along the length of the Swartkops Estuary. The yellow circle represents the current limit of *Z. capensis* in the estuary (Figure 5.2). The extensive loss of *Z. capensis* beds could potentially be due to the degraded quality of water attributed to the waste water treatment works outflow into the estuary resulting in excess nutrients and fresh water into the estuary (Adams *et al*., 2019). As *Z. capensis* is not commonly found at salinity below 15 this would play a role in the disappearance of the seagrass (Adams, 2016). This is consistent with previous studies where seagrass was lost due to freshwater inflow because the salinity decreases, and the nutrient input increased resulting in the seagrass being shaded by microalgal blooms and excessive growth of water hyacinth (Buzzelli *et al.,* 2014) — which is prevalent in the upper reaches of the Swartkops Estuary. During the Adams and Talbot (1992) study, they found an increase in the cover of *Z. capensis* when the freshwater inflow to the Kromme Estuary had decreased. The Great Brak Estuary experienced losses of *Z. capensis* because it was outcompeted by the macroalga, *Cladophora glomerate,* for light and nutrients (Human *et al.*, 2015). Furthermore, the *Ulva* bloom in the Ashmead channel in Knysna is another significant event that led to the loss of *Z. capensis* (Allanson *et al.,* 2016). Lastly the upper reaches of the Swartkops Estuary are very turbid which could also lead to shading and the loss of *Z. capensis*. Past studies found that the middle reaches of the estuary were more turbid than the riverine reaches and the mouth because of the polluted water from Markman and Motherwell canals (McLachlan and Grindley, 1974; Daniel, 1994). Scharler *et al.* (1997) held that increased turbidity was associated with increased chlorophyll *a* levels (microalgal blooms), and higher nitrogen and phosphorus concentrations — all of which was observed in the middle to upper reaches of the estuary in the current study. More recent studies had the same trends as these earlier two and can verify that the turbidity in the middle and upper reaches (Redhouse) of the estuary have continued to increase. In 2015 turbidity showed a definite decrease with distance from the mouth (Pretorious, 2015; Adams *et al.,* 2019). Similarly, turbidity and sediment suspension led to the loss of *Z. capensis* in the Mtata Estuary where it no longer occurs (Adams *et al*., 2002).

Spartina maritima area cover has remained stable in the Swartkops Estuary despite the major decline reported between 1979 and 2008 (Table 5.2). This was also found in the Keurbooms Estuary where despite the overall decline, the area cover remained stable in the lower reaches of the estuary (Mfikili, 2017). That study also showed that although the area cover decreased, *S. maritima* was still able to produce viable seeds and reproduce vegetatively, showing potential for it to colonise intertidal sand and mudflats. Declines of supratidal salt marsh are likely due to urban expansion— increased by 118 ha between 1939 and 2012 (Bornman *et al*., 2016) — but other physical human influences such as bait digging are likely responsible for the declines in the *S. maritima* stands (Colloty *et al*., 2000). *Salicornia tegetaria* has not been mapped in terms of its aerial cover as it mostly occurs as mixed stands with species such as *Bassia diffusa, Triglochin*, and *S. maritima* (Schmidt, 2013; Brown, 2017). Brown (2017) did find large stable salt marsh stands of *S. tegetaria* that were in good condition in the Olifants, Langebaan, Knysna, and Keurbooms estuaries to mention a few.

6.2 Sediment characteristics

6.2.1 Bulk density

Sediment properties and carbon stocks have been found to differ substantially between blue carbon habitats globally (Lewis *et al*., 2017; Radabaugh *et al.,* 2017; Cusack *et al*., 2018). These differences can be due to many factors such as the location of the habitat, — is it close to the limit of its extent? — or the age of the biomass and sediment carbon stocks, or the pollution status of the estuary (Chmura *et al.* 2003; Huxham *et al.,* 2018; Kinderburg *et al*., 2018). The main sediment factors considered when studying blue carbon stocks are; soil depth, bulk density, organic matter, and carbon density (Howard *et al.,* 2014). In all three species – *Z. capensis, S. maritima*, and *S. tegetaria* – there were no seasonal changes in the sediment characteristics. The mean bulk density (1.3 ± 0.004 g cm^{-3}) for *Z. capensis* was similar to that of the global mean for seagrasses (1.03 ± 0.02 g cm^{-3}) (Fourqurean *et al*., 2012), as well as for other studies done in the Red Sea seagrass beds (Serrano *et al.,* 2018), and in Shark Bay and Florida Bay (Fourqurean *et al.*, 2012a). *Zostera marina* beds occurring in East Scotland estuaries had similar bulk density (1.26 ± 0.02 g cm^{-3}) to what was found in this study, but their range was greater extending far into the zone of root growth restriction > 1.6 g. cm^{-3}, (Soane, 1990) with a maximum of 2.33 g cm^{-3} (Potouroglou, 2017). The bulk density for this study are considered low because the mean and maximum extent are below 1.6 g cm^{-3} meaning that root growth is not restricted. Sites with low bulk density and high organic carbon generally indicate organic rich sediment, while high bulk density and low organic carbon indicate mineral rich sediments (Stringer *et al*., 2015).

6.2.2 % LOI and organic carbon

Site 2 (Tippers Creek) sediment was highest in organic carbon (7.6 ± 0.6%) and had a low bulk density (1.05 ± 0.06 g cm^{-3}) beneath the *S. maritima* stand. Creeks are generally less tidally flushed and therefore the build-up of detritus may result, and more carbon is stored in the sediment. Similar findings were reported for *S. maritima* in a study that took place in Southern India — the organic carbon stocks were highest of the salt marsh species they studied (*Sesuvium portulacastim, Arthrocnemum indicum, Salicornia brachiata*) in the wet season with a carbon stock of 7.23 ± 0.09 % (Kaviarasan *et al.,* 2018). The highest sediment organic carbon stocks of *S. tegetaria* were found at Site 3 (Creek site, 5.7 ± 0.7%). This weakly flushed creek site had a factory outlet flowing into it and had distinct black sediment which smelled of H_2S when walking over it – an indication of anoxia (Karlsson *et al*., 2010). When the sediment is permanently saturated keeping it in an anaerobic state there is a continual build up in carbon over time (Chmura et al., 2003), which is why these anoxic sediments store more carbon (Trevathan-Tackett *et al*., 2017). Anoxic sediments in estuaries can provide “carbon protection” under elevated sea temperature rise despite the changing microbial activities (Trevathan-Tackett *et al*., 2017).

This study found that organic content and organic carbon decreased slightly with depth, but these changes were not significant which agrees with a UK seagrass study which also found that organic carbon decreased with depth but not significantly (Hayes *et al.,* 2017; Green *et al*., 2018). The normal trend is that there is a significant decrease of organic content and organic carbon with depth (Serrano *et al*., 2012). These changes with depth were not significant when 0.5 m cores were collected, only when the 1 m cores were collected, however, other studies have found the same trend as this with similar core lengths (0.5 m) (Lavery *et al.,* 2013; Serrano *et al.,* 2016). The biggest variation in organic carbon and organic matter in salt marsh and seagrass sediments in this study and in many others are in the top 50 cm (Choi *et al*., 2001; Johnson *et al*., 2007; Fourqurean *et al*., 2012a; Howard *et al*., 2014). Although the Carbon Pools Manual (Howard *et al*., 2014) suggests measuring carbon stocks to 1 m as the standard globally, many studies only measure the upper 30 to 50 cm of the sediment

(Potouroglou, 2017; Sousa *et al*., 2017; Chastain *et al*., 2018). Soil depth was not an important factor when determining organic carbon stocks based on mud content (Serrano, *et al*., 2016). Because the sediments of this study were more sandy than muddy, the sediment depth was important to note. Sediment textural analysis may be beneficial to do per depth so that in future soil carbon can be predicted (Serrano, *et al*., 2016). Classification of soils into “sandy and not-sandy” have been found to explain up to 37% of the variation in soil organic content (Ford *et al.*, 2018). With plant community types and GIS, up to 50% of salt marsh carbon stocks could be predicted, especially in large areas that are unaccounted for, to better understand global carbon stocks (Ford *et al.*, 2018).

6.1.3 Sediment texture

Sediment carbon storage is linked to the mineral and physical characteristics of the sediment (Rasmussen *et al*., 2007) and soils higher in clay, usually store more carbon (Schimel *et al*., 1994). This specifically plays a role in the long-term storage of carbon in a habitat (Rasmussen *et al*., 2007). The sediment texture is sandy throughout the Swartkops Estuary. This is because the deposition of sediment that has occurred is mainly sandstone and shales (Schmidt, 2013). This makes sense as the dominant sediment loading to the estuary comes from marine sand on the flood tide. Previous studies in the Swartkops Estuary also classified the sediment as sandy with some muddy creeks (Schmidt, 2013). *Zostera capensis* sediment at Site 3 was made up of 39.6 ± 2.2% silt content and *S. maritima* showed higher clay (19.3 ± 1.2 %) and silt (34.7 ± 1.2 %) content at Sites 2 and 3 respectively. These two sites were creek sites and had the highest organic carbon as well. This is still a relatively low silt deposition. This may be attributed to the low frequency of agricultural activities taking place in the catchment (Hill *et al*., 1974) or the subsoil sediments are not stoney (Finch *et al*., 2014), or the ebb and flow of the tides.

Salicornia tegetaria showed similar trends in terms of sediment composition to *S. maritima*. The silt and clay content of the sediment were greater at Sites 2 (27 ± 2%; 13.3 ± 7.7%) and 3 (37.3 ± 2.2%; 11.7 ± 0.3%) compared to the other sites. The smaller grain sizes of silt and clay sediments (larger surface area) allow them to accumulate more organic matter which essentially results in greater organic carbon storage (Serrano *et al*., 2016; Dahl *et al*., 2017). The sites that had the higher silt and clay grain sizes were also the sites that had higher organic carbon stocks in this study. This was also found in the sediments under *Z. marina* beds in Gullmar Fjord Estuary on the Swedish west coast in Europe (Dahl *et al.,* 2016). Not only do these finer sediment particle sizes result in higher organic carbon stocks due to a greater surface area, but they result in lower exchanges in oxygen which reduces remineralization rates, adding to the preservation of carbon once it has been stored (Hedges and Kiel, 1995; Pederson *et al*., 2011; Serrano *et al*., 2016). The same occurs in salt marsh sediments of fine textured soils (Serrano *et al*., 2018). Using sediment textural analysis, especially % mud, is suggested to be a proxy for sediment organic carbon as it is cheaper and can be used in countries that do not have funding for carbon projects (Erftemeijer and Koch, 2001; Ford *et al.,* 2019). For the sediment beneath each of the plant species at the mouth (Site 1) the % sand was the highest with almost no silt and clay particles present because the mouth is marine dominated. This agrees with a similar study done in an Australian salt marsh in Tasmania (Ellison and Beasy, 2018) where the invasive *Spartina anglica* had finer sediment grains as well as higher organic carbon stocks than the native *Sarcocornia quinqueflora*.

6.1.4 Total sediment carbon storage

The results of this study show that the sediment beneath *Z. capensis, S. maritima*, and *S. tegetaria* stands in the Swartkops Estuary store a total of 224.1 ± 37.9 Mg C ha^{-1}, 247.1 ± 47.7 Mg C ha^{-1}, and 212.3 ± 44 Mg C ha^{-1}, respectively. Most of the carbon stored in these habitats is likely to be allochthonous because globally approximately 50 % of sediment organic content is derived from external sources (Kennedy *et al*., 2010; Githaiga *et al*., 2017). In the Swartkops Estuary this is likely due to the waste water treatment works which release nutrient rich effluent high in organic content (Potgieter, 2008; Lemley *et al*., 2019). The sediment carbon content is similar in all three habitats. Seagrass carbon stocks are generally lower than the salt marsh according to the blue carbon manual (Howard *et al*., 2014). Fourqurean *et al.* (2012) expressed that when comparing regional and species-specific data differences they should be viewed as preliminary because of the lack of data in many areas of the world and for many species. The values for *S. maritima* and *S. tegetaria* in this study both fall within the global range for salt marsh (16 – 623 Mg C ha^{-1}), however they are slightly lower than the mean of 255 Mg C ha^{-1} (Howard *et al.,* 2014). The *Z. capensis* sediment carbon stock in this study was significantly higher than the global mean (108 Mg C ha^{-1}), but still fell within the range (10 – 829 Mg C ha^{-1}) (IPCC, 2013). These large ranges indicate the variability of carbon storage between various locations and species. This study displayed values similar to those for seagrass species (*Z. maritima*) in a South Australian subtropical seagrass meadow at Shark Bay (268.3 ± 101.7 Mg C ha^{-1}). However larger seagrass species such as *Posidonia oceanica* have been found to store up to 829.2 Mg C ha^{-1} in their sediments (Fourqurean *et al*., 2012a), but these species are found in deeper subtidal habitats. The carbon stocks of this study current are greater than many other areas across the globe (Table 6.2). The size of the seagrass therefore does not play a role in how well it captures carbon and the environmental variables may play a bigger role in how the carbon is stored. For example, *Halophila ovalis*, stored almost equivalent amounts of carbon in its sediment as *Posidonia australis* which has much larger leaves and root systems (Lavery *et al*., 2013; Githaiga *et al.,* 2017). The difference between these seagrasses was the location — *P. australis* was growing in the Mediterranean Sea, while *H. ovalis* occurred in a sheltered estuarine bay. There have been few studies on blue carbon in Africa, and except for Githaiga *et al.*, (2017, 2019), most of them are on mangrove carbon stocks (Jones *et al.,* 2014; Stringer *et al.,*2015; Gress *et al*., 2016; Benson *et al*., 2018). Githaigia *et al*. (2017) found that the carbon stocks were significantly different between seagrass species (*Thalassodendron ciliatum*, *Thalassia hemprichii, Enhalus acoroides* and *Syringodium isoetifolium*) in Gazi Bay, Kenya. These carbon stocks (160.7 - 233.8 Mg C ha^{-1}) were similar to those found in the current study. *Enhalus acoroides* stored the most carbon in its sediment (295.7 ± 63.6 Mg C ha^{-1}) and the lowest was beneath *S. isoetifolium* (160.7 ± 40.3 Mg C ha^{-1}) (Githaiga *et al.,* 2017). *Zostera capensis,* was also found in Gazi Bay but was not as extensively researched because it did not occur as a monospecific stand.

Spartina maritima in this study stored more carbon in the sediment beneath it than many other *Spartina* species (Table 6.1). *Spartina alterniflora* growing invasively in Yangtze Estuary in China stored 209.4 Mg C ha^{-1} in the sediment which was much higher than the native species — *Phragmites* and *Scirpus* (Liao *et al*., 2007). This is most similar to the carbon storage found in this study. *Phragmites* has been found to be extremely effective at storing carbon (286 Mg C ha^{-1}) as was found in a South Korean estuary (Byun *et al*., 2019). Although there has been a substantial amount of research on *Spartina* species (Table 6.2), many studies tend to research mixed salt marsh stands to include the less common species (Saintilan and Rogers, 2013; Quintana-Alcantara, 2014; Patterson, 2016). Chastain *et al*. (2018) proved that higher marsh areas stored more carbon in the sediment than the lower, intertidally influenced marsh areas. *Salicornia* and *Sarcocornia* species are said to store similar amounts of carbon in their sediment (Ellison and Beasy, 2018). As seen in Table 6.1, this study reported on more carbon in *S. tegetaria* than other similar studies of *S. quinqueflora* in estuaries in Australia that have similar climate to South Africa. The studies done by Kelleway *et al*. (2016), Ellison and Beasy (2018) and Lewis *et al.* (2018) indicate the variability in sediment carbon storage beneath the same species in the same region. This highlights that carbon stock variability is due to factors such as sampling procedures, times, weather, or analysis, and the geomorphology, dominant pollutants, and carbon inputs of specific estuaries (Lewis *et al*., 2018).

The likely reason for the higher carbon stocks in the Swartkops Estuary compared to international studies is because the estuary is highly polluted (Emmerson, 1985; Scharler and Baird, 2003; Adams *et al*., 2014). This was also found in Danish eelgrass meadows —

eutrophic estuaries had greater carbon stock than pristine estuaries (Kinderburg *et al*., 2018). This was due to the elevated nutrient levels in the water. Another reason for the high carbon stocks and little difference between the sediment carbon storage beneath each of the three habitats may be due to the carbon black factory (Algorax, Port Elizabeth) (Orion, 2015). This factory releases high amounts of brown (gases from burning fossil fuels and derived products thereof) and black (emissions that are high in organic carbon) carbon that enters the coastal environment (Nellemann *et al.,* 2010). Bond et al. (2000) found that Southern Africa is one of the largest black carbon polluters in the world, which means it is highly likely that having so many industries on the edge of the Swartkops Estuary results in greater proportion of pollution and released organic particles settling in the salt marsh and seagrass habitats. Swartkops Estuay salt marsh (*S. tegetaria*) and seagrass (*Z. capensis*) sediments stored significantly more organic carbon than the Nxaxo Estuary (5.1 ± 0.01 Mg C ha^{-1} for seagrass and 2.6 ± 0.19 Mg C ha^{-1} for salt marsh) (Mbense *et al.,* 2019, unpublished). Knysna Estuary in South Africa also stored less carbon (25 ± 6.4 Mg C ha^{-1}) beneath the *Z. capensis* beds (Els *et al.,* 2018, unpublished) than what was found in the Swartkops Estuary. Both the Nxaxo and Knysna estuaries are also permanently open to the sea and situated in the warm temperate region along South Africa’s coastline, but they experience less industrial waste pollution from the water and the air. This indicates the likelihood that the carbon black factory causes increased carbon stocks in Swartkops Estuary. This is is potentially due to fly ash — ash produced by the burning of coal and other materials which are usually carbonous and indicators of anthropogenic impact (Rose, 2001, 2015). The study of black carbon in marine eosystems is still a fairly new field, however, chemothermal oxidation methods have been used to quantify black carbon in sediments (Gustafsson *et al*., 2001) of salt marsh and estuarine habitats where black carbon is known to be deposited (Leorri *et al.* 2014; Hanke, *et al.* 2016). This is a likely indication that black carbon factories may be a source of blue carbon stocks. More research may be required to link the two variables to one another. The current study found that the carbon storage was greater in the creeks than in the main channel of the estuary because they experience less tidal action and are sheltered so that organic content can build up in the sediment. This directly addressed the second objective to determine carbon storage in the sediment and the hypothesis related to this was accepted — more carbon is stored in sheltered creeks than in the main channel.

Table 6.1: Comparison of seagrass, salt marsh grass, and salt marsh succulent organic carbon values from across the globe.

Region	**Species**	**C_{org} (%)**	**Total sediment carbon stock (Mg. ha^{-1})**	**Reference**
Saudi Arabia	*Thalassia hemprichii*	0.7	50	Serrano *et al.* (2018)
UK	*Zostera marina*	4.94	380.07	Green et al. (2018)
Australia	*Posidonia australis*	2.24	108	Rozaimi *et al.* (2016)
Kenya	*Enhalus acoroides*	N/A	295.7	Githaiga *et al.* (2017)
South Africa	*Zostera capensis*	0.86	5.1	Mbense *et al.* (2019, unpublished)
South Africa	*Zostera capensis*	2.89	224.14	This study
Australia	*Spartina anglica*	2.28	55.5	Ellison and Beasy (2018)
Portugal	*Spartina maritima*	2.25	N/A	Santos *et al*. (2019)
India	*Spartina maritima*	3.3	N/A	Kaviarasan *et al.* (2018)
South Africa	*Spartina maritima*	4.15	247.1	This study
Australia	*Sarcocornia quinqueflora*	N/A	164	Kelleway *et al*. (2016)
Australia	*Sarcocornia quinqueflora*	N/A	87.1	Lewis *et al*. (2018)
Australia	Sarcocornia *quinqueflora*	0.7	49.5	Ellison and Beasy (2018)
India	*Salicornia brachiata*	0.83	N/A	Rathore *et al*. (2016)
South Africa	*Salicornia tegeteria*	0.96	2.6	Mbense *et al.* (2019, unpublished)
South Africa	*Salicornia tegeteria*	3.51	212.3	This study

6.2 Biomass

One of the objectives of this study was to determine the change in biomass over time and the carbon stored in the biomass of the three intertidal species (*Z. capensis, S. maritima*, and *S. tegetaria*). According to the literature on blue carbon, the majority of the carbon stocks are stored in the sediment; however, the vegetative component is still an important part of the overall carbon stock assessment of an estuary (Radabbaugh *et al.,* 2017). The importance of the biomass is largely due to it acting as an effective trap allowing sediment carbon to settle because of the canopy it forms, and it reduces the water flow (Green *et al.,* 2018). Therefore, higher biomass plays a role in trapping allochthonous carbon and stabilising sediments to reduce erosion of the already buried carbon (Hemminga *et al.*, 1991; Gacia *et al.*, 2002). Without the important biomass in blue carbon ecosystems, the carbon stocks in the sediment may be much lower. All three species studied in this project showed greater carbon storage in the aboveground biomass than in the belowground biomass despite the usual trends (Cacador *et al*., 2003; Howard *et al*., 2014; Radabbaugh *et al.,* 2017) possibly because of nutrient enrichment.

6.2.1 *Zostera capensis*

The overall mean biomass (above and belowground combined) for *Z. capensis* in the Swartkops Estuary was 527.2 ± 91.9 g DW m^{-2} and 767.6 ± 134.1 g DW m^{-2} for summer and winter respectively. Contradictory to this study, Talbot and Bate (1987) found that the highest biomass occurred in the summer and not in winter, however they attributed this to recovery time as a flood took place just before the winter sampling period. The higher winter biomass found in this study may be a result of more favourable water transparency and light attenuation in winter which was found for *Z. capensis* in a Mozambique estuary (de Boer, 2000). Past data of turbidity in the Swartkops Estuary indicated higher turbidity in the summer months (November 2012) and this was attributed to the increased chlorophyll *a* levels in the water column (Pretorius, 2015). A study done in the Kromme Estuary in South Africa on *Z. capensis* biomass also found that the aboveground and belowground biomass was highest in winter however there was no seasonal variation in biomass following seasonal changes in air and water temperature, or solar radiation (Hanekom and Baird, 2010). Arendse (2011) found that there were significant differences between *Z. capensis* biomass in different seasons in the Langebaan Lagoon, but these were all site-specific changes and each site showed different trends. At many of the sites, the biomass was greater in winter. This was attributed to the greater epiphyte biomass in summer resulting in the dieback of *Z. capensis* (Arendse, 2011).

This is, however, not the case for the current study and in the Swartkops Estuary it is most likely related to the increased nutrient input to the system in the winter months which was found in a recent study (Lemley *et al.*, 2019). The mean biomass calculated for the year was 647.4 ± 112.98 g DW m^{-2} which is higher than the biomass reported by Talbot and Bate (1987) in the same estuary (124 g DW m^{-2}). The current studies biomass did fall within the range for African seagrass studies — 461–738 g DW m^{-2} (Githaiga *et al.*, 2016). The seagrass biomass considered were *Zostera, Thalassia, Halodule, Cymodocea, Halophila*, and *Thalassodendron*. The seagrass biomass is higher than any other study reported for South Africa (Christie, 1981; Hanekom and Baird, 1988; Adams and Talbot, 1992). Majority of the investment was into the aboveground biomass as was in the 1987 study. The ratio of above to belowground biomass was 2.16 for this study which is also a lot higher than the 1.28 found in the previous study (Talbot and Bate, 1987). This large increase in biomass is due to the increased nutrients that the Swartkops Estuary is facing compared to the nutrient concentrations in the 1980's (Emmerson, 1985; Adams *et al*., 2014; Lemley *et al*., 2019). In the 1980's Emmerson (1985) considered the nutrient levels in the estuary high — 0.2 mg DIN l^{-1}, however this increased to 0.98 mg l^{-1} in 2013 (Adams *et al.,* 2014) and this then increased further to 4 mg l^{-1} (Lemley *et al.,* 2019). Dissolved inorganic phosphorus (DIP) also increased in the Swartkops Estuary between 2013 and 2019 from 0.44 mg l^{-1} (Adams*, et al.,* 2014) to 2 mg l^{-1} (Lemley *et al.,* 2019).

Githaiga *et al*. (2016) established a ratio of above- to belowground biomass for African seagrasses of 0.33 which is much lower than this study (2.16 in the summer). Summer is considered the maximum growing season which is when sampling took place (Howard *et al*., 2014; Githaiga *et al*., 2016). The bulk of the seagrass biomass was found in the lower reaches of the estuary and no seagrass was found in the upper reaches, and a large portion of this was in creeks, agreeing with the earlier work by Talbot and Bate (1987). Seagrasses have been found to prefer these creek habitats in a host of international and local studies because their morphology creates greater surface areas for colonization and they are characterised by calmer conditions (Talbot and Bate, 1987; Hogarth, 2017; Cullen-Unsworth *et al*., 2018 Ferguson *et al*., 2018). In addition to this, creeks generally have higher nutrient contents (McLachlan and Grindley, 1974), and the waterlogged conditions protect the seagrass from desiccation during tidal exposure (Hogarth, 2015; Zimmermann, 2017).

The range of leaf lengths found in this study (20 – 54 cm) was smaller than that found by Talbot and Bate (1987) (2 – 103 cm). This could be due to the larger area of seagrass available for them to sample. International studies have suggested that seagrass biomass is generally higher in cold and temperate regions (Iverson and Bittaker, 1986), but in tropical regions seagrasses show aseasonal patterns (Larkum, 1977; Kirkman and Reid, 1979).

Turner (2010) found that leaf production was greater in winter than in summer for *Z. capricorni* in a New Zealand estuary. It is important to note that cautions have been made against the comparison of seagrass biomass from different geographic locations, even within the same biogeographic region, due to its variable nature, unless the biomass was collected at the same point of maximum leaf biomass (Iverson and Bittaker, 1986). The biomass recorded in this study had similar trends to a 2017 study in the Knysna Estuary in South Africa (Els, unpublished). *Zostera capensis* had higher biomass in winter (290.1 ± 25.4 g DW m^{-2}) than in summer (233.5 ± 51.2 g DW m^{-2}) in the Knysna Estuary.

Sediment carbon storage is often found to be greater below seagrass beds than bare areas (Dahl et al., 2016a; Serrano *et al.,* 2016a; Lyimo, 2016; Githaiga *et al*., 2017). This means that the biomass plays a major role in sequestering carbon. Some studies have also used biomass as a predictor of soil organic carbon (Kirwin and Mudd, 2012; Armitage and Fourqurean, 2016). In the Swartkops Estuary the carbon content of *Z. capensis* was 2.08 ± 0.49 Mg C ha^{-1} which is similar to the global average of 2.52 ± 0.48 Mg C ha^{-1} when considering the above and belowground biomass (Fourqurean *et al*., 2012). Many seagrasses store more carbon in their belowground biomass as this is usually the larger portion of biomass (Fourqurean *et al*., 2012; Belshe *et al.,* 2017) but the current study did not find this as the aboveground biomass was higher. *Zostera capensis* growing in Inhaca, Mozambique had much greater belowground biomass (198.9 ± 75 g DW m^{-2}) than aboveground biomass (25.7 ± 8.0 g DW m^{-2}) (de Boer, 2000). *Zostera noltii* growing in a Moroccan marine bay had a large range of biomass but had a larger belowground portion (167.5 ± 140.0 g DW m^{-2}) as well compared to the aboveground portion of the biomass (3.08 ± 1.12 g DW m^{-2}) because of the wave action (Bououarour *et al*., 2015). *Zostera marina* beds in Studland bay in the UK did not have this trend in the biomass estimations either and they suggested this may be due to taking samples from the centre of the seagrass bed (Green *et al.,* 2018). This could possibly be the case here as well, although it may not be the only contributing factor. Higher nutrient levels in the water column are known to increase productivity of the aboveground biomass (Koop-Jakobsen *et al*., 2015). Green *et al*. (2018) found biomass carbon values similar to the current study for *Z. marina* (2.51 ± 0.49 Mg C ha^{-1}). According to Howard *et al*. (2014) a conversion factor can be used to determine the carbon content in the seagrass, but because seagrasses differ so much in their morphology and ecology (Hogarth, 2015), species specific conversion factors should be used to avoid over or underestimation of carbon stocks. This study calculated a carbon conversion factor by means of elemental analysis specific to *Z. capensis* of 0.35 for aboveground biomass and 0.33 for belowground biomass. This is close to the mean global carbon conversion factor of 0.34 (Howard, *et al.,* 2014). This means that 35% of *Z. capensis* consists of organic carbon. Allometric equations were also determined to make this a Tier 3 assessment and followed the same methods used in Owers *et al*., (2018). The allometric equations were determined by leaf length and biomass, however this did not result in a strong enough relationship ($r^2 = 0.22$) to determine the biomass from the leaf length to reduce the destructive sampling. Seasonal changes to biomass and plant height may affect these values which does not make them accurate and it is better to rather sample the biomass and use the species-specific carbon conversion factor. Owers *et al*. (2018) suggests that accurate carbon storage depends on three things; an accurate assessment of biomass, carbon content, and the extent of the vegetation. This method is not recommended in the Carbon Pools manual as seagrass biomass is too variable (Howard *et al.,* 2019). Therefore, biomass is important for determining the organic carbon content with the species-specific carbon conversion factor, but biomass must be collected each time as a biomass versus leaf length correlation does not create a reliable allometric equation.

6.2.2 *Spartina maritima*

There was a distinct difference in the biomass of *S. maritima* in the Swartkops Estuary between Pierce (1979) and the current study. During the Pierce (1979) survey they found a biomass range of 293 – 656 g DW m^{-2} while in this study the range extended from 1903 – 3125 g DW m^{-2}. The cause of this difference in biomass is likely attributed to an increased nutrient supply derived from wastewater treatment works and urban runoff (Emmerson, 1986; Adams *et al.,* 2014; Lemley *et al*., 2019). The biomass values reported in the current study correspond to those of *Spartina alterniflora* growing at Oak Island salt marshes in North Carolina (Stroud and Cooper, 1969). Johnson *et al*. (2016) experimented on the effect that nutrient enrichment would have on a salt marsh in the Plum Island Sound Estuary.They found that the intertidal salt marsh (*Spartina alterniflora*) responded with a temporary increased aboveground biomass in the first three years, while over a longer term (nine years) the results displayed a decrease in belowground biomass. This is not consistent with what was found for *S. maritima* in this study since the study by Pierce (1979). The above- and belowground biomass has increased since the Pierce (1979) study, but the ratio of aboveground biomass to belowground biomass has changed to having greater aboveground biomass than belowground biomass. An investigation in a salt marsh in Maryland, USA showed that increased nitrogen in a system strongly favoured the growth, production and overall biomass of *Spartina patens* which resulted in a species shift from *Schoenoplectus americanus* to a less flood tolerant species, *S. patens* (Langley *et al*., 2013). This article communicated that the long-term effects of increased nitrogen may still lead to bank destabilisation because *S. patens* is not able to tolerate floods. In New England salt marshes, there was also an increase in the biomass of *S. patens* due to nutrients but not *S. alterniflora* resulting in a species shift (Fox *et al.* 2012). Both these studies suggested that nutrient enrichment can have cumulative negative effects with other environmental factors (flooding, sea-level rise, physiochemical changes). Some plants thrive in nutrient enriched conditions — *Spartina* species — while others that play important ecological roles may be lost. Castillo *et al*. (2008) found that *S. maritima* belowground biomass ranged from 1190 ± 192 to 8694 ± 1585 g DW m^{-2}, while the aboveground biomass ranged from 672 ± 84 to 1427 ± 356 g DW m^{-2} but, according to the mean values the above to belowground ratio was only 0.6. That ratio is similar to that found in this investigation (0.9). As was seen with *Z. capensis*, *S. maritima* had higher aboveground biomass in the winter season (2744.08 ± 482.04 g DW m^{-2}). This is consistent with what was found for *S. maritima* salt marsh at the Southwest Iberian Peninsula during warmer winters (Momba and Bux, 2010). Warmer winter, like what would be experienced in this temperate South African estuary, results in faster development and productivity of salt marshes plants and essentially greater biomass than regions that experience extremely cold temperatures in winter (Momba and Bux, 2010). Extremely high belowground biomass was found in the Tagus Estuary (7190 g DW m^{-2}) and this made up 96% of the total biomass (Cacador *et al*., 2003). The belowground biomass was sampled to a depth of 30 cm which is generally the standard depth sampled in most studies (Connor and Chmura, 2000; Deegan *et al*., 2012; Nelson and Zavaleta, 2012; Howard *et al*., 2014). Castillo *et al*. (2017) also found similar allocation of above and belowground biomass where the aboveground biomass was slightly higher — this was said to be due to the higher shoot densities that were all of similar height. It is well known that plants that contain excess nitrogen may result in a poorly developed root system and have a higher shoot to root ratio (Salisbury and Ross, 1985) which is what was observed in the biomass of *S. maritima* and is different from studies that took place in more pristine estuaries compared to the eutrophic Swartkops Estuary. However, when there is an oversupply of phosphorus it has been observed that the belowground biomass is enhanced (Salisbury and Ross, 1985). In the Swartkops Estuary both N and P are oversupplied which may be why similar ratios of above: belowground biomass were observed.

Biomass is necessary for carbon calculations because if the percentage of the carbon that makes up salt marsh species is low, but the biomass is high, that specific site will store high amounts of organic carbon (Sousa *et al*., 2017). There are very few published carbon conversion factors for salt marsh (Radabaugh *et al.,* 2017). Howard *et al*. (2014) reported a value of 0.45 which was based on a Chinese study in terrestrial systems (Fang *et al*., 1996). The current study determined a carbon conversion factor from elemental analysis of 0.4 for aboveground biomass and 0.25 for belowground biomass of *S. maritima*. This means over estimations of carbon in the specific habitat can be avoided. Radabaugh *et al.* (2017) reported a carbon conversion factor mean of 0.41 for 18 salt marsh species. *Juncus roemerianus* is a species with a greater percentage of carbon (conversion factor of 0.47), while *S. alterniflora* (0.42) and *S. patens* (0.46) are very close to the value reported by Howard, *et al.* (2014). These conversion factors are used together with allometric equations, determined by plotting plant height against biomass. Based on this, the current study determined a r - value of 0.34 which statistical analysis showed was a significant relationship and fit. Previous work on lowland bamboo, following the same method found that the r values ranged from 0.025 to 0.82 suggesting that this may not actually be the most accurate method of determining biomass (Gurmessa *et al.,* 2016). Salt marsh grasses have been seen to result in accurate allometric equations with r values of 0.91 (Craft *et al*., 2013). Species such as *S. alterniflora* have been found to have a r-value of 0.86 only once log transformed (Gross *et al*., 1991). Log transformations may have resulted in a better fit and a higher r-value which may be a point for consideration in future studies. However, this study suggests that only 34% of the *S. maritima* stem heights were correlated to biomass, leaving 66% of the data uncorrelated. This means that stem lengths cannot be used as a proxy for biomass in future studies. According to Clarke and Jacoby (1994), no seasonal variation in biomass is observed in the aboveground biomass of salt marsh in South east Australia, so these r-values may be enough and only one allometric equation necessary. This is likely not the case for salt marsh species globally and more detailed research is needed. Many studies have suggested that salt marsh plants vary seasonally due to growth rates, flowering, and senescence to mention a few factors (Reidenbaugh, 1983; Morris and Haskin 1990; Gonzalez Trilla *et al*. 2013). The most accurate biomass estimations are through direct — and slightly destructive — sampling methods (Howard *et al.,* 2014).

Spartina maritima stored 16.27 ± 2.86 Mg C ha^{-1} in the Swartkops Estuary. Globally the carbon stocks and extent of salt marshes are still largely uncertain with an area ranging between 22 000 and 400 000 km^{2} (Duarte *et al*., 2013; Chastain *et al.,* 2018). Our *S. maritima* stocks were similar to the carbon stocks in *Juncus kraussii* (15.97 ± 2.35 Mg ha^{-1}) *in* an Australian wetland (Owers *et al.,* 2018). This was higher than a mixed salt marsh stand of herbs, sedges, and grasses that only stored 7.51 ± 0.91 Mg C ha^{-1} (Owers *et al.,* 2018). The *J. kraussii* in this study was tidally inundated unlike the mixed salt marsh stand which received less tidal action as it was higher on the intertidal zone. These salt marsh areas were also sheltered by mangroves which may have resulted in less carbon particles being transported to the salt marsh biomass (Owers *et al.,* 2018). *Spartina maritima* in European salt marshes stored only 4.3 Mg C ha^{-1} in the aboveground biomass (Curado *et al.,* 2017). *Spartina alterniflora* also only stored 4.46 Mg C ha^{-1} in its biomass (Liu et al., 2013), both of these reported results from the aforementioned studies were much less than what was found in the current study. This is likely due to the higher nutrient levels in the Swartkops Estuary. Many *Spartina* species (*S. alterniflora*, *S. patens* and *S. perennis)* have decreased in belowground biomass with greater nutrient enrichment (Valiela *et al*., 1976; Gross *et al*., 1991; Palomo and Niell, 2009). It can be expected that the belowground biomass will decrease even more over time if the nutrient content in the estuary continues to increase.

6.2.3 *Salicornia tegetaria*

There are few studies in the literature on *S. tegetaria*, but comparisons can be made with other succulent halophytes (Krüger and Peinemann, 1996) that display similar ecological characteristics to *Salicornia. Salicornia tegetaria'*s ratio of above to belowground biomass (4.0) is high in comparison to the other dominant macrophytes in this study, but it is low in comparison to an Indian study of *Salicornia brachiata* that had higher aboveground biomass compared with belowground biomass (ratio of 12.0) (Chaudhary *et al*., 2018). *Sarcocornia perrenis* salt marsh in Argentina had very low biomass 363 ± 43 g DW m^{-2} and 242 ± 27 g DW m^{-2} for above and belowground biomass respectively (Negrin *et al*., 2015) compared to the 1056 ± 223 g DW m^{-2} and 212 ± 75 g DW m^{-2} above and belowground biomass determined in this study. A recent investigation in South Africa determined the above (1310 ± 60 g DW m^{-2}) and belowground (3660 ± 210 g DW m^{-2}) biomass of *S. tegetaria* at six different estuaries (Brown, 2018). In all the surveyed estuaries the below ground biomass was greater than the aboveground biomass (Brown, 2018), but some international findings displayed the same trend as the current study (Pallomo and Niell, 2009; Negrin *et al*., 2015; Chaudhary *et al*., 2018). Brown (2018) proposed that the higher values found for the aboveground biomass in Palomo and Niell's (2009) work was due to eutrophic conditions in the estuary in Spain but was also potentially due to the succulence in the stems in response to sediment salinity. This may also explain why the current study found the results it did. Both the average biomass for this study and that of Brown (2018) however, fell within the range that has been reported for *Salicornia spp*. biomass (530 to 3400 g DW m^{-2}) (Curco *et al.,* 2002; Scarton *et al.*, 2002; Palomo and Niell, 2009). Palomo and Niell (2002) stated that the same species may even differ in biomass between sites, which is evident looking at the vast range for mean global biomass for *Salicornia*. What is important to note is that the biomass production is directly related to the nutrient retention of the salt marsh macrophytes and nutrients in the soil (Shao *et al*., 2013). According to Negrin *et al.* (2015) there are significant amounts of carbon, nitrogen, and phosphorus cycled through *Sarcocornia* which implies it may be an effective filter of these nutrients.

The carbon conversion factor calculated through elemental analysis in this study for *S. tegetaria* was 0.32 for aboveground biomass and 0.38 for belowground biomass. There are very few conversion factors for salt marsh succulents and the closest species that this has been determined for is a salt marsh shrub, *Tecticornia*, native to Australia (Saintilan *et al*., 2009; Howard *et al*., 2014). The blue carbon manual suggests that a carbon conversion factor of between 0.45 and 0.5 should be used. This would result in overestimations of carbon in *S. tegetaria*. Similar carbon conversion factors were obtained for *Salicornia virginica* (0.33) (Radabaugh *et al*., 2017). Salt marsh succulents are known to have lower carbon content than grasses, sedges, and reeds, likely due to the fact that some of them, like *S. virginica*, do not have C_4 type carbon fixation (Dawes, 1998). *Batis maritima*, a salt marsh succulent stores one of the lowest percentages of carbon in its biomass (carbon conversion factor of 0.23) (Radabaugh *et al.,* 2017). This study found a good relationship between stem height and biomass (r = 0.48). The closest r value to this was for *Fimbristylis cymose*, a sedge (r = 0.46) and *Sporobolus virginicus* (r = 0.553) (Radabaugh *et al.,* 2017). These species may vary seasonally because they may have inflorescence but, in this study, none was noted during sampling. *Salicaornia tegetaria* flowers seasonally (May and June – winter) (Riddin and Adams, 2019) so this would not be an effective way to determine biomass in the future.

This is the first dataset available on the carbon storage potential of *S. tegetaria* and globally there are little data available on other *Salicornia* species. *Salicornia tegetaria* biomass had a mean carbon stock of 4.28 ± 0.72 Mg C ha^{-1} which is less than what was found for other succulent salt marsh species. *Sarcocornia quinqueflora* in Australia stored 6.88 ± 1.38 Mg ha^{-1}, while *Samolus repens* stored 5.51 ± 0.80 Mg ha^{-1} (Owers *et al*., 2018). Salt marsh plants in arid areas have slightly lower carbon stocks (range from 1.9 to 7.2 Mg C ha^{-1}), with a mean of 3.6 Mg C ha^{-1} (Schile *et al*., 2017) which is lower than the current study. This is one of the lower carbon stocks reported globally, after Schile *et al*. (2017), and it makes sense because the biomass is, especially the belowground component, is lower than that found elsewhere (Curcó *et al*., 2002, Neves *et al*., 2010).

6.3 Epiphyte biomass

The epiphyte biomass is suggested to be a good indicator of eutrophication in estuaries because they are normally more prominent in polluted or nutrient enriched estuaries (Borowitzka and Lethbridge, 1989; Harlin, 1995; Nelson, 2009; Thomsen *et al*., 2012; Nelson, 2017). This study, however, showed a completely opposite trend where epiphytes were not good indicators of nutrient enrichment. The chlorophyll *a* values (15.1 ± 3.7 mg chl-*a* m^{-2}) are much lower than would be expected in a eutrophic system. A biomass ranging between 100 to 150 mg chl-*a* m^{-2} is the threshold at which epiphytes become a problem (generally indicating nutrient enrichment) (Welch *et al.,* 1988). At levels greater than 100 mg chl-*a* m^{-2} filamentous algae tend to dominate the epiphytic community (Lemley *et al*., 2017). These values are much lower than the epiphyte biomass found by Talbot and Bate (1987) and Lemley *et al.* (2017) in the Swartkops Estuary. The epiphyte biomass has no correlation to the leaf length and although Site 1 showed the highest seagrass biomass (655.3 ± 100.2 g DW m^{-2}), it did not have the longest leaf length (Site 3, 28.3 cm). This agrees with the findings of Talbot and Bate (1987). Although majority of epiphyte studies suggest that they are good indicators of nutrient enrichment, they agree that epiphytes alone cannot be used as indicators of eutrophication. Frankovich and Fourqurean (1997) studied the effect of nutrient enrichment in Florida Bay and found that the relationship between nutrient availability and epiphyte biomass alone cannot predict nutrient enrichment. Active uptake of nutrients from the water column by macrophytes, especially submerged aquatic vegetation (SAV), reduces the availability of nutrients to epiphytes (Lin *et al*., 1996). This along with top-down grazer control of epiphytes and macroalgal biomass may mask the effects of nutrient enrichment (Neckles *et al*., 1993 and 1994). It is well known that the Swartkops Estuary is high in nutrient pollution which is why it is eutrophic, so if epiphytes do not display this, plant tissue N and P may be better indicators as was found in several studies globally (Lin *et al*., 1996; Inglett and Reddy, 2006; Burkholder *et al*., 2007; Hood, 2012). One study went as far as to say "especially tissue nutrient content (C, N, P)" are useful in identifying nutrient enriched areas (Burkholder *et al.,* 2007).

6.4 Nutrient storage stocks

Salt marsh halophytes can alter the chemistry of the rhizosediment related to their specific processes and seasonal changes in biomass and nutrient dynamics (Koop-Jakobsen *et al*., 2015). An example of this is *S. maritima* which has been known to colonize anoxic sediments and change the sediment to an oxygenated state by transporting oxygen to the roots (Sousa *et al*., 2008). In this study *S. maritima* showed higher biomass and nitrogen and phosphorus storage than *Z. capensis* and *S. tegetaria*. *Spartina maritima* stored 1.37 ± 0.03 Mg N ha^{-1} and 1.13 ± 0.05 Mg P ha^{-1} in summer and substantially more in winter (1.60 ± 0.13 Mg N ha^{-1}; 1.20 ± 0.12 Mg P ha^{-1}). Pierce (1979) also studied the composition of *S. maritima* in the Swartkops Estuary and she found that the nutrient content in the tissues were prone to seasonal fluctuations. She measured the nitrogen in the plant biomass and found that it made up approximately 1.3% of the dry plant mass. This is less than this study found (3.9 %) because comparing the nitrogen input data from Pierce (1972), the nitrogen inputs recently recorded (Lemley *et al.,* 2019) are much higher. This shows how much the estuary can change within a matter of 40 years with extreme amounts of anthropogenic inputs. The current study found spatial and seasonal variation between nutrient stocks in the plant which agrees with what was found in the Mondego Estuary — more nutrients were stored in plants closer to wastewater inlets to the estuary (Sousa *et al.,* 2008). Approximately 0.7 Mg N ha^{-1} was stored in the aboveground biomass and 0.2 Mg N ha^{-1} of *Spartina* which is similar to the nitrogen stored in the summer season in this study's *S. maritima* above- (0.97 ± 0.01 Mg N ha^{-1}) and below-ground biomass (0.41 ± 0.02 Mg N ha^{-1}). This estuary is highly polluted in the lower regions similar to the Swartkops Estuary with urban development along the banks.

Zostera capensis had higher nitrogen and phosphorus stocks in its aboveground biomass compared to belowground biomass because of the greater quantity of aboveground biomass, which has been seen in a number of studies for both seagrass and salt marsh (Frankovich and Fourqurean, 1997; Flindt *et al.,* 1999; Boyer *et al.,* 2001; Sousa *et al.,* 2010). This is due to macrophytes in the intertidal zone taking up nutrients from both the water column and the sediment. Pederson *et al*. (1997) suggested that leaf tissues have a higher affinity to take up nutrients than the roots especially if growing in the water column. A study in Florida Bay showed this as the water column was the main source of nutrients to the seagrass and showed a strong relationship between the water column nitrogen and phosphorus and the nitrogen and phosphorus content of the aboveground biomass (Frankovich and Fourqurean, 1997). *Zostera capensis* stored 0.21 ± 0.003 Mg N ha^{-1} and 0.13 ± 0.01 Mg P ha^{-1} in summer and 0.42 ± 0.03 Mg N ha^{-1} and 0.36 ± 0.03 Mg P ha^{-1} in winter. In European *Z. marina* meadows much lower nitrogen and phosphorus was found to be stored in the plant tissues (0.02 Mg N ha^{-1}; 0.003 Mg P ha^{-1}) compared to the current study (Flindt *et al.*, 1999). The same experiment compared the sediment nutrients with those beneath vegetated meadows and bare ground and found that estuaries with more vegetation had a generally cleaner water column (Flindt *et al.*, 1999). *Zostera noltii* stored less nitrogen than the current study (0.01 Mg N ha^{-1}), but a different seagrass with similar size leaves — *Cymodea nodosa* — also stored less than the current study (0.04 Mg N ha^{-1}) but more than *Z. noltii* which is smaller than *Z. capensis*. This was in a more pristine estuary compared to the Swartkops Estuary. *Zostera noltii* in a different estuary — Palmones River estuary in Spain — also stored less phosphorus (0.01 Mg P ha^{-1}) but showed seasonal variations in the phosphorus strorage — the highest stocks were seen in winter and the lowest in summer (Perez-Llorenz and Niell, 1993). This estuary experiences oil spills and is prone to waste from boats in the harbour (Perez-Llorenz and Niell, 1993). *Zostera marina* growing in an estuary similar to Swartkops in terms of its pollution sources and permanently open status, but not overall size stored nitrogen most similar to that of this study (0.35 Mg N ha^{-1}) (Pederson and Borum, 1993). This means that higher nutrient inputs to the estuary result in more of a specific nutrient in the plant tissues. Higher nitrogen and phosphorus stocks in winter agrees with what was found in the seagrass *Halodule wrightii* in Texas in winter (Kowalski, *et al*., 2009).

Salicornia tegetaria stored the least nutrients of the plants both percentage wise and overall. This supports the findings of Boyer *et al.* (2001) that nutrient storage capacities are not related to biomass. Overall *S. tegetaria* has higher biomass and different structure from *Z. capensis* so it is impossible to accurately compare biomass. Species that cover a larger area generally results in significant amounts of a nutrient being stored in the estuary. *Salicornia tegetaria* stored 0.15 ± 0.03 Mg N ha^{-1} and 0.35 ± 0.04 Mg P ha^{-1} (greatest *S. tegetaria* P stock) in summer and 0.37 ± 0.02 Mg N ha^{-1} and 0.2 ± 0.01 Mg P ha^{-1} in winter. All three species stored greater amounts of nutrients in the aboveground biomass despite the seasonal changes. These findings differ from that which was found in a Portugal salt marsh where no seasonal variation was observed in *S. maritima. Salicornia brachiata* however, did display a seasonal difference in the salt marshes of India where that the maximum nitrogen and phosphorus content was found in the plant tissues in winter (0.048 Mg N ha^{-1}; 0.004 Mg P ha^{-1}) (Chaudhary *et al*., 2018). This same study found significant spatial and temporal differences which were attributed to different sediment characteristics which may also be the case in the Swartkops Estuary *S. tegetaria*, but the aboveground biomass always stored more nitrogen and phosphorus. *Salicornia virginica* stored significantly more nitrogen and phosphorus in winter in the protected Mugu Lagoon salt marsh in Southern California (Boyer *et al*., 2001). This study measured the total nitrogen in the tissues as a percentage of the biomass —

approximately 3.5% of the total biomass (succulent and woody parts of the plant). This resulted in an approximate nitrogen storage of 0.7 Mg N ha^{-1} in *S. virginica*. The Tagus Estuary stored nitrogen and phosphorus in its five dominant halophytes across an area of 4400 ha, but 90% of the storage was in the upper salt marsh plants (Sousa *et al*., 2017). Seasonal trends in nitrogen storage were the same with all three species having the greatest stocks occurring in winter. The same trend was seen in phosphorus stocks for *Z. capensis* and *S. maritima* in winter, but *S. tegetaria* stored more phosphorus in summer. This is likely because of its placement above *S. maritima* on the intertidal zone or it may be due to its physiology that it is unable to accumulate nutrients as well (Rathore *et al*., 2016). Boyer *et al.* (2001) also noted an increase in tissue nitrogen content in the winter season in *Salicornia virginica*, while phosphorus was greater at the end of the growing season.

It is key to note that worldwide species affinity to take up nutrients and store them is significantly different (Shardendu *et al.,* 2012). Thiebaut (2008) found that slower growing species had a lower nutrient storage capability than faster growing species. *Spartina maritima* is a C_4 plant while *S. tegetaria* is a C_3 plant. Studies have shown that in warm temperatures C_4 plants grow fatser than C_3 plants because of their ability to bind oxygen with RUBISCO rather than with carbon dioxide (Wang *et al*., 2012; Jothiramshekar *et al.*, 2018). Oxygen tends to reduce the photosynthetic ability in C_3 plants resulting in them growing slower than C_4 plants like *S. maritima* (Wang *et al*., 2012). This could explain why *S. tegetaria* stored less nutrients than *S. maritima*. A global study on seagrass tissue nutrients suggested that environmental factors and nutrient concentrations at specific locations may be the main drivers of seagrass tissue content rather than the physiology of the plant (Vonk *et al*., 2017). Other researchers suggest that all environmental factors and physiological features of the plant should be taken into account when interpreting tissue nutrient content results, however more specialized and recent research is required in the physiology of aquatic plants (Agawin *et al.,* 1996; Fourqurean *et al*.,1997; Udy and Dennison, 1997). This will give a better understanding of salt marsh plant-nutrient interaction because currently nutrient levels are not well established for halophytes (Rathore *et al*., 2016). Sousa *et al.* (2010) discovered that *S. maritima* was more effective at storing nutrients than *Sarcocornia* species because it has a higher affinity to store nutrients long-term.

6.4.1 Nutrient Ratios

Carbon sequestration can be closely studied with nutrient enrichment in plant biomass tissues, but they act on different spatial and temporal scales (Armitage and Fourqurean, 2016). This study has understood the temporal differences on a short-term scale due to time constraints and the seasonal fluctuations noted here may just be due to a snapshot in time. Extending the time frame of this study to investigate the nutrient accumulation in the tissues of seagrass and salt marsh plants may give a better understanding on the variability of the ecosystem. The nutrient ratios determined in this study indicate the reason for the observed increased biomass. This is also evidence towards the final hypothesis that biomass increased because of increased nutrient input to the estuary. Seagrass are more commonly used as nutrient pollution indicators, but this study shows that salt marsh may also be used to indicate enrichment of estuarine waters. The nitrogen to biomass ratio is most commonly used as this indicator (Lee *et al*., 2004; Burkholder *et al.,* 2007). Macrophytes found in low nutrient habitats usually have high C:N and C:P ratios and those growing in nutrient rich habitats have low ratios (Atkinson and Smith, 1984; Duarte, 1990; Yang *et al*., 2018). Nutrient pollution indicator (NPI) values of eelgrass in New England estuaries varied throughout the estuary, but higher NPI values were observed in the upper reaches of the estuary (Lee *et al*., 2004). Spatial changes in nutrient content of tissues is largely dependent on the main source of N or P input — if the ocean is the main source of N the C:N ratio will be greater at the mouth and vise versa (Fourqurean *et al*., 1997).

A study done on three estuaries with *Zostera* species that experience nutrient enrichment (Great Bay, Narragansett Bay, and Waquoit Bay) saw N: biomass ratios between 0.3 and 2.5 (Lee *et al*., 2004; Burkholder *et al*., 2007) which is much higher than what was found in this study (0.01). This shows how enriched the Swartkops Estuary was compared to these international studies. Kennish and Haag (2014) studied *Z. marina* as an indicator of pollution using the same index at Barnegat Estuary in the northern hemisphere and noted distinct temporal changes in the NPI values.

The first comprehensive study on N and P in the tissues of submerged macrophytes in South Africa found that there were shifts in the amount of total N and P between submerged macrophytes at a given time depending on the state of the mouth (Human, 2013). The current study did not note strong spatial changes in nutrient ratios with N: biomass ranging between 0.01 and 0.31, however, Fourqurean *et al*. (2002) found that *Thalassia testudinum* nutrient ratios in an estuary in the Gulf of Mexico changed significantly from one side of the estuary to the other. *Thalassia testudinum* N:P values of 30 were recorded which is high indicating low nutrient contents in the tissues leading to phosphorus limitation, but not N-limitation (Patriquin, 1972; Fourqurean *et al*., 2002). In the Swartkops Estuary neither N or P are limiting (Lemley, *et al.,* 2019). The present study showed significantly lower C:N (4.1 - 7.1), C:P (4.7 – 8.2), and N:P (1 – 1.6) ratios in winter, meaning the estuary is more nutrient enriched in winter than in summer. The same trend was seen in *Z. marina* in Tomales Bay — lower C:N ratios (21) were noted in winter, but no seasonal changes were apparent for C:P (Fourqurean *et al.*, 1997). Yang *et al*. (2018) determined a benchmark value differentiating between eutrophic and low-nitrogen values. This value was determined to be 18 and anything below this was considered eutrophic. Different species of seagrasses and those in different locations have vastly different nutrient concentrations in the tissues making the inputs to the estuary coupled with factors such as light availability responsible for the nutrient ratios in the plant (Patriquin, 1972; Atkinson and Smith, 1983; Fourqurean *et al.,* 1997). Sterner (2009) found that C:P and C:N increased with light availability and decreased with increased nutrient input. Therefore, just as N:P ratios are acceptable ways of determining whether there is a deficit of either N or P in a system, N: seagrass biomass is an effective and acceptable measure of determining whether an estuary is nutrient enriched.

Salt marsh macrophytes have not really been used as indicators of nutrient enrichment to estuaries and coastal waters but this study shows that they can be used but they do not show as much seasonal and spatial variation as seagrasses that are predominantly submerged. Deegan *et al.* (2012) found that lower salt marsh areas were lost while higher salt marsh were not when N and P was added from sewage treatment plants and runoff. *Spartina maritima* C:N (7 – 15.7), C:P (11 – 21.4), N:P (1.2 – 2.1), and N:biomass (0.01 – 0.04) ratios in this study did not differ seasonally but C:N (6.7 – 12) in *S. tegetaria* was lower in winter which means that the nutrient concentrations in the tissues were higher. This again indicates the higher nutrient enrichment to the estuary in winter. The same was found for *Salicornia virginica* in a Southern California salt marsh (Boyer *et al*., 2001). Literature shows that nutrient inputs can shift species composition, and this generally favours the succulent salt marsh species such as *Salicornia* (Covin and Zedler, 1988; Boyer and Zedler, 1999; Boyer *et al.,* 2001). *Spartina maritima* (0.02) and *S. tegetaria* (0.04) had similar N: biomass ratios as *Z. capensis* (0.08) so they may also indicate nutrient enrichment and this study shows that they can be indicators of enrichment, however, seagrass likely respond quicker to environemental changes and nutrient additions.

6.5 Blue carbon and nutrient stocks

The decrease in area of estuarine coastal ecosystems is of concern as it affects the ecosystem services associated with these habitats (Barbier *et al*., 2011). It is therefore critically important that a baseline understanding of the services provided by these ecosystems be obtained. Currently, South African policy has not yet addressed the value of blue carbon and nutrient storage in coastal ecosystems. However, the Paris Agreement was signed with the objective of increasing research and understanding in these areas to mitigate climate change. Therefore, opportunities for carbon trading, restoration, and payment for ecosystem services may become apparent sooner than expected. Ecosystem services are not as simple as they seem and are in fact interconnected in some way or another. This makes studying each service in isolation difficult to relate back to the bigger picture. This work shows that salt marsh and seagrass halophytes can successfully contribute to the reduction of eutrophication by accumulation and retention of nitrogen and phosphorus in their biomass. Carbon storage is increased under nitrogen enrichment (Sanders *et al*., 2014). This study supports these results because the estuary is enriched with high levels of nitrogen and higher carbon stocks than many other similar species across the globe.

The decrease in estuarine coastal ecosystems is said to have a major impact on viable fisheries which have already seen a 33% decline (Worm *et al*., 2006). Nursery habitats have declined by 69% and nutrient cycling and filtering has decreased by 63% to date (Barbier *et al.*, 2011). If there is protection of the studied salt marsh and seagrass plants, they will function better as blue carbon and nutrient sinks aiding in the purification of water and better fisheries for locals and tourists and functional nursery habitats. This will only be possible as management and communities make a mutual decision to protect and rehabilitate what has been destroyed with the goal of increasing the EHI of the Swartkops Estuary to at least a C or B and hopefully restore the estuary to as close as possible to its reference sate.

7. Conclusion

This study defines the status of carbon, nitrogen, and phosphorus storage in the highly urbanised Swartkops Estuary with specific reference to nutrient cycle regulation as an ecosystem service. This study can add to the carbon inventory for South Africa and contribute to filling knowledge gaps. The role of *Z. capensis, S. maritima*, and *S. tegetaria* in storing excess nutrients in the system is of critical importance because one of the main threats to South African estuaries is deteriorating water quality. Increased human impacts on these systems result in an increase in ecosystem usage, nutrient pollution runoff and development adding to the loss of blue carbon habitats. Studies show that macrophytes are good potential indicators of nutrient enrichment because they take up nutrients from the water column, are widely distributed and long lived.

Overall the Swartkops Estuary stored 1 808.43 ± 324.76 Mg C, 189.80 ± 15.01 Mg N, and 143.24 ± 18.60 Mg P in the *Z. capensis, S. maritima*, and *S. tegetaria* biomass combined in an area of 185.53 ha. *Spartina maritima* stored significantly more C, N, and P in its biomass than the other species, but *Z. capensis* N:biomass value (0.8) was the most effective at indicating nutrient enrichment because it responded to seasonal and spatial changes more than the salt marsh macrophytes. The N and P stocks in the plants fluctuated seasonally in relation to the nutrient input to the estuary. This also indicated that the estuary is more enriched in winter than in summer. The sediment made up the larger carbon pool, storing 224.14 ± 37.93 Mg C ha^{-1} beneath *Z. capensis*, 247 ± 48 Mg C ha^{-1} beneath *S. maritima*, and 212 ± 44 Mg C. ha^{-1} in the sediment of *S. tegetaria*. The sediment carbon stocks did not differ significantly depending on species. In the Swartkops Estuary seagrass beds and salt marshes, carbon, nitrogen, and phosphorus stocks were generally higher than that found elsewhere in the world. This is because of the eutrophic state of the estuary. Carbon sequestration and storage in blue carbon ecosystem sediments is linked to the aboveground and belowground biomass and productivity, which is directly influenced by nutrient input (Armitage and Fourqurean, 2016). Future research should investigate tissue nutrient content, plant biomass and the role of estuarine macrophytes as a filter for nutrient pollution. Kinderburg *et al.* (2018) suggested that sediment properties, especially grain analysis, and the level of eutrophication should be included when evaluating carbon, nitrogen, and phosphorus storage and capacity in estuarine systems. Further investigation into sediment pore water nutrients would add further value to the study because the nutrient cycle is interconnected with the plant, sediment and water column and they do not act in isolation. To further improve this study all the individual species could be mapped so that higher accuracy can be obtained, and area cover changes can be more accurately observed. Future South African carbon storage studies should include remote sensing methods to help determine the standing biomass and carbon stocks as has been done in other countries around the world (Wicaksono *et al*., 2016; Byrd *et al.,* 2018; Pham *et al.,* 2019; Zhang *et al.,* 2019).

This study confirmed that blue carbon ecosystems are globally variable and therefore detailed full spectrum research — all species, habitats, and physiochemical factors affecting these spheres need to be considered to draw accurate conclusions. Salt marsh habitats, especially *S. maritima* stands may be a good idea to plant near waste water treatment work outlets because it is the most efficient at storing excess nutrients, but this must not be to the detriment of naturally occurring salt marsh species. This study proved the effectiveness of N: biomass and N:P ratios to be used as indicators of nutrient enrichment. This research is required in many more South African estuaries so that a national understanding can be determined. A better approach may be to first restore estuarine ecosystems to their reference state and monitor climate change. If this is effective, then the trading of carbon credits and carbon offset projects can be determined. This agrees with McLeod et al. (2011) that while efforts to restore and rehabilitate these systems may reduce the impacts of anthropogenic carbon dioxide emissions, it should not be viewed as a replacement for carbon dioxide emissions reduction strategies.

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9. Appendices

9.1 Appendix 1: Site locations

Site 1: 33°52'8.16"S; 25°37'42.87"E

Site 2: 33°51'11.47"S; 25°36'50.17"E

Site 3: 33°52'9.20"S; 25°36'53.11"E

Site 4: 33°51'57.52"S; 25°36'37.51"E

Site 5: 33°51'1.30"S; 25°35'48.04"E

Site 6: 33°50'15.02"S; 25°35'19.35"E

9.2 Appendix 2: Raw data

Table 9.1: *Zostera capensis* sediment characteristics

			Summer			Winter		
	Site	Depth (cm)	Mean	Std D	Std E	Mean	Std D	Std E
Bulk density (g. cm^{-3})	1	0	1,458	0,069	0,028	1,458	0,069	0,028
		10	1,564	0,034	0,014	1,564	0,034	0,014
		25	1,666	0,101	0,041	1,666	0,101	0,041
		50	1,608	0,051	0,021	1,608	0,051	0,021
	2	0	0,973	0,090	0,037	0,973	0,090	0,037
		10	1,287	0,165	0,067	1,287	0,165	0,067
		25	1,222	0,222	0,091	1,222	0,222	0,091
		50	1,404	0,149	0,061	1,404	0,149	0,061
	3	0	1,058	0,136	0,056	1,058	0,136	0,056
		10	1,257	0,324	0,132	1,257	0,324	0,132
		25	1,445	0,144	0,059	1,445	0,144	0,059
		50	1,670	0,281	0,115	1,670	0,281	0,115
	4	0	1,086	0,210	0,086	1,086	0,210	0,086
		10	1,191	0,139	0,057	1,191	0,139	0,057
		25	1,314	0,301	0,123	1,314	0,301	0,123
		50	1,321	0,264	0,108	1,321	0,264	0,108
	5	0	1,460	0,109	0,045	1,460	0,109	0,045
		10	1,504	0,083	0,034	1,504	0,083	0,034
		25	1,412	0,271	0,111	1,412	0,271	0,111
		50	1,380	0,055	0,023	1,380	0,055	0,023
	6	0	1,458	0,095	0,039	1,458	0,095	0,039
		10	1,224	0,147	0,060	1,224	0,147	0,060
		25	1,164	0,171	0,070	1,164	0,171	0,070
		50	1,291	0,144	0,059	1,291	0,144	0,059

Organic matter (%)	1	0	2,050	0,612	0,250	1,985	0,301	0,123
		10	2,154	0,719	0,294	1,655	0,192	0,078
		25	2,097	1,423	0,581	1,493	0,161	0,066
		50	1,972	0,397	0,162	1,520	0,209	0,085
	2	0	5,652	1,491	0,609	4,604	0,581	0,237
		10	4,311	1,075	0,439	3,531	0,204	0,083
		25	3,723	0,920	0,375	3,093	1,536	0,627
		50	3,341	1,415	0,578	3,083	0,576	0,235
	3	0	4,238	0,880	0,359	4,601	0,749	0,306
		10	3,690	0,440	0,179	3,573	0,704	0,287
		25	3,581	0,663	0,270	3,093	0,690	0,282
		50	2,825	0,730	0,298	2,209	0,881	0,360
	4	0	5,672	0,942	0,385	4,241	0,632	0,258
		10	4,575	1,181	0,482	3,311	0,235	0,096
		25	3,802	0,663	0,270	3,025	0,535	0,218
		50	3,323	0,567	0,231	2,298	0,611	0,250
	5	0	2,533	0,236	0,106	2,730	0,394	0,161
		10	2,603	0,620	0,253	2,726	0,193	0,079
		25	2,318	0,484	0,198	3,244	0,331	0,135
		50	2,190	0,375	0,153	2,770	0,782	0,319
	6	0	2,653	0,313	0,128	2,897	0,220	0,090
		10	3,092	0,344	0,140	3,113	0,376	0,153
		25	3,217	0,916	0,374	2,947	0,222	0,091
		50	3,730	0,525	0,214	2,997	0,223	0,091
Organic carbon (%)	1	0	1,970	0,552	0,225	1,912	0,272	0,111
		10	2,064	0,649	0,265	1,614	0,173	0,071
		25	2,012	1,285	0,524	1,468	0,145	0,059
		50	2,329	0,794	0,459	1,492	0,189	0,077
	2	0	5,222	1,346	0,549	4,276	0,524	0,214
		10	4,011	0,970	0,396	3,307	0,184	0,075
		25	3,480	0,830	0,339	2,911	1,387	0,566
		50	3,136	1,277	0,521	2,903	0,520	0,212
	3	0	3,945	0,795	0,324	4,272	0,676	0,276
		10	3,451	0,397	0,162	3,345	0,635	0,259
		25	3,352	0,828	0,338	2,912	0,623	0,254
		50	2,669	0,659	0,269	2,114	0,795	0,325
	4	0	5,239	0,850	0,347	3,948	0,571	0,233
		10	4,249	1,066	0,435	3,108	0,212	0,087
		25	3,552	0,598	0,244	2,850	0,483	0,197
		50	3,120	0,512	0,209	2,194	0,552	0,225
	5	0	2,406	0,213	0,087	2,584	0,355	0,145
		10	2,078	1,082	0,442	2,580	0,174	0,071
		25	2,212	0,437	0,178	3,048	0,299	0,122
		50	2,097	0,338	0,138	2,620	0,706	0,288
	6	0	2,514	0,282	0,115	2,735	0,198	0,081

		10	2,911	0,311	0,127	2,930	0,339	0,138
		25	3,024	0,827	0,338	2,780	0,201	0,082
		50	3,487	0,474	0,194	2,825	0,201	0,082
Carbon density (g. cm^{-3})	1	0	0,033	0,011	0,008	0,038	0,001	0,000
		10	0,046	0,003	0,002	0,028	0,000	0,000
		25	0,049	0,032	0,023	0,023	0,000	0,000
		50	0,035	0,004	0,003	0,029	0,000	0,000
	2	0	0,042	0,010	0,007	0,049	0,004	0,003
		10	0,044	0,009	0,007	0,043	0,005	0,003
		25	0,038	0,006	0,004	0,023	0,018	0,013
		50	0,026	0,012	0,008	0,033	0,005	0,004
	3	0	0,046	0,001	0,001	0,044	0,005	0,003
		10	0,041	0,002	0,002	0,040	0,003	0,002
		25	0,036	0,004	0,003	0,042	0,000	0,000
		50	0,034	0,003	0,002	0,029	0,006	0,004
	4	0	0,055	0,007	0,005	0,164	0,035	0,025
		10	0,064	0,032	0,023	0,106	0,005	0,003
		25	0,055	0,004	0,003	0,094	0,012	0,009
		50	0,044	0,011	0,008	0,042	0,041	0,029
	5	0	0,038	0,002	0,001	0,040	0,006	0,004
		10	0,034	0,001	0,001	0,040	0,003	0,002
		25	0,030	0,006	0,004	0,039	0,004	0,003
		50	0,027	0,007	0,005	0,034	0,004	0,003
	6	0	0,038	0,009	0,006	0,040	0,002	0,001
		10	0,044	0,001	0,000	0,041	0,009	0,007
		25	0,037	0,019	0,013	0,033	0,006	0,004
		50	0,049	0,014	0,010	0,036	0,005	0,004

Table 9.2: *Spartina maritima* sediment characteristics

			Summer			Winter		
	Site	Depth (cm)	Mean	Std D	Std E	Mean	Std D	Std E
Bulk density (g. cm^{-3})	1	0	1,403	0,101	0,041	1,486	0,100	0,041
		10	1,502	0,160	0,072	1,462	0,060	0,027
		25	1,604	0,144	0,059	1,521	0,101	0,041
		50	1,516	0,101	0,041	1,521	0,026	0,010
	2	0	1,045	0,110	0,045	1,047	0,184	0,075
		10	1,018	0,229	0,103	1,014	0,114	0,051
		25	0,977	0,144	0,059	1,159	0,178	0,072
		50	1,068	0,145	0,059	1,091	0,081	0,033
	3	0	1,288	0,282	0,115	1,210	0,180	0,074
		10	1,164	0,290	0,130	1,274	0,269	0,120
		25	1,169	0,238	0,097	1,396	0,246	0,100

		50	1,147	0,232	0,095	1,507	0,379	0,155
	4	0	0,894	0,180	0,073	1,047	0,255	0,104
		10	0,958	0,120	0,054	1,189	0,144	0,065
		25	1,253	0,823	0,336	1,414	0,184	0,075
		50	1,124	0,233	0,095	1,342	0,138	0,056
	5	0	1,105	0,115	0,047	1,042	0,216	0,088
		10	1,345	0,068	0,031	1,305	0,152	0,068
		25	1,381	0,141	0,058	1,495	0,209	0,085
		50	1,436	0,151	0,062	1,550	0,071	0,029
	6	0	-	-	-	0,738	0,117	0,048
		10	-	-	-	1,092	0,301	0,135
		25	-	-	-	0,950	0,639	0,261
		50	-	-	-	0,933	0,111	0,045
Organic matter (%)	1	0	2,281	0,604	0,247	1,859	0,238	0,097
		10	1,870	0,278	0,114	3,476	2,756	1,125
		25	1,908	0,269	0,110	1,875	0,194	0,079
		50	1,632	0,215	0,088	1,953	0,269	0,110
	2	0	8,765	1,202	0,491	6,413	1,758	0,718
		10	10,947	5,239	2,139	5,837	0,654	0,267
		25	9,885	4,129	1,686	5,722	1,189	0,485
		50	6,328	1,970	0,804	5,970	1,380	0,564
	3	0	5,106	1,410	0,576	6,303	0,850	0,347
		10	5,467	2,695	1,100	6,111	1,092	0,446
		25	4,173	0,710	0,290	4,382	1,153	0,471
		50	4,488	1,197	0,489	4,079	1,161	0,474
	4	0	6,350	1,504	0,614	5,244	0,799	0,326
		10	5,689	1,243	0,507	4,643	0,576	0,235
		25	5,881	3,735	1,525	4,079	0,218	0,089
		50	4,023	2,543	1,038	3,311	0,616	0,252
	5	0	4,512	0,816	0,333	5,036	1,308	0,534
		10	3,706	0,594	0,243	3,661	1,122	0,458
		25	3,586	0,351	0,143	3,346	0,435	0,178
		50	3,067	0,471	0,192	3,273	0,988	0,403
	6	0	-	-	-	7,167	0,953	0,389
		10	-	-	-	2,930	0,471	0,192
		25	-	-	-	2,489	0,300	0,123
		50	-	-	-	3,004	0,503	0,205
Organic carbon (%)	1	0	1,708	0,685	0,280	1,229	0,270	0,110
		10	1,241	0,316	0,141	3,063	3,126	1,276
		25	1,284	0,305	0,124	1,246	0,220	0,090
		50	0,971	0,244	0,100	1,336	0,305	0,125
	2	0	9,063	1,364	0,557	6,395	1,995	0,814
		10	11,538	5,944	2,427	5,742	0,742	0,303
		25	10,334	4,685	1,913	5,611	1,349	0,551

		50	6,298	2,234	0,912	5,893	1,566	0,639
	3	0	4,913	1,599	0,653	6,270	0,964	0,394
		10	5,321	3,058	1,248	6,052	1,239	0,506
		25	3,854	0,806	0,329	4,091	1,308	0,534
		50	4,211	1,359	0,555	3,747	1,318	0,538
	4	0	6,323	1,706	0,697	5,068	0,906	0,370
		10	5,574	1,410	0,576	4,387	0,654	0,267
		25	5,791	4,237	1,730	3,747	0,248	0,101
		50	3,683	2,885	1,178	2,876	0,699	0,285
	5	0	4,238	0,926	0,378	4,832	1,484	0,606
		10	3,323	0,674	0,275	3,273	1,273	0,520
		25	3,187	0,398	0,163	2,916	0,494	0,202
		50	2,599	0,534	0,218	2,833	1,121	0,457
	6	0	-	-	-	7,251	1,081	0,441
		10	-	-	-	2,443	0,534	0,218
		25	-	-	-	1,943	0,341	0,139
		50	-	-	-	2,528	0,571	0,233
Carbon density (g. cm^{-3})	1	0	0,021	0,003	0,002	0,015	0,000	0,000
		10	0,018	0,003	0,002	0,076	0,078	0,017
		25	0,019	0,000	0,000	0,022	0,007	0,001
		50	0,017	0,003	0,002	0,024	0,002	0,000
	2	0	0,091	0,003	0,002	0,058	0,027	0,006
		10	0,073	0,004	0,003	0,060	0,008	0,002
		25	0,131	0,015	0,011	0,065	0,003	0,001
		50	0,073	0,002	0,001	0,066	0,008	0,002
	3	0	0,049	0,012	0,009	0,075	0,011	0,002
		10	0,048	0,012	0,008	0,080	0,006	0,001
		25	0,040	0,010	0,007	0,070	0,011	0,003
		50	0,033	0,011	0,008	0,051	0,002	0,000
	4	0	0,048	0,013	0,009	0,058	0,002	0,000
		10	0,042	0,011	0,008	0,049	0,014	0,003
		25	0,027	0,005	0,003	0,055	0,013	0,003
		50	0,021	0,004	0,003	0,050	0,012	0,003
	5	0	0,044	0,007	0,005	0,047	0,038	0,009
		10	0,054	0,006	0,004	0,057	0,021	0,005
		25	0,044	0,007	0,005	0,048	0,014	0,003
		50	0,035	0,009	0,006	0,036	0,000	0,000
	6	0	-	-	-	0,059	0,020	0,005
		10	-	-	-	0,026	0,001	0,000
		25	-	-	-	0,014	0,000	0,000
		50	-	-	-	0,023	0,002	0,001

Table 9.3: *Sarcocornia tegetaria* sediment characteristics

				Summer			Winter	

	Site	Depth (cm)	Mean	Std D	Std E	Mean	Std D	Std E
Bulk density (g. cm^{-3})	1	0	1,377	0,154	0,063	1,499	0,041	0,017
		10	1,500	0,064	0,029	1,505	0,048	0,021
		25	1,452	0,159	0,065	1,539	0,130	0,053
		50	1,446	0,114	0,047	1,574	0,102	0,042
	2	0	1,087	0,160	0,065	1,125	0,137	0,056
		10	1,471	0,253	0,113	1,164	0,099	0,044
		25	1,508	0,149	0,061	1,228	0,075	0,031
		50	1,263	0,217	0,097	1,220	0,096	0,039
	3	0	1,018	0,137	0,056	1,293	0,217	0,088
		10	1,047	0,154	0,069	1,168	0,309	0,138
		25	1,132	0,162	0,066	1,365	0,198	0,081
		50	1,157	0,143	0,064	1,479	0,111	0,046
	4	0	1,195	0,045	0,018	1,277	0,058	0,024
		10	1,425	0,080	0,036	1,396	0,088	0,039
		25	1,322	0,324	0,132	1,392	0,125	0,051
		50	1,468	0,123	0,050	1,477	0,080	0,033
	5	0	1,389	0,092	0,038	1,140	0,198	0,081
		10	1,272	0,097	0,043	1,310	0,107	0,048
		25	1,377	0,069	0,028	1,303	0,163	0,067
		50	1,368	0,091	0,037	1,363	0,089	0,037
	6	0	-	-	-	0,893	0,185	0,075
		10	-	-	-	0,954	0,183	0,082
		25	-	-	-	0,860	0,140	0,057
		50	-	-	-	0,780	0,430	0,175
Organic matter (%)	1	0	3,626	3,051	1,246	1,780	0,232	0,095
		10	4,250	4,867	1,987	1,640	0,206	0,084
		25	1,947	0,741	0,303	3,009	3,377	1,378
		50	3,066	2,155	0,880	1,502	0,122	0,050
	2	0	4,761	1,431	0,584	8,468	0,820	0,335
		10	1,839	0,485	0,198	6,045	1,036	0,423
		25	1,920	0,498	0,204	4,270	0,322	0,131
		50	2,306	0,478	0,195	4,046	0,712	0,291
	3	0	8,231	1,736	0,709	5,817	1,713	0,699
		10	8,720	3,897	1,591	8,992	2,392	0,977
		25	5,873	1,381	0,564	4,917	1,375	0,561
		50	5,071	1,535	0,627	3,666	0,739	0,302
	4	0	7,505	0,974	0,398	4,363	1,219	0,498
		10	1,613	0,114	0,046	2,684	1,193	0,487
		25	3,119	4,029	1,645	4,477	0,562	0,230
		50	3,923	0,926	0,378	3,741	0,446	0,182
	5	0	2,757	0,459	0,187	5,790	1,164	0,475
		10	2,857	0,460	0,188	3,683	0,729	0,297
		25	2,530	0,526	0,215	4,579	1,253	0,512

		50	2,118	0,569	0,232	3,973	0,420	0,172
	6	0	-	-	-	3,676	0,824	0,337
		10	-	-	-	3,004	2,046	0,835
		25	-	-	-	2,379	0,388	0,159
		50	-	-	-	2,292	0,517	0,211
Organic carbon (%)	1	0	3,299	2,612	1,066	1,719	0,199	0,081
		10	3,833	4,166	1,701	1,599	0,176	0,072
		25	1,862	0,634	0,259	2,771	2,890	1,180
		50	2,820	1,845	0,753	1,481	0,104	0,043
	2	0	4,270	1,225	0,500	7,443	0,702	0,286
		10	1,769	0,415	0,170	5,369	0,886	0,362
		25	1,839	0,427	0,174	3,850	0,276	0,113
		50	1,840	0,885	0,361	3,658	0,609	0,249
	3	0	7,240	1,486	0,607	5,174	1,466	0,599
		10	7,659	3,335	1,362	7,891	2,048	0,836
		25	5,222	1,182	0,483	4,404	1,177	0,480
		50	4,536	1,314	0,536	3,333	0,633	0,258
	4	0	6,619	0,834	0,340	3,930	1,044	0,426
		10	1,576	0,097	0,040	2,492	1,021	0,417
		25	2,865	3,449	1,408	4,027	0,481	0,197
		50	3,553	0,792	0,323	3,397	0,382	0,156
	5	0	2,555	0,393	0,160	5,097	1,029	0,420
		10	2,641	0,393	0,161	3,455	0,759	0,310
		25	2,361	0,451	0,184	4,196	1,078	0,440
		50	2,008	0,487	0,199	3,707	0,504	0,206
	6	0	-	-	-	3,342	0,705	0,288
		10	-	-	-	2,766	1,752	0,715
		25	-	-	-	2,231	0,332	0,136
		50	-	-	-	2,157	0,443	0,198
Carbon density (g. cm^{-3})	1	0	0,039	0,015	0,010	0,027	0,000	0,000
		10	0,024	0,000	0,000	0,026	0,005	0,003
		25	0,023	0,003	0,002	0,023	0,001	0,001
		50	0,025	0,006	0,004	0,022	0,000	0,000
	2	0	0,045	0,004	0,003	0,079	0,012	0,008
		10	0,027	0,002	0,001	0,067	0,001	0,001
		25	0,030	0,010	0,007	0,046	0,009	0,006
		50	0,026	0,001	0,001	0,041	0,007	0,005
	3	0	0,063	0,005	0,004	0,067	0,018	0,013
		10	0,082	0,031	0,022	0,083	0,019	0,014
		25	0,037	0,003	0,002	0,050	0,007	0,005
		50	0,048	0,003	0,002	0,054	0,009	0,006
	4	0	0,072	0,004	0,003	0,056	0,000	0,000
		10	0,020	0,000	0,000	0,024	0,000	0,000

	25	0,081	0,088	0,062	0,057	0,002	0,002
	50	0,054	0,003	0,002	0,059	0,001	0,001
5	0	0,031	0,000	0,000	0,053	0,003	0,002
	10	0,031	0,007	0,005	0,054	0,009	0,007
	25	0,029	0,003	0,002	0,050	0,015	0,010
	50	0,027	0,013	0,009	0,057	0,010	0,007
6	0	-	-	-	0,036	0,006	0,004
	10	-	-	-	0,012	0,005	0,003
	25	-	-	-	0,016	0,003	0,002
	50	-	-	-	0,019	0,001	0,001

Table 9.4: Macrophyte biomass data

Season	**Species**	**Site**	**Replicate**	**Biomass**	**Biomass (g. m^{-2})**	**Leaf length/ Stem height (cm)**	**Carbon content (g. m^{-2})**
Summer	Zostera	1	1	Above	893,22	25,97	115,10
Summer	Zostera	1	2	Above	328,87	22,89	209,25
Summer	Zostera	1	3	Above	597,85	22,15	163,77
Summer	Zostera	1	4	Above	467,92	22,96	198,94
Summer	Zostera	1	5	Above	568,41	19,60	165,90
Summer	Zostera	1	6	Above	474,01	21,02	71,41
Summer	Zostera	2	1	Above	204,02	21,86	132,16
Summer	Zostera	2	2	Above	377,59	20,76	56,84
Summer	Zostera	2	3	Above	162,40	20,65	231,63
Summer	Zostera	2	4	Above	661,79	27,94	138,91
Summer	Zostera	2	5	Above	396,87	19,72	367,69
Summer	Zostera	3	1	Above	113,28	29,71	39,65
Summer	Zostera	3	2	Above	162,50	22,70	56,88
Summer	Zostera	3	3	Above	540,80	24,72	189,28
Summer	Zostera	3	4	Above	133,88	40,67	46,86
Summer	Zostera	3	5	Above	408,75	19,24	143,06
Summer	Zostera	3	6	Above	200,67	25,37	70,23
Summer	Zostera	4	1	Above	331,71	33,49	116,10
Summer	Zostera	4	2	Above	178,85	27,80	62,60
Summer	Zostera	4	3	Above	243,20	30,34	85,12
Summer	Zostera	4	4	Above	643,72	26,62	225,30
Summer	Zostera	4	5	Above	455,64	39,91	159,47
Summer	Zostera	4	6	Above	504,46	30,39	176,56
Summer	Zostera	5	1	Above	288,06	31,62	100,82
Summer	Zostera	5	2	Above	440,62	28,51	154,22
Summer	Zostera	5	3	Above	323,69	28,67	113,29
Summer	Zostera	5	4	Above	279,84	30,66	97,94
Summer	Zostera	5	5	Above	502,13	32,60	175,75
Summer	Zostera	5	6	Above	525,88	29,03	184,06

Summer	Zostera	6	1	Above	60,90	26,08	21,32
Summer	Zostera	6	2	Above	62,93	16,96	22,03
Summer	Zostera	6	3	Above	135,00	18,24	47,25
Summer	Zostera	6	4	Above	100,49	19,30	35,17
Summer	Zostera	6	5	Above	74,10	17,17	25,93
Summer	Zostera	6	6	Above	79,17	16,95	27,71
Summer	Zostera	1	1	Below	239,04	-	74,10
Summer	Zostera	1	2	Below	11,67	-	57,87
Summer	Zostera	1	3	Below	146,87	-	42,60
Summer	Zostera	1	4	Below	126,37	-	119,82
Summer	Zostera	1	5	Below	127,08	-	39,30
Summer	Zostera	1	6	Below	202,60	-	29,61
Summer	Zostera	2	1	Below	186,66	-	3,62
Summer	Zostera	2	2	Below	264,92	-	82,13
Summer	Zostera	2	3	Below	61,71	-	56,83
Summer	Zostera	2	4	Below	275,68	-	88,01
Summer	Zostera	2	5	Below	237,51	-	11,55
Summer	Zostera	2	6	Below	534,91	-	40,50
Summer	Zostera	3	1	Below	137,43	-	45,53
Summer	Zostera	3	2	Below	183,31	-	19,13
Summer	Zostera	3	3	Below	119,98	-	37,19
Summer	Zostera	3	4	Below	86,07	-	41,79
Summer	Zostera	3	5	Below	182,91	-	18,88
Summer	Zostera	3	6	Below	191,23	-	38,07
Summer	Zostera	4	1	Below	386,52	-	39,17
Summer	Zostera	4	2	Below	283,90	-	85,46
Summer	Zostera	4	3	Below	134,79	-	26,68
Summer	Zostera	4	4	Below	165,96	-	51,45
Summer	Zostera	4	5	Below	144,03	-	61,07
Summer	Zostera	4	6	Below	170,73	-	28,48
Summer	Zostera	5	1	Below	126,78	-	39,39
Summer	Zostera	5	2	Below	37,25	-	73,63
Summer	Zostera	5	3	Below	60,90	-	56,70
Summer	Zostera	5	4	Below	197,02	-	44,65
Summer	Zostera	5	5	Below	173,26	-	53,71
Summer	Zostera	5	6	Below	164,13	-	41,53
Summer	Zostera	6	1	Below	95,51	-	62,81
Summer	Zostera	6	2	Below	130,63	-	165,82
Summer	Zostera	6	3	Below	122,82	-	59,28
Summer	Zostera	6	4	Below	91,86	-	52,93
Summer	Zostera	6	5	Below	133,98	-	50,88
Summer	Zostera	6	6	Below	67,60	-	20,96
Winter	Zostera	1	1	Above	785,62	35,53	274,97
Winter	Zostera	1	2	Above	1264,71	39,24	442,65
Winter	Zostera	1	3	Above	702,39	25,99	245,84
Winter	Zostera	1	4	Above	381,65	34,20	133,58

Winter	Zostera	1	5	Above	631,34	38,06	220,97
Winter	Zostera	1	6	Above	767,35	32,51	268,57
Winter	Zostera	2	1	Above	641,49	18,52	224,52
Winter	Zostera	2	2	Above	1057,65	26,81	370,18
Winter	Zostera	2	3	Above	356,27	29,53	124,70
Winter	Zostera	2	4	Above	845,51	29,58	295,93
Winter	Zostera	2	5	Above	1377,38	22,92	482,08
Winter	Zostera	2	6	Above	557,25	27,53	195,04
Winter	Zostera	3	1	Above	501,42	53,63	175,50
Winter	Zostera	3	2	Above	332,82	42,64	116,49
Winter	Zostera	3	3	Above	264,92	47,47	92,72
Winter	Zostera	3	4	Above	261,47	50,78	91,51
Winter	Zostera	3	5	Above	422,25	18,87	147,79
Winter	Zostera	3	6	Above	423,87	36,35	148,36
Winter	Zostera	4	1	Above	193,87	37,03	67,85
Winter	Zostera	4	2	Above	1104,34	36,57	386,52
Winter	Zostera	4	3	Above	985,58	35,84	344,95
Winter	Zostera	4	4	Above	1054,60	34,97	511,21
Winter	Zostera	4	5	Above	955,13	27,53	405,35
Winter	Zostera	4	6	Above	694,27	22,82	243,00
Winter	Zostera	5	1	Above	490,25	22,82	171,59
Winter	Zostera	5	2	Above	403,98	26,20	141,39
Winter	Zostera	5	3	Above	699,35	25,99	244,77
Winter	Zostera	5	4	Above	503,45	30,84	176,21
Winter	Zostera	5	5	Above	1165,24	11,17	407,83
Winter	Zostera	5	6	Above	727,77	16,77	254,72
Winter	Zostera	6	1	Above	136,01	16,10	47,60
Winter	Zostera	6	2	Above	249,69	13,86	87,39
Winter	Zostera	6	3	Above	347,14	12,45	121,50
Winter	Zostera	6	4	Above	154,28	13,94	54,00
Winter	Zostera	6	5	Above	114,70	-	40,14
Winter	Zostera	6	6	Above	297,40	-	104,09
Winter	Zostera	1	1	Below	78,16	-	24,23
Winter	Zostera	1	2	Below	112,67	-	34,93
Winter	Zostera	1	3	Below	43,65	-	13,53
Winter	Zostera	1	4	Below	114,70	-	35,56
Winter	Zostera	1	5	Below	163,42	-	50,66
Winter	Zostera	1	6	Below	70,04	-	21,71
Winter	Zostera	2	1	Below	259,84	-	80,55
Winter	Zostera	2	2	Below	275,07	-	85,27
Winter	Zostera	2	3	Below	121,80	-	37,76
Winter	Zostera	2	4	Below	187,78	-	58,21
Winter	Zostera	2	5	Below	367,44	-	113,91
Winter	Zostera	2	6	Below	145,15	-	45,00
Winter	Zostera	3	1	Below	259,84	-	80,55
Winter	Zostera	3	2	Below	238,53	-	73,94

Winter	Zostera	3	3	Below	164,43	-	50,97
Winter	Zostera	3	4	Below	90,34	-	28,00
Winter	Zostera	4	1	Below	56,84	-	17,62
Winter	Zostera	4	2	Below	724,72	-	224,66
Winter	Zostera	4	3	Below	162,40	-	50,34
Winter	Zostera	4	4	Below	159,36	-	49,40
Winter	Zostera	4	5	Below	155,30	-	48,14
Winter	Zostera	4	6	Below	218,23	-	67,65
Winter	Zostera	5	1	Below	76,13	-	23,60
Winter	Zostera	5	2	Below	98,46	-	30,52
Winter	Zostera	5	3	Below	138,04	-	42,79
Winter	Zostera	5	4	Below	94,40	-	29,26
Winter	Zostera	5	5	Below	54,81	-	16,99
Winter	Zostera	5	6	Below	86,28	-	26,75
Winter	Zostera	6	1	Below	89,32	-	27,69
Winter	Zostera	6	2	Below	100,49	-	31,15
Winter	Zostera	6	3	Below	74,10	-	22,97
Winter	Zostera	6	4	Below	46,69	-	14,47
Winter	Zostera	6	5	Below	136,01	-	42,16
Winter	Zostera	6	6	Below	122,82	-	38,07
Summer	Spartina	1	1	Above	996,75	20,30	398,70
Summer	Spartina	1	2	Above	1799,63	32,63	719,85
Summer	Spartina	1	3	Above	1796,58	25,77	718,63
Summer	Spartina	1	4	Above	2962,84	32,45	1185,14
Summer	Spartina	1	5	Above	1911,28	27,30	764,51
Summer	Spartina	1	6	Above	1949,85	21,96	779,94
Summer	Spartina	2	1	Above	2168,08	30,87	867,23
Summer	Spartina	2	2	Above	1281,97	21,25	512,79
Summer	Spartina	2	3	Above	2393,41	28,06	957,37
Summer	Spartina	2	4	Above	1983,35	28,03	793,34
Summer	Spartina	2	5	Above	2370,07	30,62	948,03
Summer	Spartina	2	6	Above	3693,65	38,38	1477,46
Summer	Spartina	3	1	Above	2230,00	33,38	892,00
Summer	Spartina	3	2	Above	1962,03	30,63	784,81
Summer	Spartina	3	3	Above	3154,68	42,96	1261,87
Summer	Spartina	3	4	Above	3464,26	41,10	1385,70
Summer	Spartina	3	5	Above	4224,51	39,70	1689,80
Summer	Spartina	3	6	Above	3714,97	35,18	1485,99
Summer	Spartina	4	1	Above	1606,77	42,45	642,71
Summer	Spartina	4	2	Above	5074,08	52,10	2029,63
Summer	Spartina	4	3	Above	2105,15	46,70	842,06
Summer	Spartina	4	4	Above	2568,00	54,69	1027,20
Summer	Spartina	4	5	Above	2077,74	40,04	831,10
Summer	Spartina	4	6	Above	3106,97	42,35	1242,79
Summer	Spartina	5	1	Above	2645,14	40,61	1058,06
Summer	Spartina	5	2	Above	1580,38	37,87	632,15

Summer	Spartina	5	3	Above	2085,86	42,00	834,35
Summer	Spartina	5	4	Above	1851,39	40,24	740,56
Summer	Spartina	5	5	Above	3578,96	42,30	1431,58
Summer	Spartina	5	6	Above	4273,23	45,00	1709,29
Summer	Spartina	1	1	Below	744,01	-	186,00
Summer	Spartina	1	2	Below	448,64	-	112,16
Summer	Spartina	1	3	Below	1905,19	-	476,30
Summer	Spartina	1	4	Below	2341,65	-	585,41
Summer	Spartina	1	5	Below	3158,74	-	789,68
Summer	Spartina	1	6	Below	1358,10	-	339,52
Summer	Spartina	2	1	Below	3821,55	-	955,39
Summer	Spartina	2	2	Below	2181,28	-	545,32
Summer	Spartina	2	3	Below	3841,85	-	960,46
Summer	Spartina	2	4	Below	3519,07	-	879,77
Summer	Spartina	2	5	Below	2779,12	-	694,78
Summer	Spartina	2	6	Below	4341,24	-	1085,31
Summer	Spartina	3	1	Below	2811,60	-	702,90
Summer	Spartina	3	2	Below	2706,04	-	676,51
Summer	Spartina	3	3	Below	2482,74	-	620,68
Summer	Spartina	3	4	Below	2932,39	-	733,10
Summer	Spartina	3	5	Below	4917,77	-	1229,44
Summer	Spartina	3	6	Below	3267,35	-	816,84
Summer	Spartina	4	1	Below	1502,23	-	375,56
Summer	Spartina	4	2	Below	3780,94	-	945,24
Summer	Spartina	4	3	Below	1989,44	-	497,36
Summer	Spartina	4	4	Below	2128,49	-	532,12
Summer	Spartina	4	5	Below	2768,97	-	692,24
Summer	Spartina	4	6	Below	4002,22	-	1000,55
Summer	Spartina	5	1	Below	2935,43	-	733,86
Summer	Spartina	5	2	Below	3171,93	-	792,98
Summer	Spartina	5	3	Below	4008,31	-	1002,08
Summer	Spartina	5	4	Below	2867,43	-	716,86
Summer	Spartina	5	5	Below	2444,17	-	611,04
Summer	Spartina	5	6	Below	3942,33	-	985,58
Winter	Spartina	1	1	Above	4574,69	36,21	1829,88
Winter	Spartina	1	2	Above	4225,52	36,08	1690,21
Winter	Spartina	1	3	Above	4121,99	41,72	1648,80
Winter	Spartina	1	4	Above	2019,89	28,41	807,95
Winter	Spartina	1	5	Above	3031,86	36,44	1212,74
Winter	Spartina	1	6	Above	3147,57	33,05	1259,03
Winter	Spartina	2	1	Above	1871,69	49,08	748,68
Winter	Spartina	2	2	Above	661,79	36,74	264,72
Winter	Spartina	2	3	Above	1145,96	39,88	458,38
Winter	Spartina	2	4	Above	1462,64	43,99	585,06
Winter	Spartina	2	5	Above	1785,42	33,96	714,17
Winter	Spartina	2	6	Above	1009,94	42,38	403,98

Winter	Spartina	3	1	Above	2901,94	35,89	1160,78
Winter	Spartina	3	2	Above	1997,56	26,11	799,02
Winter	Spartina	3	3	Above	4658,94	29,35	1863,57
Winter	Spartina	3	4	Above	2907,01	30,84	1162,81
Winter	Spartina	3	5	Above	1854,44	28,94	741,78
Winter	Spartina	3	6	Above	3383,06	32,23	1353,22
Winter	Spartina	4	1	Above	1970,15	30,57	788,06
Winter	Spartina	4	2	Above	1981,32	33,76	792,53
Winter	Spartina	4	3	Above	4110,83	34,07	1644,33
Winter	Spartina	4	4	Above	1612,86	35,72	645,15
Winter	Spartina	4	5	Above	1967,11	33,74	786,84
Winter	Spartina	4	6	Above	3462,23	35,09	1384,89
Winter	Spartina	5	1	Above	1347,94	38,96	539,18
Winter	Spartina	5	2	Above	1649,41	35,12	659,76
Winter	Spartina	5	3	Above	1489,03	32,15	595,61
Winter	Spartina	5	4	Above	1312,42	30,05	524,97
Winter	Spartina	5	5	Above	911,49	30,13	364,59
Winter	Spartina	5	6	Above	1865,60	37,57	746,24
Winter	Spartina	6	1	Above	3840,83	39,45	1536,33
Winter	Spartina	6	2	Above	5581,59	39,16	2232,64
Winter	Spartina	6	3	Above	7950,67	40,93	3180,27
Winter	Spartina	6	4	Above	5760,25	40,20	2304,10
Winter	Spartina	6	5	Above	2779,13	38,47	1111,65
Winter	Spartina	6	6	Above	2431,99	36,28	972,80
Winter	Spartina	1	1	Below	3092,76	-	773,19
Winter	Spartina	1	2	Below	2455,33	-	461,33
Winter	Spartina	1	3	Below	2253,34	-	632,86
Winter	Spartina	1	4	Below	1475,84	-	317,95
Winter	Spartina	1	5	Below	2650,21	-	257,05
Winter	Spartina	1	6	Below	1793,54	-	642,76
Winter	Spartina	2	1	Below	1845,30	-	613,83
Winter	Spartina	2	2	Below	519,69	-	129,92
Winter	Spartina	2	3	Below	1563,13	-	342,06
Winter	Spartina	2	4	Below	767,35	-	331,66
Winter	Spartina	2	5	Below	2399,50	-	236,50
Winter	Spartina	2	6	Below	695,29	-	1184,02
Winter	Spartina	3	1	Below	2531,46	-	563,34
Winter	Spartina	3	2	Below	1368,25	-	390,78
Winter	Spartina	3	3	Below	2032,07	-	508,02
Winter	Spartina	3	4	Below	2575,10	-	633,37
Winter	Spartina	3	5	Below	1947,82	-	352,47
Winter	Spartina	3	6	Below	2626,87	-	-
Winter	Spartina	4	1	Below	1271,82	-	368,96
Winter	Spartina	4	2	Below	1326,63	-	191,84
Winter	Spartina	4	3	Below	2533,49	-	643,78
Winter	Spartina	4	4	Below	8460,18	-	-

Winter	Spartina	4	5	Below	1425,09	-	372,51
Winter	Spartina	4	6	Below	2166,05	-	1410,88
Winter	Spartina	5	1	Below	1028,21	-	662,55
Winter	Spartina	5	2	Below	946,00	-	599,88
Winter	Spartina	5	3	Below	1409,86	-	486,96
Winter	Spartina	5	4	Below	1490,05	-	356,27
Winter	Spartina	5	5	Below	807,95	-	201,99
Winter	Spartina	5	6	Below	1305,31	-	640,48
Winter	Spartina	6	1	Below	2571,04	-	448,38
Winter	Spartina	6	2	Below	4736,08	-	173,82
Winter	Spartina	6	3	Below	12857,29	-	656,72
Winter	Spartina	6	4	Below	5643,52	-	541,51
Winter	Spartina	6	5	Below	2561,92	-	326,33
Winter	Spartina	6	6	Below	1594,60	-	398,65
Summer	Sarcocornia	1	1	Above	527,81	11,30	168,90
Summer	Sarcocornia	1	2	Above	424,28	11,03	135,77
Summer	Sarcocornia	1	3	Above	683,11	14,52	218,59
Summer	Sarcocornia	1	4	Above	417,17	10,98	133,50
Summer	Sarcocornia	1	5	Above	437,47	11,24	139,99
Summer	Sarcocornia	1	6	Above	501,42	8,56	160,45
Summer	Sarcocornia	2	1	Above	1126,67	10,23	360,53
Summer	Sarcocornia	2	2	Above	992,69	12,47	317,66
Summer	Sarcocornia	2	3	Above	802,88	12,08	256,92
Summer	Sarcocornia	2	4	Above	698,33	10,18	223,47
Summer	Sarcocornia	2	5	Above	136,01	10,65	43,52
Summer	Sarcocornia	2	6	Above	171,54	15,65	54,89
Summer	Sarcocornia	3	1	Above	1403,77	15,44	449,21
Summer	Sarcocornia	3	3	Above	644,54	39,93	206,25
Summer	Sarcocornia	3	4	Above	1837,18	15,01	587,90
Summer	Sarcocornia	3	5	Above	2566,98	34,50	821,43
Summer	Sarcocornia	3	6	Above	2278,72	24,62	729,19
Summer	Sarcocornia	4	1	Above	993,70	25,81	317,99
Summer	Sarcocornia	4	2	Above	1321,55	10,07	422,90
Summer	Sarcocornia	4	3	Above	1016,03	10,30	325,13
Summer	Sarcocornia	4	4	Above	1124,64	11,62	359,89
Summer	Sarcocornia	4	5	Above	839,42	10,48	268,61
Summer	Sarcocornia	4	6	Above	1386,52	9,49	443,69
Summer	Sarcocornia	5	1	Above	1202,80	11,21	384,90
Summer	Sarcocornia	5	2	Above	2240,15	22,42	716,85
Summer	Sarcocornia	5	3	Above	455,74	45,43	145,84
Summer	Sarcocornia	5	4	Above	1376,37	12,08	440,44
Summer	Sarcocornia	5	5	Above	479,09	36,23	153,31
Summer	Sarcocornia	5	6	Above	1841,24	24,94	589,20
Summer	Sarcocornia	1	1	Below	644,54	-	244,92
Summer	Sarcocornia	1	2	Below	444,58	-	168,94
Summer	Sarcocornia	1	3	Below	789,68	-	300,08

Summer	Sarcocornia	1	4	Below	315,67	-	119,95
Summer	Sarcocornia	1	5	Below	456,76	-	173,57
Summer	Sarcocornia	1	6	Below	382,66	-	145,41
Summer	Sarcocornia	2	1	Below	33,50	-	12,73
Summer	Sarcocornia	2	2	Below	360,33	-	136,93
Summer	Sarcocornia	2	3	Below	91,35	-	34,71
Summer	Sarcocornia	2	4	Below	205,03	-	77,91
Summer	Sarcocornia	2	5	Below	136,01	-	51,68
Summer	Sarcocornia	2	6	Below	171,54	-	65,18
Summer	Sarcocornia	3	1	Below	70,04	-	26,61
Summer	Sarcocornia	3	2	Below	190,82	-	72,51
Summer	Sarcocornia	3	3	Below	68,01	-	25,84
Summer	Sarcocornia	3	4	Below	121,80	-	46,28
Summer	Sarcocornia	3	5	Below	117,74	-	44,74
Summer	Sarcocornia	3	6	Below	140,07	-	53,23
Summer	Sarcocornia	4	1	Below	48,72	-	18,51
Summer	Sarcocornia	4	2	Below	123,83	-	47,06
Summer	Sarcocornia	4	3	Below	80,19	-	30,47
Summer	Sarcocornia	4	4	Below	65,98	-	25,07
Summer	Sarcocornia	4	5	Below	24,36	-	9,26
Summer	Sarcocornia	4	6	Below	258,83	-	98,36
Summer	Sarcocornia	5	1	Below	193,87	-	73,67
Summer	Sarcocornia	5	2	Below	234,47	-	89,10
Summer	Sarcocornia	5	3	Below	124,85	-	47,44
Summer	Sarcocornia	5	4	Below	234,47	-	89,10
Summer	Sarcocornia	5	5	Below	197,93	-	75,21
Summer	Sarcocornia	5	6	Below	145,15	-	55,16
Winter	Sarcocornia	1	1	Above	406,01	9,96	129,92
Winter	Sarcocornia	1	2	Above	545,07	11,98	174,42
Winter	Sarcocornia	1	3	Above	178,64	10,43	57,17
Winter	Sarcocornia	1	4	Above	224,32	6,92	71,78
Winter	Sarcocornia	1	5	Above	561,31	8,64	179,62
Winter	Sarcocornia	1	6	Above	482,13	10,13	154,28
Winter	Sarcocornia	2	1	Above	779,53	11,18	249,45
Winter	Sarcocornia	2	2	Above	684,12	11,15	218,92
Winter	Sarcocornia	2	3	Above	1091,15	10,93	349,17
Winter	Sarcocornia	2	4	Above	759,23	9,39	242,95
Winter	Sarcocornia	2	5	Above	1406,82	9,25	450,18
Winter	Sarcocornia	2	6	Above	1082,01	9,11	346,24
Winter	Sarcocornia	3	1	Above	990,66	10,33	317,01
Winter	Sarcocornia	3	2	Above	931,79	16,30	298,17
Winter	Sarcocornia	3	3	Above	1167,27	11,80	373,53
Winter	Sarcocornia	3	4	Above	820,14	7,18	262,44
Winter	Sarcocornia	3	5	Above	765,32	11,32	244,90
Winter	Sarcocornia	3	6	Above	837,39	11,53	267,96
Winter	Sarcocornia	4	1	Above	898,29	10,07	287,45

Winter	Sarcocornia	4	2	Above	547,10	9,47	175,07
Winter	Sarcocornia	4	3	Above	875,96	8,79	280,31
Winter	Sarcocornia	4	4	Above	984,57	10,94	315,06
Winter	Sarcocornia	4	5	Above	659,76	10,87	211,12
Winter	Sarcocornia	4	6	Above	511,57	10,91	163,70
Winter	Sarcocornia	5	1	Above	696,30	12,84	222,82
Winter	Sarcocornia	5	2	Above	669,91	11,49	214,37
Winter	Sarcocornia	5	3	Above	736,90	10,10	235,81
Winter	Sarcocornia	5	4	Above	888,14	11,81	284,21
Winter	Sarcocornia	5	5	Above	951,07	12,53	304,34
Winter	Sarcocornia	5	6	Above	499,39	15,96	159,80
Winter	Sarcocornia	6	1	Above	928,74	8,55	297,20
Winter	Sarcocornia	6	2	Above	1519,48	29,85	486,23
Winter	Sarcocornia	6	3	Above	833,33	8,00	266,67
Winter	Sarcocornia	6	4	Above	1059,68	8,58	339,10
Winter	Sarcocornia	6	5	Above	359,32	10,25	114,98
Winter	Sarcocornia	6	6	Above	796,79	12,23	254,97
Winter	Sarcocornia	1	1	Below	157,33	-	59,78
Winter	Sarcocornia	1	2	Below	213,15	-	81,00
Winter	Sarcocornia	1	3	Below	325,82	-	123,81
Winter	Sarcocornia	1	4	Below	1009,94	-	383,78
Winter	Sarcocornia	1	5	Below	231,42	-	87,94
Winter	Sarcocornia	1	6	Below	75,11	-	28,54
Winter	Sarcocornia	2	1	Below	368,45	-	140,01
Winter	Sarcocornia	2	2	Below	265,93	-	101,06
Winter	Sarcocornia	2	3	Below	102,52	-	38,96
Winter	Sarcocornia	2	4	Below	231,42	-	87,94
Winter	Sarcocornia	2	5	Below	146,16	-	55,54
Winter	Sarcocornia	2	6	Below	163,42	-	62,10
Winter	Sarcocornia	3	1	Below	283,19	-	107,61
Winter	Sarcocornia	3	2	Below	269,99	-	102,60
Winter	Sarcocornia	3	3	Below	148,19	-	56,31
Winter	Sarcocornia	3	4	Below	457,77	-	173,95
Winter	Sarcocornia	3	5	Below	264,92	-	100,67
Winter	Sarcocornia	3	6	Below	235,48	-	89,48
Winter	Sarcocornia	4	1	Below	193,87	-	73,67
Winter	Sarcocornia	4	2	Below	499,39	-	189,77
Winter	Sarcocornia	4	3	Below	300,45	-	114,17
Winter	Sarcocornia	4	4	Below	285,22	-	108,38
Winter	Sarcocornia	4	5	Below	288,27	-	109,54
Winter	Sarcocornia	4	6	Below	167,48	-	63,64
Winter	Sarcocornia	5	1	Below	243,60	-	92,57
Winter	Sarcocornia	5	2	Below	335,97	-	127,67
Winter	Sarcocornia	5	3	Below	223,30	-	84,86
Winter	Sarcocornia	5	4	Below	226,35	-	86,01
Winter	Sarcocornia	5	5	Below	342,06	-	129,98

Winter	Sarcocornia	5	6	Below	631,34	-	239,91
Winter	Sarcocornia	6	1	Below	594,80	-	-
Winter	Sarcocornia	6	2	Below	323,79	-	916,83
Winter	Sarcocornia	6	3	Below	214,17	-	371,82
Winter	Sarcocornia	6	4	Below	189,81	-	317,44
Winter	Sarcocornia	6	5	Below	201,99	-	579,33
Winter	Sarcocornia	6	6	Below	179,66	-	471,72

Table 9.5: Nutrient data for plant material

Season	**Species**	**Site**	**Replicate**	**Biomass**	**Phosphorus (g/kg)**	**Nitrogen (g/kg)**
Summer	Zostera	1	1	Above	19,77304	1,59068
Summer	Zostera	1	2	Above	18,85668	1,69512
Summer	Zostera	1	3	Above	16,03568	1,28072
Summer	Zostera	1	4	Above	22,61822	1,56016
Summer	Zostera	1	5	Above	22,70068	1,30088
Summer	Zostera	1	6	Above	23,54078	1,463
Summer	Zostera	2	1	Above	19,5765	1,59404
Summer	Zostera	2	2	Above	20,00988	1,58676
Summer	Zostera	2	3	Above	19,24356	1,56072
Summer	Zostera	2	4	Above	17,97504	1,30452
Summer	Zostera	2	5	Above	19,0774	1,18384
Summer	Zostera	2	6	Above	21,8023	1,897
Summer	Zostera	3	1	Above	27,2211	1,5078
Summer	Zostera	3	2	Above	26,28676	1,63436
Summer	Zostera	3	3	Above	27,13306	1,67608
Summer	Zostera	3	4	Above	23,33742	0,79044
Summer	Zostera	3	5	Above	14,29534	0,90832
Summer	Zostera	3	6	Above	20,57656	1,3356
Summer	Zostera	4	1	Above	18,32968	1,2964
Summer	Zostera	4	2	Above	10,28642	0,87024
Summer	Zostera	4	3	Above	13,54328	0,87808
Summer	Zostera	4	4	Above	21,7775	1,078
Summer	Zostera	4	5	Above	19,90262	0,80948
Summer	Zostera	4	6	Above	19,01664	0,92372
Summer	Zostera	5	1	Above	28,65206	1,54504
Summer	Zostera	5	2	Above	29,70544	1,7402
Summer	Zostera	5	3	Above	30,473	1,86508
Summer	Zostera	5	4	Above	30,00304	1,32188
Summer	Zostera	5	5	Above	29,21874	1,5428
Summer	Zostera	5	6	Above	28,68678	1,14352
Summer	Zostera	6	1	Above	23,64928	1,46888
Summer	Zostera	6	2	Above	18,7271	1,04944
Summer	Zostera	6	3	Above	18,22924	0,70448

Summer	Zostera	6	4	Above	21,9201	1,14996
Summer	Zostera	6	5	Above	23,13406	1,071
Summer	Zostera	6	6	Above	21,8116	1,20736
Summer	Zostera	1	1	Below	15,33756	0
Summer	Zostera	1	2	Below	15,62586	0
Summer	Zostera	1	3	Below	15,15156	0,31332
Summer	Zostera	1	4	Below	11,12528	0
Summer	Zostera	1	5	Below	10,52264	0
Summer	Zostera	1	6	Below	10,60262	0,74452
Summer	Zostera	2	1	Below	14,46832	0,21196
Summer	Zostera	2	2	Below	14,71942	0,13804
Summer	Zostera	2	3	Below	12,88856	0,00476
Summer	Zostera	2	4	Below	18,42082	0,43092
Summer	Zostera	2	5	Below	15,903	0,31444
Summer	Zostera	2	6	Below	17,79462	0,1876
Summer	Zostera	3	1	Below	22,5463	0,08036
Summer	Zostera	3	2	Below	22,13896	0
Summer	Zostera	3	3	Below	19,97392	0
Summer	Zostera	3	4	Below	16,06482	0
Summer	Zostera	3	5	Below	16,43434	0
Summer	Zostera	3	6	Below	17,18392	0
Summer	Zostera	4	1	Below	24,23394	0
Summer	Zostera	4	2	Below	15,00276	0
Summer	Zostera	4	3	Below	16,79952	0
Summer	Zostera	4	4	Below	18,32596	0
Summer	Zostera	4	5	Below	15,7604	0,31668
Summer	Zostera	4	6	Below	15,8596	0,2086
Summer	Zostera	5	1	Below	64,33616	0,9534
Summer	Zostera	5	2	Below	51,82332	0
Summer	Zostera	5	3	Below	72,58154	1,2628
Summer	Zostera	5	4	Below	56,17944	0
Summer	Zostera	5	5	Below	69,98994	0
Summer	Zostera	5	6	Below	77,30532	0
Summer	Zostera	6	1	Below	82,96592	0
Summer	Zostera	6	2	Below	96,86198	0
Summer	Zostera	6	3	Below	53,34232	2,41668
Summer	Zostera	6	4	Below	66,39146	5,432
Summer	Zostera	6	5	Below	72,92936	4,8356
Summer	Zostera	6	6	Below	119,90738	0
Winter	Zostera	1	1	Above	86,298	23,37244
Winter	Zostera	1	2	Above	81,703	22,35716
Winter	Zostera	1	3	Above	70,699	21,97132
Winter	Zostera	1	4	Above	78,201	21,9338
Winter	Zostera	1	5	Above	73,563	19,43424
Winter	Zostera	1	6	Above	70,744	19,79796
Winter	Zostera	2	1	Above	91,408	17,96004

Winter	Zostera	2	2	Above	98,205	18,87984
Winter	Zostera	2	3	Above	91,31	17,39612
Winter	Zostera	2	4	Above	97,589	20,03512
Winter	Zostera	2	5	Above	86,481	19,07388
Winter	Zostera	2	6	Above	85,404	19,68344
Winter	Zostera	3	1	Above	74,894	16,35676
Winter	Zostera	3	2	Above	77,502	15,00492
Winter	Zostera	3	3	Above	75,751	15,38348
Winter	Zostera	3	4	Above	55,292	10,89172
Winter	Zostera	3	5	Above	52,101	9,48108
Winter	Zostera	3	6	Above	56,117	9,71936
Winter	Zostera	4	1	Above	84,967	14,8344
Winter	Zostera	4	2	Above	88,407	15,841
Winter	Zostera	4	3	Above	82,978	16,59952
Winter	Zostera	4	4	Above	63,956	14,364
Winter	Zostera	4	5	Above	54,42	12,91808
Winter	Zostera	4	6	Above	50,549	11,1216
Winter	Zostera	5	1	Above	93,457	14,85204
Winter	Zostera	5	2	Above	92,007	14,46004
Winter	Zostera	5	3	Above	86,175	14,28448
Winter	Zostera	5	4	Above	84,853	14,50876
Winter	Zostera	5	5	Above	82,39	14,53536
Winter	Zostera	5	6	Above	87,166	14,47348
Winter	Zostera	6	1	Above	93,448	17,82396
Winter	Zostera	6	2	Above	97,537	21,19964
Winter	Zostera	6	3	Above	94,638	21,88228
Winter	Zostera	6	4	Above	89,72	17,50756
Winter	Zostera	6	5	Above	93,771	17,23932
Winter	Zostera	6	6	Above	88,42	16,81596
Winter	Zostera	1	1	Below	19,91068	8,2404
Winter	Zostera	1	2	Below	42,31562	8,33196
Winter	Zostera	1	3	Below	31,45198	6,804
Winter	Zostera	1	4	Below	30,7489	6,42348
Winter	Zostera	1	5	Below	42,08002	8,30592
Winter	Zostera	1	6	Below	43,76146	9,9162
Winter	Zostera	2	1	Below	42,92384	10,0408
Winter	Zostera	2	2	Below	33,4242	8,4392
Winter	Zostera	2	3	Below	34,7045	9,39428
Winter	Zostera	2	4	Below	33,945	7,6062
Winter	Zostera	2	5	Below	42,27656	9,49648
Winter	Zostera	2	6	Below	19,7067	6,0368
Winter	Zostera	3	1	Below	15,96748	5,5272
Winter	Zostera	3	2	Below	19,5331	6,35096
Winter	Zostera	3	3	Below	18,80212	5,46196
Winter	Zostera	3	4	Below	20,23432	6,96052
Winter	Zostera	3	5	Below	26,54468	5,69604

Winter	Zostera	3	6	Below	25,27554	5,31328
Winter	Zostera	4	1	Below	32,94618	9,26492
Winter	Zostera	4	2	Below	37,4666	10,7114
Winter	Zostera	4	3	Below	25,05172	7,518
Winter	Zostera	4	4	Below	33,67716	9,61184
Winter	Zostera	4	5	Below	22,83956	7,04648
Winter	Zostera	4	6	Below	24,25626	7,1778
Winter	Zostera	5	1	Below	47,3897	9,82912
Winter	Zostera	5	2	Below	47,3928	9,7384
Winter	Zostera	5	3	Below	51,56664	10,4902
Winter	Zostera	5	4	Below	64,97662	13,7158
Winter	Zostera	5	5	Below	57,59738	12,26316
Winter	Zostera	5	6	Below	62,87916	12,55268
Winter	Zostera	6	1	Below	49,00604	18,06028
Winter	Zostera	6	2	Below	50,25472	17,82508
Winter	Zostera	6	3	Below	49,38052	18,3778
Winter	Zostera	6	4	Below	46,97058	16,29264
Winter	Zostera	6	5	Below	43,52896	13,80932
Winter	Zostera	6	6	Below	46,0412	13,89164
Summer	Spartina	1	1	Above	24,347	7,66248
Summer	Spartina	1	2	Above	29,712	7,92792
Summer	Spartina	1	3	Above	41,12	23,01544
Summer	Spartina	1	4	Above	46,159	11,50576
Summer	Spartina	1	5	Above	42,424	11,96944
Summer	Spartina	1	6	Above	45,995	9,78012
Summer	Spartina	2	1	Above	39,899	6,75892
Summer	Spartina	2	2	Above	41,205	7,2296
Summer	Spartina	2	3	Above	38,689	6,7802
Summer	Spartina	2	4	Above	45,535	11,17788
Summer	Spartina	2	5	Above	46,321	11,23248
Summer	Spartina	2	6	Above	49,966	10,62796
Summer	Spartina	3	1	Above	38,709	6,4106
Summer	Spartina	3	2	Above	40,465	6,7774
Summer	Spartina	3	3	Above	41,812	5,33372
Summer	Spartina	3	4	Above	42,486	6,80064
Summer	Spartina	3	5	Above	41,803	7,53424
Summer	Spartina	3	6	Above	37,068	6,90536
Summer	Spartina	4	1	Above	40,495	7,05796
Summer	Spartina	4	2	Above	45,123	8,73964
Summer	Spartina	4	3	Above	42,273	8,1858
Summer	Spartina	4	4	Above	55,634	12,10468
Summer	Spartina	4	5	Above	48,708	8,41232
Summer	Spartina	4	6	Above	51,089	9,15488
Summer	Spartina	5	1	Above	45,784	7,65436
Summer	Spartina	5	2	Above	49,15	8,90568
Summer	Spartina	5	3	Above	42,134	7,83468

Summer	Spartina	5	4	Above	44,388	8,79732
Summer	Spartina	5	5	Above	41,792	6,37588
Summer	Spartina	5	6	Above	35,834	7,71708
Summer	Spartina	1	1	Below	16,86772	7,72212
Summer	Spartina	1	2	Below	14,19242	4,07708
Summer	Spartina	1	3	Below	15,8193	5,90464
Summer	Spartina	1	4	Below	15,1249	4,59172
Summer	Spartina	1	5	Below	14,41624	4,35652
Summer	Spartina	1	6	Below	13,41804	5,047
Summer	Spartina	2	1	Below	19,50086	3,97236
Summer	Spartina	2	2	Below	18,69114	3,3124
Summer	Spartina	2	3	Below	19,53682	2,80784
Summer	Spartina	2	4	Below	20,37258	0,7028
Summer	Spartina	2	5	Below	19,8648	1,8886
Summer	Spartina	2	6	Below	20,77248	1,29892
Summer	Spartina	3	1	Below	11,64298	0,7182
Summer	Spartina	3	2	Below	11,0267	0,21112
Summer	Spartina	3	3	Below	11,84448	0,29764
Summer	Spartina	3	4	Below	8,89452	0
Summer	Spartina	3	5	Below	13,51476	0
Summer	Spartina	3	6	Below	12,97226	0
Summer	Spartina	4	1	Below	24,06592	7,65464
Summer	Spartina	4	2	Below	22,00566	4,28624
Summer	Spartina	4	3	Below	20,7421	4,739
Summer	Spartina	4	4	Below	15,18814	2,50404
Summer	Spartina	4	5	Below	15,82674	2,66112
Summer	Spartina	4	6	Below	15,64694	2,62752
Summer	Spartina	5	1	Below	14,04052	1,16172
Summer	Spartina	5	2	Below	12,15634	0,60592
Summer	Spartina	5	3	Below	13,59474	1,2026
Summer	Spartina	5	4	Below	16,73132	2,49452
Summer	Spartina	5	5	Below	17,55034	2,06864
Summer	Spartina	5	6	Below	16,30352	2,83248
Winter	Spartina	1	1	Above	22,2983	10,91552
Winter	Spartina	1	2	Above	23,00882	12,66748
Winter	Spartina	1	3	Above	24,07646	12,12484
Winter	Spartina	1	4	Above	24,27176	14,08288
Winter	Spartina	1	5	Above	23,54636	12,2514
Winter	Spartina	1	6	Above	24,24324	13,29132
Winter	Spartina	2	1	Above	22,7974	15,39216
Winter	Spartina	2	2	Above	24,0684	14,3136
Winter	Spartina	2	3	Above	24,16698	15,7794
Winter	Spartina	2	4	Above	22,46942	11,45256
Winter	Spartina	2	5	Above	22,4347	10,06768
Winter	Spartina	2	6	Above	22,79802	10,68732
Winter	Spartina	3	1	Above	21,421	8,617

Winter	Spartina	3	2	Above	20,85556	8,34484
Winter	Spartina	3	3	Above	20,07746	8,58732
Winter	Spartina	3	4	Above	19,40352	7,42112
Winter	Spartina	3	5	Above	18,569	4,54608
Winter	Spartina	3	6	Above	19,12452	5,369
Winter	Spartina	4	1	Above	34,51354	10,94772
Winter	Spartina	4	2	Above	33,46574	12,28416
Winter	Spartina	4	3	Above	33,98778	11,60236
Winter	Spartina	4	4	Above	26,6817	9,96688
Winter	Spartina	4	5	Above	24,75226	8,43752
Winter	Spartina	4	6	Above	29,3012	9,80056
Winter	Spartina	5	1	Above	28,26642	10,96704
Winter	Spartina	5	2	Above	30,14378	11,9168
Winter	Spartina	5	3	Above	31,44702	11,3232
Winter	Spartina	5	4	Above	29,6081	9,30412
Winter	Spartina	5	5	Above	27,46786	9,80112
Winter	Spartina	5	6	Above	27,19754	9,53568
Winter	Spartina	6	1	Above	32,72174	10,43728
Winter	Spartina	6	2	Above	30,48664	9,71152
Winter	Spartina	6	3	Above	31,26102	11,31816
Winter	Spartina	6	4	Above	33,40932	10,85364
Winter	Spartina	6	5	Above	27,21986	10,14636
Winter	Spartina	6	6	Above	29,93856	9,97024
Winter	Spartina	1	1	Below	24,993	9,71068
Winter	Spartina	1	2	Below	27,05	8,02704
Winter	Spartina	1	3	Below	22,733	7,9618
Winter	Spartina	1	4	Below	22,444	7,15484
Winter	Spartina	1	5	Below	22,36	6,01356
Winter	Spartina	1	6	Below	20,254	4,39012
Winter	Spartina	2	1	Below	23,847	7,52668
Winter	Spartina	2	2	Below	25,1	7,8834
Winter	Spartina	2	3	Below	26,055	6,51224
Winter	Spartina	2	4	Below	29,954	7,15232
Winter	Spartina	2	5	Below	28,662	6,54472
Winter	Spartina	2	6	Below	30,762	7,5096
Winter	Spartina	3	1	Below	24,811	4,6816
Winter	Spartina	3	2	Below	22,064	4,61608
Winter	Spartina	3	3	Below	22,145	5,21556
Winter	Spartina	3	4	Below	26,032	5,43928
Winter	Spartina	3	5	Below	25,053	5,73272
Winter	Spartina	3	6	Below	26,303	5,29452
Winter	Spartina	4	1	Below	44,243	7,09296
Winter	Spartina	4	2	Below	42,179	7,6202
Winter	Spartina	4	3	Below	39,142	6,4638
Winter	Spartina	4	4	Below	46,709	8,05168
Winter	Spartina	4	5	Below	42,439	5,51544

Winter	Spartina	4	6	Below	44,138	6,32324
Winter	Spartina	5	1	Below	31,152	6,132
Winter	Spartina	5	2	Below	30,981	5,24384
Winter	Spartina	5	3	Below	35,335	8,1956
Winter	Spartina	5	4	Below	36,982	7,43064
Winter	Spartina	5	5	Below	31,741	5,43312
Winter	Spartina	5	6	Below	37,402	6,58588
Winter	Spartina	6	1	Below	29,112	4,66424
Winter	Spartina	6	2	Below	29,257	4,86668
Winter	Spartina	6	3	Below	29,092	4,86892
Winter	Spartina	6	4	Below	30,573	5,04448
Winter	Spartina	6	5	Below	35,376	5,24636
Winter	Spartina	6	6	Below	34,124	5,65768
Summer	Sarcocornia	1	1	Above	26,80198	0
Summer	Sarcocornia	1	2	Above	28,50698	0,04564
Summer	Sarcocornia	1	3	Above	32,82156	2,30104
Summer	Sarcocornia	1	4	Above	26,11316	3,69656
Summer	Sarcocornia	1	5	Above	34,82168	0
Summer	Sarcocornia	1	6	Above	32,45762	3,661
Summer	Sarcocornia	2	1	Above	30,44758	3,99952
Summer	Sarcocornia	2	2	Above	26,75424	2,75548
Summer	Sarcocornia	2	3	Above	29,95468	1,6422
Summer	Sarcocornia	2	4	Above	28,55596	1,5176
Summer	Sarcocornia	2	5	Above	28,9106	3,6148
Summer	Sarcocornia	2	6	Above	18,2807	2,00256
Summer	Sarcocornia	3	1	Above	22,59962	0,56364
Summer	Sarcocornia	3	2	Above	21,15192	2,57824
Summer	Sarcocornia	3	3	Above	21,94924	0,4606
Summer	Sarcocornia	3	4	Above	20,14504	1,61672
Summer	Sarcocornia	3	5	Above	27,83676	4,32908
Summer	Sarcocornia	3	6	Above	16,54284	0,42924
Summer	Sarcocornia	4	1	Above	32,56612	3,35664
Summer	Sarcocornia	4	2	Above	33,38266	0,7182
Summer	Sarcocornia	4	3	Above	30,01792	1,78136
Summer	Sarcocornia	4	4	Above	35,11742	8,48624
Summer	Sarcocornia	4	5	Above	48,54724	4,63092
Summer	Sarcocornia	4	6	Above	39,54422	4,40776
Summer	Sarcocornia	5	1	Above	28,98128	3,03968
Summer	Sarcocornia	5	2	Above	26,05116	2,57516
Summer	Sarcocornia	5	3	Above	31,60202	2,84004
Summer	Sarcocornia	5	4	Above	22,70006	1,90316
Summer	Sarcocornia	5	5	Above	21,53384	0,34272
Summer	Sarcocornia	5	6	Above	22,43284	0
Summer	Sarcocornia	1	1	Below	27,03448	1,15276
Summer	Sarcocornia	1	2	Below	21,19036	0,21672
Summer	Sarcocornia	1	3	Below	22,35038	0

Summer	Sarcocornia	1	4	Below	36,63828	0
Summer	Sarcocornia	1	5	Below	23,1632	0
Summer	Sarcocornia	1	6	Below	40,35828	0
Summer	Sarcocornia	2	1	Below	40,77554	1,85472
Summer	Sarcocornia	2	2	Below	28,84612	0
Summer	Sarcocornia	2	3	Below	38,9763	0,93548
Summer	Sarcocornia	2	4	Below	76,96184	5,54316
Summer	Sarcocornia	2	5	Below	35,75354	1,3706
Summer	Sarcocornia	2	6	Below	49,82444	1,53636
Summer	Sarcocornia	3	1	Below	22,2859	1,11216
Summer	Sarcocornia	3	2	Below	22,65232	0,5782
Summer	Sarcocornia	3	3	Below	19,6757	2,32568
Summer	Sarcocornia	3	4	Below	27,49018	2,56508
Summer	Sarcocornia	3	5	Below	29,38428	4,37584
Summer	Sarcocornia	3	6	Below	22,18546	0,4074
Summer	Sarcocornia	4	1	Below	25,56198	12,67056
Summer	Sarcocornia	4	2	Below	24,36476	10,71252
Summer	Sarcocornia	4	3	Below	23,48002	9,569
Summer	Sarcocornia	4	4	Below	17,12378	7,54852
Summer	Sarcocornia	4	5	Below	21,66156	10,68032
Summer	Sarcocornia	4	6	Below	15,64942	8,06232
Summer	Sarcocornia	5	1	Below	25,40078	7,97692
Summer	Sarcocornia	5	2	Below	22,81414	7,16884
Summer	Sarcocornia	5	3	Below	39,36938	12,85536
Summer	Sarcocornia	5	4	Below	26,08278	7,651
Summer	Sarcocornia	5	5	Below	36,88566	9,90836
Summer	Sarcocornia	5	6	Below	26,14664	7,56952
Winter	Sarcocornia	1	1	Above	38,26454	19,69184
Winter	Sarcocornia	1	2	Above	24,91656	10,67416
Winter	Sarcocornia	1	3	Above	22,90962	10,60472
Winter	Sarcocornia	1	4	Above	23,45336	10,41796
Winter	Sarcocornia	1	5	Above	25,46774	12,0064
Winter	Sarcocornia	1	6	Above	22,1557	10,30232
Winter	Sarcocornia	2	1	Above	17,89444	9,64432
Winter	Sarcocornia	2	2	Above	18,32162	9,3548
Winter	Sarcocornia	2	3	Above	18,34766	9,695
Winter	Sarcocornia	2	4	Above	22,2177	9,282
Winter	Sarcocornia	2	5	Above	17,85104	10,00552
Winter	Sarcocornia	2	6	Above	15,87448	8,41176
Winter	Sarcocornia	3	1	Above	15,64632	9,70676
Winter	Sarcocornia	3	2	Above	15,79512	9,39736
Winter	Sarcocornia	3	3	Above	15,83666	9,64096
Winter	Sarcocornia	3	4	Above	15,19248	8,5442
Winter	Sarcocornia	3	5	Above	14,24388	7,90384
Winter	Sarcocornia	3	6	Above	12,82284	6,42908
Winter	Sarcocornia	4	1	Above	14,88	8,70856

Winter	Sarcocornia	4	2	Above	14,67912	8,2572
Winter	Sarcocornia	4	3	Above	15,09948	8,11748
Winter	Sarcocornia	4	4	Above	17,85786	9,01096
Winter	Sarcocornia	4	5	Above	16,9539	8,63352
Winter	Sarcocornia	4	6	Above	17,77602	9,31224
Winter	Sarcocornia	5	1	Above	18,67688	9,32904
Winter	Sarcocornia	5	2	Above	18,42392	7,93548
Winter	Sarcocornia	5	3	Above	17,21244	7,38724
Winter	Sarcocornia	5	4	Above	18,51506	6,88604
Winter	Sarcocornia	5	5	Above	17,88142	7,52612
Winter	Sarcocornia	5	6	Above	18,54048	7,43484
Winter	Sarcocornia	6	1	Above	19,6168	13,26556
Winter	Sarcocornia	6	2	Above	18,76616	12,999
Winter	Sarcocornia	6	3	Above	19,83628	11,14512
Winter	Sarcocornia	6	4	Above	21,8519	12,1058
Winter	Sarcocornia	6	5	Above	23,20102	9,91816
Winter	Sarcocornia	6	6	Above	20,61686	9,08768
Winter	Sarcocornia	1	1	Below	16,36552	5,75344
Winter	Sarcocornia	1	2	Below	15,09824	4,63008
Winter	Sarcocornia	1	3	Below	16,06482	4,61244
Winter	Sarcocornia	1	4	Below	20,00864	6,97732
Winter	Sarcocornia	1	5	Below	19,10096	7,87052
Winter	Sarcocornia	1	6	Below	18,91868	7,17976
Winter	Sarcocornia	2	1	Below	20,41722	7,12124
Winter	Sarcocornia	2	2	Below	19,92742	7,86464
Winter	Sarcocornia	2	3	Below	18,89202	7,38864
Winter	Sarcocornia	2	4	Below	24,17628	7,8694
Winter	Sarcocornia	2	5	Below	25,69466	9,3954
Winter	Sarcocornia	2	6	Below	24,29966	7,36512
Winter	Sarcocornia	3	1	Below	16,28988	13,75416
Winter	Sarcocornia	3	2	Below	17,31474	14,63028
Winter	Sarcocornia	3	3	Below	16,05056	12,754
Winter	Sarcocornia	3	4	Below	15,15094	13,18492
Winter	Sarcocornia	3	5	Below	14,21412	11,84848
Winter	Sarcocornia	3	6	Below	14,61402	10,49636
Winter	Sarcocornia	4	1	Below	14,03742	11,21372
Winter	Sarcocornia	4	2	Below	13,96178	11,5878
Winter	Sarcocornia	4	3	Below	14,20358	10,33396
Winter	Sarcocornia	4	4	Below	13,98038	10,14104
Winter	Sarcocornia	4	5	Below	14,2848	10,91888
Winter	Sarcocornia	4	6	Below	13,5129	10,43336
Winter	Sarcocornia	5	1	Below	17,11386	11,46124
Winter	Sarcocornia	5	2	Below	18,042	12,63108
Winter	Sarcocornia	5	3	Below	17,81322	11,62196
Winter	Sarcocornia	5	4	Below	19,16172	12,43172
Winter	Sarcocornia	5	5	Below	20,64724	14,19824

Winter	Sarcocornia	5	6	Below	16,41884	9,92684
Winter	Sarcocornia	6	1	Below	33,59284	13,3196
Winter	Sarcocornia	6	2	Below	35,82732	12,00612
Winter	Sarcocornia	6	3	Below	34,49494	12,94916
Winter	Sarcocornia	6	4	Below	32,42042	11,68748
Winter	Sarcocornia	6	5	Below	38,98622	10,80212
Winter	Sarcocornia	6	6	Below	40,18158	11,08352

Table 9.6: Epiphyte biomass (Chl a content) on the *Zostera capensis* leaf blades

Season	Site	Replicate	Chlorophyll a content (mg. m^{-2})
Summer	1	1	14,11
Summer	1	2	6,09
Summer	1	3	6,23
Summer	1	4	7,31
Summer	1	5	8,03
Summer	1	6	3,10
Summer	2	1	0,21
Summer	2	2	0,23
Summer	2	3	0,35
Summer	2	4	0,40
Summer	2	5	1,16
Summer	2	6	0,75
Summer	3	1	2,93
Summer	3	2	4,14
Summer	3	3	4,68
Summer	3	4	3,43
Summer	3	5	1,73
Summer	3	6	3,38
Summer	4	1	0,36
Summer	4	2	0,49
Summer	4	3	0,31
Summer	4	4	0,20
Summer	4	5	0,60
Summer	4	6	0,18
Summer	5	1	1,83
Summer	5	2	1,68
Summer	5	3	2,03
Summer	5	4	1,73
Summer	5	5	1,69
Summer	5	6	2,27
Summer	6	1	6,40
Summer	6	2	2,80
Summer	6	3	2,80
Summer	6	4	3,28

Summer	6	5	4,83
Summer	6	6	1,28
Winter	1	1	30,87
Winter	1	2	7,17
Winter	1	3	38,21
Winter	1	4	40,34
Winter	1	5	8,10
Winter	1	6	5,22
Winter	2	1	2,54
Winter	2	2	10,18
Winter	2	3	15,97
Winter	2	4	3,76
Winter	2	5	6,16
Winter	2	6	9,75
Winter	3	1	58,35
Winter	3	2	72,41
Winter	3	3	-
Winter	3	4	65,07
Winter	3	5	51,25
Winter	3	6	33,95
Winter	4	1	5,25
Winter	4	2	2,90
Winter	4	3	4,46
Winter	4	4	8,60
Winter	4	5	4,83
Winter	4	6	0,51
Winter	5	1	15,51
Winter	5	2	14,42
Winter	5	3	8,31
Winter	5	4	43,55
Winter	5	5	18,19
Winter	5	6	18,19
Winter	6	1	8,81
Winter	6	2	90,39
Winter	6	3	10,21
Winter	6	4	93,39
Winter	6	5	112,70
Winter	6	6	5,42