African Journal of Aquatic Science

ISSN: 1608-5914 (Print) 1727-9364 (Online) Journal homepage: https://www.tandfonline.com/loi/taas20

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To cite this article: CE Brown & A Rajkaran (2020) Biomass partitioning in an endemic southern African salt marsh species *Salicornia tegetaria* (Chenopodiaceae), African Journal of Aquatic Science, 45:1-2, 41-48, DOI: 10.2989/16085914.2019.1687419

To link to this article: https://doi.org/10.2989/16085914.2019.1687419

African Journal of Aquatic Science 2020, 45(1–2): 41–48
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AFRICAN JOURNAL OF AQUATIC SCIENCE
ISSN 1608-5914 EISSN 1727-9364
https://doi.org/10.2989/16085914.2019.1687419

Biomass partitioning in an endemic southern African salt marsh species *Salicornia tegetaria* (Chenopodiaceae)

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The below ground biomass of salt marsh species accounts for more than half of the total plant biomass in salt marsh systems, yet no biomass data exist for salt marsh species in South Africa. The aims of the current study were to compare the biomass allocation of *Salicornia tegetaria* in six estuaries and relate findings to their environmental conditions. The current study measured the physico-chemical variables of the sediment (moisture content, organic matter content, electrical conductivity, pH) and pore water (temperature, salinity, pH, depth) at Olifants, Berg, Langebaan, Heuningnes, Nahoon and Kwelerha estuaries. Above and below ground biomass and stem height measurements were also collected. The below ground biomass (1.51 ± 0.24 kg m^{-2}) and root/shoot ratio (1.36 ± 0.17) was the lowest at Heuningnes Estuary with no significant difference at the remaining estuaries, suggesting that factors, such as geomorphology and sedimentological processes, could have a stronger effect on the biomass allocation in this species. Important drivers of biomass allocation were sediment pH, redox potential and pore water depth. The current study provides baseline information for *S. tegetaria,* an endemic salt marsh species, for which there is a paucity of data. This species plays a major role in the ecology of the lower intertidal zone, which will be vulnerable to sea-level rise.

Keywords: climate change, root/shoot ratio, salinity, sediment particle size, sea-level rise

Supplementary material: available online at https://doi.org/10.2989/16085914.2019.1687419

Introduction

Vegetated coastal habitats play a large role in climate mitigation through the global capture and storage of carbon (Mcleod et al. 2011). Salt marshes have a high rate of below ground production and grow in anoxic sediments (Connor and Chmura 2000; Chmura et al. 2003; Barbier et al. 2011; Chmura 2013). Anoxic sediments allow for a slower rate of decay resulting in a long-term carbon sink (Ponnamperuma 1972; Chmura 2013). The below ground biomass of halophytic species accounts for more than half of the total plant biomass in salt marsh systems (Schubauer and Hopkinson 1984; Ouyang et al. 2017).

South Africa has more than 300 estuaries unequally distributed along 3 400 km of coastline with approximately 11 400 ha of intertidal and supratidal salt marsh (Van Niekerk and Turpie 2012). No studies to date have measured biomass for salt marsh species, such as *Salicornia tegetaria* (S Steffen, Mucina & G Kadereit) Piirainen & G Kadereit, 2017, which is widely distributed in these systems. The species has recently undergone a name change. It was previously described as *Sarcocornia tegetaria* S Steffen, Mucina & G Kadereit, 2009 (Steffen et al. 2009). *Salicornia tegetaria* is a succulent, low-growing shrub endemic to South Africa, Namibia and Mozambique found in the lower to middle intertidal zone of estuaries.

Extensive literature describes the above ground biomass (AGB), below ground biomass (BGB) and biomass production of other salt marsh macrophytes from estuaries along the North American Atlantic coast (Schubauer and Hopkinson 1984; Gross et al. 1991; Connor and Chmura 2000), tropical coast of the Gulf of Mexico (De La Cruz and Hackney 1977; Hackney and De La Cruz 1986) and the Mediterranean (Castellanos et al. 1994; Scarton and Rismondo 2002; Palomo and Niell 2009), but the measurement of physico-chemical variables are often lacking from these studies.

Salt marsh vegetation distribution is governed by a gradient of physico-chemical conditions that change with elevation (Veldkornet et al. 2016). In the lower intertidal environment, the most important variables determining physico-chemical conditions and plant growth are salinity and tidal inundation (Pennings and Callaway 1992; Bertness and Hacker 1994; Guo and Pennings 2012). It has been shown that low growing clonal plants from the lower marsh zone, where there is an increase in stress, because of marine salinity and waterlogging, had a high allocation to roots and rhizomes (Minden et al. 2012).

Clay content in the sediment determines drainage and influences the nutrient, water and oxygen availability (Olff et al. 1997; Bai et al. 2005) and the ground water table additionally determines the oxygen status and therefore the redox potential of the sediment (Armstrong et al. 1985). Well-drained and oxygenated soils have higher pH and lower salinity, a higher rate of organic matter decomposition, higher nutrient availability and above ground production (Angiolini et al. 2013; Costa et al. 2003; Husson 2013). The redox potential and pH level of the soil is important in the rhizosphere. At +350 mV the root medium becomes oxygen deficient, which can reduce the rate of photosynthesis, cause energy deficiency in the roots and reduce water and nutrient uptake (Pezeshki and DeLaune 2012). Roots require a positive membrane potential and a transmembrane pH gradient for the transport of nutrients as H^+-translocating ATPases drives the transmembrane flux of other ions (Braun et al. 1986).

Salt marshes have shown responses consistent with Brouwer's (1962) theory and Tilman's (1988) allocation model in relation to a nutrient gradient, where allocation to below ground biomass was high in nutrient poor soils and allocation to above ground biomass was high in nutrient rich soils (Minden 2012).

The current study measured the standing above and below ground biomass of *S. tegetaria* in six estuaries along the coast of South Africa (Figure 1). *Salicornia tegetaria* displays a high degree of plasticity and grows in a wide range of physico-chemical conditions (Veldkornet et al. 2016). It is expected that the physico-chemical conditions could vary among individual estuaries and that these differences could influence resource allocation. The current study measured sediment pH, moisture content, organic matter content and electrical conductivity (EC), as well as pore water temperature, salinity, pH and depth. Relating the biomass allocation of these plants to physico-chemical conditions might provide insights to the shifts that could occur as a result of anthropogenic impacts.

Eutrophication and water abstraction alters the lower intertidal zone with a resulting increase in nutrients, lower freshwater runoff and higher salinity (Van Niekerk and Turpie 2012). Major shifts in climate are expected over the next century (Stocker et al. 2013), which might affect the potential of wetlands to be valuable as global carbon and methane sinks (Bartlett et al. 1987; Chmura et al. 2003; Adams et al. 2012; Ouyang and Lee 2014).

Estuaries will be affected by changes to freshwater supply, increased storm frequency and intensity, increased temperatures and increased inundation, because of sea-level rise (SLR) (Van Niekerk and Turpie 2012). Salt marshes adapt to SLR by trapping sediment or increasing below ground biomass (Larsen and Harvey 2010; Marani and D'Alpaos 2013; Bornman et al. 2016).

In this study, we hypothesised that 1) higher salinity/EC would result in an increased allocation to below ground biomass and that 2) higher pH, redox potential, soil moisture and organic matter content would result in higher above ground allocation.

Materials and methods

Descriptions of the study sites

The study was conducted in six estuaries: Olifants, Berg, Langebaan, Heuningnes, Nahoon and Kwelerha (Figure 1). These estuaries were chosen for their large intertidal areas, where monospecific patches of *S. tegetaria* could be found. Olifants, Berg, Nahoon and Kwelerha are predominantly open estuaries. Four of the six estuaries (Olifants, Berg, Heuningnes and Nahoon) have been affected by flow modification and habitat loss (Van Niekerk and Turpie 2012). Olifants and Berg estuaries maintain their open state through river flow, whereas Nahoon and Kwelerha estuaries are maintained in the open state by tidal currents (Allanson and Baird 2008). Both the Olifants Estuary and Berg Estuary are under high flow modification pressure, mainly as a result of large dams in their catchment. Hence, the Olifants Estuary remains marine dominated for most of the year (Lamberth et al. 2008).

The Heuningnes Estuary is located on a stretch of coastline with extensive flood plains and vast mobile dune fields that, driven by strong winds, periodically blocked the river mouth leading to the flooding of farmland. Since the early 20th century the mouth has been kept artificially open most of the time by the introduction of *Ammophila arenaria* (L.) Link (European beach grass) to stabilise dunes and fix drift sand movement (Lubke and Hertling 2001).

Langebaan is a unique estuarine system type in South Africa (estuarine lagoon). The body of water in the estuarine lagoon is fed by ground water in certain sections rather than receiving freshwater from river input. Typical estuarine species occur in the lagoon, including a large portion of South Africa's total salt marsh vegetation (Whitfield 2005; Mucina et al. 2006).

Olifants, Berg and Langebaan estuaries fall within the semiarid Mediterranean climate with winter rainfall of the cool temperate biogeographical region (Bickerton 1984). Heuningnes, Nahoon and Kwelerha estuaries fall within the warm-temperate biogeographical region where the rainfall pattern is highly variable throughout the year and is usually slightly higher during autumn (March) and spring (October/November) and at a minimum in winter (June) (Schulze 1965; Heydorn and Tinley 1980; Jury and Levey 1993). Temperature and rainfall data were provided by the South African Weather Service (SAWS) (Supplementary Figure S1).

Sample collection

Biomass, pore water and sediment sampling were undertaken twice at each estuary during low tide, once during the winter of 2016 and once during the summer of 2017. Monospecific patches of 100% *S. tegetaria* cover were identified in the lower intertidal zone of each estuary. Three permanent transects were demarcated and divided into a lower, middle and upper zone. A quadrat was identified in each zone containing 100% *S. tegetaria* cover, providing a total of 18 replicates per estuary.

Sediment cores were collected at the surface and at 50 cm depth within each quadrat, giving 18 replicates each at 0 cm and 50 cm. Sediment pH (Black et al. 1965), moisture content, organic matter content (Briggs 1977; Heiri et al. 2001) and electrical conductivity (EC) (Barnard 1990) were measured in the laboratory. Sediments were analysed for redox potential *in situ* with a HANNA redox/pH metre by placing the probe into the sediment at each quadrat (Black et al. 1965). Sediment pH and redox potential were measured in summer when equipment became available, giving a total of nine replicates per estuary.

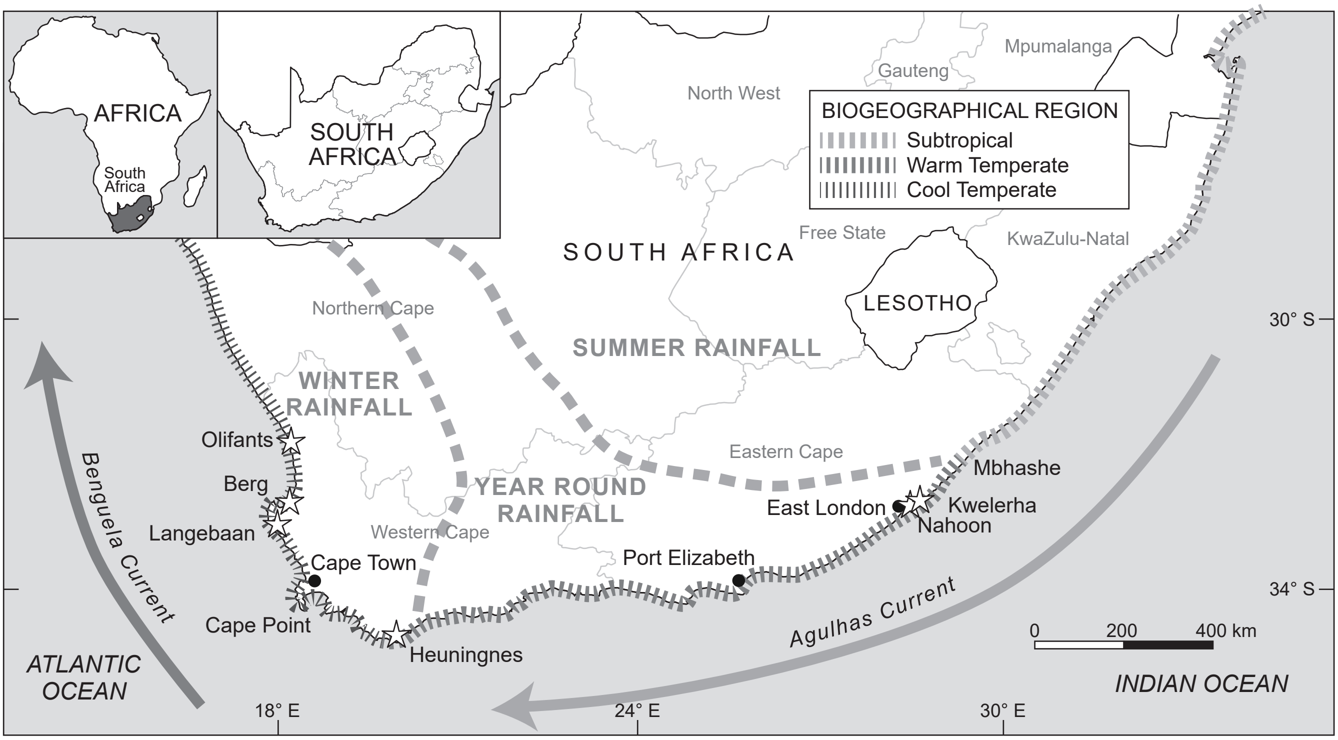

Figure 1: Map of South Africa showing rainfall zones and biogeographical regions. Study sites are shown as white stars

Pore water was measured in the quadrats as water filled the wells in which biomass and sediment were collected, giving 18 replicates per estuary. In each augured well, pore water temperature, salinity and pH were measured using a YSI Professional Plus multimeter. Pore water depth was measured as the level to which water filled the wells at low tide. Wells were augured to a depth of 1 m, and recorded as >1 m if water did not enter the well.

Plant height was measured for ten *S. tegetaria* stems from tip to ground/lateral branch in each quadrat (180 replicates per estuary). All the AGB was harvested from the sediment surface within a 0.15 m × 0.15 m area in each quadrat. The AGB was rinsed with water and any attached litter removed by hand (Schubauer and Hopkinson 1984; Gross et al. 1991). Following the removal of AGB, BGB was collected by removing the sediment containing the roots to a depth of 10 cm in the same 0.15 m × 0.15 m area as above ground biomass. Most of the roots were found down to a depth of 10 cm (Curcó et al. 2002; Palomo and Niell 2009).

The below ground biomass was washed by hand with water to remove the bulk of sediment using a 1 mm sieve to collect fine roots. The water was passed through the sieve until all the roots in each sample were recovered. A second wash with 10 g sodium polyphosphate in water removed the rest of the sediment. The above and below ground biomass was dried for 48 h at 60 °C and then weighed as per Hopkinson and Dunn (1984).

Statistical analysis

Statistical analyses were performed using R Statistical Software (R Core Team 2013). Data were tested for normality using Shapiro–Wilk normality test and non-parametric tests were used when data were not distributed normally. A *t*-test of sediment variables between samples collected at 0 cm and 50 cm did not show a significant difference and the data were pooled for additional analyses. The number of replicates (*N*) was 108 for biomass, sediment EC, moisture and organic content, 54 for sediment pH and redox and 89 (excluding wells where water was >1 m deep) for pore water temperature, pH and salinity.

Values are reported as means (± SE). A Kruskal–Wallis non-parametric analysis of variance (ANOVA) was used to test the variance of biological and physico-chemical variables between estuaries. A Dunn's test was used to perform *post hoc* analyses when the ANOVA found variables to be significantly different between estuaries, and *p*-values were adjusted with the Benjamini–Hochberg method using the R package FSA version 0.8.24 (Ogle et al. 2019) and rcompanion version 2.2.1 (Mangiafico 2019). Spearman's correlation tests were used to test the relationship between physico-chemical and biological variables within each individual estuary. Statistical significance was determined at $p < 0.05$.

Results

Olifants and Berg estuaries had significantly higher sediment moisture content, Berg Estuary had significantly higher sediment EC and Heuningnes Estuary had significantly lower sediment EC. Heuningnes Estuary also had significantly higher pore water pH than found at the other estuaries (Table 1). Plants at Berg Estuary and Nahoon Estuary were significantly taller than those at the Langebaan and Heuningnes estuaries were (Figure 2). The

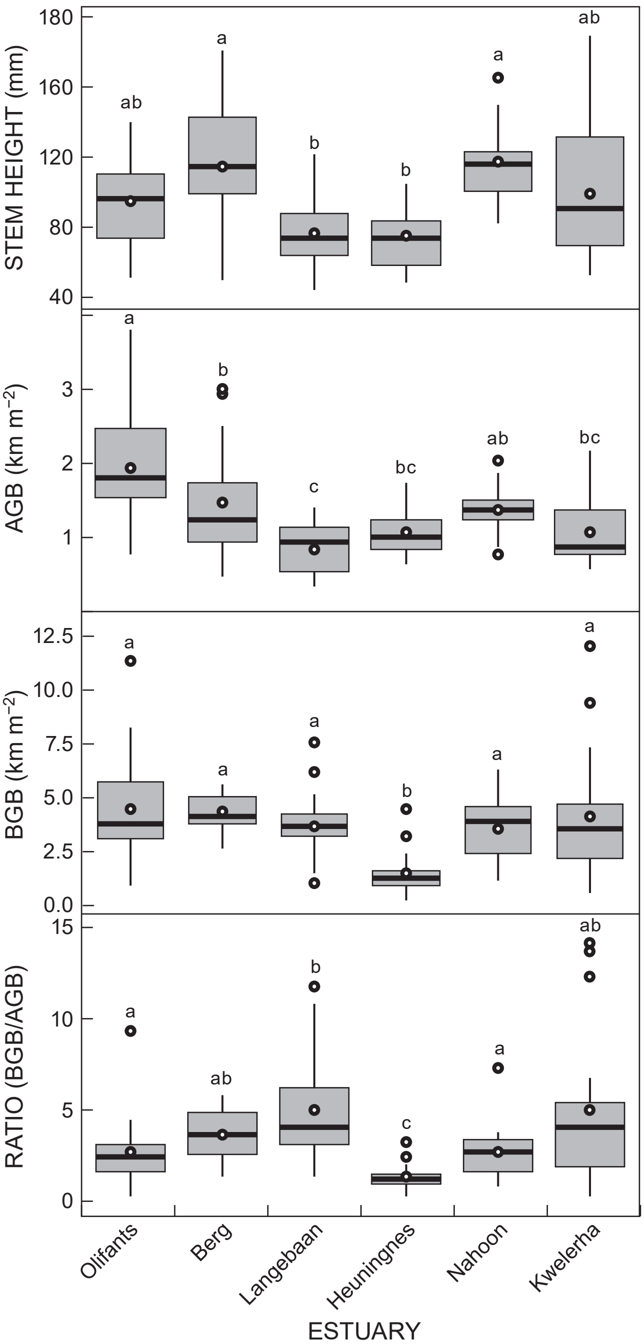

Figure 2: Boxplots of biological variables among estuaries. The line indicates the median and points inside the boxes show the mean. Outliers are shown as points outside the boxes. Estuaries sharing a letter are not significantly different ($p < 0.05$) (Kruskal–Wallis multiple comparison test)

AGB at Berg, Heuningnes, Nahoon and Kwelerha estuaries were similar. The AGB at Olifants Estuary was significantly higher than at Langebaan, Heuningnes and Kwelerha estuaries. Langebaan Lagoon had the lowest AGB of 0.86 ± 0.09 kg m^{-2} and the lowest recovered in winter 2016 (0.59 ± 0.08 kg m^{-2}), but the AGB at Langebaan Estuary was not significantly different from Heuningnes or Kwelerha

Table 1: Sediment and pore water characteristics at each estuary (mean ± SE)

Estuary	Sediment moisture (%)	Sediment organic (%)	Sediment redox (mV)	Sediment EC (m s^{-1})	Sediment pH	Pore water temperature (°C)	Pore water salinity	Pore water pH	Pore water depth (cm)
Olifants	55.2 ± 2.0	12.8 ± 1.1	−165.3 ± 28.6	43.8 ± 4.4	6.9 ± 0.1	15.3 ± 0.6	38.2 ± 2.7	7.2 ± 0.1	37.5 ± 4.2
Berg	62.0 ± 1.5	18.0 ± 0.9	128.9 ± 32.5	59.9 ± 3.2	6.6 ± 0.1	15.0 ± 0.8	39.9 ± 2.4	6.9 ± 0.2	29.7 ± 4.0
Langebaan	37.8 ± 2.7	9.9 ± 1.7	183.9 ± 11.8	44.0 ± 2.2	6.5 ± 0.1	18.0 ± 0.4	33.8 ± 2.2	7.1 ± 0.2	27.5 ± 5.7
Heuningnes	24.1 ± 0.7	3.9 ± 0.4	232.0 ± 23.1	30.8 ± 1.1	9.4 ± 0.0	16.8 ± 0.4	25.8 ± 2.0	8.5 ± 0.3	27.1 ± 1.0
Nahoon	35.6 ± 1.4	11.7 ± 2.4	168.1 ± 29.2	38.1 ± 1.7	7.8 ± 0.1	17.9 ± 1.0	40.4 ± 1.8	7.6 ± 0.2	37.0 ± 5.0
Kwelerha	30.6 ± 1.2	5.8 ± 0.4	13.9 ± 35.6	39.4 ± 2.1	7.1 ± 0.1	18.9 ± 1.0	44.5 ± 2.4	7.0 ± 0.1	50.8 ± 3.8

estuaries. Although washing the roots from the different estuaries it was evident that *S. tegetaria* in Heuningnes Estuary grew in sandier, coarser-grained sediment compared with the other estuaries, and had visibly fewer roots. Heuningnes Estuary had significantly lower BGB than found at the other estuaries (1.51 ± 0.24 kg m^{-2}), but overall the BGB was not significantly different between the other estuaries. The root/shoot ratio was significantly lower at Heuningnes Estuary (1.36) than at the other five estuaries sampled.

At Olifants, Langebaan and Heuningnes estuaries, sediment pH was negatively correlated to BGB and at Langebaan and Heuningnes estuaries it was negatively correlated to AGB. In the Olifants, Nahoon and Kwelerha estuaries, the AGB was higher in quadrats where the pore water depth was shallower. At Langebaan Lagoon (where pore water was often found at the surface and it did not exceed 60 cm during sampling), the AGB was lower where the pore water depth was shallower. At Berg Estuary the depth to water level exceeded 1 m in six quadrats during summer and at Heuningnes Estuary water level depth exceeded 1 m in all nine quadrats in winter. The sediment redox potential was strongly positively correlated to AGB at Langebaan Lagoon and BGB at Kwelerha Estuary. Kwelerha Estuary had a higher BGB/AGB ratio during winter sampling and resulted in a negative correlation to pore water temperature. At Heuningnes Estuary the AGB was higher in quadrats with higher sediment organic content (Table 2).

Table 2: Spearman's correlations of physico-chemical variables with AGB, BGB and the BGB/AGB ratio, for each estuary. Significant values are given as $^{*}p < 0.05$; $^{**}p < 0.001$; $^{***}p < 0.0001$

Estuary	Biological variable	Physico-chemical variable	*r*
Olifants	BGB	Sediment pH	−0.54*
	AGB	Pore water Depth	−0.56*
Berg	AGB	Sediment moisture	−0.55*
	Ratio	Sediment moisture	0.49*
Langebaan	AGB	Sediment redox	0.73**
	AGB	Sediment pH	−0.63*
	BGB	Sediment pH	−0.50*
	AGB	Pore water depth	0.77***
	Ratio	Pore water depth	−0.65*
Heuningnes	AGB	Sediment organic	0.52*
	AGB	Sediment pH	−0.53*
	BGB	Sediment pH	−0.53*
Nahoon	AGB	Pore water depth	−0.51*
Kwelerha	BGB	Sediment redox	0.71**
	Ratio	Sediment redox	0.70**
	BGB	Pore water temperature	−0.51*
	Ratio	Pore water temperature	−0.54*

Discussion

The current study represents the first quantification of biomass allocation and the standing biomass of *S. tegetaria* in estuaries in South Africa. The AGB of *S. tegetaria* (1.31 kg m^{-2}) was within the range reported for other *Salicornia* species (0.53–3.40 kg m^{-2}) (Mahall and Park 1976; Castellanos et al. 1994; Curcó et al. 2002; Scarton and Rismondo 2002; Palomo and Niell 2009) (Figure 2). The high AGB (3.40 kg m^{-2}) and low root/shoot ratio (0.68) of *S. perennis* subsp. *alpini* reported by Palomo and Niell (2009) was likely because of nutrient enrichment of the system studied in Spain, whereby an increase in a limiting nutrient resulted in an increase in AGB (Darby and Turner 2008).

The BGB of *S. tegetaria* (3.66 kg m^{-2}) was higher than that of *Salicornia perennis* (approximately 1.67–2.33 kg m^{-2}), which is found at a similar elevation in the lower intertidal zones of the Mediterranean salt marshes (Castellanos et al. 1994; Davy et al. 2006; Palomo and Niell 2009). The higher BGB found in the current study might be because of the variation at the species level, but might also indicate an environment that promotes below ground production (Schubauer and Hopkinson 1984; Colmer and Voesenek 2009; Minden and Kleyer 2011).

Veldkornet et al. (2016) recorded similar values for ground water depth, sediment EC and sediment pH compared with the current study, whereas the sediment moisture and organic content found in the current study was higher than recorded by Veldkornet et al. (2016) and Geldenhuys et al. (2016). The importance of sediment particle size on below ground processes was evident when individual estuaries were compared. The sediment at the historically river-dominated Olifants and Berg estuaries was finer than at the other estuaries with a clay/silt loam texture and had higher moisture content (Bornman et al. 2002). The higher surface tension of soils with higher organic and clay/silt content, result in a higher water and nutrient holding capacity than sandy soils (Barko and Smart 1986; Gómez-Plaza et al. 2001; Bai et al. 2005).

Nahoon and Kwelerha estuaries had similar sediment profiles, measured at 50% sand, 35% clay and 15% silt in the lower salt marsh of Nahoon Estuary (Reddering 1987; Geldenhuys et al. 2016). The sandy nature of the sediment near to the mouth of Heuningnes Estuary where samples were collected, was most likely the result of an influx of sand from the sea (Bickerton 1984). A decrease in pH with an increase in salinity (Redondo-Gómez et al. 2007; Arslan and Demir 2013) and a decrease in pH with an increase in soil moisture (Rogel et al. 2000) have been reported in other salt marsh studies. The roots at Langebaan Lagoon were highly condensed in the top layer (± 2–3 cm), which trapped fine sediment, with a coarse sandy layer and little roots continuing beneath. This is probably because no river flows into the estuarine lagoon and sediment input to the salt marsh is of marine or aeolian origin (Flemming 1977).

A decrease in sediment redox potential is expected with an increase in tidal inundation period and frequency over the long term in the lower intertidal zone (Seybold et al. 2002). Shallower ground water tables had a positive effect on AGB in Olifants, Nahoon and Kwelerha estuaries, though this was not the case at Langebaan Lagoon. At Langebaan, an increase in the depth of the ground water level had a strong positive correlation to AGB, which affected the BGB/AGB ratio.

A phosphate-mining license has been granted in the Langebaan area above the aquifer that supplies ground water to the salt marsh vegetation as its only source of freshwater (Whitfield 2005). Phosphate mining affects the hydrology and water quality of the environment (Reta et al. 2018) and could have an impact on vegetation in the estuarine lagoon and reduce the BGB/AGB ratio.

Following submergence, the redox potential in the sediment becomes lower as oxygen is depleted in the sediment by roots, microorganisms and soil reductants that are formed when oxidised compounds are used as electron acceptors and carbon dioxide accumulates (Pezeshki and DeLaune 2012). Sediment redox potentials were positively correlated to BGB and the BGB/AGB ratio (Table 2) at Langebaan Lagoon. The top layer of fine sediment and dense roots could have impeded the drainage of water and had a strong effect on the redox potential and BGB/AGB ratio.

Heuningnes Estuary is a sand-dominated estuary. The resulting high availability of oxygen and low salinity increases organic matter decomposition and above ground growth (Valiela et al. 1976; Poluektov and Topazh 2005; Darby and Turner 2008; Husson 2013; Ouyang et al. 2017). This is supported by the significantly lower BGB recorded. Other salt marsh species, including *Spartina alterniflora* Loisel., *S. patens* and *S. perennis* subsp. *alpini* have shown a decrease in BGB with higher nutrient availability (Valiela et al. 1976; Gross et al. 1991; Palomo and Niell 2009).

Geldenhuys et al. (2016) found that sediment pH was an important determinant in salt marsh species distribution at Nahoon Estuary. Studies have shown that nutrients become more soluble at lower pH levels, promoting plant growth (Ponnamperuma 1972; Peterson and Graves 2009; Husson 2013). H^+ translocating activity in saline conditions was found to be optimum at pH 6.2 in the halophyte *Atriplex nummularia* Lindl. (Braun et al. 1986). At higher pH, *S. tegetaria* showed a decrease in both BGB and AGB. The optimum pH at which plants grow best in the natural environment do not necessarily reflect the optimum pH for plant growth (Peterson and Graves 2009), which is additionally complicated by salinity (Braun et al. 1986) and waterlogging (Adams and Bate 1994) in the salt marsh environment.

The different sediment sources and quantities of sediment delivered to estuaries could have implications on BGB production. Inappropriate development, such as dams and bridges, reduces the inflow from rivers and reduces the scouring of marine sediments in the lower reaches of estuaries (Schumann 2003). An increase in sea storms could cause an increase in wave height and an increase in marine sediment along areas of sediment-rich coastline, which could affect the biomass of salt marsh macrophytes near the mouth of estuaries, e.g. Heuningnes (Van Niekerk and Turpie 2012).

Salt marshes are classified as blue carbon ecosystems that sequester carbon within the sediment over the long term, and AGB and BGB over the short term, at a higher rate than terrestrial ecosystems (Chmura et al. 2003; Mcleod et al. 2011). The accumulation of organic matter is linked to the production of AGB import or export and the production and decomposition of BGB. Measuring the BGB and organic matter in salt marshes will aid estimates of the amount of carbon they store (Ouyang et al. 2017), which in turn affects the response of salt marshes to sea-level rise that depends on sediment supply and accretion (Lovelock et al. 2015). *Salicornia tegetaria* is a common species endemic to southern African estuaries where it forms large monospecific stands in the lower intertidal zone that will be vulnerable to SLR. Biomass allocation is an important mechanism by which plants respond to resource based and non-resource-based environmental stress (Bazzaz et al. 1987; Minden et al. 2012) and long-term monitoring could identify processes that could affect the patterns of biomass allocation in this species.

Acknowledgements — Funding for this project is gratefully acknowledged from the South African National Research Foundation (NRF) (Thuthuka TTK14060668458) and the Early Career Fellowship provided by the University of the Western Cape. Sampling permits were obtained from Cape Nature (permit no. 0028-AAA008-00240), the DAFF (permit no. RES2016/107) and SANPARKS (permit no. CRC/2017-2018/009-2016/V1). The grant holder acknowledges that opinions, findings and conclusions or recommendations expressed in any publication generated by this NRF supported research are that of the authors, and that the NRF accepts no liability whatsoever in this regard.

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Manuscript received: 9 July 2019, revised: 13 October 2019, accepted: 29 October 2019
Associate Editor: J Adams