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The broad-scale impacts of livestock grazing on saltmarsh carbon stocks

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The Broad-Scale Impacts of Livestock Grazing on Saltmarsh Carbon Stocks

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Overall Thesis Summary

In light of recent upward trends in atmospheric carbon dioxide concentration, efforts have turned to methods of sequestering atmospheric carbon into other stable carbon sinks. Enhancing carbon sequestration by natural systems is an effective way of managing carbon sequestration. Due to high productivity and high sedimentation rates, salt marshes are extremely efficient at capturing and storing carbon, and provide the ideal environment for enhancing carbon sequestration rates through the management of livestock grazing, a common use of salt marshes. However, salt marshes are subject to a range of environmental stressors, which can vary considerably over a large spatial scale. It is therefore important to understand the implications of environmental and contextual variability on the use of livestock grazing as a carbon management tool. Twenty-two salt marshes were selected along the coasts of north Wales and north-west England to assess the impact of grazers on above and below-ground carbon stocks and processes in relation to broader contextual variables. The impacts of seasonality on carbon sequestration rates were also assessed by investigating a salt marsh carbon budget over the course of one year. Grazing was found to have a negative impact on several above-ground plant characteristics, but no impact on soil carbon stocks or overall carbon sequestration rates. Instead, below-ground processes were explained more by the broader environmental variables and seasonal changes. While this study does not discount the fact that grazing may affect soil carbon stocks on the small-scale, or after initial introduction, it shows that grazing impacts are insignificant relative to broader contextual factors on marshes with well-established grazing regimes.

Acknowledgements

I would like first of all to thank my three supervisors, Martin Skov, Angus Garbutt and Steve Hawkins. Martin was the driving force behind this project; he sat through long hours of pondering over stats, read countless drafts of chapters and conference presentations, and was always ready with new and interesting ideas, provided he'd had enough coffee. Despite working a demanding job in the Centre for Ecology and Hydrology, Angus was always on hand for down to earth, sensible advice on anything to do with working on salt marshes. He provided me with many key references and reports he'd collected from various salt marsh chums, advised me on the tried and tested ways of measuring a range of variables, and more often than not he had just the piece of equipment I needed sitting in his desk drawer. Steve was incredibly good at advising on broader scientific theories; a half hour meeting with Steve would leave me with lots of new ideas to test, and usually a new way of looking at my data. Luckily, a move down to Southampton did not stop Steve's involvement with the project; he was heavily involved with proof reading thesis chapters and again provided new ideas for analyses and discussion points. Without the support and advice from my three supervisors, I would not have developed my scientific skills to the extent I have, and for that I will always be grateful. They have also made this PhD a genuinely enjoyable three and a half years.

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Although salt marshes are a fairly niche subject, falling between terrestrial and marine sciences, there is a small group of salt marsh scientists in Bangor, who have helped me broaden my knowledge, understand my findings, and generally have more fun working on salt marshes. Tom Davies was a PhD student at Bangor whose work took him to Malltraeth salt marsh. As his field assistant for one summer, this was my first taste of working in the salt marsh environment; without his help and encouragement I would not have been accepted as a PhD candidate. Hilary Ford was a PhD student in CEH and is now a post doctoral researcher at Bangor University. She has provided advice and support throughout this project for which I am extremely grateful. I also had the opportunity to help her collect some of her data, which gave me an insight to processes and procedures I have not been able to cover in this project.

I am indebted to the army of fieldwork assistants that I had helping me throughout the long field days. In particular, Marc Brouard, Kate Batchelor, Caroline Lamarque and the three Masters students, Matt Lundquist, Aoife Ni Neachtain and Cai Ladd, who all put in many long days out on the marshes in all conditions, and often endured carrying heavy loads, getting lost in the vegetation and occasionally getting caught out by the tide.

Finally, I would not have made it through this PhD or my years in Bangor leading up to it without the love and support from my family and friends. Since the age of 13, I wanted to study and do research in ocean sciences at Bangor, and my parents have supported me right through. Special thanks to my Dad for agreeing to learn how to track changes on Word and then spending long hours proof reading final thesis chapters (including the references)! Last but not least is my fiancé Gareth Harvey. He too has had his share of proof reading over the years, and has given me a lot of advice on statistical analyses, writing styles and thesis formatting. He has been my anchor throughout these years and with him I have many an intellectual debate, many mountain adventures, and many silly challenges (a combination perhaps only Gareth can achieve), which all kept me sane and happy throughout my time at Bangor.

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PART 1: INTRODUCTION

Chapter 1: General Introduction: The Role of Coastal Wetlands in Mitigating Climate Change

In the context of climate change adaptation and mitigation, this thesis addresses how the grazing regime of salt marshes influences above-ground vegetation patterns, and whether this has any influence on ecosystem services, particularly those below-ground such as carbon sequestration. Such carbon sequestration may also be important in mitigating climate change by targeted management of wetlands and other grazed pastoral ecosystems. The remainder of this chapter sets the scene by briefly reviewing climate change, the role of wetlands in carbon sequestration, and basic salt marsh ecology before considering the importance of grazing in salt marshes. The aims and rationale of the rest of the thesis are then outlined.

1.1 A Changing Climate

The words 'climate change' have woven themselves into the consciousness of the general public worldwide (Lorenzoni & Pidgeon, 2006); the familiar graphs depicting an increase in global temperatures (Crowley, 2000; Hansen et al., 2006; Mann, Bradley, & Hughes, 1999; Trenberth et al., 2007) have increased awareness and concern for environmental issues (Bord, Fisher, & O'Connor, 1998). According to the Intergovernmental Panel for Climate Change (IPCC 2007) temperatures have risen 0.76°C ± 0.19°C since the western industrial revolution, and warming over the past 50 years is nearly twice that of the last 100 years (Trenberth et al., 2007).

The causes of climate change have been extensively researched (Lindzen, 1997) and it is widely accepted that both natural and anthropogenic factors contribute to climate change (Prentice et al., 2001). Before 1850 (pre-industrial times in Europe and the USA) regional warming or cooling events could be explained by natural variations in environmental forcings: the Little Ice Age in the 1500s is thought to be linked to increased volcanic activity, whereas a warm period in the Middle Ages is believed to be linked to solar variation (Crowley, 2000). However, Crowley (2000) states that volcanism and solar radiation only contribute to a quarter of the increase in temperatures over the 20th century. Ice cores have shown that carbon dioxide (CO_2) levels have increased since pre-industrial times (Neftel, Moor, Oeschger, & Stauffer, 1985); this is chiefly due to anthropogenic activities such as the burning of fossil fuels (Marland, Rotty, & Treat, 1985; Raupach et al., 2007) made worse by deforestation (van de Werf et al., 2009) and other land use change (Bernoux, Da Conceicao Santana Carvalho, Volkoff, & Cerri, 2001). CO_2 is one of the major greenhouse gases (Lal, 2008; Lashof & Ahuja, 1990) that contribute to the 'greenhouse effect' (Schneider, 1989) and thus the increase in CO_2 levels is thought to be the main contributor to this recent rise in global temperature (Crowley, 2000; Meehl et al., 2005; Prentice et al., 2001; Trenberth et al., 2007). Furthermore, the situation is exacerbated by a positive feedback loop between CO_2 and global temperature: an increase in temperature causes more CO_2 to be released from natural systems through respiration, which then feeds back into the warming of the greenhouse effect (Scheffer, Brovkin, & Cox, 2006).

Another significant greenhouse gas is methane (Forster et al., 2007). Although the lifetime of methane in the atmosphere (around 10 years) is much shorter than that of carbon dioxide, it is approximately 25 times more potent over a 100 year period (Lelieveld, Crutzen, & Dentener, 1997). The largest natural source of methane is produced naturally from terrestrial wetlands, but there are also other natural methane sources such as termites, volcanoes, and oceans (Lal, 2008). However, around 60% of total methane emissions come from human activities such as natural gas and petroleum production, agricultural practices, and waste (Forster et al., 2007).

Carbon sequestration is the locking away of atmospheric carbon by biological or geological processes into other long-term carbon sinks, from which it cannot be easily re-emitted (Lal, 2008). There are five major long-term carbon stores: the oceans, the atmosphere (from which carbon needs to be removed), fossil fuels (which are being consumed), biotic (living organisms) and soils (Lal, 2008). These sinks have a finite capacity for carbon uptake (Chmura, 2009; Forster et al., 2007; Lal, 2008; Sabine et al., 2004) and carbon is in constant flux between atmospheric, oceanic and terrestrial sinks (Falkowski et al., 2000). Consequently measures can be taken to enhance the capacity of the biotic, oceanic and soil sinks to remove carbon from the atmosphere (Chmura, 2009; Falkowski et al., 2000). In terrestrial and coastal systems, sequestration of carbon into the biotic and soil sinks via natural processes, such as sedimentation and afforestation, is a simple and effective way of storing carbon (Lal, 2008; Milne & Brown, 1997). Despite a high carbon stock in soils (1462-1548 pita-grams (Pg) of organic matter in the top metre (Batjes, 1996), and a further 842 Pg in the second and third metres (Jobbagy & Jackson, 2000)), soils allow for only relatively low rates of carbon sequestration (0.4 x1015 g C yr-1) particularly in land used for agriculture (Schlesinger, 1990). The biotic sink has a much higher rate of carbon sequestration (Schlesinger, 1990), yet carbon is also emitted at high rates and turnover is fast – on the decadal scale – rather than long-term (Falkowski et al., 2000). Vegetation, however, plays a key linking role in transferring carbon from the biotic pool into the more stable pool in soils through root biomass and litter from vegetation (Bardgett & Wardle, 2003; De Deyn, Cornelissen, & Bardgett, 2008; Yu & Chmura, 2010).

Terrestrial wetlands have a huge potential for sequestering carbon due to high plant productivity and high organic content of the soils. For example, peatlands only occupy 3% of the terrestrial global surface, yet they contain 16-33% of the global soil carbon pool (Bridgham, Maegonigal, Keller, Bliss, & Trettin, 2006). Terrestrial wetlands, however, also act as a significant source of carbon by the production of carbon dioxide and methane through aerobic and anaerobic decay of organic matter (Baird, Holden, & Chapman, 2010; Wang, Zeng, & Partrick, 1996).

1.2 The Role of Coastal Wetlands

Coastal saline wetlands, including tidal salt marshes and mangroves, sequester carbon at an overall average rate of 210 grams of carbon per metre squared per year (g (C) m^{-2} y^{-1} (Chmura, Anisfeld, Cahoon, & Lynch, 2003), which is an order of magnitude greater than that of peatlands (20-30 g (C) m^{-2} y^{-1}) (Chmura, 2009). Plant productivity is the main contributor to these high rates of carbon sequestration (Chmura et al., 2003; Niering & Scott Warren, 1980), and salt marshes have an estimated net primary production and carbon output of 100-200 g (CO_2) m^{-2} y^{-1} (Boorman, 2000; Hussein & Rabenhorst, 2002). The majority of this productivity is channeled below-ground, with root production being roughly 1.6 times that of above-ground production (Schubauer & Hopkinson, 1984). Below-ground production is particularly important for carbon sequestration: roots can be deeper than one metre (Saunders, Megonigal, & Reynolds, 2006) and are not easily broken down in the anoxic conditions of a salt marsh or mangrove (Hussein & Rabenhorst, 2002; Scanlon & Moore, 2000); thus carbon stores in below-ground biomass are long-term (Boorman, 2000; De Deyn et al., 2008; Yu & Chmura, 2010).

Coastal wetlands are regularly waterlogged and anoxic conditions prevail in the low marsh where tidal inundation is frequent (Pennings & Callaway, 1992). Anaerobic soils favour methane-producing microbial communities (methanogens), a significant factor affecting the carbon output of terrestrial wetlands and other terrestrial soils (W. H. Schlesinger & J. A. Andrews, 1999). In coastal wetlands, however, the presence of sulphates in the soil deposited by tidal inundation significantly inhibits the production of methane (Chmura et al., 2003; Magenheimer, Moore, Chmura, & Daoust, 1996) as methane-producing bacteria are inhibited by sulphate-reducing bacteria due to competition for the products of anaerobic fermentation: hydrogen and acetate (Winfrey & Ward, 1983). As coastal wetlands are regularly inundated with sea water, the sulphate levels of the soil are regularly replenished (Winfrey & Ward, 1983), thus methane production by coastal wetlands is significantly lower than that by terrestrial wetlands (Magenheimer et al., 1996; Yu & Chmura, 2010).

Saline marshes sequester on average 2.5 mm sediment per year from marine fluvial and tidal processes, (Flessa, Constantine, & Cushman, 1977). This high rate of sedimentation is mainly due to vegetation, which traps particles otherwise too small to settle out of the water (Brix, 1997; Stumpf, 1983). These particles are then transported into the soil by rain water, invertebrate detrivores or grazers, or by the plants decomposing (Stumpf, 1983). The trapped sediment is often rich in inorganic carbon thus sediment trapping significantly contributes to carbon sequestration by salt marshes (Connor, Chmura, & Beecher, 2001). Marshes with denser and taller vegetation trap more sediment and thus contribute more to carbon sequestration (Chmura, 2009; Chmura et al., 2003; Woodwell, Whitney, Hall, & Houghton, 1977).

1.3 The Salt Marsh Environment

Salt marshes are areas dominated by halophytic herbs, grasses or low shrubs bordering saline water bodies, which are exposed to the air for the majority of the time but are periodically inundated with saline water (Adam, 1990b). These occur worldwide in temperate areas; there are extensive salt marshes across Europe and the UK (Figure 1.1), with large expanses in the Wadden Sea and in the large estuaries of the UK (Boorman, 2003). Salt marshes form in low energy environments, limiting them to sheltered environments such as estuaries or behind barrier islands where fine sediment accumulates, providing a suitable substrate for pioneer plant species (Adam, 1990b; Boorman, 2003).

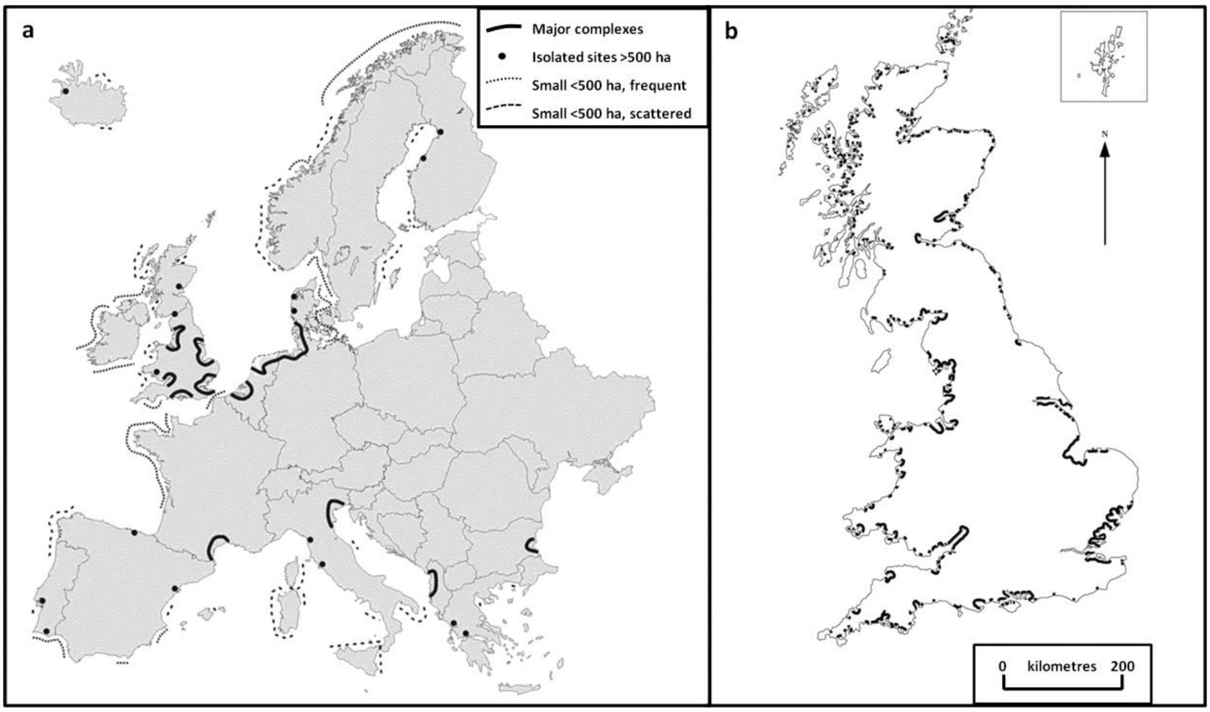


Figure 1.1 | Salt marsh distribution. European (a) and UK (b) salt marsh distribution based on (Boorman, 2003).

Spartina species are typical pioneer salt marsh plants that colonise mudflats in circular patches; these patches eventually join up forming a uniform sward (D.S. Ranwell, 1964a; Sanchez, SanLeon, & Izco, 2001). Once established, rhizome root structures ensure the stability of these *Spartina* patches and sediment trapping by the roots leads to elevation of the marsh surface (D.S. Ranwell, 1964a; Sanchez et al., 2001; Stumpf, 1983). Shading by the plants slows evaporation and thus reduces soil salinity, allowing less salt-tolerant but competitively superior species to colonise (Adam, 1990b; Sanchez et al., 2001; Shumway & Bertness, 1994).

Continuing salt marsh growth often results in distinct zonation according to tidal elevation, each zone representing a different stage of salt marsh succession, with the most mature marsh at the highest elevations (Adam, 1990b; Boorman, 2003; Chapman, 1940; Feagin et al., 2011; Weisbrod, 1964). The plant species that dominate these zones are ultimately determined by a variety of physical stress factors, the nature and severity of which depends on geographical location (Pennings & Bertness, 2001). Competition and facilitation can be important proximate factors in settling zonation patterns on a marsh (Bertness & Ellison, 1987; Bertness & Hacker, 1994; Bertness & Shumway, 1993). All salt marshes are frequently inundated with saline water, resulting in waterlogged soils with little oxygen, yet due to the nature of tidal cycles, high marsh areas are flooded less frequently than lower marsh areas. As a consequence the soils in high marsh areas are less waterlogged than low marsh soils (Adam, 1990b; Chapman, 1938; Pennings & Bertness, 2001). Accumulation of organic matter, either by deposition of material by tides or breakdown of in-situ plant material, leads to further depletion of oxygen in the soil by decomposition and microbial activity and, subsequently, the soil becomes anoxic (Bertness & Ellison, 1987; Pennings & Bertness, 2001; Pennings & Callaway, 1992). In warmer regions, evaporation of saline water results in higher soil salinities in the high marsh where inundation is infrequent and freshwater influence is minimal, whereas at lower elevations inundation is frequent enough to dilute the salinity of the soil (Adam, 1990b; Chapman, 1939; Parrondo, Gosselink, & Hopkinson, 1978; Pennings & Bertness, 2001; Pennings & Callaway, 1992). Salt marsh plants are also subject to direct physical stress from water movement and, in the northern latitudes, ice scour (Adam, 1990b; Belanger & Bedard, 1994; Pennings & Bertness, 2001). It is due to these harsh physical conditions that salt marsh plants have developed various coping strategies including additional surface roots to facilitate oxygen transport to deeper roots, aerenchyma tissue to transport oxygen directly to the roots, and osmotic adaption of cell cytoplasm to counteract high salinity (Burdick, 1989; Flowers, 1985; Parrondo et al., 1978). In general, the lower limits of species in salt marshes are set by physical disturbance or stress, and in the upper limits by biological interactions such as competition. Facilitation can, however, enable species to extend further into hostile conditions in the lower marsh (Bertness & Ellison, 1987; Bertness & Hacker, 1994; Bertness & Shumway, 1993).

Although the specialised vegetation is the primary defining factor of a salt marsh, another distinctive feature of most salt marshes is a network of creeks across the marsh, often occupying a large part of the total marsh area (Adam, 1990b; Boorman, 2003). These creeks are formed as the marsh is developing: pioneer plant species develop around existing creeks on the mudflats or new channels are cut between vegetation stands by tidal flow (Adam, 1990b; Chapman, 1939; Perillo & Iribarne, 2003). Although very stable, salt marsh creeks are not static: creeks can continue to extend through the marsh, joining up with other creeks and salt pans, and in the case of extreme storm events smaller creeks may change position completely (Adam, 1990b; Perillo & Iribarne, 2003). Creek networks are the primary pathways for both tidal flooding and drainage of the marsh, and well-drained soils can be found on the creek banks, while waterlogged conditions persist in areas furthest from the creeks (Pennings & Bertness, 2001; Pennings & Callaway, 1992; Temmerman, Bouma, Govers, & Lauwaet, 2005). Creeks also play an important role in sediment and nutrient transport into and out of the marsh; heavier coarse sediment and organic material is deposited on the creek banks and finer sediment is transported in suspension beyond the creeks, with the finest particles only settling at slack water (Stumpf, 1983).

Salt pans are another common feature of salt marshes and there are many ways in which these small pools can be formed (Adam, 1990b). Vegetation may form around a depression in the initial stages of salt marsh formation, leaving a bare patch that remains waterlogged, making it difficult for plants to colonise (Yapp, Johns, & Jones, 1917). Salt pans may also develop on a mature marsh due to disturbance by tidal litter or ice floes, seasonal waterlogging of depressions in the marsh surface, or subsidence of the marsh surface after sub-surface drainage (Boston, 1983). Elongated salt pans can be formed by the blockage of creeks, either by vegetation growth or the accumulation or sediment or tidal litter; these elongated pans have sloping banks and more vegetation growth due to the invasion of vegetation at the shallower edges (Yapp et al., 1917).

Salt marshes provide many ecosystem goods and services from direct provisioning services, such as harvesting of salt marsh plants for food, animal fodder, grazing and thatch, to regulating services such as nutrient filtering, carbon sequestration and coastal defence (Costanza et al., 1997; Gedan, Silliman, & Bertness, 2009; Krutilla, 1967).

1.4 The Importance of Grazers

Salt marshes are natural grazing grounds, and evidence of large herbivores on salt marshes can be found as far back as the late Pleistocene (Koch, Hoppe, & Webb, 1998; Levin, Ellis, Petrik, & Hay, 2002). It is possible that salt marshes, like many terrestrial grasslands, have evolved alongside large herbivores (Milchunas, Sala, & Laurenroth, 1988; Olff & Ritchie, 1998). Early human settlers were drawn to these natural grazing grounds and salt marshes have been grazed by domestic herbivores since the Bronze Age (Britton, Muldner, & Bell, 2008).

Grazing has a significant impact on both vegetation and soil characteristics (Jensen, 1985). Loss of vegetation height and density occurs under all grazing regimes (Andresen, Bakker, Brongers, Heydenmann, & Irmler, 1990; V. Bouchard et al., 2003; Jensen, 1985; Kiehl, I., Gettner, & Walter, 1996), but different grazer species affect the vegetation in different ways (Jensen, 1985). Sheep are selective grazers and create patchy vegetation; they preferentially select grazing patches, plant species and individual plants within an area, and are even selective over different leaves on an individual plant (J. P. Bakker, de Leeuw, & van Wieren, 1984; Parsons, Newman, Penning, Harvey, & Orr, 1994). Geese are also selective grazers and many species graze only on plant roots leaving the rest of the plant on the marsh surface; this is destructive to individual plants but like sheep they can create patchiness (Smith III & Odum, 1981). In contrast, cows are generalist grazers and continually graze as they move across the turf, regardless of vegetation type; this results in a more uniform vegetation cover (Jensen, 1985; Wallis De Vries, Laca, & Demment, 1999). Preferential sheep grazing leads to stands of ungrazed undesirable plant species such as *Juncus maritimus* or *Atriplex portulacoides*, which are denser and taller than the surrounding vegetation (J. P. Bakker et al., 1984; D. S. Ranwell, 1961). Grazing in shorter vegetation patches is easier than in taller vegetation, resulting in a higher grazing intensity in the shorter patches and an increased difference between the patches of desirable and undesirable species (Wallis De Vries et al., 1999). If the same area was grazed by cattle however, this patchiness is less likely to arise and vegetation height and density will be more uniform across the turf (Wallis De Vries et al., 1999). Furthermore, the intensity of grazing has a significant impact on the effects of grazing: intense grazing generally leads to very a short, uniform vegetation sward, while light grazing often results in an uneven patchy sward (Table 1.1) (Jensen, 1985; Kiehl et al., 1996).

Grazing significantly influences species richness (the number of species) (Sala et al., 2000)): on an un-grazed sward, species richness is low due to the dominance of one competitively dominant species, but light grazing opens up the sward for less competitively dominant, more opportunistic species, and thus increases species richness (Table 1.1) (Augustine & McNaughton, 1998; V. Bouchard et al., 2003; Marty, 2004). This does not occur in all cases as the increase in species richness depends on the initial plant community (Schroder, Kiehl, & Stock, 2002) and the above process occurs only if the dominant species is a palatable species. If the dominant species is an unpalatable species, less dominant species are grazed, decreasing competition for the dominant species, further reducing species richness (Lubchenco, 1978). Under an intense grazing regime species richness will decrease regardless of preferential grazing, resulting in a less diverse sward of grazing-resistant species (Fleischner, 1994; Olff & Ritchie, 1998).

The opening up of the sward under a light grazing regime results in reverse succession, as more resilient, earlier successional species invade open patches (Andresen et al., 1990; J. P. Bakker, 1985; Fleischner, 1994). Smaller herbivores such as hares have a preference for these opportunistic species, that would otherwise be unavailable (Hewson, 1989), thus large herbivores facilitate for small herbivores (Kuijper, 2004a, 2004b; Kuijper, Beek, & Bakker, 2004). In the absence of large herbivores salt marsh succession would continue towards a monoculture of an apex species despite the presence of the small herbivores, which can only slow vegetation succession (Kuijper, 2004a, 2004b; Kuijper et al., 2004).

Grazing has a detrimental effect on root systems (Table 1.1) (Schuster, 1964) but the extent of root damage depends on the grazer species: cows damage and deracinate roots both by grazing and by trampling (Wallis De Vries et al., 1999) whereas sheep have a less destructive method of grazing, and the impact of trampling is less due to their smaller size (Parsons et al., 1994). Geese feed on root structures and can often leave large open patches resembling salt pans (Belanger & Bedard, 1994; Pedersen, Speed, & Tombre, 2013; Smith III & Odum, 1981), especially in stands of desirable plant species such as *Scirpus maritimus* in soft sediments (Jensen, 1985). Despite the damage caused by grazers, light levels of grazing often lead to increased root density in the upper layers of sediment due to changes in the allocation of plant productivity from above-ground to below-ground, however these roots are finer and shallower than those found in un-grazed areas (J. N. Holland, Cheng, & Crossley, 1996). Intense grazing significantly reduces both root depth and root density at all depths, and ultimately sediment stability is significantly reduced (Schuster, 1964).

A less obvious but equally substantial effect of large herbivores is trampling (Jensen, 1985), and in high stocking densities this can be more detrimental than grazing (Turner, 1987). The primary effect of trampling is the compaction of the soil (Table 1.1), which results in reduced root growth and reduced pore size; consequently soil moisture and temperature are altered, water infiltration rates are reduced as drainage is poor, and ultimately anoxic conditions prevail (Fleischner, 1994; Yates, Norton, & Hobbs, 2000). The anoxic conditions created by soil compaction create harsh conditions across the marsh akin to those found in the lower elevations and thus trampling causes an upward shift of zonation boundaries (Kiehl et al., 1996; Schroder et al., 2002).

These primary impacts of grazing have knock-on effects on the ecosystem services salt marshes provide. Saltmarsh vegetation plays an important role in coastal defence by attenuating waves (Moeller, 2006), and stabilising the coastal fringe by accreting sediment and reducing erosion (Moeller & Spencer, 2002). Therefore, reduction of vegetation height and density by grazing has a significant impact on wave attenuation across a marsh (Moeller, 2006). Taller and denser vegetation provides shading reducing soil temperature and moisture loss from the soil through evaporation and consequently prevents an increase in soil salinity, which has significant impacts on saltmarsh flora and fauna (Andresen et al., 1990). Tall vegetation also provides habitat for invertebrates, which are an important food source for many bird and small mammal species (Andresen et al., 1990; Vickery et al., 2001). These are perhaps arguments against any grazing on salt marshes, but there are several advantages to a light grazing regime. An uneven vegetation height provides habitat for breeding birds (Vickery et al., 2001), and an in increase in species richness increases the potential for the presence of plant species that contribute to ecosystem services, such as those with woody stems that effectively attenuate waves, those with complex root systems that trap sediment, or those with high rates of carbon allocation to their root systems (Adler, Raff, & Lauenroth, 2001). Despite the ecological benefits of an ungrazed or lightly grazed regime, the capital generated from livestock is greatest under an intense grazing regime. There is, therefore, a fine balance between finding the best ecological solution and the best economical solution.

Table 1.1 | Grazing impacts. Summary of the effects of different grazing intensities on vegetation height, species richness, soil compaction and root biomass, with relevant citations.

Effects	Un-grazed	Lightly Grazed	Intensively Grazed	Citations
Vegetation Height	Tall	Mixed	Short	Jensen 1985 Andresen et al. 1990 Kiehl et al. 1996 Bouchard et al 2003
Species Richness	Low	High	Low	Fleischner 1994 Augustine and McNaughton 1998 Olaf and Ritchie 1998 Adler 2001 Bouchard et al. 2003 Marty 2004
Root Biomass	Dense	Very Dense	Low	Schuster 1964 Jensen 1985 Smith III and Odum 1981 Parsons et al. 1994 Wallis de Vries et al. 1999
Soil Compaction	Low	High	Very High	Jensen 1985 Turner 1987 Fleischner 1994 Yates et al. 2000

1.5 Thesis Aims and Overarching Hypotheses

The overall aim of this thesis was to investigate how grazing influenced the goods (i.e. livestock production) and services (e.g. carbon sequestration) provided by salt marshes. The main focus has been on how grazing influences above-ground vegetation patterns, and the consequences of this for below-ground processes involved in carbon sequestration. A broad-scale comparative approach using the marshes of west Wales and north-west England has been adopted. The overarching hypotheses were:

H1: Livestock grazing significantly reduces plant biomass on salt marshes

H2a: Salt marsh species richness is highest under a light grazing regime

H2b: Species richness does not significantly differ between un-grazed and intensively grazed salt marshes

H3: Livestock grazing results in reverse vegetation succession on salt marshes

H4a: Root biomass is greatest under a light grazing regime

H4b: Root biomass is lowest under an intensive grazing regime

H5: Salt marsh carbon sequestration rates are lower on a grazed marsh than on an un-grazed marsh

The following chapters have addressed these overarching hypotheses in turn. The thesis starts by describing study sites and general methods used throughout the subsequent chapters (Chapter 2). The thesis then addresses potential influence of livestock grazing on above-ground patterns in the context of broad-scale environmental variation (Chapter 3). This chapter investigates whether the impacts of grazing override the impacts of environmental variables, as shown in previous small-scale studies (Jensen, 1985; Kiehl et al., 1996), but on the broad-scale.

Chapter 4 tests whether the above-ground impacts of grazing translate to below-ground carbon stocks, to inform potential management schemes for optimising the ecosystem service of carbon sequestration. This chapter specifically asks the question: how do grazing impacts compare with other environmental variables in determining below-ground carbon stocks?

Chapter 5 builds on Chapter 4 by quantifying carbon fluxes and pools, and building a carbon budget model for an un-grazed salt marsh, to further understanding of the processes associated with carbon sequestration rates on salt marshes. Chapter 6 extends the modelling approach to grazed marshes to explore the impact of grazing in the context of multiple environmental variables on salt marsh carbon budgets. Chapters 5 and 6 address the main factors contributing to soil carbon sequestration on salt marshes, and Chapter 6 quantifies the relative importance of grazing as a disturbance on carbon sequestration rates in relation to broad-scale contextual variables. Finally, the discussion integrates the thesis and briefly explores the management implications of the work.

Chapter 2: General Methods and Study Sites

2.1 Study Region and Site Selection

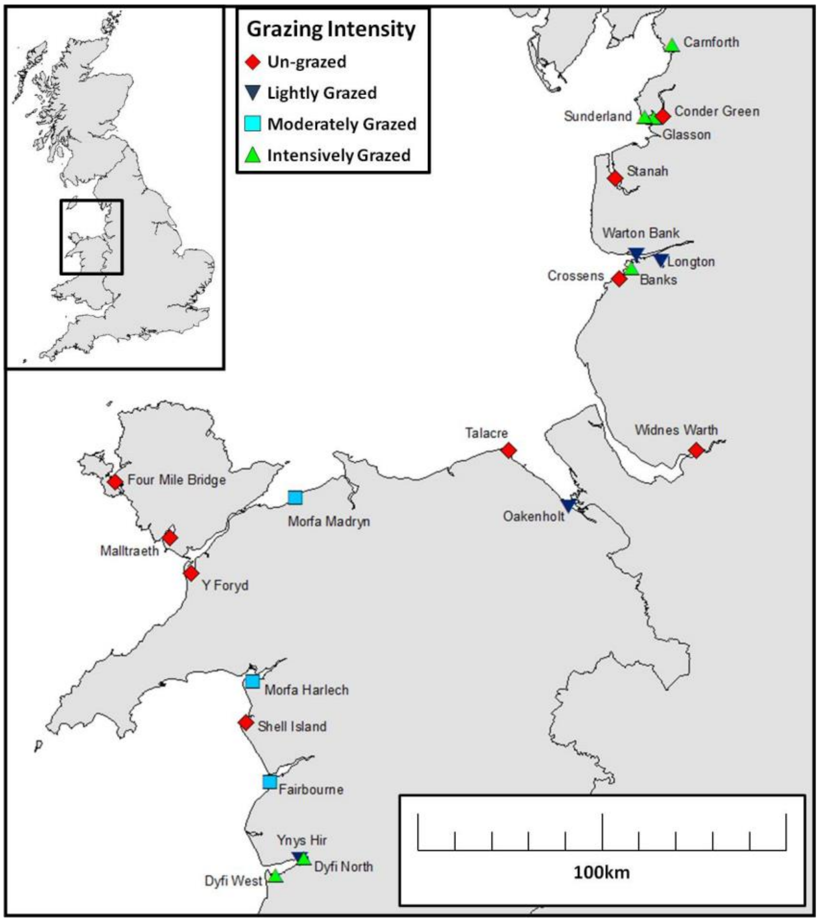


Figure 2.1 | Study area and site locations. Twenty-two salt marshes were selected across the ~650 km coastline between the Dyfi Estuary, Mid Wales, and Morecambe Bay, NW England.

An approximately 650 km stretch of coastline between the Dyfi Estuary, Mid Wales, and Morecambe Bay, NW England was selected for study (Figure 2.1). The study area was defined by biogeographical limits. Salt marshes in the UK occur in one of four biogeographical regions characterised by distinct vegetation communities: south eastern, western, western Scottish and eastern Scottish regions (Adam, 1990g). To reduce variability in the data, the 22 study sites were selected to be within the western biogeographical region. The northern sites in Morecambe Bay (Figure 2.1) were near the northern limit of the western biogeographical region. The southern limit of the study area was in the Dyfi Estuary (Figure 2.1). The western biogeographical zone extends further south than the Dyfi Estuary, but sites were selected to be within a three-hour drive from Bangor, Gwynedd. There were approximately 35 salt marshes within the study area. Only 22 were sampled, however, the remaining marshes were either unsuitable for the study (i.e. too small or too freshwater dominated), or access was refused by the land owner. Table 2.1 lists the general characteristics of each site.

Table 2.1 | Study site details. Environmental and grazing characteristics for the 22 study sites. Marsh area was measured using ArcGIS software (ArcMap 10) and Ordnance Survey 1:25,000 Land Ranger maps from Edina Digimaps (EDINA, 2010). Marsh geomorphology was classified according to Allen (2000). The grain size was determined as a mean for all marsh zones within each marsh, where clay = 0.2-2 µm silt = 2-20 µm, fine sand = 20-200 µm, and coarse sand = 200-2000 µm. Grazing intensity was determined for each site using the calculated stocking density per hectare per year. Historical grazing information is also shown for each marsh.

Marsh Name	BNG Grid Reference	Thesis Chapters Featuring the Site	Area (ha)	Marsh Geomorphology	Zones Sampled	NVC Plant Community by Zone	Average Marsh Grain Size (5-7cm depth)	Grazing Intensity Category	Current Stocking Rate (LSU/ha/yr)	Livestock Type	Livestock Numbers	Grazing Duration per year	Historical Grazing Details
Dyfi West	SN 62749 93642	3, 4, 5 & 6	134	Estuarine back-barrier	Mid Low Pioneer	SM16c SM13a SM9	Silt + Fine Sand	Intensively Grazed	0.79	Sheep (Geese)	200 2500	All year	As current
Ynys Hir	SN 67857 97121	3, 4, 5 & 6	225	Estuarine fringing	High Mid	SM16b SM13	Silt + Fine Sand	Lightly Grazed	0.26	Sheep (Geese)	500 2500	140 days/year	Intensive sheep and cattle grazing before 2000
Dyfi North	SN 68761 97392	3 & 4	54	Estuarine fringing	High	SM13	Silt	Intensively Grazed	3.45	Sheep Cattle (Geese)	400 50 2500	All year	As current
Fairbourne	SH 61474 13776	3, 4, 5 & 6	41	Estuarine back-barrier	Mid Low Pioneer	SM13d SM13a SM10	Silt	Moderately Grazed	0.70	Sheep	270 108	Aug-Mar Mar-Jul	As current
Shell Island	SH 56065 26477	3 & 4	60	Restricted-entrance embayment	High Mid Low	SM15 SM13d SM12a	Silt	Un-grazed	0.00	N/A	N/A	N/A	As current
Morfa Harlech	SH 57690 35232	3, 4, 5 & 6	236	Estuarine back-barrier	High Mid Low Pioneer	SM18a SM13a SM13a SM6	Silt + Fine Sand	Moderately Grazed	0.40	Sheep Cattle	200 20	May - October	As current
Y Foryd	SH 44482 58512	3, 4, 5 & 6	111	Restricted-entrance embayment	High Mid Low Pioneer	SM16d SM16d SM13d SM6	Silt (2-20µm)	Un-grazed	0.00	N/A	N/A	N/A	As current
Malltraeth	SH 39742 66134	3, 4, 5 & 6	80	Restricted-entrance embayment	High Mid Low Pioneer	SM8 SM13d SM13a SM16d	Fine Sand	Un-grazed	0.00	N/A	N/A	N/A	As current
Four Mile Bridge	SH 28148 78038	3 & 4	5	Restricted-entrance embayment	High Mid Low Pioneer	SM15 SM13d SM16d SM15	Fine Sand	Un-grazed	0.00	N/A	N/A	N/A	As current

Table 2.1 (Cont.) | Marsh details.

Marsh Name	BNG Grid Reference	Thesis Chapters Featuring the Site	Area (ha)	Marsh Geomorphology	Zones Sampled	NVC Plant Community by Zone	Average Marsh Grain Size (5-7cm depth)	Grazing Intensity Category	Current Stocking Rate (LSU/ha/yr)	Livestock Type	Livestock Numbers	Grazing Duration per year	Historical Grazing Details
Morfa Madryn	SH 66919 74629	3, 4, 5 & 6	14	Open coast back-barrier	Mid	SM13a	Silt + Fine Sand	Moderately Grazed	0.70	Sheep	60-70	All year	As current
Talacre	SJ 12550 84799	3 & 4	11	Estuarine back-barrier	Mid Low	SM14a SM10	Silt	Un-grazed	0.00	N/A	N/A	N/A	As current
Oakenholt	SJ 25667 72756	3, 4, 5 & 6	63	Estuarine fringing	Mid Low	SM13 SM13	Silt	Lightly Grazed	0.29	Sheep	120	All year	As current
Widnes Warth	SJ 52747 84954	3 & 4	41	Estuarine fringing	High	SM28	Silt	Un-grazed	0.00	N/A	N/A	N/A	Light cattle grazing before 1999
Crossens*	SD 36189 21676	3, 4, 5 & 6	58	Open coast	High Mid Low	SM16a/SM28 SM16d SM13a	Silt	Lightly Grazed / Un-grazed	0.1 (high marsh only)	Cattle / N/A	25 / N/A	May - October	As current
Banks Marsh†	SD 39078 23861	3 & 4	704	Estuarine fringing	Mid	SM13/SM13a	Silt	Intensively Grazed / Un-grazed	0.82	Cattle	575	All year	As current
Longton	SD 45374 25461	3 & 4	312	Estuarine fringing	High	SM16d	Silt	Lightly Grazed	0.24	Sheep Cattle	400 40-50	Cattle on Dec - Mar	As current
Warton Bank	SD 40208 26614	3, 4, 5 & 6	237	Estuarine fringing	High Mid	SM13 SM13a	Silt + Fine Sand	Lightly Grazed	0.19	Cattle	80-100	April - September	As current

* Crossens is a large marsh which is mostly un-grazed. The top of the marsh (the landward side of the high marsh zone) is fenced off and is lightly grazed by 100 cattle for half of the year. The seaward half of the high marsh zone, the mid and the low marsh zones all remain un-grazed. The community composition in the grazed high marsh is SM16a and the community composition in the un-grazed high marsh is SM28.

† Banks Marsh is a large marsh that is intensively grazed by sheep and cattle along the landward edges. An extensive creek system makes access to the seaward edge of the marsh difficult for livestock; as such the seaward edge of the marsh remains un-grazed. The community composition in the grazed area is SM13 and the community composition in the un-grazed area is SM13a.

Table 2.1 (Cont.) | Marsh details.

Marsh Name	BNG Grid Reference	Thesis Chapters Featuring the Site	Area (ha)	Marsh Geomorphology	Zones Sampled	NVC Plant Community by Zone	Average Marsh Grain Size (5-7cm depth)	Grazing Intensity Category	Current Stocking Rate (LSU/ha/yr)	Livestock Type	Livestock Numbers	Grazing Duration per year	Historical Grazing Details
Stanah	SD 35472 43247	3 & 4	21	Estuarine fringing	Mid Low	SM14a SM13a	Silt	Un-grazed	0.00	N/A	N/A	N/A	As current
Glasson	SD 43981 56127	3 & 4	35	Open embayment	High Mid Low Pioneer	SM16d SM16d SM6 SM6	Silt	Intensively Grazed	2.26	Sheep Cattle	1000 10-100	140 days per year	As current
Conder Green	SD 45673 56416	3 & 4	26	Estuarine fringing	High Mid Low Pioneer	SM28 SM16d SM13a SM6	Silt	Un-grazed	0.00	N/A	N/A	N/A	Light sheep grazing before 1990
Sunderland	SD 41860 56333	3, 4, 5 & 6	53	Open coast	High Mid Low Pioneer	SM16c SM16c SM13a SM8	Silt	Intensively Grazed	0.82	Cattle	50-80	March - September	As current
Carnforth	SD 47808 71776	3, 4, 5 & 6	110	Open coast	High Mid	SM16e SM16d	Fine Sand	Intensively Grazed	0.72	Sheep	650 400	Mar - Sept Sept - Mar	As current

2.2 Grazing Regimes

2.2.1 Site grazing information

Information on current and historical livestock density for each marsh was obtained from Natural England (NE), Natural Resources Wales (NRW, formerly Countryside Council for Wales), and individual landowners. The sites were subject to a range of grazing regimes (Table 2.1). Most marshes had had a consistent grazing regime for the past 30 years or more (Table 2.1). Three marshes had been previously grazed at a different grazing intensity than the current grazing regime: Ynys Hir, Widnes Warth and Conder Green. Conder Green was grazed more than 20 years before the study was conducted. Ynys Hir was intensively grazed until 10 years before the study. Widnes Warth was lightly grazed until 11 years before the study.

2.2.2 Quantifying grazing regimes

Marshes were grazed by cattle and sheep (Table 2.1). The study used Livestock Units per hectare per year (LSU ha^{-1} yr^{-1}) to standardise livestock density across grazer types where one LSU = 1 cow or 6.6 sheep (DEFRA guidelines; (Woodend, 2010)). Governmental grazing regulators, such as NRW, typically distinguish four levels of grazing intensity: un-grazed, lightly grazed, moderately grazed and intensively grazed. To make the study comparable to management schemes and other grazing studies, we categorized our marshes into un-grazed (0 LSU $ha^{-1}yr^{-1}$), lightly grazed (<0.3 LSU $ha^{-1}yr^{-1}$), moderately grazed (0.3-0.7 LSU $ha^{-1}yr^{-1}$) and intensively grazed (>0.7 LSU$ha^{-1}yr^{-1}$) using a scale adapted from *Tir Gofal*, an agri-environment scheme in Wales (Table 2.2). Grazing intensity categories of the marshes surveyed were comparable to those observed in the general literature on grazing (Appendix 1: Grazing Intensities in Other Studies). There was no systematic geographical pattern in grazing intensities across the study area.

Table 2.2 | Total number of marshes and zones sampled within each grazing intensity category. Two marshes (Crossens and Banks Marsh) had distinct un-grazed and grazed areas (Table 2.1) and thus are included in two grazing intensity categories.

	Un-grazed	Lightly Grazed	Moderately Grazed	Intensively Grazed
Total Marshes	**10**	**4**	**5**	**6**
High Marsh Zones	7	4	1	4
Mid Marsh Zones	9	2	4	5
Low Marsh Zones	8	0	3	3
Pioneer Marsh Zones	5	0	2	3

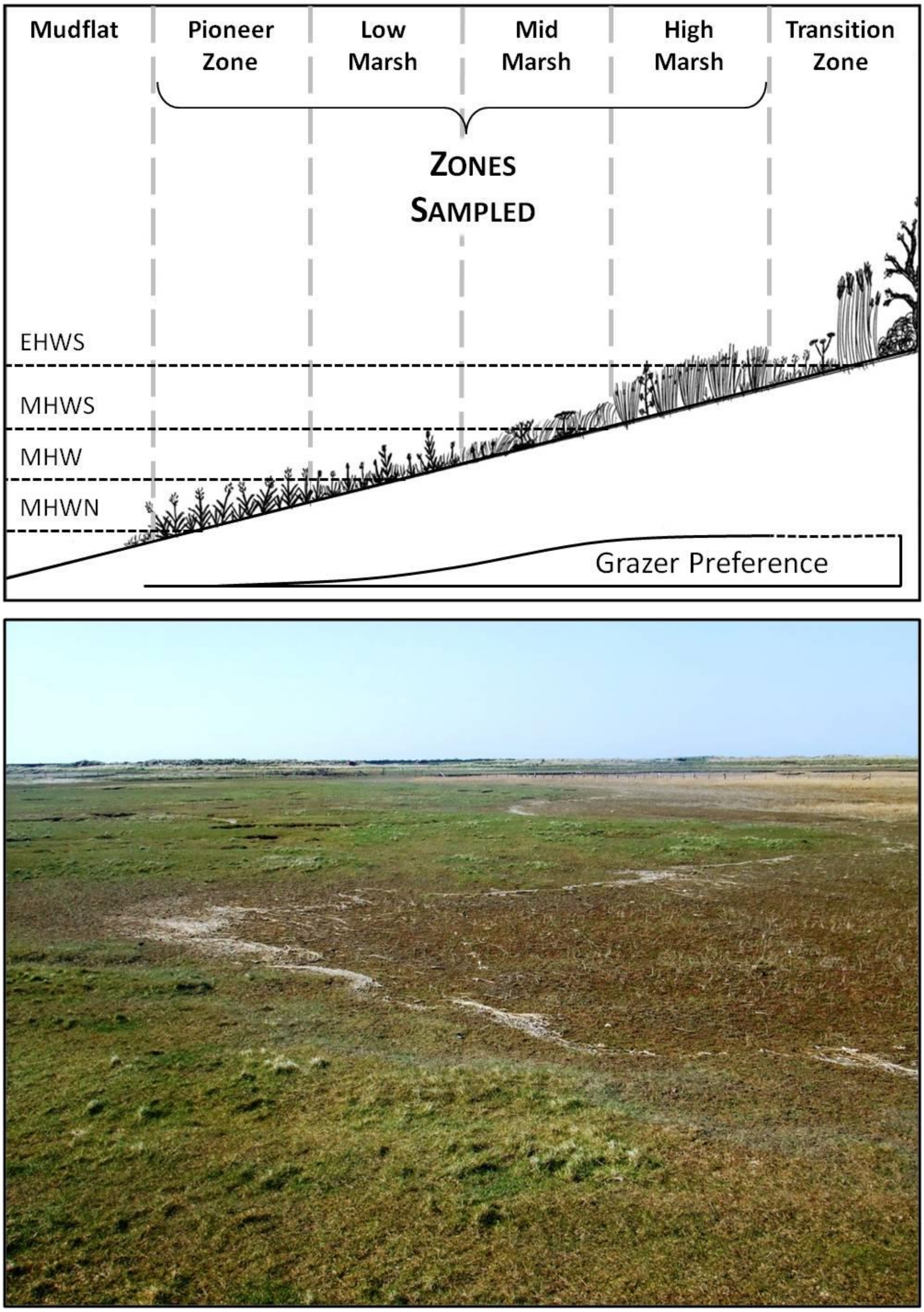
a
b


Figure 2.2 | Zonation in a salt marsh. a) A diagrammatic representation of a salt marsh showing zonation according to tidal inundation: extreme high water spring (EHWS), mean high water spring (MHWS), mean high water (MHW) and mean high water neap (MHWN). Only the pioneer, low, mid and high zones were sampled in this study. Grazer preference is indicated showing decreased grazing activity in the lower zones. **b)** An example of clear zonation between a low marsh zone and a pioneer marsh zone. The edge of the zone is indicated by a change in elevation, a strand line and a change in plant community composition.

2.3 Determination of Vertical Marsh Zones

Saltmarsh vegetation composition, flooding frequency and sedimentation rates change relative to shore elevation from seaward to landward edges of the marsh (Moeller, Spencer, French, Leggett, & Dixon, 1999; Stumpf, 1983). As such, four distinct marsh zones are classically recognised in the literature (pioneer, low, mid and high) (Figure 2.2a) (Adam, 1990b). The extent of each zone was determined using a combination of strand line position, marsh topography, tidal inundation observations, and vegetation community composition characteristics (Figure 2.2b). More emphasis was put on the first three techniques as grazing alters community composition (Jensen, 1985) and can cause reverse succession (J. P. Bakker, 1985; Kuijper & Bakker, 2004a); therefore on a grazed marsh, a higher marsh zone may be colonized by species from lower marsh zones. Fifteen of the 22 sites did not have all four zones present due to embankments at the landward edge of the marsh, or saltmarsh cliffs or riverbanks at the seaward edge of the marsh (Table 2.1).

2.4 General Sampling Design

The same general sampling design was used for each experimental chapter, thus some quadrats were sampled both above-ground and below-ground. The direct coupling of above and below-ground observations facilitated evaluations of above-below-ground relationships in Chapters 4, 5 and 6. Chapters 3 and 4 used all 22 study marshes in the study area to investigate the broad-scale impacts of livestock grazing on above-ground plant community characteristics and below-ground carbon stocks. A sub-set of 12 marshes were used to investigate the processes related to a salt marsh carbon budget and the effects of grazing and environmental context on salt marsh carbon budgets. The 12 sites were selected to incorporate a range of grazing intensities and contextual environmental variables as part of a balanced experimental design. Chapter 5 only used the three un-grazed marshes of the 12-marsh sub-set to construct a carbon budget for un-grazed salt marshes and to investigate the effects of seasonality and environmental setting on salt marsh carbon budgets. Chapter 6 used the nine grazed marshes in the sub-set to investigate the impact of livestock grazing on salt marsh carbon budgets in relation to environmental setting and seasonality.

2.4.1 Sample size and power

A priori power analyses using G*Power 3.1.5 (Faul, Erdfelder, Lang, & Buchner, 2007) were used to determine the required sample size per group (grazing intensity category) for each of the targeted predictor variables. The analysis used data from previous Masters projects from the study region (Honey, 2009; Lundquist, 2010) and data from comparable studies in the literature (Andresen et al., 1990; J. P. Bakker, 1985; Jensen, 1985; Kiehl et al., 1996). Effect size calculations predicted that the study data set was likely to show very large effect sizes (F>0.40) for each predictor variable (Cohen, 1988) (Table 2.3). The total number of samples taken in the study for above and below-ground sampling is shown in Table 2.4. The minimum total sample size for soil organic carbon (36 samples, Table 2.3) could not be met in lightly grazed and moderately grazed marshes due to regional scarcity in the numbers of marshes with these grazing intensity categories.

Table 2.3 | Effect sizes of simulated data. Simulated data set estimated from previous Masters projects and the literature with predicted effect size (Cohen's F) for each predictor variable by grazing intensity.

	Un-grazed		Lightly Grazed		Moderately Grazed		Intensively Grazed		Effect Size	Minimum Sample
Predictor variable	$\bar{x}$	*SD*	$\bar{x}$	*SD*	$\bar{x}$	*SD*	$\bar{x}$	*SD*	**(*F*)**	**Size (*n*)**
Species richness (d)	0.9	0.1	1.2	0.1	1.3	0.10	0.6	0.1	2.74	8
Overall % cover	100.0	10.0	95.0	10.0	75.0	10.0	50.0	10.0	1.97	12
Vegetation height (cm)	17.9	4.6	15.5	2.75	10.6	1.25	7.5	1.2	1.66	12
Above-ground biomass (g cm^{-3})	1.5	0.5	1.0	0.3	0.7	0.3	0.5	0.2	1.16	16
Vegetation litter (g cm^{-3})	0.5	0.2	0.1	0.1	0.0	0.0	0.0	0.0	2.38	8
Root biomass (g cm^{-3})	3.2	1.3	2.7	0.1	3.0	0.6	4.8	1.9	0.79	32
Maximum root depth (cm)	40.0	20.0	30.0	15.0	25.0	10.0	10.0	7.0	0.83	24
Soil organic carbon (%)	22.7	1.2	14.6	6.7	15.8	10.3	23.1	1.6	0.78	36

Table 2.4 | Study sample size. Total number of above-ground (AG) and below-ground (BG) samples per grazing intensity in the study followed by total number of above and below-ground samples per zone (pioneer, low, mid and high) per grazing intensity. Overall total number of above-ground and below-ground samples and totals for each zone are shown in the bottom row.

	Total	Total	Pioneer		Low		Mid		High	
Grazing Intensity	**AG**	**BG**	**AG**	**BG**	**AG**	**BG**	**AG**	**BG**	**AG**	**BG**
Un-grazed	280	112	40	16	80	32	90	36	70	28
Lightly grazed	90	32	0	0	10	4	30	12	40	16
Moderately grazed	80	32	20	8	20	8	30	12	10	4
Intensively grazed	150	60	30	12	30	12	50	20	40	16
Overall Total	**600**	**236**	**100**	**36**	**140**	**56**	**200**	**80**	**160**	**64**

2.4.2 Sampling design

Sampling was stratified by the four marsh zones (pioneer, low, mid and high) (Adam, 1990b). A representative 100 metre cross shore belt was selected within each marsh zone. Salt marsh vegetation can be patchy across large areas (van de Koppel, van der Wal, Bakker, & Herman, 2005), and on some marsh sites, the cross shore belts had to be split into two sections to more accurately represent the overall vegetation community within a zone. A random number generator was used to place ten 2×2 metre plots along each cross-shore belt. Salt pans, pools and areas less than 2 metres from creek edges were excluded from the sample belt. All 10 plots were used for the study investigating the impacts of grazing on above-ground plant community characteristics (Chapter 3). Four of the ten plots per zone (plot numbers 1, 4, 7 and 10) were selected for the broad-scale below-ground measurements (Chapter 4). This was to reduce the number of soil cores sampled, minimizing the risk of root matter degradation before the laboratory analysis was complete. The carbon budget study (Chapters 5 & 6) focused on the mid marsh exclusively. The mid marsh was considered representative of the whole marsh; it is not subject to the extremes wave and tidal disturbance of the pioneer zone or the terrestrial influences of the high marsh, yet it is still subject to regular tidal flooding and it is colonized by halophytic plants from across all the marsh zones (Adam, 1990b). There were also more than two mid marsh zones within each grazing intensity category (Table 2.3). The four below-ground plots (plot numbers 1, 4, 7 and 10) from the broad-scale study were used in the carbon budget study so that comparisons could be drawn to both above and below-ground parameters in the broad-scale study.

2.5 Sampling of Contextual Environmental Variables

The study collected the following contextual environmental variables as indicators of contextual drivers of salt marsh productivity and carbon storing processes.

2.5.1 Marsh size and geomorphology

The size and geomorphology of a marsh are determined by the physical setting of the marsh and the relative impact of tidal range and wave exposure. Several contextual variables depend on marsh area and geomorphology, such as wave stress, nutrient regimes and sediment regimes (Allen, 2000). These contextual variables all potentially impact soil organic carbon stocks; wave stress is directly related to sedimentation and erosion rates across a marsh (Spencer, Moeller, & French, 1995), nutrient regimes affect plant growth rates (Anisfeld & Hill, 2012; Loomis & Craft, 2010), and the sediment regime dictates several below-ground processes (Warnaars & Eavis, 1972). The area of each study site was calculated in ArcGIS software (ArcMap 10) based on Ordnance Survey 1:25,000 Landranger maps from Edina Digimap (EDINA, 2010). Marsh morphology was classified into seven marsh types (open coast, open coast back-barrier, open embayment, restricted entrance embayment, estuarine fringing, estuarine back-barrier, ria/loch-head) according to the geomorphological classifications from Allen (2000) (Table 2.4).

2.5.2 Wave fetch

Wave fetch is directly related to wave height and energy; the greater the fetch, the greater the wave height and energy (Burrows, Harvey, & Robb, 2008). Wave energy is an environmental stress for the salt marsh plant community (Spencer et al., 1995), and is related to small and large-scale erosion on salt marshes (Moeller, Spencer, French, Leggett, & Dixon, 2001), which can be a significant output of carbon from salt marshes to the marine system (Boorman, 2000; Chalmers, Wiegert, & Wolf, 1985; Marani, D'Alpaos, Lanzoni, & Santalucia, 2011; van de Koppel et al., 2005). Wave fetch was measured according to methods outlined by Burrows et al. (2008): using Ordnance Survey 1:25,000 Landranger maps and UK and Ireland coastal outlines in ArcGIS software (ArcMap 10), the maximum potential wave fetch was calculated by measuring the greatest uninterrupted distance to land from the low intertidal edge of each marsh. Wave fetch was also calculated from the direction of the prevailing wind. The prevailing wind direction was calculated from daily weather data from nearby weather stations for each marsh (Steremberg, 2010); the distance to the nearest coastline in the direction of the prevailing wind was calculated. In some cases the prevailing wind was an offshore wind (i.e. came from the landward edge of the marsh, rather than the seaward edge) and thus prevailing wave fetch was recorded as zero.

2.5.3 Tidal range

Tidal range determines the relative size of each salt marsh zone, the upper and lower limits of each zone and marsh, and thus determines many of the soil and plant properties across the marsh (Adam, 1990a). Tidal range was calculated using Tide Plotter 2010-13 from Belfield Software (BelfieldSoftware, 2010).

2.5.4 Particle size distribution

Particle size distribution (grain size) is a soil physical parameter that can affect several below-ground processes, such as soil porosity, root growth rates, and soil stability (Warnaars & Eavis, 1972). Grain size samples were taken from the soil cores taken at each study site. The 5-7 cm depth sample was analysed for all cores to give an estimation of the soil grain size in the depth with the highest root biomass. A range of depths (0-2cm, 5-7cm, 11-13cm, 22-24cm and 44-46cm) were analysed from a sub-set of cores to give a general overview of how grain size changes down the soil profile. Samples were dried at 30°C for ~ 1 week and then broken up gently using a small pestle and mortar. Approximately three grams of each sample was used and organic matter was removed by adding 5ml of 6% Hydrogen Peroxide (H_2O_2) followed by 1-5 drops of 30% H_2O_2 until the supernatant of each sample was clear; samples were heated to 80°C for 1.5 hours each time H_2O_2 was added. A Mastersizer 2000 laser particle sizer was then used to measure the grain size of each sample: 99

grain size fractions were measured on a logarithmic scale from 0.2-2000μm and the percentage of each fraction within each sample was recorded.

2.5.5 Water quality

Water quality and nutrient variables were obtained from the Environment Agency. These included nutrients that relate to plant productivity (dissolved inorganic nitrogen, orthophosphate and silicates), plant stressors (water pH and water salinity) and physical parameters (suspended solids) (Howard & Mendelssohn, 1998; Parrondo et al., 1978; Valiela, Teal, & Persson, 1976). The data did not cover all marshes, as it was available only for those situated in large estuaries. These data were therefore only used in models with a reduced number of marshes throughout the data analyses.

2.6 The Study Site Details

Dyfi West (Dyfi Estuary)

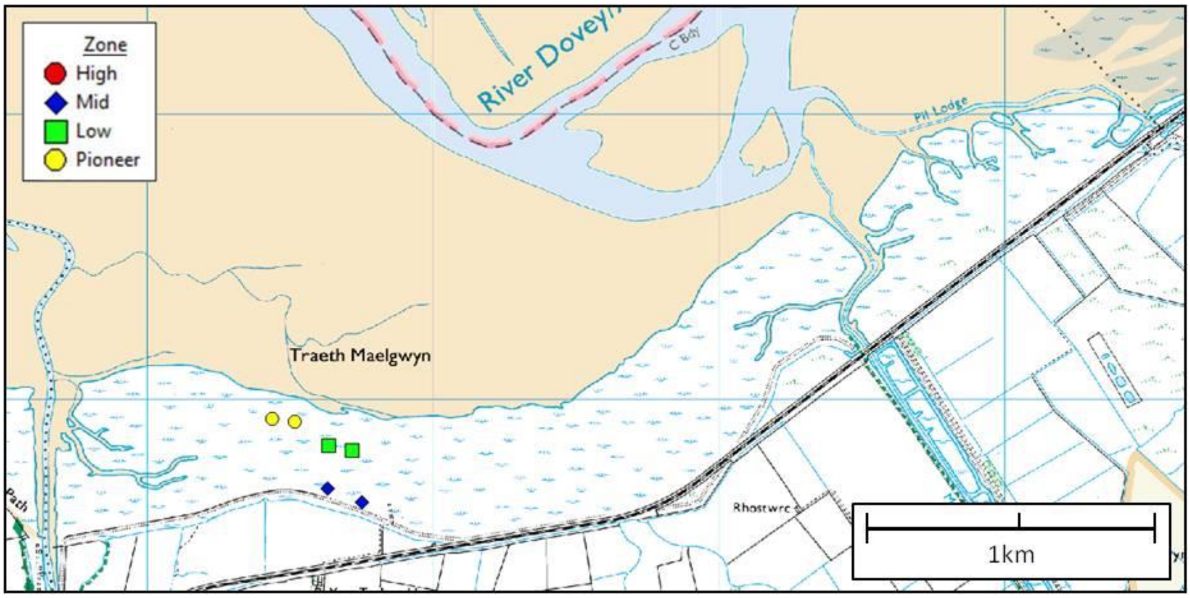


Figure 2.3 | Map of Dyfi West marsh. Ordnance Survey Map OL23 (2010k) showing start and end points of mid, low and pioneer zone cross-shore sample belts.

Grid Reference (BNG): SN 627 936

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Estuarine back-barrier

Zones Present: Mid, Low & Pioneer

Grazing Intensity: Intensive (0.79 LSU ha^{-1} yr^{-1})

Situated at the seaward end of the Dyfi Estuary on the south bank, Dyfi West is owned by a local farmer and managed by Natural Resources Wales (NRW) below mean high water neap (below the pioneer zone). The marsh is grazed by sheep and geese. The Dyfi Estuary hosts the largest population of Canada geese in the UK so in this estuary alone, geese have been included in the LSU calculations where 1 LSU = 22 geese. There is no high marsh zone due to the presence of an embankment. The mid marsh zone is intermittent and situated along the southern edge of the marsh, next to the embankment; it consists of a closely grazed *Puccinellia maritima* sward and patches of *Juncus maritimus* with *Atriplex prostrata*. The low marsh is fairly extensive, particularly further east, and is broken up by several small creeks. It is dominated by *Puccinellia maritima* and *Suaeda maritima*. The pioneer zone is more extensive to the west and consists mainly of *Spartina anglica* and *Suaeda maritima*.

Ynys Hir (Dyfi Estuary)

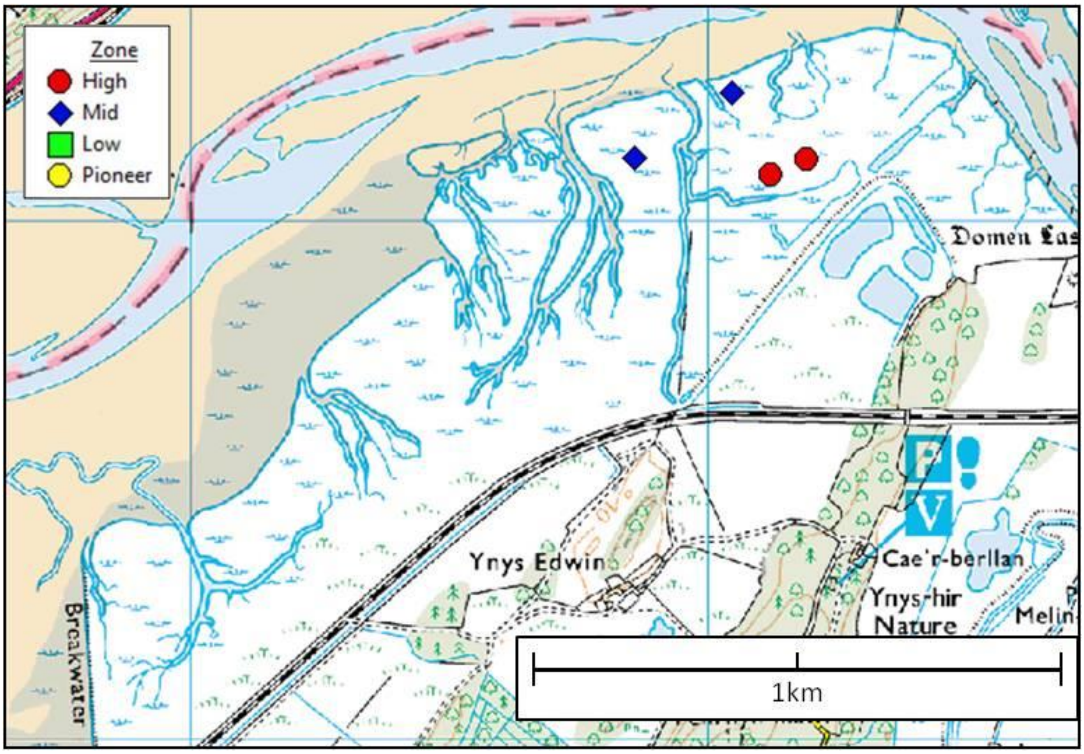


Figure 2.4 | Map of Ynys Hir marsh. Ordnance Survey Map OL23 (2010k) showing start and end points of high and mid zone cross-shore sample belts.

Grid Reference (BNG): SN 678 971

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Estuarine fringing

Zones Present: High & Mid

Grazing Intensity: Light (0.26 LSU ha^{-1} yr^{-1})

Ynys Hir is situated on the south bank of the Dyfi Estuary between Afon Clettwr and Glandyfi. It is owned by the RSPB and hosts the bulk of the largest population of Canada geese in the UK (around 2,500), as well as Greenland White Fronted geese and Barnacle geese. For this reason, the marshes on the Dyfi Estuary have geese included in the LSU calculations (where 22 geese = 1 LSU). This marsh is lightly grazed by sheep, but until 2001 there were up to 2,500 sheep on the marsh. High and mid marsh zones are present, with some *Glaux maritima* (<5% cover) on the sand flats in front of the marsh. The mid marsh consists of heavily grazed *Armeria maritima* and *Puccinellia maritima* between *Juncus maritimus* patches, while the high marsh is more evenly grazed with a relatively tall *Festuca rubra* sward. Due to the heterogeneity of the vegetation in the mid marsh, the cross-shore sample belt was split into two parts to best represent the marsh vegetation. The mid marsh is truncated by the estuarine channel, with cliffs at the seaward edge of the marsh.

Dyfi North (Dyfi Estuary)

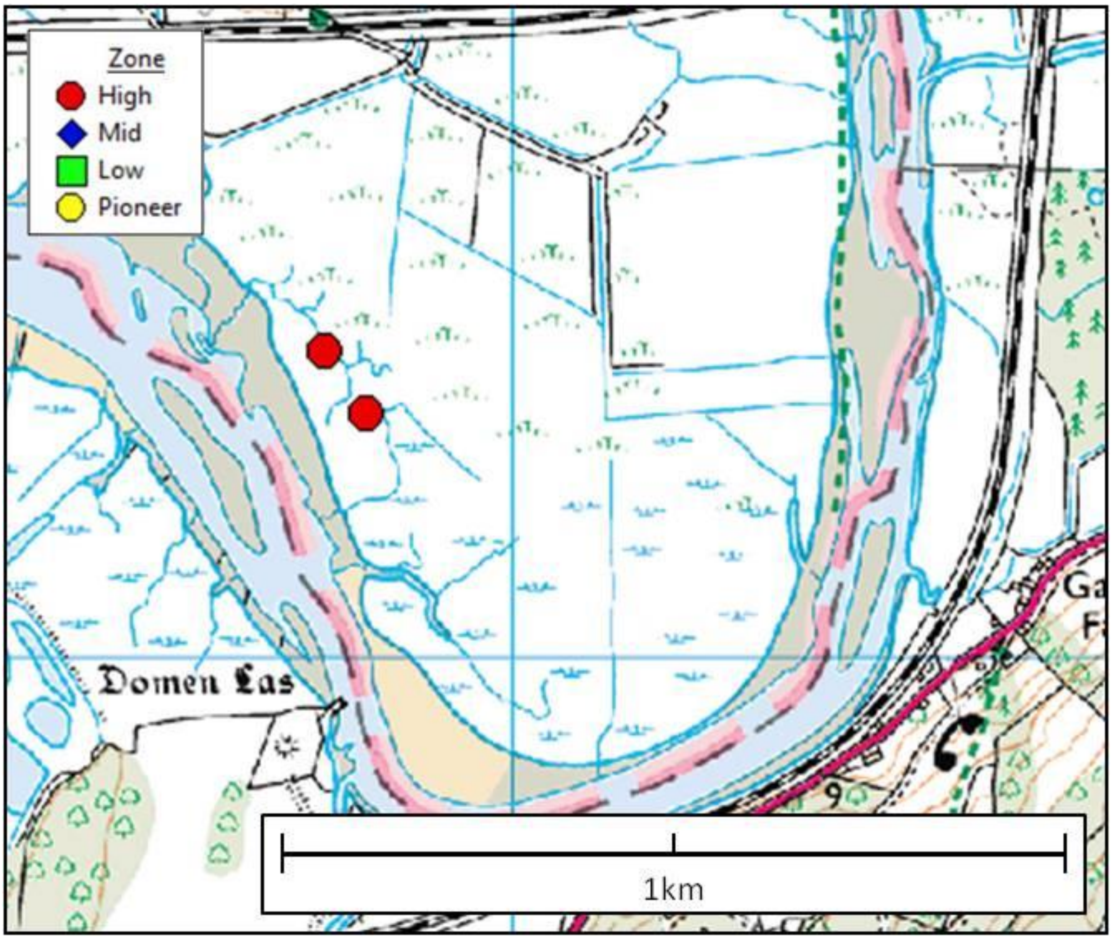


Figure 2.5 | Map of Dyfi North marsh. Ordnance Survey Map OL23 (2010k) showing start and end points of high zone cross shore sample belt.

Grid Reference (BNG): SN 687 973

Used in Chapters: 3 & 4

Marsh Type: Estuarine fringing

Zones Present: High

Grazing Intensity: Intensive (3.45 LSU ha^{-1} yr^{-1})

Situated on the north (Gwynedd) bank of the Dyfi Estuary, this marsh is owned by Montgomery Wildlife Trust and a local land owner who leases it out to a local farmer as grazing pasture. It is grazed by cattle, sheep and geese, which have been included in the LSU calculations. The salt marsh only occupies the fringe of the marsh area; the rest of the marsh area is a brackish marsh, which only occasionally gets flooded. Only the high marsh zone is present and it is dominated by a closely cropped *Puccinellia maritima* sward with small *Juncus maritimus* patches. The marsh is truncated by the estuarine channel, with cliffs at the seaward edge of the marsh.

Fairbourne (Mawddach Estuary)

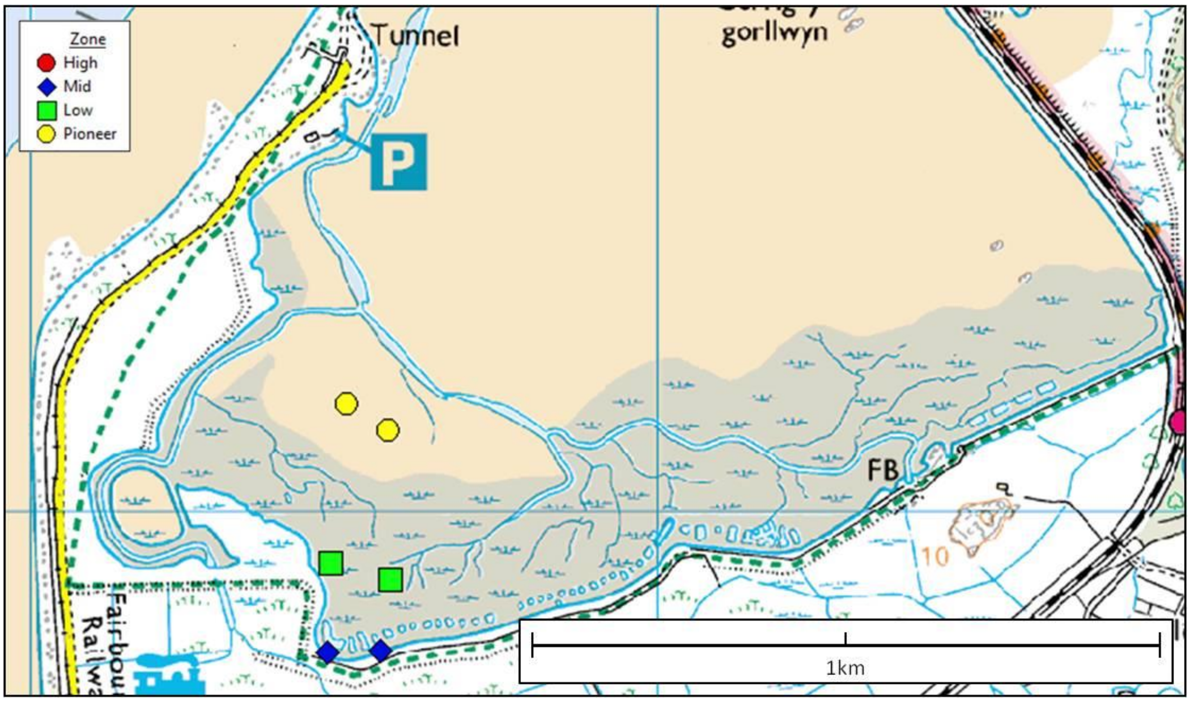


Figure 2.6 | Map of Fairbourne marsh. Ordnance Survey Map OL23 (2010k) showing start and end points of mid, low and pioneer zone cross-shore sample belts.

Grid Reference (BNG): SH 614 137

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Estuarine back-barrier

Zones Present: Mid, Low & Pioneer

Grazing Intensity: Moderate (0.70 LSU ha^{-1} yr^{-1})

This is a patchy and diverse marsh that has formed behind a spit of land at the end of the Mawddach Estuary near Fairbourne. It is managed by NRW and it is moderately grazed by sheep. There are some high marsh *Festuca rubra* patches along the west edge of the marsh but the marsh is truncated by an embankment around most of the marsh, limiting the extent of any high marsh vegetation communities. There is a narrow strip of mid marsh along the southern edge of the marsh, which is dominated by a closely cropped *Armeria maritima* sward. To the north of this is an extensive low marsh area dominated by *Spartina anglica* and *Festuca rubra*. Much of this area remains relatively un-grazed as deep creeks hinder access by sheep. The pioneer zone extends across the sand flats at the northern edge of the marsh and is dominated by *Salicornia europaea*.

Shell Island

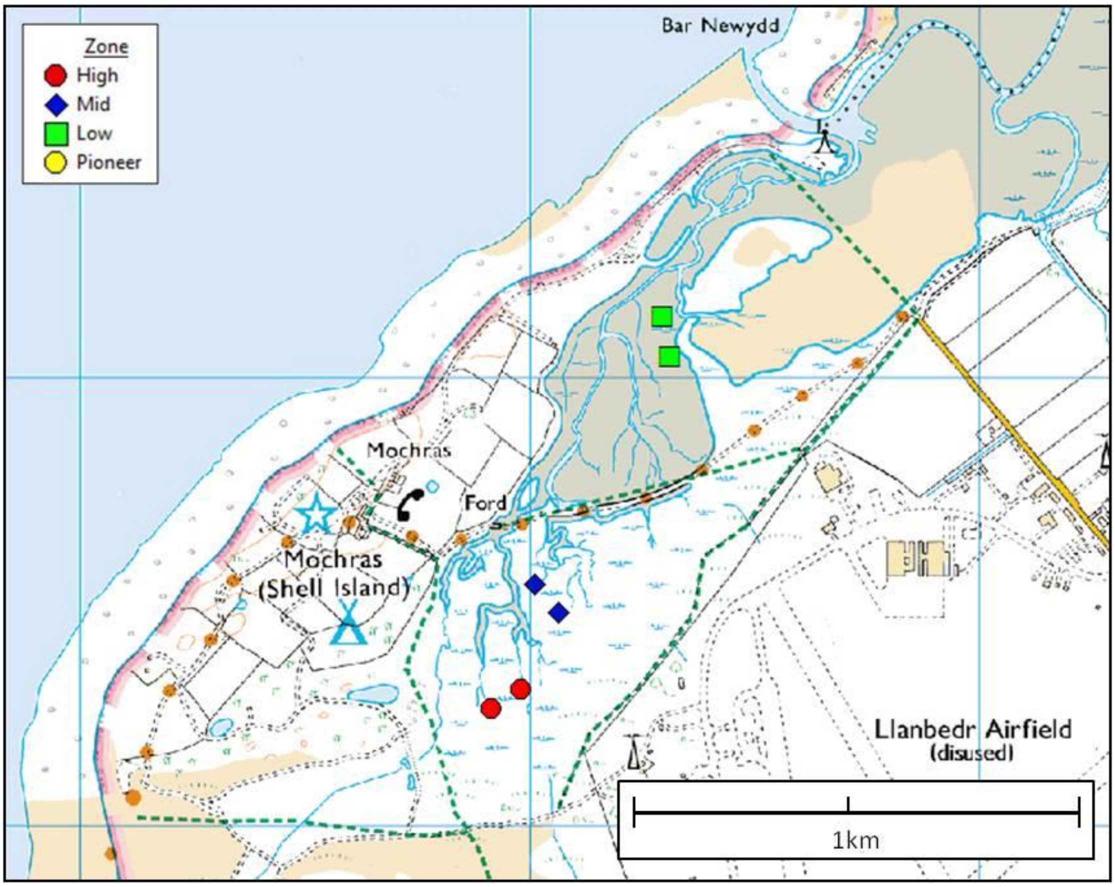


Figure 2.7 | Map of Shell Island marsh. Ordnance Survey Map OL18 (2010j) showing start and end points of high, mid and low zone cross-shore sample belts.

Grid Reference (BNG): SH 560 264

Used in Chapters: 3 & 4

Marsh Type: Restricted entrance embayment

Zones Present: High, Mid & Low

Grazing Intensity: Un-grazed

This marsh is situated in an enclosed embayment behind Shell Island. The marsh is bisected by an access road to the island. The island and the salt marsh are both owned by the campsite on Shell Island. At the top of the marsh there is a narrow *Phragmites australis* stand, below which is a narrow band of high marsh dominated by *Juncus maritimus* and *Atriplex prostrata.* The extensive mid marsh is diverse with relatively tall *Aster tripolium* and *Limonium humile*. *Atriplex portulacoides* bushes can be found along the banks of the large creeks, particularly in the mid and lower marsh. The low marsh on the northern edge of the marsh consists of *Spartina anglica* and *Suaeda maritima*. There is no pioneer zone and the marsh is bounded by a large creek.

Morfa Harlech

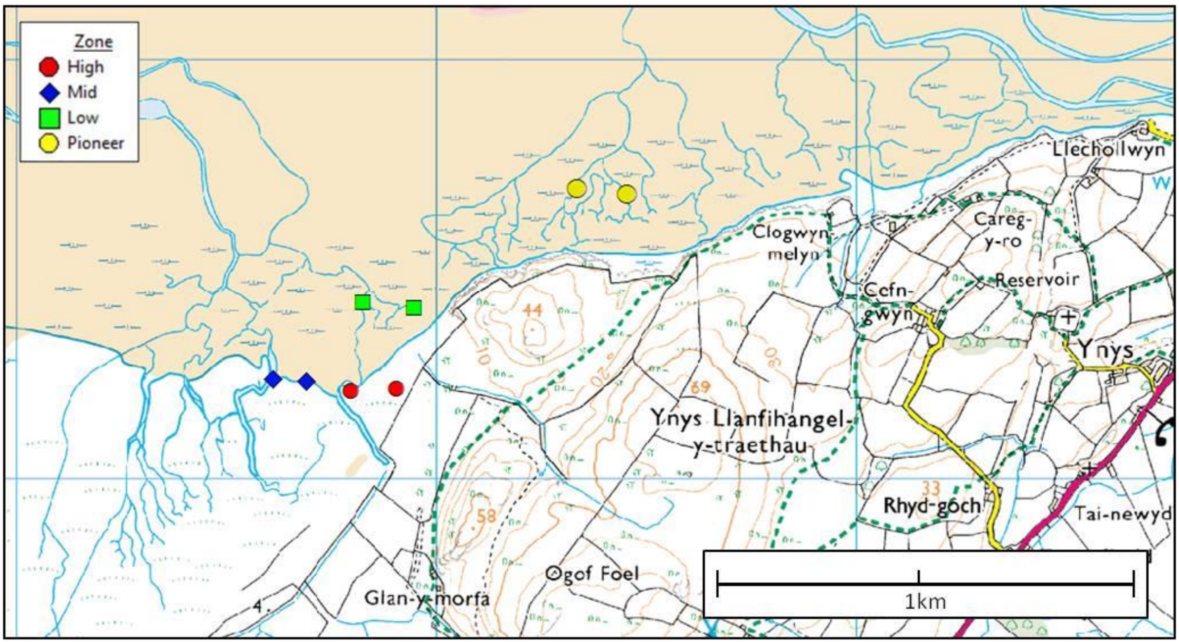


Figure 2.8 | Map of Morfa Harlech marsh. Ordnance Survey Map OL18 (2010j) showing start and end points of high, mid, low and pioneer zone cross-shore sample belts.

Grid Reference (BNG): SH 576 352

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Estuarine back-barrier

Zones Present: High, Mid, Low & Pioneer

Grazing Intensity: Moderate (0.40 LSU ha^{-1} yr^{-1})

This is a large marsh situated to the south of the Glaslyn Estuary, just north of Harlech. It is bordered by a large sand dune system to the south and west and it is owned by a local farmer and managed by NRW. Morfa Harlech is grazed mostly by cattle but there is also a small flock of sheep. The high marsh consists of extensive *Juncus maritimus* patches, while the mid marsh consists of a closely cropped yet highly diverse vegetation sward. There is little poaching (damage caused by trampling) in the mid marsh, possibly due to high levels of soil compaction. The low marsh also has a highly diverse sward but there is intensive poaching by the livestock, providing a very heterogeneous soil surface. The pioneer zone is an extensive, well-developed *Spartina anglica* sward. There are many large creeks and the marsh is difficult to cross in places; however, the presence of hoof prints indicates that the cattle seem to be able to reach all areas of the marsh.

Y Foryd

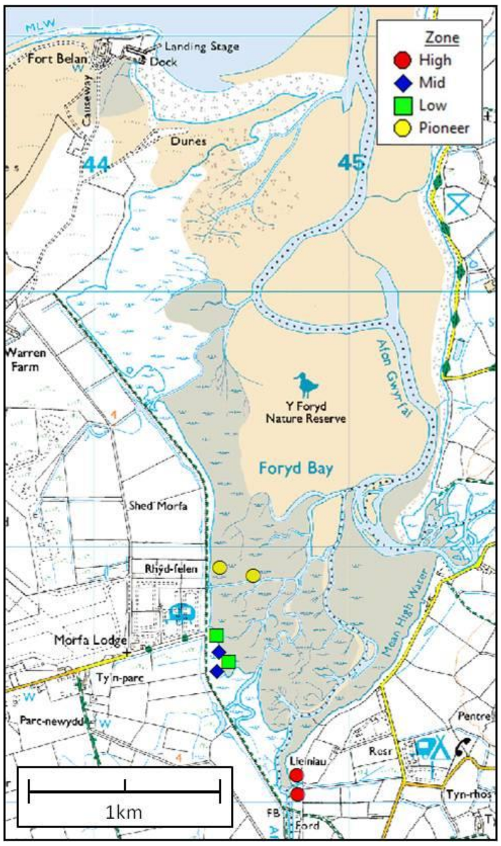


Figure 2.9 | Map of Y Foryd marsh. Ordnance Survey Map OL18 (2010i) showing start and end points of high, mid, low and pioneer zone cross-shore sample belts.

Grid Reference (BNG): SH 444 585

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Restricted entrance embayment

Zones Present: High, Mid, Low & Pioneer

Grazing Intensity: Un-grazed

This is a large marsh situated in the sheltered Afon Gwyrfai estuary west of Caernarfon. It is owned and managed by Gwynedd Council. On the eastern side of the river in the south-eastern corner there is a small patch of high marsh dominated by *Festuca rubra* and *Juncus maritimus*. The narrow mid marsh to the west of the river is truncated by an embankment on the western side and dominated by a diverse *Festuca rubra* community. The low marsh consists of a narrow band of a diverse *Plantago maritima* community along the eastern edge of the mid marsh zone. The pioneer zone covers a large area to the north of the mid and low marsh zones and is largely dominated by *Spartina anglica*.

Malltraeth

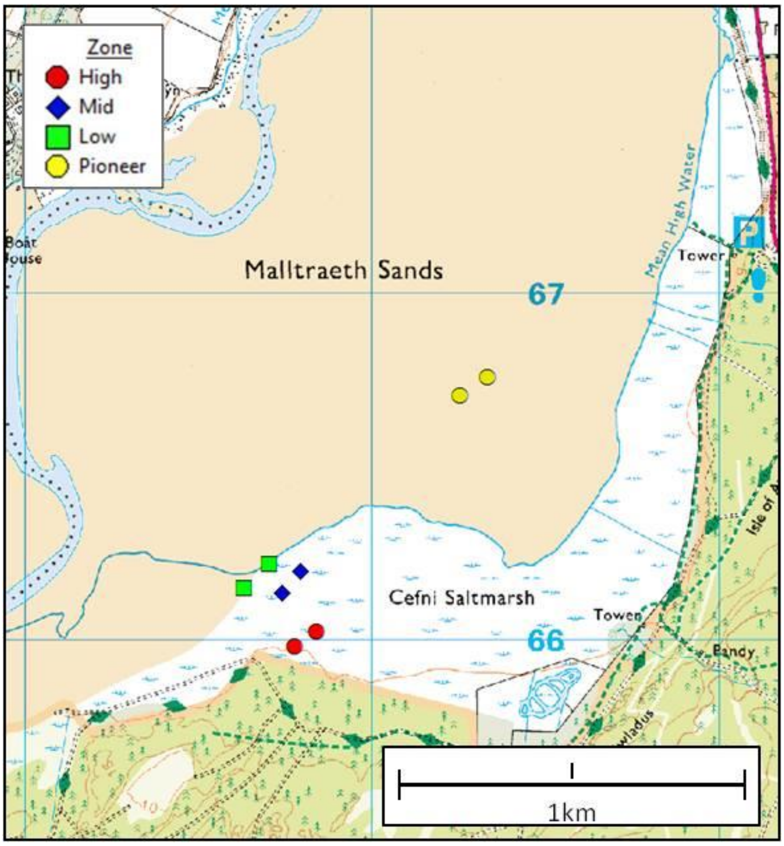


Figure 2.10 | Map of Malltraeth marsh (Cefni Saltmarsh). Ordnance Survey Map 263 (2010b) showing start and end points of high, mid, low and pioneer zone cross-shore sample belts.

Grid Reference (BNG): SH 397 661

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Restricted entrance embayment

Zones Present: High, Mid, Low & Pioneer

Grazing Intensity: Un-grazed

This marsh is situated just north-west of Newborough, Anglesey. It is owned and managed by NRW. The marsh is dominated by brackish water plants along the eastern edge, and west of this is an extensive high marsh, dominated by *Juncus maritimus* and *Festuca rubra*. The mid marsh zone is west of the high marsh zone and is more extensive to the south. It is dominated by a short, diverse sward punctuated by *Atriplex portulacoides* and *Juncus maritimus* patches. The low marsh is found along the western fringes of the marsh with more extensive patches to the south. It consists of a patchy sward dominated by *Spartina anglica* and *Puccinellia maritima*. The pioneer zone consists of large patches of *Salicornia europaea* on the sand flats to the north-west of the main marsh.

Four Mile Bridge

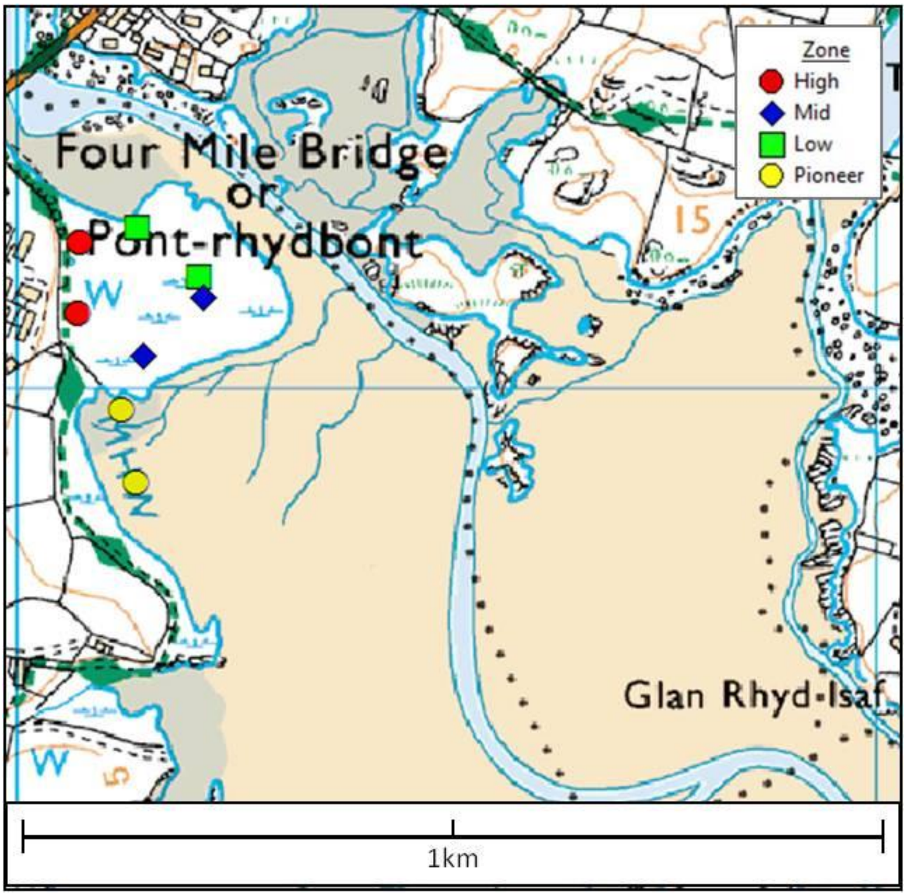


Figure 2.11 | Map of Four Mile Bridge marsh. Ordnance Survey Map 262 (2010a) showing start and end points of high, mid, low and pioneer zone cross-shore sample belts.

Grid Reference (BNG): SH 281 780

Used in Chapters: 3 & 4

Marsh Type: Restricted entrance embayment

Zones Present: High, Mid, Low & Pioneer

Grazing Intensity: Un-grazed

This is a small marsh situated on the edge of Holy Island, Anglesey, just north-west of RAF Valley. It is owned by a local farmer. The high marsh is a narrow strip near the footpath to the west of the marsh; it is dominated by *Juncus maritimus*. The low marsh is a small patch to the north of the marsh and is dominated by a short, diverse *Plantago maritima* sward. The mid marsh forms a sandy ridge running roughly south-west to north-east on the southern edge of the marsh and it is dominated by *Festuca rubra*. The pioneer zone is a large patch of *Spartina anglica* to the south of the main marsh.

Morfa Madryn

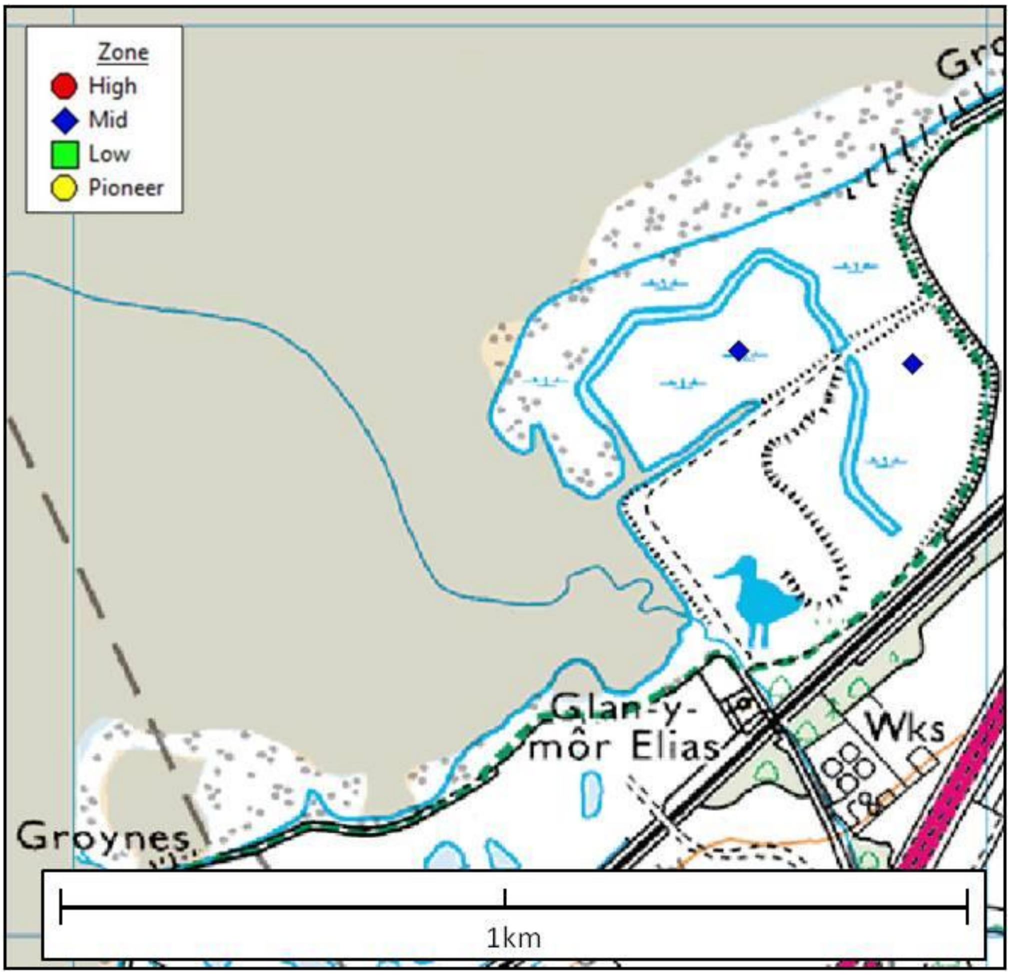


Figure 2.12 | Map of Morfa Madryn marsh. Ordnance Survey Map OL17 (2010i) showing start and end points of mid zone cross-shore sample belt.

Grid Reference (BNG): SH 669 746

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Open coast back-barrier

Zones Present: Mid

Grazing Intensity: Moderate (0.70 LSU ha^{-1} yr^{-1})

This is a small marsh situated behind a small spit of land to the south-east of Llanfairfechan. It is owned by Conwy Council and a local farmer has grazing rights. The marsh is bisected by an embankment and tidal flooding in the area to the south-east of the embankment occurs only via one large creek. Morfa Madryn is moderately grazed by sheep throughout the year. The marsh consists only of a mid marsh zone dominated by *Puccinellia maritima* but there are some patches of *Juncus gerardii* on the south-eastern section of the marsh.

Talacre (Dee Estuary)

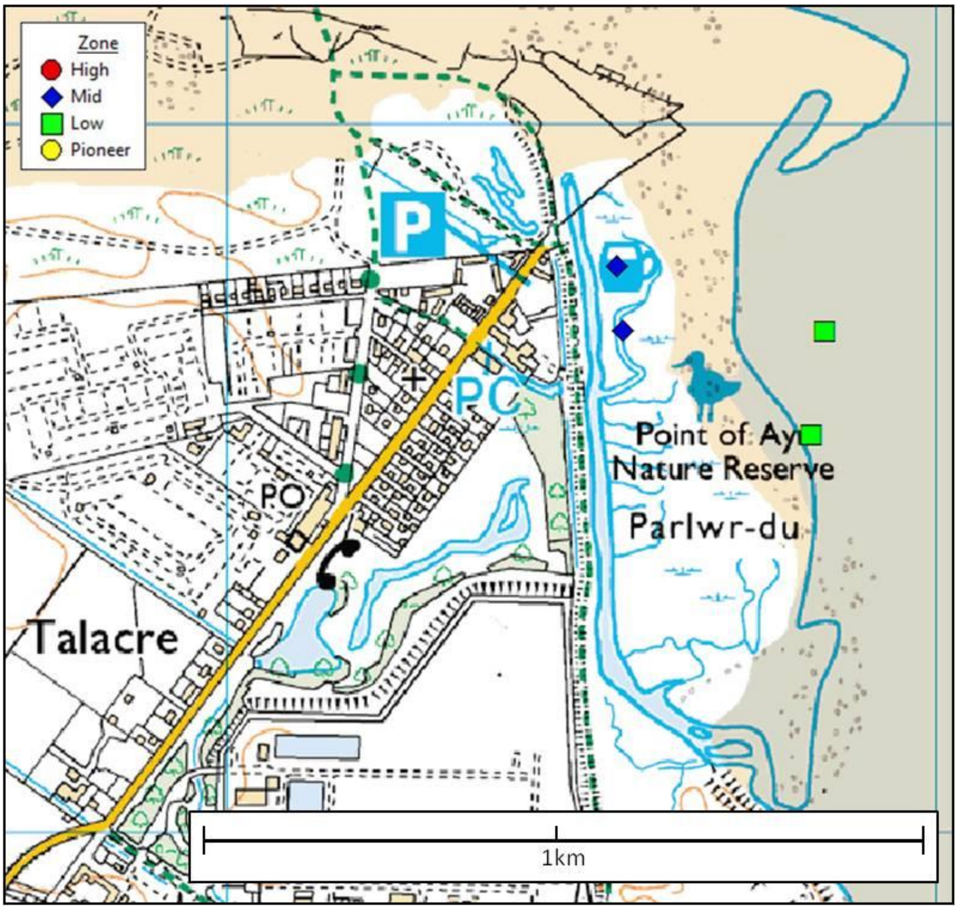


Figure 2.13 | Map of Talacre marsh. Ordnance Survey Map 265 (2010c) showing start and end points of mid and low zone cross-shore sample belts.

Grid Reference (BNG): SJ 125 847

Used in Chapters: 3 & 4

Marsh Type: Estuarine back-barrier

Zones Present: Mid & Low

Grazing Intensity: Un-grazed

Talacre is a small marsh developed behind a sand spit and dune system at the end of the Dee estuary on the Welsh (western) bank. It is owned and managed by Environment Agency Wales and the nearby gas plant (BHP Billiton). As the marsh is truncated by a steep embankment at the top, there is no high marsh present. The mid marsh is dominated by large *Atriplex portulacoides* bushes with some small patches of *Festuca rubra*. The low marsh is dominated by *Spartina anglica* and *Salicornia europaea*. In some raised areas of the marsh, the soil is very sandy, suggesting the marsh was formed over old sand dunes.

Oakenholt (Dee Estuary)

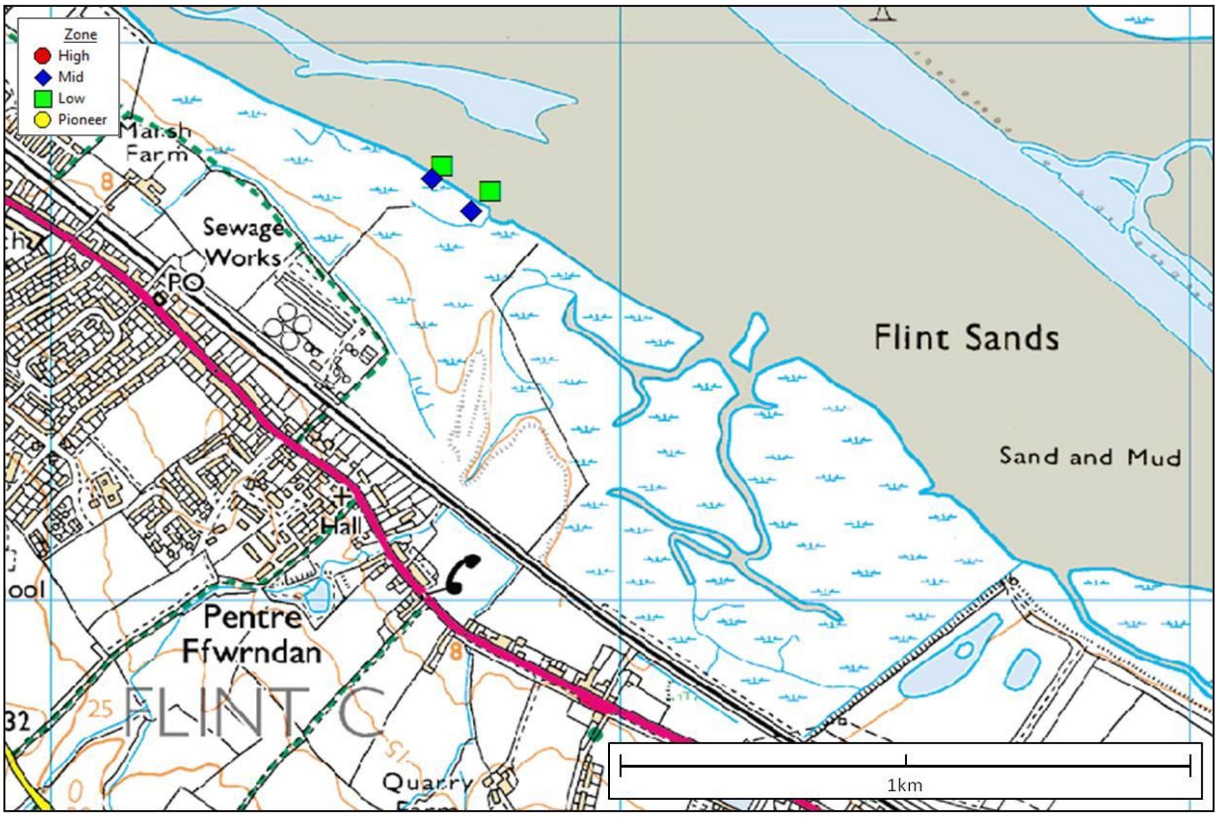


Figure 2.14 | Map of Oakenholt marsh. Ordnance Survey Map 266 (2010d) showing start and end points of mid and low zone cross-shore sample belts.

Grid Reference (BNG): SJ 256 727

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Estuarine fringing

Zones Present: Mid & Low

Grazing Intensity: Light (0.29 LSU ha^{-1} yr^{-1})

Oakenholt marsh is a long and narrow salt marsh situated on the Welsh bank of the Dee Estuary just south of Fflint. The southeastern area of the marsh is owned by the Royal Society for the Protection of Birds (RSPB) and the north-western part of the marsh, where this study was conducted, is owned by a local farmer. Oakenholt is moderately grazed by sheep. The high marsh consists only of a few isolated *Juncus maritimus* patches along the landward edge of the marsh. The extensive mid marsh consists of a short *Puccinellia maritima* community and is separated from the low marsh by a small salt marsh cliff. The low marsh is a narrow band along the seaward edge of the marsh dominated by *Spartina anglica* and *Puccinellia maritima*.

Widnes Warth (Mersey Estuary)

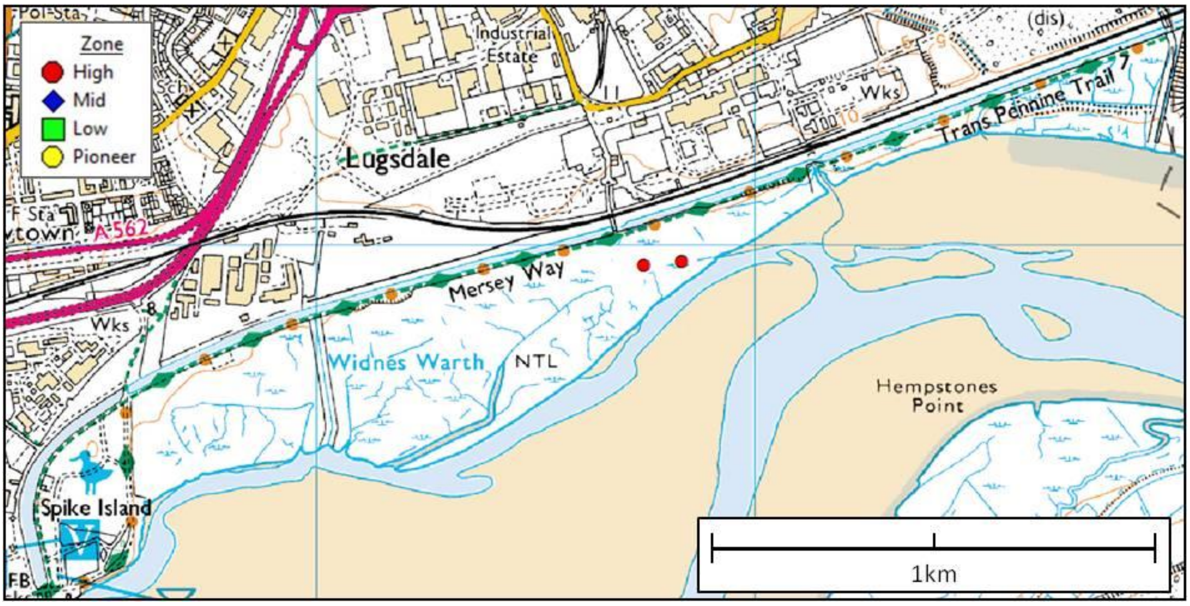


Figure 2.15 | Map of Widnes Warth marsh. Ordnance Survey Map 275 (2010e) showing start and end points of high zone cross-shore sample belt.

Grid Reference (BNG): SJ 527 849

Used in Chapters: 3 & 4

Marsh Type: Estuarine fringing

Zones Present: High

Grazing Intensity: Un-grazed (at time of survey)

This is a small marsh situated on the north bank of the Mersey at Widnes. It is owned by Halton Borough Council and is currently part of the Mersey Gateway Project, a construction program for a new bridge in 2012-14. As part of this project, six long-horn cattle were introduced to half of the marsh in 2011 for half the year, resulting in an intensive regime. The sampling on this site was completed in 2010, a year before the long-horned cattle were initially introduced. At the time of sampling the marsh was un-grazed and had not been grazed for 11 years. The site consists of a high marsh zone only, which is dominated by *Elymus repens* and *Atriplex prostrata*. There is a steep river bank at the edge of the marsh.

Crossens (Ribble Estuary)

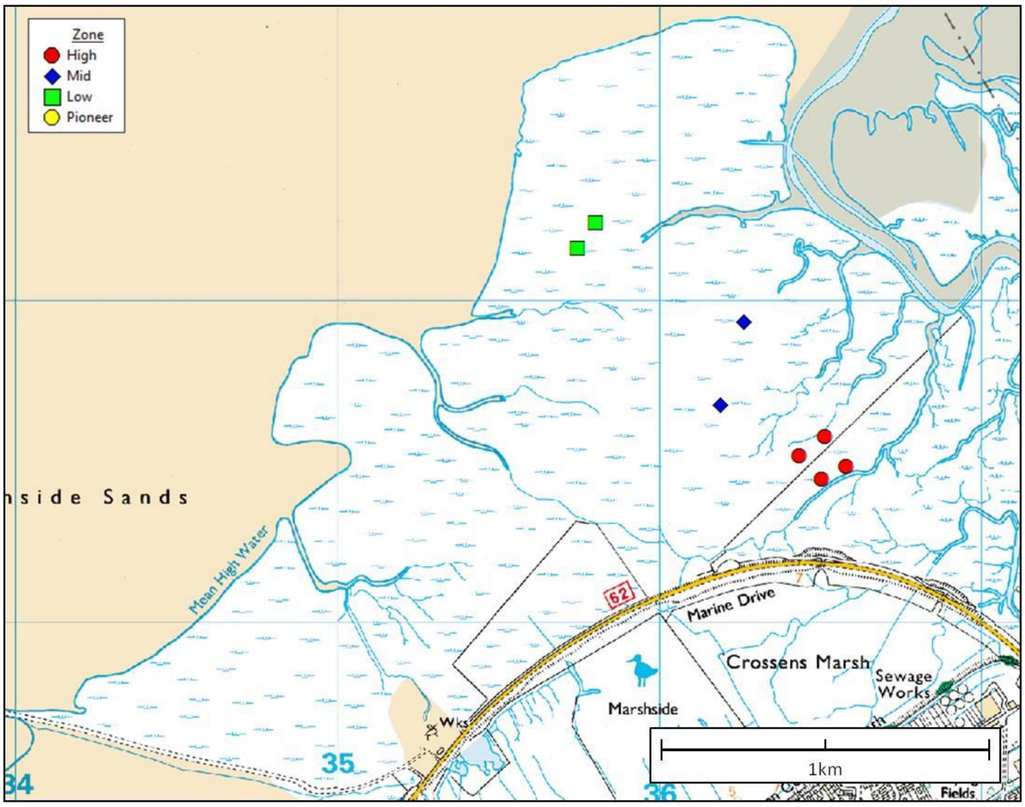


Figure 2.16 | Map of Crossens marsh. Ordnance Survey Map 286 (2010f) showing start and end points of high, mid and low zone cross-shore sample belts.

Grid Reference (BNG): SD 361 216

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Open coast

Zones Present: High, Mid & Low

Grazing Intensity: Light (0.10 LSU ha^{-1} yr^{-1}) – part of high marsh only

This is a large marsh situated on the end of the Ribble Estuary just north of Southport. It is owned and managed by Natural England. Apart from a small area lightly grazed by cattle at the top (east) of the marsh, this marsh is un-grazed. The grazed high marsh is dominated by a diverse *Puccinellia maritima* community while the more extensive un-grazed high marsh to the west of the fence line is dominated by tall *Elymus repens*. The mid marsh covers most of the marsh and consists of several large patches either dominated by *Aster tripolium* or *Puccinellia maritima*. The low marsh forms an approximately 100 metre wide band towards the west of the marsh, which becomes more extensive to the south. It is dominated by a diverse *Puccinellia maritima* and *Suaeda maritima* sward. There is a steep salt marsh cliff separating the low marsh from the extensive mud flats to the west.

Banks Marsh (Ribble Estuary)

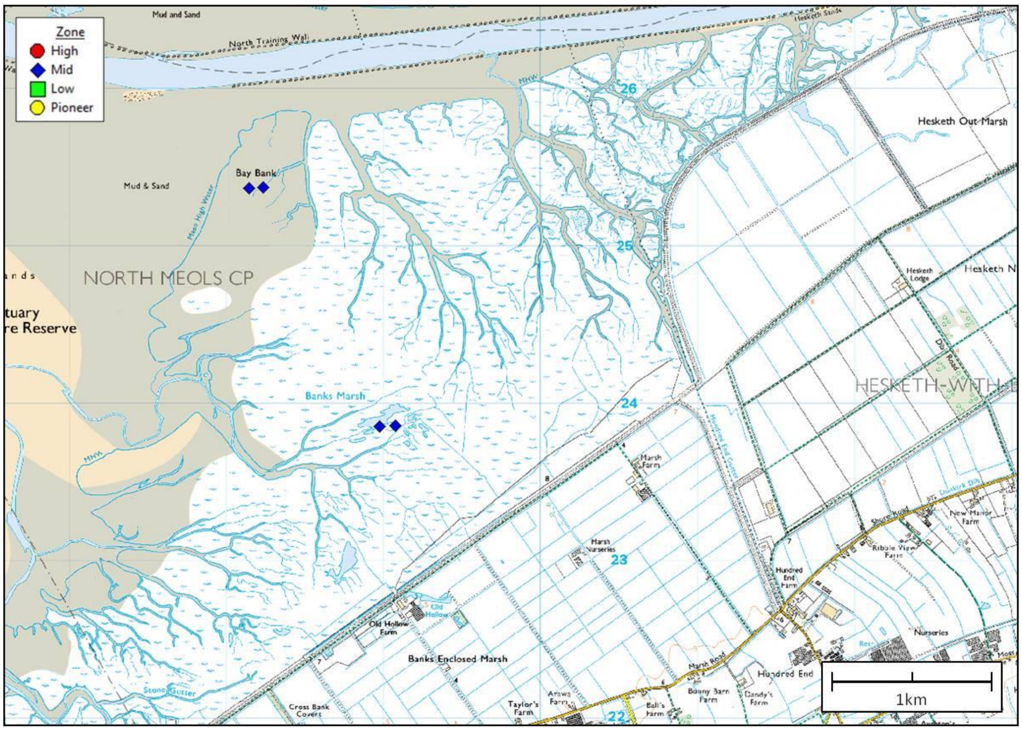


Figure 2.17 | Map of Banks Marsh. Ordnance Survey Map 286 (2010f) showing start and end points of mid zone cross-shore sample belts.

Grid Reference (BNG): SD 390 238

Used in Chapters: 3 & 4

Marsh Type: Estuarine fringing

Zones Present: Mid

Grazing Intensity: Intensive (0.82 LSU ha^{-1} yr^{-1}) – only in the southern half of the marsh

Banks Marsh is a large marsh situated on the south bank of the Ribble estuary. It is owned and managed by RSPB and Natural England. There is intensive sheep grazing to the east, and intensive cattle grazing along the south-east edge of the marsh. The livestock are not cut off from the rest of the marsh by fences but several large creeks make it difficult for livestock to reach the seaward (northern) half of the marsh. As a result, the northern part of the marsh is un-grazed. The upper marsh has been reclaimed as farm land and the main marsh consists of a large mid marsh zone north of a large embankment. The northern edge of the marsh is truncated by the estuarine channel, with cliffs at the seaward edge of the marsh. Samples were taken in both the grazed and the un-grazed areas of the marsh. The southern half of the marsh (grazed area) is dominated by *Puccinellia maritima*, and the bottom of the marsh (un-grazed area) is dominated by diverse *Atriplex portulacoides* and *Puccinellia maritima* swards.

Longton (Ribble Estuary)

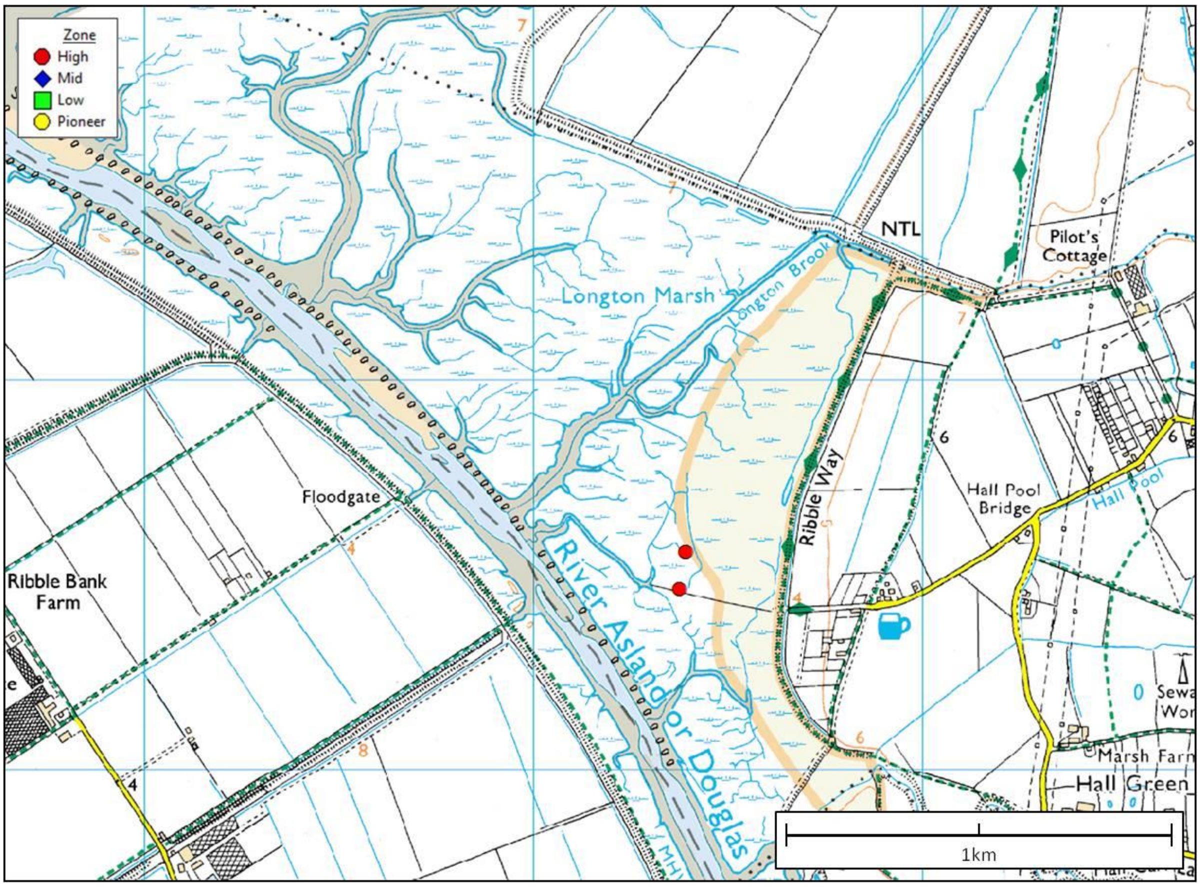


Figure 2.18 | Map of Longton Marsh. Ordnance Survey Map 286 (2010f) showing start and end points of high zone cross-shore sample belt.

Grid Reference (BNG): SD 453 254

Used in Chapters: 3 & 4

Marsh Type: Estuarine fringing

Zones Present: High

Grazing Intensity: Light (0.24 LSU ha^{-1} yr^{-1})

This marsh is situated on the south bank of the Ribble along one of its tributaries (River Asland/Douglas). The south of the marsh (the sample area) is owned by the RSPB and a local farmer, and a large area to the north is owned by a local wildfowlers association. Longton Marsh is currently lightly grazed by sheep and it has been grazed at this, or a similar stocking density for at least 150 years. There is an extensive high marsh dominated by *Festuca rubra*, but steep river cliffs to the west truncate the marsh so there are no lower marsh zones.

Warton Bank (Ribble Estuary)

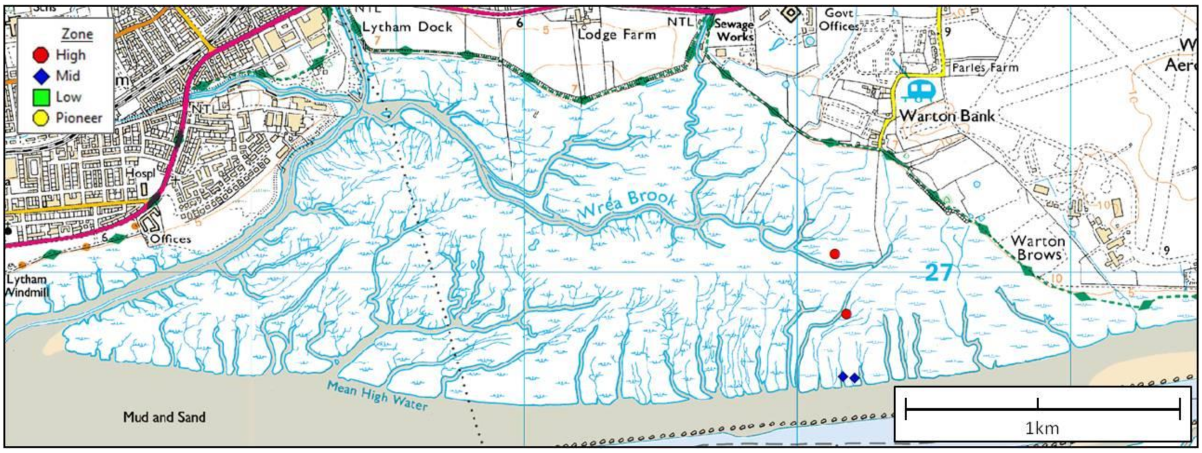


Figure 2.19 | Map of Warton Bank marsh. Ordnance Survey Map 286 (2010f) showing start and end points of high and mid zone cross-shore sample belts.

Grid Reference (BNG): SD 402 266

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Estuarine fringing

Zones Present: High & Mid

Grazing Intensity: Light (0.19 LSU ha^{-1} yr^{-1})

Warton Bank marsh is situated on the north bank of the Ribble Estuary opposite Banks Marsh. It is owned and managed by Lytham & District Wildfowlers Association and thus access is restricted during winter months due to wildfowl shooting. Warton Bank is lightly grazed throughout the summer months by cattle and has been grazed at a similar stocking density for at least 80 years. The mid marsh runs along the south edge of the marsh where many deep creeks make some areas difficult for livestock to access. It is dominated by a diverse *Puccinellia maritima* and *Spartina anglica* sward, and *Atriplex portulacoides* bushes can be found along the edges of the creeks. The high marsh is heavily poached (damage caused by the feet of livestock) in some areas, particularly around the access track. It is dominated by a diverse *Puccinellia maritima* sward interspersed with large patches of *Festuca rubra* and *Atriplex prostrata*. Due to this heterogeneity in the high marsh, the cross-shore sample belt was split into two sections to more accurately represent the vegetation composition of the marsh.

Stanah

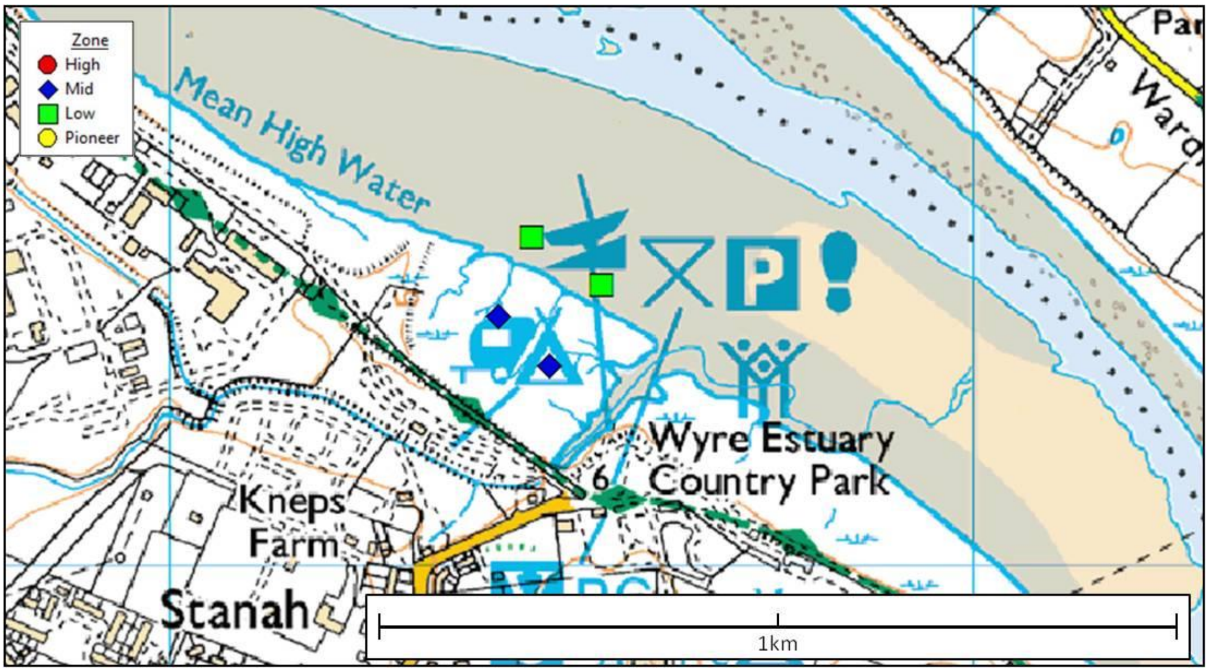


Figure 2.20 | Map of Stanah marsh. Ordnance Survey Map 296 (2010g) showing start and end points of mid and low zone cross-shore sample belts.

Grid Reference (BNG): SD 354 432

Used in Chapters: 3 & 4

Marsh Type: Estuarine fringing

Zones Present: Mid & Low

Grazing Intensity: Un-grazed

Stanah is a small, narrow marsh situated on the western bank of the Wyre Estuary, just south of Fleetwood. It is owned and managed by the Wyre Estuary Country Park and Wyre Borough Council. The mid marsh is dominated by large *Atriplex portulacoides* bushes and it is truncated by a large embankment at the land-ward edge of the marsh. The low marsh is situated along the river edge of the marsh and is dominated by a diverse *Puccinellia maritima*/*Suaeda maritima* sward.

Glasson (Lune Estuary)

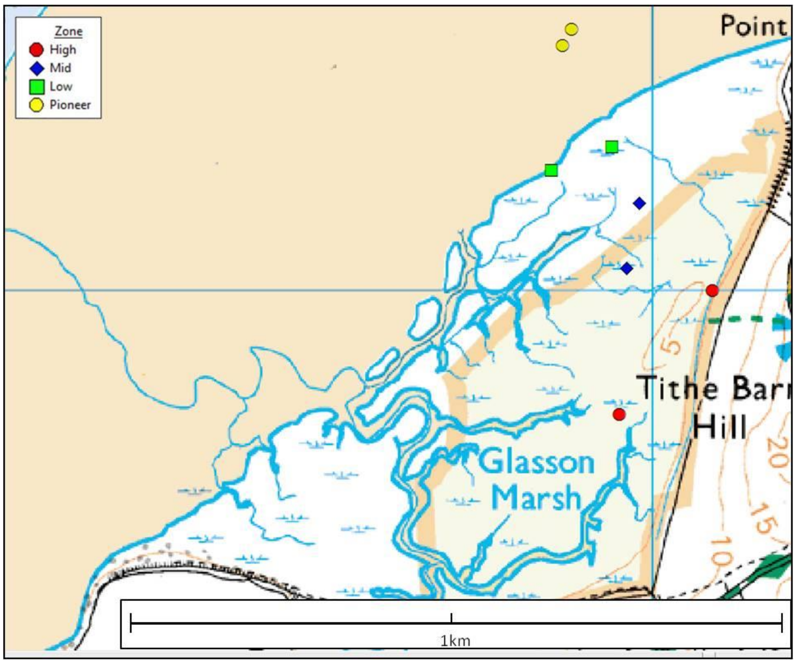


Figure 2.21 | Map of Glasson Marsh. Ordnance Survey Map 296 (2010g) showing start and end points of high, mid, low and pioneer zone cross-shore sample belts.

Grid Reference (BNG): SD 439 561

Used in Chapters: 3 & 4

Marsh Type: Open embayment

Zones Present: High, Mid, Low & Pioneer

Grazing Intensity: Intensive (2.26 LSU ha^{-1} yr^{-1})

Glasson Marsh is situated on the southern bank of the Lune Estuary, south of Lancaster. It is owned by two local farmers and is intensively grazed by both sheep and cattle. However, these livestock have access to adjacent terrestrial land so it is hard to quantify the stocking density of the marsh with confidence. There is an extensive high marsh zone below a steep hill (Tithe Barn Hill) to the east of the marsh. This high marsh is dominated by a diverse *Festuca rubra* sward interjected with large *Juncus maritimus* patches; the cross-shore sample belt was bisected to compensate for this heterogeneity. The mid marsh forms a sandy ridge in the middle of the low marsh zone and is dominated by low *Atriplex portulacoides* bushes. Due to an extensive creek system, the low marsh covers most of the marsh, starting just below the high marsh zone; it is dominated by a short *Puccinellia maritima* sward. The pioneer zone is a narrow band on the edge of the sand flats and is dominated by a sparse *Spartina anglica* sward.

Conder Green (Lune Estuary)

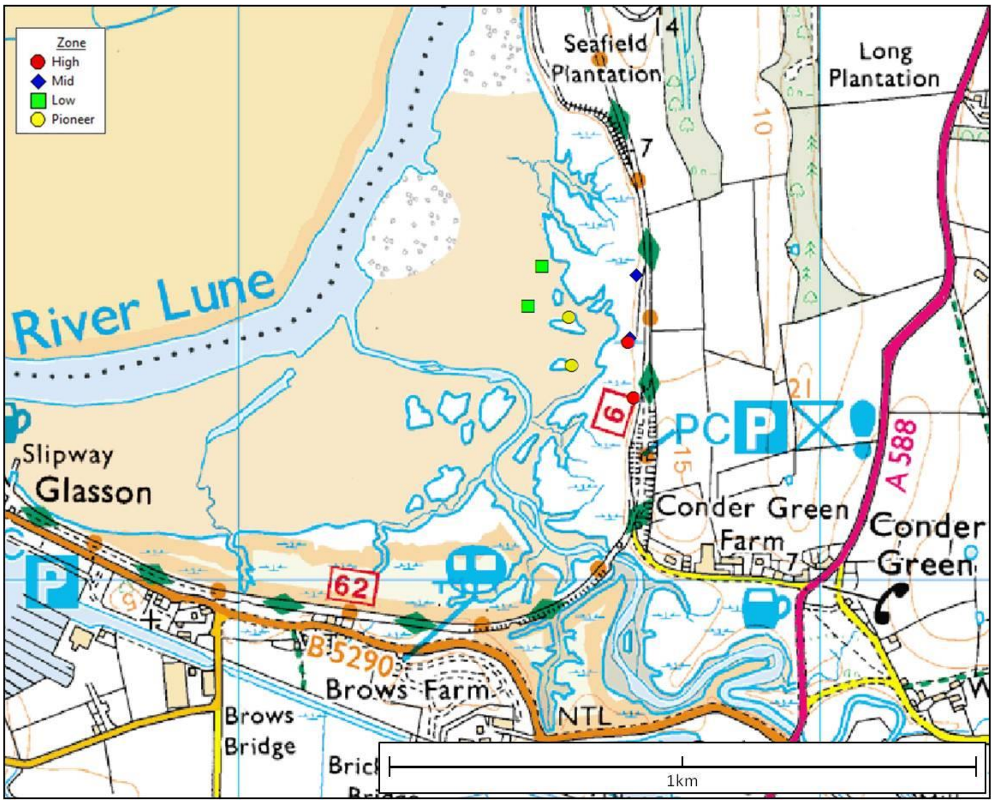


Figure 2.22 | Map of Conder Green. Ordnance Survey Map 296 (2010g) marsh showing start and end points of high, mid, low and pioneer zone cross-shore sample belts.

Grid Reference (BNG): SD 456 564

Used in Chapters: 3 & 4

Marsh Type: Estuarine fringing

Zones Present: High, Mid, Low & Pioneer

Grazing Intensity: Un-grazed

Conder Green is a small marsh situated on the south bank of the Lune Estuary along one of the tributaries. It is owned by a local land owner and has not been grazed in 20-30 years; before that it was lightly grazed by sheep. The high and mid marsh are truncated by a large embankment and are therefore within ten metres of the upper marsh edge. The high marsh along the south-east edge of the marsh is dominated by *Elymus repens*, and the mid marsh along the north-east edge of the marsh is dominated by a diverse *Festuca rubra* sward. The high and mid marsh drop down sharply to an extensive pioneer zone dominated by *Spartina anglica*. The low marsh forms a ridge on the river edge of the marsh and is truncated by a steep river bank; it is dominated by a diverse *Puccinellia maritima*/*Suaeda maritima* sward.

Sunderland (Morecambe Bay)

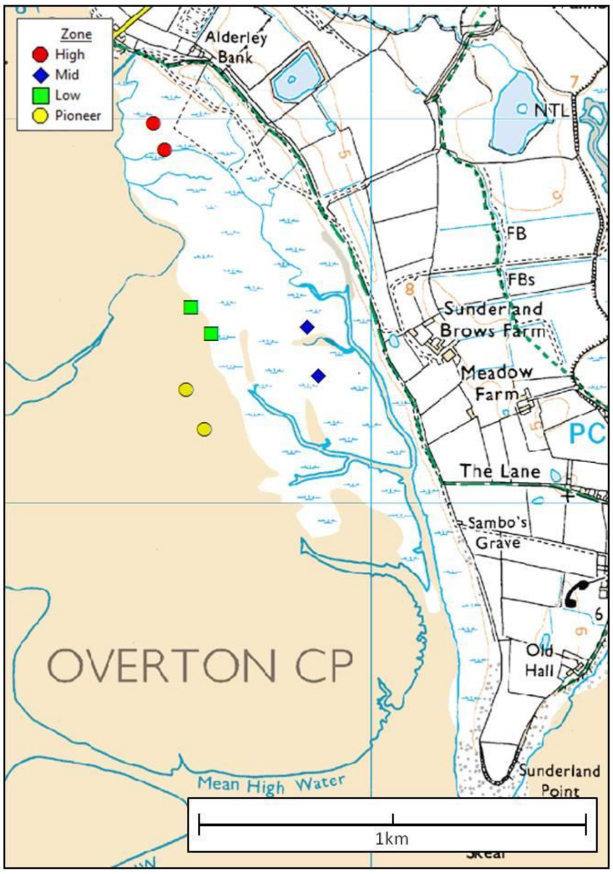


Figure 2.23 | Map of Sunderland marsh. Ordnance Survey Map 296 (2010g) showing start and end points of high, mid, low and pioneer zone cross-shore sample belts.

Grid Reference (BNG): SD 418 563

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Open coast

Zones Present: High, Mid, Low & Pioneer

Grazing Intensity: Intensive (0.82 LSU ha^{-1} yr^{-1})

Sunderland is a long and relatively narrow marsh situated on the coast to the north of the Lune Estuary. It is owned by a local farmer and heavily grazed by young cattle. The high marsh to the north of the marsh is dominated by a short *Festuca rubra* sward. The extensive mid marsh covers most of the marsh area and is also dominated by a short *Festuca rubra* sward; however it is broken up by several large *Juncus maritimus* patches. The low marsh is a narrow strip along the western edge of the marsh and consists of many hummocks that are dominated by a diverse *Puccinellia maritima* sward. The pioneer zone is a sparse but expansive *Salicornia* patch on the sand flats to the west of the marsh.

Carnforth (Morecambe Bay)

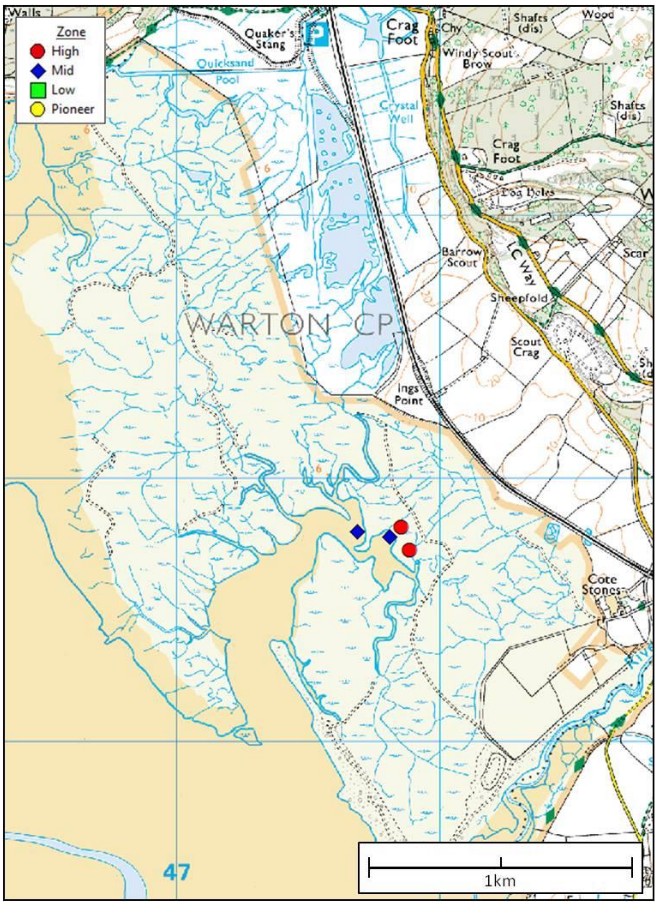


Figure 2.24 | Map of Carnforth marsh. Ordnance Survey Map OL7 (2010h) showing start and end points of high and mid zone cross-shore sample belts.

Grid Reference (BNG): SD 478 717

Used in Chapters: 3, 4, 5 & 6

Marsh Type: Open coast

Zones Present: High & Mid

Grazing Intensity: Intensive (0.72 LSU ha^{-1} yr^{-1})

Carnforth marsh (also known as Warton Marsh) is a large marsh situated just north of Carnforth, near Lancaster. It is mostly owned by a local farmer and managed by Morecambe Bay Wildfowlers Association, but the RSPB also own a section of the marsh to the north. It is intensively grazed by sheep throughout the year. The extensive high marsh is dominated by a closely cropped *Festuca rubra* and *Agrostis stolonifera* sward with extensive *Juncus maritimus* patches to the north. The mid marsh extends to the west and is dominated by a sparse and short *Festuca rubra* sward. This marsh is very sandy and highly dynamic in places.

PART 2: THE IMPACTS OF GRAZERS

Chapter 3: The Importance of Context – The Above-Ground Impacts of Grazers in a Naturally Variable System

3.1 Introduction

3.1.1 The impacts of grazers on above-ground plant communities

Livestock grazing is a common disturbance in grasslands and wetlands as livestock are used for both meat production and for management of vegetated landscapes (Reid, Galvin, & Kruska, 2008). Disturbance by livestock grazing has significant above-ground impacts on vegetation community characteristics such as vegetation height and biomass, species diversity, and community composition (Jensen, 1985) (Figure 3.1). Grazing disturbance can thus have significant knock-on effects on several ecosystem functions such as carbon sequestration (R. Conant, Paustian, & Elliott, 2000; R. T. Conant & Paustian, 2002; Reeder & Schuman, 2002), biodiversity (Kruess & Tscharntke, 2002; Loucougaray, Bonis, & Bouzille, 2004; Olff & Ritchie, 1998) and habitat provision (Baldi, Batary, & Erdos, 2005; Schmidt, Olsen, Bildsoe, Sluydts, & Leirs, 2005; Vickery et al., 2001). Loss of vegetation height, biomass and cover occurs under all grazing regimes (Hayes & Holl, 2003; Jensen, 1985; Jones, 2000; H.-L. Zhao, Zhao, Zhao, Zhang, & Drake, 2005) and the overall stocking density of livestock determines the extent of this loss. A high stocking density is likely to lead to a short and uniform sward with low vegetation cover, as grazing disturbance significantly reduces plant biomass and height across all species (Jensen, 1985; Kiehl et al., 1996). In contrast, a low stocking density is likely to lead to a patchy vegetation sward, as grazing disturbance reduces above-ground biomass of grazer-sensitive and palatable species, giving opportunity for grazer resilient species to thrive with reduced interspecific competition (Grime, 1974; Jensen, 1985; Kiehl et al., 1996). Different grazer species affect vegetation structure in different ways (Jensen, 1985). Sheep are selective grazers; they preferentially select grazing patches, plant species and even individual plants within an area, which can result in a patchy vegetation sward (Adler et al., 2001; J. P. Bakker et al., 1984; Parsons et al., 1994; D. S. Ranwell, 1961). It is easier for sheep to graze short vegetation patches than tall vegetation, resulting in a higher grazing intensity and frequency in shorter vegetation patches and an increased difference between the patches of desirable and undesirable species (Graff, Aguiar, & Chaneton, 2007; Wallis De Vries et al., 1999). In contrast, cows are generalist grazers and tend to continually graze as they move across the turf, regardless of vegetation type, resulting in a more uniform sward (Jensen, 1985; Wallis De Vries et al., 1999).

Livestock grazing can significantly influence the species richness of vegetation communities (Sala et al., 2000). Species richness is often low in un-grazed swards due to the dominance of one competitively dominant species, while light grazing can open up the sward, allowing less competitively dominant, more opportunistic species to grow, and thus increase species richness (Augustine & McNaughton, 1998; V. Bouchard et al., 2003; Marty, 2004). The latter may not occur in all cases as the increase in species richness depends on the palatability of the initial plant community (Graff et al., 2007; Schroder et al., 2002). If the dominant species are unpalatable, less dominant species may then be preferentially grazed, decreasing competition for the dominant species and further reducing species richness (Lubchenco, 1978; Olff & Ritchie, 1998; Parsons et al., 1994). Under an intense grazing regime species richness will decrease regardless of preferential grazing, resulting in a low-diversity sward dominated by grazing-resistant species (Fleischner, 1994; Olff & Ritchie, 1998).

3.1.2 The salt marsh environment

Salt marshes are at the interface of the marine and terrestrial systems; they are subjected to stressors and disturbances from both the marine environment, such as tidal inundation, salinity gradients and wave action, and the terrestrial environment, such as herbivory, freezing and dessication (Adam, 1990a; Jimenez, Lugo, & Cintron, 1985). Salt marshes are frequently inundated with saline water resulting in waterlogged soils with little oxygen (Adam, 1990a, 1990b; Chapman, 1938). High marsh areas are flooded less frequently than lower marsh areas (Adam, 1990b; Chapman, 1938) (Figure 3.2); as a consequence the soils in high marsh areas are less waterlogged than low marsh soils (Adam, 1990b; Chapman, 1938; Pennings & Bertness, 2001). In warmer regions, evaporation of saline water results in high soil salinities in the high marsh, where inundation is infrequent and freshwater influence is minimal; at lower marsh elevations water inundation is frequent enough to dilute the salinity of the soil (Adam, 1990b; Chapman, 1939; Parrondo et al., 1978; Pennings & Bertness, 2001; Pennings & Callaway, 1992). Salt marsh plants are also subject to direct physical stress from water movement and, in northern latitudes, ice scour (Adam, 1990b; Belanger & Bedard, 1994; Pennings & Bertness, 2001).

3.1.3 Above-ground impacts of grazing on salt marshes

Livestock grazing is used both as a conservational management tool and for agricultural production on salt marshes (Adam, 1990c). Conservation management usually necessitates an absence of grazers or a low to moderate livestock density, while agricultural production typically requires high stocking densities (Andresen et al., 1990; J.P. Bakker, De Bie, Dallinga, Tjaden, & De Vries, 1983; Jensen, 1985; Kiehl et al., 1996). Because of this range in stocking densities and environmental stress gradients, salt marshes provide an ideal environment for studying the relative importance of grazing disturbance in relation to environmental stressors.

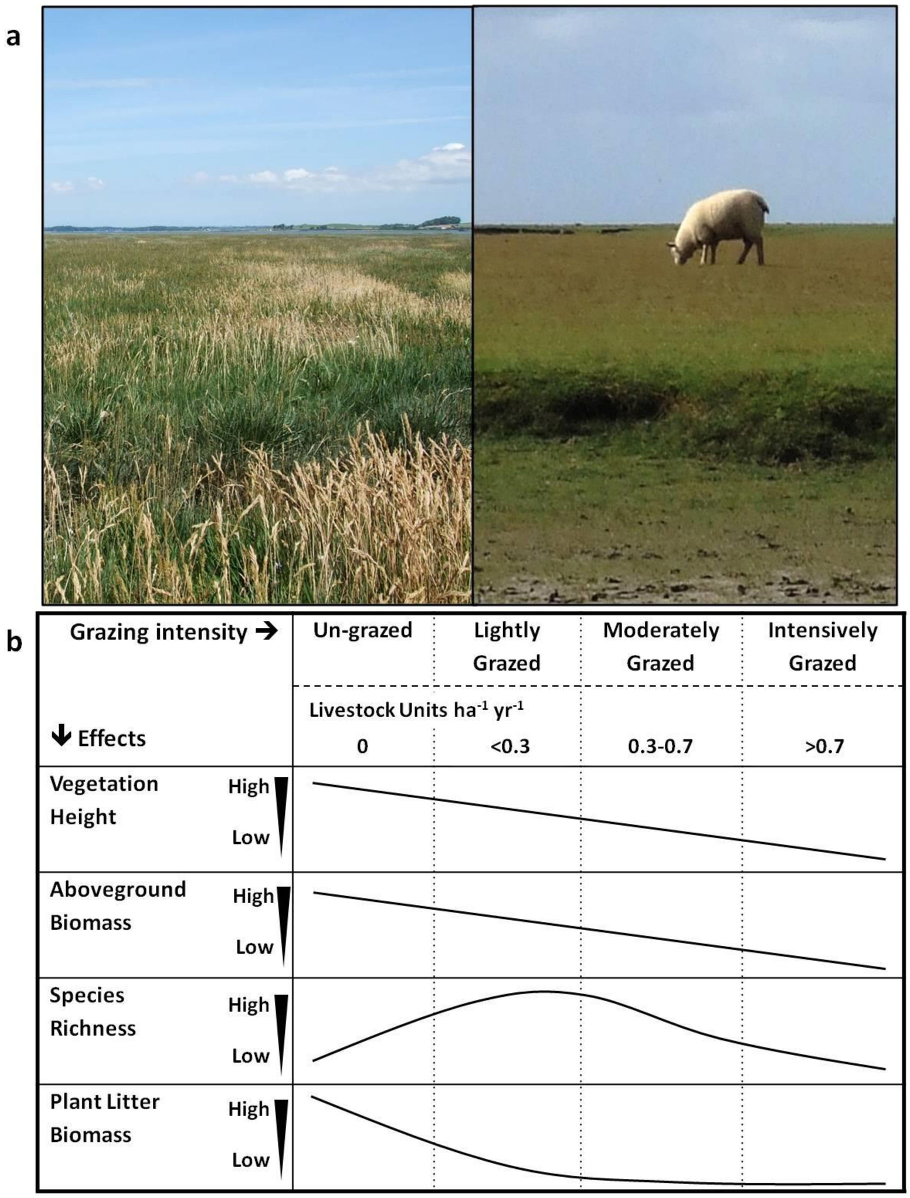


Figure 3.1 | The impacts of livestock grazing. a) The contrast between an un-grazed (left) and an intensively grazed (right) salt marsh. **b)** Predicted effects of a range of grazing intensities on vegetation height, above-ground biomass, species richness and plant litter biomass according to the literature (Andresen et al., 1990; Augustine & McNaughton, 1998; Jensen, 1985; Kiehl et al., 1996). Grazing is shown as 'Grazing Intensity' category (un-grazed, lightly grazed, moderately grazed and intensively grazed) and Livestock Units per hectare per year (LSU ha^{-1} yr^{-1}).

Grazers are likely to have significant impacts on salt marsh vegetation. Plant height, biomass and cover will decrease with an increase in stocking density (Andresen et al., 1990; V. Bouchard et al., 2003; Jensen, 1985; Kiehl et al., 1996). Species richness is likely to peak under a light grazing regime as an intensively grazed sward will consist of only disturbance-resistant species, and an un-grazed sward will be dominated by a competitively dominant monoculture, particularly in the higher marsh zones where soil physical conditions are more favourable (Adam, 1990a; Kiehl, Schroder, & Stock, 2007; Pennings & Callaway, 1992). In the absence of grazing, salt marshes have distinct zonation of the vegetation according to elevation (Adam, 1990b). Each zone represents a different stage of salt marsh succession, with the pioneer zone at the seaward edge of the marsh representing the newest, early-successional vegetation communities, and higher marsh zones representing increasingly later successional vegetation communities as shore elevation increases (Adam, 1990b; Boorman, 2003; Davy, Brown, Mossman, & Grant, 2011; Krull & Craft, 2009; Packham & Liddle, 1970; Pennings & Callaway, 1992; D.S. Ranwell, 1964a) (Figure 3.2). Under the influence of large herbivores, community composition is likely to revert to an earlier successional stage; higher marsh zones will become dominated by the communities found lower down the shore, as disturbance will open up the sward and facilitate for more robust, competitively inferior species (J. P. Bakker, 1985; Bos, Bakker, De Vries, & van Lieshout, 2002). The relative impact of grazers is likely to differ between marsh zones; livestock normally avoid the pioneer marsh zone (Figure 3.2) as it is dominated by unpalatable species and can be difficult to reach, due to complex creek systems (Adam, 1990b; Boorman, 2003; Kiehl et al., 1996).

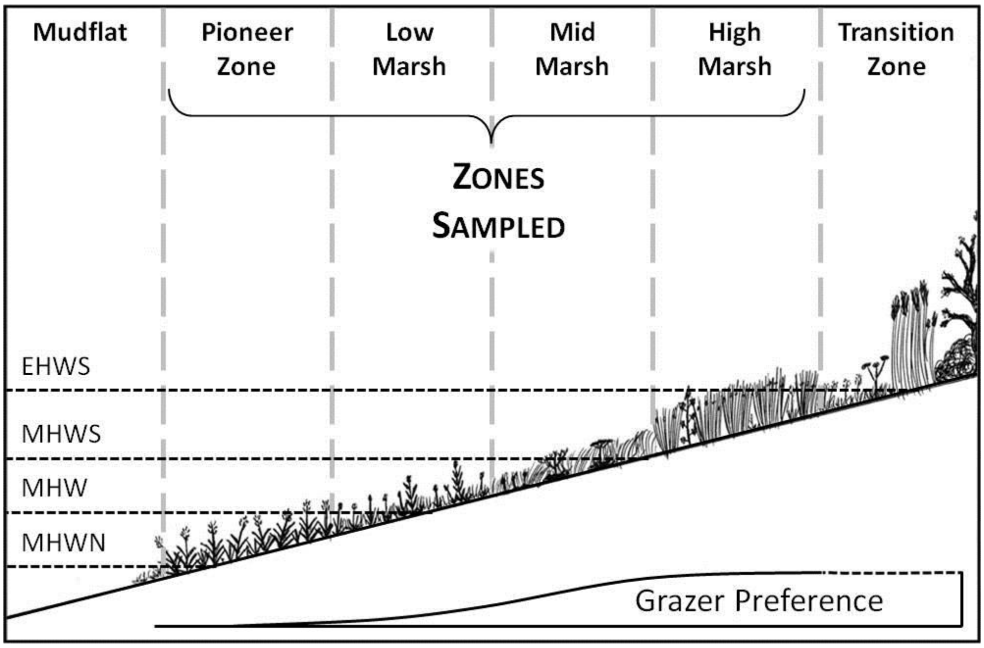


Figure 3.2 | Zonation on a salt marsh. A diagrammatic representation of a salt marsh showing zonation according to tidal inundation: extreme high water spring (EHWS), mean high water spring (MHWS), mean high water (MHW) and mean high water neap (MHWN). Only the pioneer, low, mid and high zones were sampled in this study. Grazer preference is indicated showing decreased grazing activity in the lower zones.

3.1.4 The importance of environmental setting

Environmental context is known to moderate grazer control of vegetation composition in a range of ecosystems (Chaneton, Perelman, Omacini, & Leon, 2002; Ren, Schonbach, Wan, Gierus, & Taube, 2012; Stohlgren, Schell, & Vanden Heuvel, 1999). Salt marshes, being intertidal systems, are naturally exposed to a large variety of environmental stressors and are, as a consequence, spatially and temporally highly variable (Adam, 1990b). As yet, no study has investigated how broad-scale environmental context affects grazing impacts on salt marsh vegetation. In natural systems, plant community composition, diversity and morphology are determined by a combination of stress gradients, and inter and intraspecific competition (Grime, 1974). Variation in such stressors naturally increase with an increase in spatial and temporal scales (Sprugel, 1991). In small-scale studies, the impact of grazing is clearly detectable (Jensen, 1985; Kiehl et al., 1996), however, over a large spatial scale, the impact of grazers on above-ground processes would have to be substantial and consistent enough to overcome the large-scale natural variation to be detectable. In the higher marsh zones, where livestock preferentially graze, the impact of grazing is likely to be substantial enough to be detectable over the impacts of environmental stressors. However, due to preferential grazing (Figure 3.2), the impact of grazers is less likely to be detectable over the impacts of environmental stressors in the lower marsh zones.

3.1.5 Study aims

The overall aim of this study was to examine the broad-scale relationships between livestock grazing and above-ground plant community characteristics in relation to large-scale environmental variation. The overarching hypothesis was that grazing has consistent effects on salt marsh plant communities, as indicated in previous small scale-studies (Jensen, 1985; Kiehl et al., 1996), and that these effects are detectable across a large spatial scale. To address this hypothesis, above-ground plant morphology and community characteristics were sampled across 22 salt marshes along the north-west coast of Wales and the north-west coast of England. Sites had a large range of livestock stocking densities and environmental settings (Chapter 2). Plant height, live biomass, litter biomass and percent cover were all expected to show a significant negative response to an increase in livestock density. Species diversity was expected to peak under a light grazing regime and community composition was expected to revert to that of a lower marsh zone community with an increase in stocking density. The study also investigated the interaction between grazing and the impact of tidal elevation (zone) on plant community characteristics. Plant height, live biomass, litter biomass and percent cover were all expected to be greatest in the high marsh, where physical stress and disturbance levels are lowest, regardless of grazing intensity (Adam, 1990b). Community composition was expected to significantly differ between marsh zones; the lower marsh zones were expected to be dominated by halophytic, early successional species, while the higher marsh zones were expected to be dominated by less salt-tolerant, competitively dominant species. Species diversity was expected to be lowest in the pioneer zone where physical stress and disturbance is highest (Adam, 1990b). Finally, the study contrasted the influence of livestock grazing with the influence of environmental contextual variables such as wave exposure, tidal range and marsh geomorphology on above-ground plant community characteristics. Tidal range was expected to be a significant driver of plant community characteristics in un-grazed marshes as tidal range dictates many of the physical stresses and disturbances on a salt marsh and defines the position and extent of the marsh zones (Adam, 1990b). It was expected that the impact of livestock grazing would be detectable above the impacts of environmental stressors in the higher marsh zones but not in the lower marsh zones.

3.2 Materials and Methods

3.2.1 Site selection, determination of zones and quadrat selection

The study sites and sampling design are described in detail in Chapter 2. Twenty-two salt marshes were selected between the Dyfi Estuary, Mid Wales, and Morecambe Bay, NW England (Chapter 2). Marshes varied in grazing intensity from un-grazed to intensively grazed (Chapter 2: Table 2.1). Marsh zones were determined using a combination of strand line position, marsh topography, and direct observations of tidal inundation (Chapter 2). Each zone was sampled by ten 2 x 2 metre plots that were randomly placed along a representative cross-shore 100m belt (Chapter 2).

3.2.2 Sampled response variables

3.2.2.1 Total vegetation cover and community composition: Total vegetation cover and community composition were recorded according to the National Vegetation Classification (NVC) guidelines (Rodwell et al., 2000): the total percentage cover of bare ground and of vegetation in each 2 x 2 metre plot (Figure 3.3a) was assessed by eye; 5-10 minutes were then spent identifying each species within the plot before the percentage cover of each species was estimated.

3.2.2.2 Vegetation height: Five measurements of vegetation height were taken from each plot (Figure 3.3b), one from each corner and one from the middle; the five observations were then averaged. To measure vegetation height, a flat surface was placed level with 80% of the vegetation and a ruler was used to measure the height according to the direct vegetation height method by Stewart, Bourn, and Thomas (2001). The maximum vegetation height was also measured for each plot and the species of the tallest plant was recorded.

3.2.2.3 Above-ground live biomass and litter biomass: Above-ground live biomass and litter biomass were measured using a 25 x 50cm quadrat placed in a representative area of each plot, defined by the spread and abundance of each species present within the plot (Figure 3.3c). Any vegetation litter within the quadrat was collected. The living vegetation was then cut down to the soil and also collected. In the laboratory, both above-ground and litter samples were placed in pre-weighed paper bags, dried at 80°C for 3 days, and weighed. Total dry weight was calculated and expressed per centimetre squared.

3.2.2.4 Species diversity: Species diversity takes into account both species richness (number of species) and species evenness (how evenly individuals are distributed among different species).

Species diversity was calculated from the community composition data matrix using DIVERSE in the PRIMER statistical package (K. R. Clarke & Warwick, 2001). Species diversity was recorded as the Shannon-Wiener Diversity Index (H' $\log_e$):

$$H' = -\sum_i p_i \log_e(p_i)$$

where p_i was the proportion of the total count arising from the i^{th} species (K. R. Clarke & Warwick, 2001).

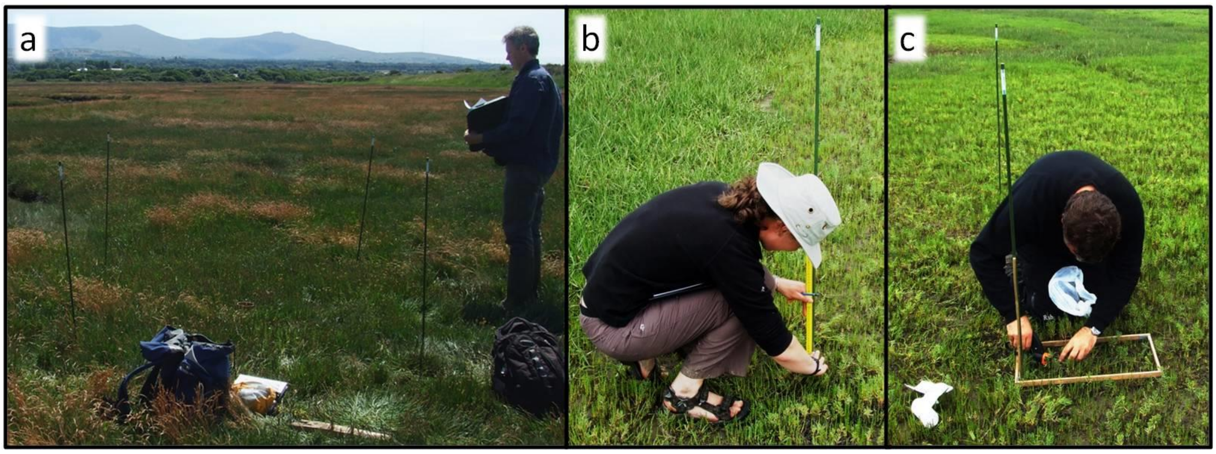


Figure 3.3 | The quadrat and the measurements. **a)** The 2 x 2m quadrat used for the above-ground measurements. **b)** Taking a vegetation height measurement at a plot corner. **c)** Clipping the vegetation after having collected any vegetation litter within the 25 x 50cm quadrat.

3.2.3 Determination of stocking density and contextual environmental variables

The method of quantifying livestock density is outlined in Chapter 2 (Section 2.2). The stocking density was expressed as livestock units (Woodend, 2010) per hectare per year (LSU ha^{-1} yr^{-1}) (Chapter 2). As well as considering grazing as a continuous variable, the marshes were also categorised into four grazing intensities: un-grazed, lightly grazed, moderately grazed and intensively grazed. This was to relate to local management schemes and grazing intensities used in other studies (Chapter 2). Several contextual environmental variables were sampled as indicators of environmental drivers of salt marsh productivity and carbon storing processes (Chapter 2).

3.2.4 Statistical analysis

Due to the considerable differences between saltmarsh zones, separate analyses were used for each zone as well as the overall data set (all zones). As management schemes stipulate grazing pressure by categorizing sites into a range of grazing intensities, the data were analysed with grazing as both a continuous variable (LSU) and as an ordinal categorical variable (four categories of grazing intensity). LSU is a continuous measurement of stocking density; however, it does not lend itself to factorial-type analyses such as ANOVA. Grazing intensity categories are arbitrary and somewhat subjective classifications of grazing regime. They were included in this analysis to relate to current management schemes that use these categories. The data analysis was divided into three parts:

i) Regression analyses with grazing intensity as a continuous variable (LSU ha^{-1} yr^{-1}) for a continuous determination of grazing impacts on below-ground measures (Section 3.2.4.1).

ii) An analysis of grazing impacts using categorical levels of grazing intensity (un-grazed, lightly grazed, moderately grazed, or intensely grazed), as stipulated by management schemes, using ANOVAs (Section 3.2.4.2), PERMANOVA (Section 3.2.4.3), and ANCOVA (Section 3.2.4.4).

iii) Analyses of the impacts of grazing in relation to a series of environmental variables (3.2.4.5 DistLM; 3.2.4.6 Mixed effects model).

3.2.4.1 Regression: A series of regression analyses investigated the effect of livestock stocking density (LSU ha^{-1} yr^{-1}) on the above-ground response variables. Analyses were run on the overall data set (all marshes, all zones) and separately for each zone (high, mid, low or pioneer). False discovery rate (FDR) control *p*-values were calculated to compensate for the large number of tests. FDR control is similar to a Bonferroni correction as it reduces the risk of a Type I error by lowering the *p*-value threshold; but instead of lowering the *p*-value threshold by a set amount, FDR control takes into account the rank order of the tests (Verhoeven, Simonsen, & McIntyre, 2004). Partial *eta* squared effect size was calculated for each test where ≥0.0099 (0.99% of the variation explained) was a small effect, ≥0.0588 (5.88% of the variation explained) was a medium effect, and ≥0.1379 (13.79% of the variation explained) was a large effect (Cohen, 1988; Richardson, 2011). Square root and log_{10} transformations were used when necessary to meet the test assumptions.

3.2.4.2 ANOVA: Analyses of variance (ANOVAs) were run alongside the regression analyses to investigate the impact of categorical levels of grazing intensity on the above-ground response variables (plant height, biomass, percentage cover, and species richness) and their coefficients of variation (spread in the data). To analyse the impact of grazing on plant structure and species richness in the overall data set, a three-way, between-group factorial ANOVA was run with the model *Grazing Intensity | Zone + Marsh(Grazing Intensity*). This model determined both independent effects of grazing, zone and marsh, as well as interaction effects of grazing and zone. Marsh a random factor and was nested within grazing intensity so no interaction terms could be determined for marsh. To analyse the impact of grazing on plant structure and species richness within each zone, a 2-way ANOVA was run for each zone (high, mid, low and pioneer) with the model *Grazing Intensity + Marsh(Grazing Intensity)*. This model determined the independent effects of grazing and marsh within each zone. Tukey HSD *post hoc* tests were used to determine where any between-group significant differences lay. False discovery rate control p-values were calculated for the main factor, 'Grazing', to compensate for the large number of analyses. Partial *eta* squared effect size was calculated for each test. For non-parametric analyses (litter biomass in all zones, and overall percentage cover in the high and mid zones), a Kruskal-Wallis multiple Comparisons test was used.

3.2.4.3 PERMANOVA: A permutational analysis of variance (PERMANOVA) (Anderson, 2005) was used to analyse the effects of grazing on community composition. The PERMANOVA design included the factors:

i) Grazing intensity (GI): Fixed factor; 4 levels (un-grazed, lightly grazed, moderately grazed, intensively grazed)
ii) Marsh: Random factor; 22 marshes; nested in GI
iii) Zone: Fixed factor; up to 4 levels per marsh (pioneer, low, mid, high)

The PERMANOVA was run with 9999 permutations on a log transformed Bray-Curtis similarity matrix. A permutational analysis of dispersions (PERMDISP) was used to analyse heterogeneity of the spread of the data between groups (grazing intensities) within each zone.

3.2.4.4 MDS and SIMPER: Community composition of marsh zones were compared using multi-dimensional scaling (MDS) plots on log transformed Bray-Curtis similarity matrixes (K. R. Clarke & Warwick, 2001). MDS analyses were followed by SIMPER analyses to establish which species best explained the similarities or dissimilarities between the grazing intensity categories and between the zones.

3.2.4.5 Mixed Effects Model: A mixed effects model was used to analyse the impact of multiple environmental and contextual factors (including LSU) on above-ground response variables. The model was run on the overall data set for un-grazed marshes, the combined high zone and mid zone data for grazed marshes (zones most likely to be influenced by grazers), and the combined low zone and pioneer zone data for grazed marshes (zones least likely to be influenced by grazers).

3.2.4.6 DistLM: A distance based linear model (DistLM) (Anderson, 2005) was used to determine the relative impacts of grazing and several environmental variables on community composition using multiple regression techniques. A Best selection procedure was used and an AICc (Akaike's Information Criterion (AIC corrected for data sets with a small 'number of samples –number of variables' ratio) selection criterion was used. A reduced model (fewer marshes) was used to test for effects of environmental variables for which data was not available for all marshes.

3.3 Results

3.3.1 The impact of grazing on vegetation structure

Vegetation height decreased significantly in response to an increase in stocking density (LSU), irrespective of whether analyses were done collectively across all zones (the overall marsh), or separately for each zone; only in the pioneer zone was there no significant relationship between grazing and vegetation height (Regression analyses: Table 3.1; Figure 3.4). Vegetation height varied significantly between the four categorical levels of grazing but there was also significant variation between marsh sites (ANOVA Table 3.2). Overall, and in the high and mid marsh zones, the mean and maximum vegetation height in un-grazed and lightly grazed marshes was significantly higher than that in moderately and intensively grazed marshes (*post hoc* Tukey HSD tests: Table 3.2). Vegetation height was not significantly affected by grazing in the low and pioneer zones (Table 3.2).

Above-ground live biomass showed a significant but weak negative relationship with livestock stocking density across the marsh as a whole (Regression: Table 3.1; Figure 3.4). Above-ground live biomass did not significantly differ between grazing intensity categories but there were significant, large effects of marsh site (ANOVA: Table 3.2). Considering the zones separately, above-ground live biomass decreased with an increase stocking density in the high, mid and low marsh zones (Regression: Table 3.1; Figure 3.4). Interestingly, there was a significant positive relationship with grazing in the pioneer zone (Regression: Table 3.1; Figure 3.4).

There was a significant effect of grazing on litter biomass both collectively across all marsh zones (the overall marsh) and within each zone (Kruskal-Wallis multiple comparisons: Table 3.3, Figure 3.4). Overall and in the high, mid and pioneer marsh zones, there was significantly more litter biomass in un-grazed marshes than in grazed marshes (Kruskal-Wallis multiple comparisons: Table 3.3). In the high marsh, there was a more gradual reduction of litter biomass with grazing than in the other zones as there was significantly more litter in the lightly grazed marshes than in moderately and intensively grazed marshes (Kruskal-Wallis multiple comparisons: Table 3.3). In the mid and pioneer zones, however, litter biomass did not significantly differ between grazed treatments, and in the low marsh, litter biomass was significantly greater in intensively grazed marshes than in lightly grazed marshes (Kruskal-Wallis multiple comparisons: Table 3.3).

3.3.2 Changes in vegetation structure across the salt marsh zones

Vegetation height significantly differed between marsh zones (ANOVA Table 3.2). Vegetation height was significantly greater in the high zone ($\bar{x}$ = 22.33, *SE* = 1.51) than in the mid ($\bar{x}$ = 11.94, *SE* = 0.73) low ($\bar{x}$ = 16.06, *SE* = 0.88) and pioneer zones ($\bar{x}$ = 11.40, *SE* = 1.18) (*post hoc* Tukey HSD tests).

Above-ground live biomass significantly differed between marsh zones (ANOVA: Table 3.2. Above-ground biomass was greater in the high marsh zone ($\bar{x}$ = 0.044, *SE* = 0.002) than in the pioneer zone ($\bar{x}$ = 0.031, *SE* = 0.003) (*post hoc* Tukey HSD tests). Litter biomass also significantly differed between marsh zones (Kruskal-Wallis multiple comparisons: H_3 = 34.57, p <0.001). The high marsh had significantly more litter biomass ($\tilde{x}$= 0.0001, *IQR* = 0.0167) than mid ($\tilde{x}$= 0.0000, *IQR* = 0.0012), low ($\tilde{x}$= 0.0000, *IQR* = 0.0000) and pioneer zones ($\tilde{x}$= 0.0000, *IQR* = 0.0000), and there was significantly less litter biomass in the low marsh than in the pioneer marsh (Kruskal-Wallis multiple comparisons).

Table 3.1 | Regression analyses for above-ground variables against LSU. Results of regression analyses for each predictor variable vs. LSU ha^{-1} yr^{-1} for overall data set followed by analysis by zone (high, mid, low and pioneer). Results of ANOVA (*df*, *F* and *p*) are shown along with FDR *p*-value thresholds (FDR $p_{(i)}$). An emboldened *p*-value denotes a significant effect. The results of the regression are shown in the last three columns: R^2, Intercept (*b*) and Slope (*m*).

Predictor Variable	*df*	*F*	*p*	FDR $p_{(i)}$	R^2	*b*	*m*
Overall							
Sqrt Average Plant Height (cm)	1, 598	84.04	**<0.001**	0.033	12.3	3.920	-0.892
Maximum Plant Height (cm)	1, 598	52.19	**<0.001**	0.025	8.0	42.000	-9.930
Sqrt Above-ground Biomass (g cm^{-2})	1, 598	15.73	**<0.001**	0.008	2.6	0.202	-0.021
Overall % Cover	1, 598	19.50	**<0.001**	0.017	3.2	88.800	-5.930
Species Diversity (H' $\log_e$)	1, 598	2.59	0.108	0.042	0.4		
High Marsh							
Ln10 Average Plant Height (cm)	1, 158	75.86	**<0.001**	0.030	32.4	1.290	-0.303
Maximum Plant Height (cm)	1, 158	40.99	**<0.001**	0.020	20.6	55.700	-14.100
Above-ground Biomass (g cm^{-2})	1, 158	15.13	**<0.001**	0.010	8.7	0.049	-0.009
Species Diversity (H' $\log_e$)	1, 158	1.25	0.265	0.040	0.8		
Mid Marsh							
Average Plant Height (cm)	1, 198	47.29	**<0.001**	0.030	19.3	15.300	-8.450
Maximum Plant Height (cm)	1, 198	46.43	**<0.001**	0.020	19.0	38.500	-17.400
Sqrt Above-ground Biomass (g cm^{-2})	1, 198	10.56	**0.001**	0.010	5.1	0.211	-0.041
Species Diversity (H' $\log_e$)	1, 198	0.01	0.936	0.050	0.0		
Low Marsh							
Average Plant Height (cm)	1, 138	4.29	0.040	0.042	3.0		
Maximum Plant Height (cm)	1, 138	0.50	0.479	0.050	0.4		
Above-ground Biomass (g cm^{-2})	1, 138	10.65	**<0.001**	0.008	7.2	0.061	-0.019
Overall % Cover	1, 138	23.94	**<0.001**	0.025	14.8	93.700	-5.770
Species Diversity (H' $\log_e$)	1, 138	32.89	**<0.001**	0.033	19.2	1.440	-0.317
Pioneer Marsh							
Average Plant Height (cm)	1,98	3.95	0.050	0.033	3.9		
Maximum Plant Height (cm)	1,98	0.14	0.708	0.042	0.1		
Above-ground Biomass (g cm^{-2})	1,98	14.95	**<0.001**	0.008	13.2	0.022	0.017
Overall % Cover	1,98	9.83	**0.002**	0.017	9.1	54.600	-14.000
Species Diversity (H' $\log_e$)	1,98	0.00	0.994	0.050	0.0		

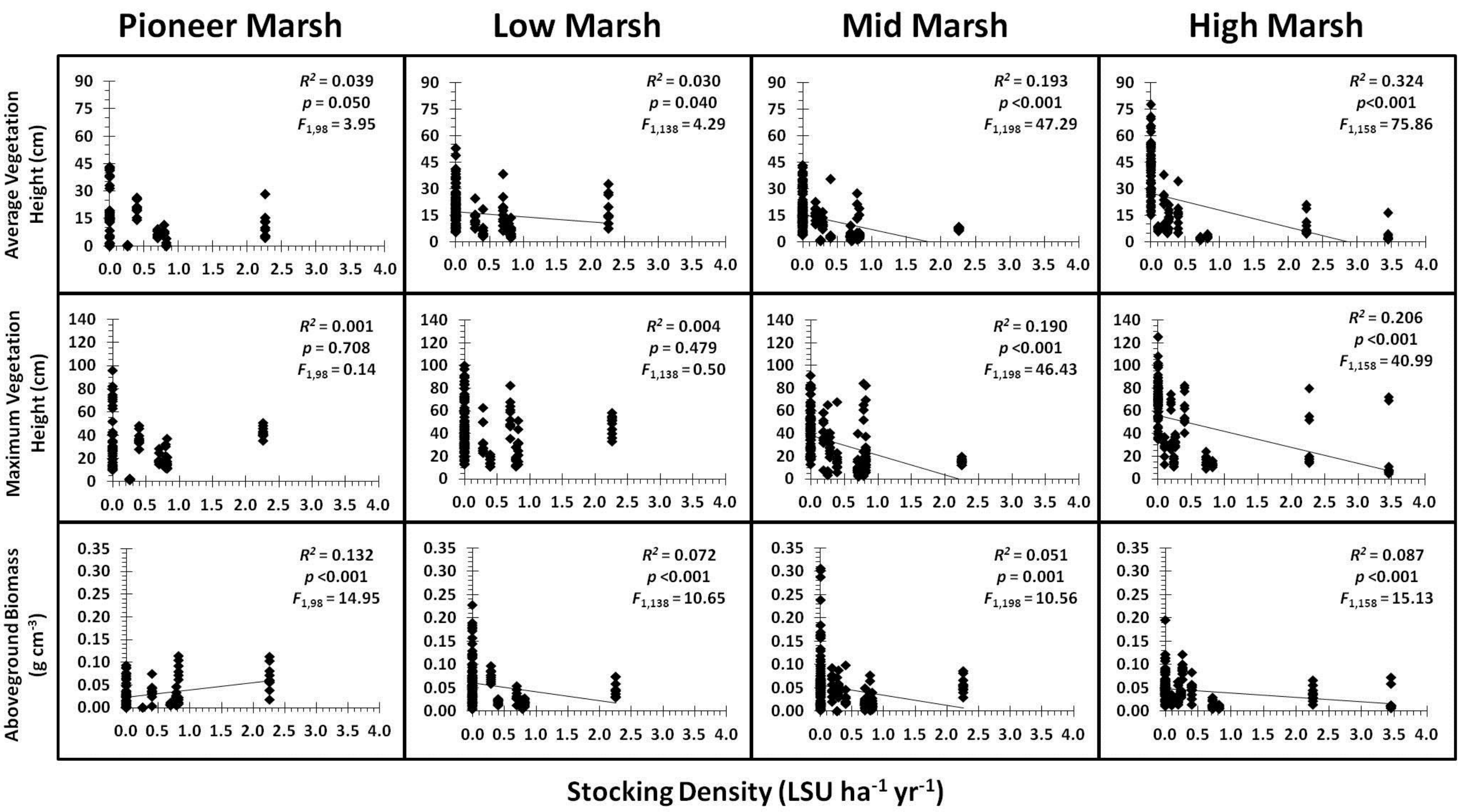


Figure 3.4 | Above-ground variables vs. livestock units by zone. Scatter plots showing the relationships between the above-ground variables (plant height and plant biomass) and grazing intensity (LSU ha^{-1} yr^{-1}) for each zone. The marsh with the highest grazing intensity had only a high marsh zone, so these data are missing from the mid, low and pioneer plots. The results (R^2, *p* and *F*) of a regression analysis are also shown for parametric analyses, while Kruskal-Wallis multiple comparisons *p*-values and *H*-values are shown for non-parametric analyses.

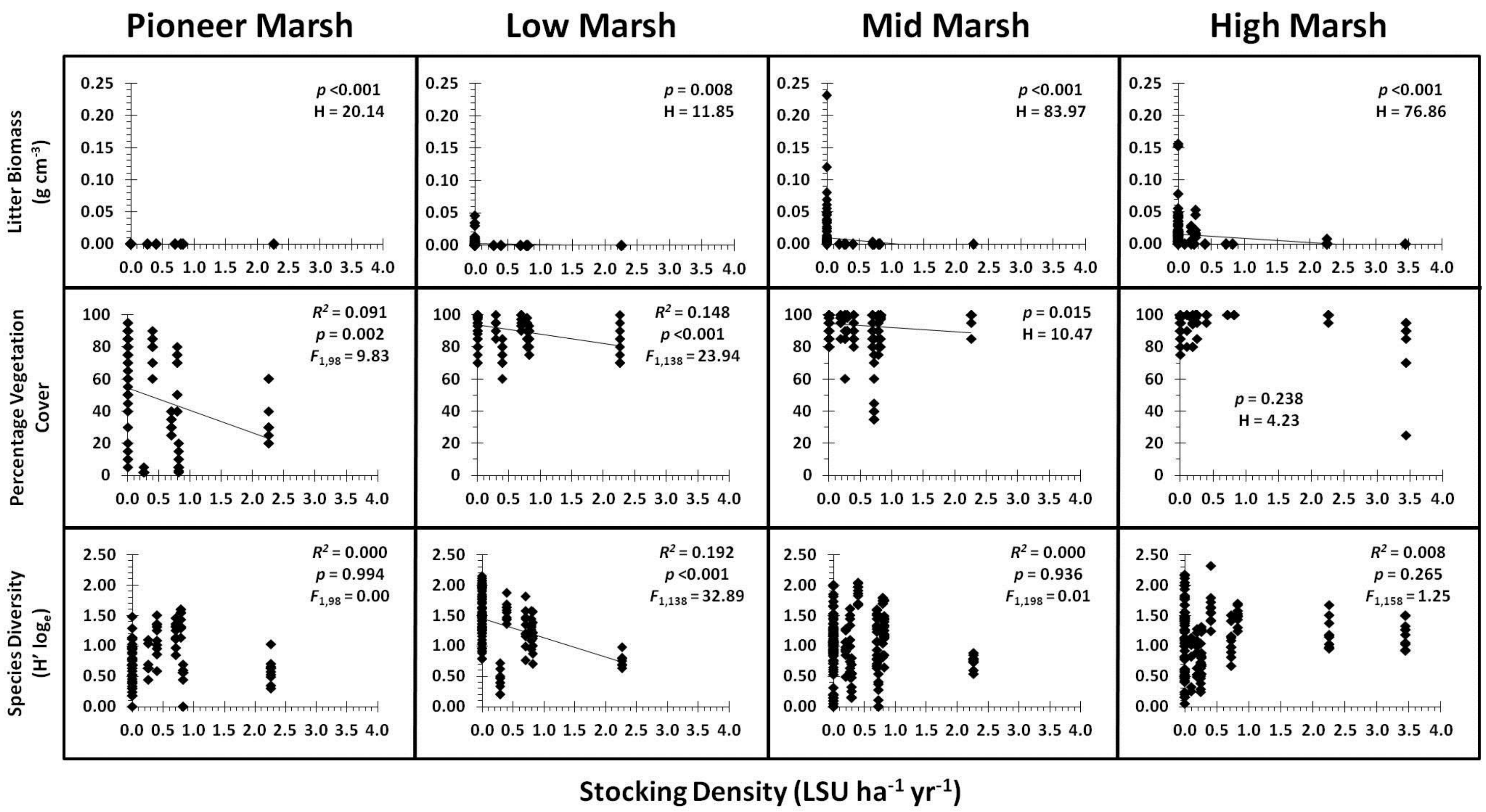


Figure 3.4 (cont) | Above-ground variables vs. livestock units by zone. Scatter plots showing the relationships between the above-ground variables (litter biomass, percent vegetation cover, and species diversity) and grazing intensity (LSU ha^{-1} yr^{-1}) for each zone. The marsh with the highest grazing intensity had only a high marsh zone, so these data are missing from the mid, low and pioneer plots. The results (R^2, p and F) of a regression analysis are also shown for parametric analyses, while Kruskal-Wallis multiple comparisons p-values and H-values are shown for non-parametric analyses.

Table 3.2 | ANOVA results of above-ground variables by grazing intensity. Results of a factorial ANOVA for the overall data set ('Overall') with the model Grazing | Zone + Marsh(Grazing), and a 2-way ANOVA for each zone ('High', 'Mid', 'Low', and 'Pioneer') with the model Grazing + Marsh(Grazing). Column headers depict degrees of freedom (df: numerator, denominator), F-values (F), p-values (p), False Discovery Rate control thresholds (FDR p(i)), and partial eta squared effect size (ηp2). An emboldened p-value denoted a significant effect. Means ($\bar{x}$) and Standard Deviation (SD) are shown by Grazing for each predictor variable with the results of Tukey HSD post hoc tests (superscript); groups that share the same number are significantly different.

Predictor Variable		ANOVA *df*	*F*	*p*	FDR $p_{(i)}$	η_p^2	Un-grazed $\bar{x}$	*SE*	Light $\bar{x}$	*SE*	Moderate $\bar{x}$	*SE*	Intensive $\bar{x}$	*SE*
Overall														
Average Plant Height (cm)	Grazing	3, 9	17.67	**<0.001**	0.010	0.494	24.045	0.914 [123]	10.072	0.748 [14]	9.766	0.977 [245]	6.195	0.506 [35]
	Marsh(Gr)	21, 9	17.33	**<0.001**	0.030	0.381								
	Zone	3, 9	23.99	**<0.001**	0.040	0.263								
	Gr x Zo	9, 9	19.97	**<0.001**	0.030									
Ln10 Maximum Plant Height (cm)	Grazing	3, 9	15.14	**<0.001**	0.020	0.403	50.320	1.450 [123]	28.300	1.870 [1]	29.090	2.400 [24]	23.600	1.460 [34]
	Marsh(Gr)	21, 9	13.83	**<0.001**	0.040	0.329								
	Zone	3, 9	69.61	**<0.001**	0.020	0.197								
	Gr x Zo	9, 9	22.66	**<0.001**	0.020									
Above-ground Biomass (g cm^{-2})	Grazing	3, 9	3.29	0.040	0.040	0.181	0.059	0.003	0.044	0.003	0.026	0.002	0.03	0.002
	Marsh(Gr)	21, 9	21.14	**<0.001**	0.020	0.428								
	Zone	3, 9	6.68	**<0.001**	0.051	0.046								
	Gr x Zo	9, 9	7.42	**<0.001**	0.050									
Overall Percent Cover	Grazing	3, 9	6.96	**0.002**	0.030	0.198	91.579	0.941 [12]	85.520	3.200 [1]	82.560	2.410 [3]	78.430	2.360 [23]
	Marsh(Gr)	21, 9	10.87	**<0.001**	0.050	0.278								
	Zone	3, 9	419.51	**<0.001**	0.010	0.708								
	Gr x Zo	9, 9	26.81	**<0.001**	0.010									
Species Diversity (*H'* loge)	Grazing	3, 9	1.06	0.387	0.050	0.072	1.128	0.032	0.766	0.036	1.359	0.042	1.041	0.034
	Marsh(Gr)	21, 9	22.98	**<0.001**	0.010	0.449								
	Zone	3, 9	31.38	**<0.001**	0.030	0.244								
	Gr x Zo	9, 9	14.99	**<0.001**	0.040									
High Marsh														
Average Plant Height (cm)	Grazing	3, 12	26.68	**<0.001**	0.013	0.770	40.020	1.730 [123]	11.370	1.160 [14]	14.350	2.740 [25]	4.350	0.733 [345]
	Marsh(Gr)	12, 12	6.03	**<0.001**	0.038	0.334								
Maximum Plant Height (cm)	Grazing	3, 12	20.71	**<0.001**	0.025	0.718	72.280	2.270 [12]	31.480	2.580 [134]	61.500	4.510 [35]	19.820	2.910 [245]
	Marsh(Gr)	12, 12	5.90	**<0.001**	0.050	0.330								
Above-ground Biomass (g cm^{-2})	Grazing	3, 12	2.44	0.115	0.038	0.326	0.054	0.004	0.048	0.005	0.047	0.006	0.021	0.003
	Marsh(Gr)	12, 12	9.52	**<0.001**	0.025	0.442								
Species Diversity (*H'* loge)	Grazing	3, 12	1.57	0.248	0.050	0.388	1.165	0.067	0.818	0.050	1.627	0.092	1.240	0.042
	Marsh(Gr)	12, 12	19.41	**<0.001**	0.013	0.618								

Table 3.2 (Cont.) | ANOVA results of above-ground variables by grazing intensity.

		ANOVA					Un-grazed		Light		Moderate		Intensive	
Predictor Variable		***df***	***F***	***p***	**FDR $p_{(i)}$**	η_p^2	$\bar{x}$	***SE***	$\bar{x}$	***SE***	$\bar{x}$	***SE***	$\bar{x}$	***SE***
							Mid Marsh							
Sqrt Average Plant Height (cm)	Grazing	3, 16	7.91	**0.002**	0.013	0.663	18.660	1.100 [123]	10.780	1.070 [145]	4.210	1.100 [24]	5.180	0.770 [35]
	Marsh(Gr)	16, 16	14.90	**<0.001**	0.038	0.570								
Maximum Plant Height (cm)	Grazing	3, 16	5.30	**0.010**	0.025	0.457	43.870	1.990 [123]	30.480	3.070 [145]	14.100	2.240 [24]	20.540	2.800 [35]
	Marsh(Gr)	16, 16	9.53	**<0.001**	0.050	0.459								
Sqrt Above-ground Biomass (g cm^{-2})	Grazing	3, 16	1.92	0.167	0.038	0.445	0.070	0.007	0.044	0.005	0.022	0.003	0.026	0.003
	Marsh(Gr)	16, 16	25.03	**<0.001**	0.025	0.690								
Species Diversity (*H'* loge)	Grazing	3, 16	0.84	0.491	0.050	0.261	0.957	0.050	0.825	0.072	1.349	0.086	1.006	0.070
	Marsh(Gr)	16, 16	25.27	**<0.001**	0.013	0.692								
							Low Marsh							
Average Plant Height (cm)	Grazing	3, 10	1.04	0.418	0.040	0.401	19.760	1.180	12.770	1.570	11.780	2.040	10.150	1.400
	Marsh(Gr)	10, 10	27.13	**<0.001**	0.020	0.683								
Maximum Plant Height (cm)	Grazing	3, 10	0.36	0.784	0.050	0.281	45.030	2.510	35.200	4.410	36.250	5.070	31.130	2.780
	Marsh(Gr)	10, 10	45.72	**<0.001**	0.010	0.784								
Above-ground Biomass (g cm^{-2})	Grazing	3, 10	1.46	0.283	0.020	0.474	0.070	0.005	0.077	0.004	0.027	0.002	0.026	0.003
	Marsh(Gr)	10, 10	25.94	**<0.001**	0.050	0.673								
Overall Percent Cover	Grazing	3, 10	1.95	0.186	0.030	0.349	94.737	0.763	94.000	1.450	85.500	2.810	85.970	1.590
	Marsh(Gr)	10, 10	11.54	**<0.001**	0.030	0.478								
Species Diversity (*H'* loge)	Grazing	3, 10	5.23	0.020	0.010	0.698	1.510	0.040	0.434	0.051	1.435	0.061	1.058	0.051
	Marsh(Gr)	10, 10	18.52	**<0.001**	0.040	0.595								
							Pioneer Marsh							
Sqrt Average Plant Height (cm)	Grazing	3, 6	1.01	0.453	0.030	0.789	16.780	2.310	0.070	0.040	13.800	1.760	6.400	1.10
	Marsh(Gr)	6, 6	111.39	**<0.001**	0.010	0.881								
Maximum Plant Height (cm)	Grazing	3, 6	0.81	0.535	0.050	0.714	36.950	3.710	2.150	0.107	28.200	0.350	26.200	2.440
	Marsh(Gr)	6, 6	93.03	**<0.001**	0.020	0.861								
Above-ground Biomass (g cm^{-2})	Grazing	3, 6	4.22	0.063	0.010	0.418	0.029	0.004	<0.001	<0.001	0.022	0.004	0.049	0.006
	Marsh(Gr)	6, 6	49.70	**<0.001**	0.030	0.584								
Overall Percent Cover	Grazing	3, 6	2.08	0.205	0.020	0.690	64.500	4.090	2.300	0.300	55.500	5.420	33.830	4.510
	Marsh(Gr)	6, 6	32.18	**<0.001**	0.040	0.682								
Species Diversity (*H'* loge)	Grazing	3, 6	0.89	0.497	0.040	0.391	0.680	0.054	0.710	0.063	1.163	0.052	0.819	0.086
	Marsh(Gr)	6, 6	21.56	**<0.001**	0.050	0.590								

Table 3.3 | Kruskal-Wallis multiple comparisons results non-parametric results. H-values, degrees of freedom and p-values from Kruskal-Wallis multiple comparisons test between grazing intensities for the non-parametric predictor variables for the overall data set ('Overall') and for each zone ('High', 'Mid', 'Low', and 'Pioneer'). Means ($\bar{x}$) and Standard Deviation (SD) are shown by Grazing for each predictor variable with the comparison results of the Kruskal Wallis multiple comparisons tests (superscript); groups that share the same number are significantly different.

Predictor Variable	Kruskal-Wallis			Un-grazed		Light		Moderate		Intensive	
	H	*df*	*p*	$\tilde{x}$	*IQR*	$\tilde{x}$	*IQR*	$\tilde{x}$	*IQR*	$\tilde{x}$	*IQR*
Overall											
Litter Biomass	135.12	3	**<0.001**	0.001	0.015 ^{123}	0.000	<0.001 ^{14}	0.000	<0.001 ^{245}	0.000	<0.001 ^{35}
High Marsh											
Litter Biomass	76.86	3	**<0.001**	0.015	0.025 ^{123}	0.000	0.015 ^{145}	0.000	<0.001 ^{24}	0.001	<0.001 ^{35}
Overall % Cover	4.23	3	0.238	100.0	5.000	100.0	4.500	99.50	0.000	99.50	5.00
Mid Marsh											
Litter Biomass	83.97	3	**<0.001**	0.002	0.012 ^{123}	0.000	<0.000 ^{1}	0.000	<0.000 ^{2}	0.000	<0.000 ^{3}
Overall % Cover	10.47	3	**0.015**	100.0	5.000 ^{12}	100.0	6.250	95.00	15.00 ^{1}	99.50	16.25 ^{2}
Low Marsh											
Litter Biomass	11.85	3	**0.008**	0.000	<0.001 ^{1}	0.000	<0.001 ^{12}	0.000	<0.001 ^{3}	0.000	0.009 ^{23}
Pioneer Marsh											
Litter Biomass	20.14	3	**<0.001**	0.000	0.022 ^{123}	0.000	<0.001 ^{1}	0.000	<0.001 ^{2}	0.000	<0.001 ^{3}

3.3.3 The impact of grazing on percentage vegetation cover

Percentage vegetation cover had a significantly negative response to an increase in stocking density when considering all the marsh zones combined, and when considering the low and pioneer zones separately (Regression; Tables 3.1; Figure 3.4). However, an analysis with grazing as a categorical factor showed a significant effect of grazing on vegetation cover across the combined marsh zones (the overall marsh) and in the mid marsh, but no significant impact of grazing in the high, low and pioneer zones (ANOVA; Kruskal-Wallis multiple comparisons: Tables 3.2 & 3.3). Across the overall marsh and in the mid marsh, vegetation cover was greater on un-grazed marshes than on grazed marshes but vegetation cover was also high in moderately and lightly grazed marshes respectively (*post hoc* Tukey HSD tests; Kruskal-Wallis multiple comparisons: Tables 3.2 & 3.3)

3.3.4 Changes in percentage vegetation cover across the salt marsh zones

Percentage cover significantly differed between zones (Table 3.2). Vegetation cover decreased down the shore: vegetation cover was significantly greater in the high marsh ($\bar{x}$ = 96.44, *SE* = 0.65) than in the mid marsh ($\bar{x}$ = 93.71, *SE* = 0.87), which had significantly greater vegetation cover than the low marsh ($\bar{x}$ = 91.49, *SE* = 0.77), which had significantly greater vegetation cover than the pioneer zone ($\bar{x}$ = 47.28, *SE* = 3.08).

3.3.5 The impact of grazing on community composition and species diversity

There was a significant impact of grazing on community composition in the mid marsh (PERMANOVA: Pseudo $F_{(3)}$ = 2.071, P(perm) = 0.029) but grazing did not have a significant impact on community composition in the high, low or pioneer marsh zones (Figure 3.5). SIMPER analyses showed that *Puccinellia maritima, Festuca rubra*, *Plantago maritima*, *Atriplex portulacoides* and *Salicornia europaea* contributed to most of the dissimilarity between grazing intensities in the mid marsh zone (Table 3.4). *Puccinellia maritima* largely dominated lightly grazed and moderately grazed plots, *Festuca rubra* largely dominated un-grazed and intensively grazed plots, *Plantago maritima* dominated mostly un-grazed plots but also a small number of intensively grazed plots, *Atriplex portulacoides* dominated only un-grazed and some lightly grazed plots, and *Salicornia europaea* dominated only moderately grazed plots (Figure 3.6; Table 3.4).

Species diversity was not significantly affected by stocking density when considering the zones combined, or in the high and mid marsh zones, but there was a significant negative response in the low marsh zone, and a significant positive response to grazing in the pioneer marsh zone (Regression: Table 3.1; Figure 3.4). When considering grazing as a categorical factor there was no impact of grazing on species diversity in any zone but there were significant, large effects of marsh site (ANOVA: Table 3.2).

3.3.6 Changes in community composition and diversity across the salt marsh zones

Community composition depended heavily on marsh zone (PERMANOVA: Pseudo $F_{(3)}$ = 11.809, P(perm) = 0.001) and marsh site (PERMANOVA: Pseudo $F_{(8)}$ = 55.325, P(perm) = 0.001). Pioneer marsh zones had a higher abundance of *Spartina anglica* than other zones, low marsh zones had a higher abundance of *Puccinellia maritima* than other zones and a higher abundance of *Spartina anglica* than mid and high marsh zones, mid marsh zones had a higher abundance of *Plantago maritima* than other marsh zones and a higher abundance of *Festuca rubra* than pioneer and low marsh zones, and high marsh zones had higher abundances of *Festuca rubra* and *Atriplex prostrata* than other marsh zones (SIMPER: Table 3.5).

Species richness significantly differed between marsh zones (Table 3.2). Species diversity in the low marsh zone ($\bar{x}$ = 1.33, SE = 0.04) was significantly higher than in the mid ($\bar{x}$ = 1.01, SE = 0.03) and pioneer marsh zones ($\bar{x}$ = 0.82, SE = 0.04) but did not significantly differ from the high marsh ($\bar{x}$ = 1.13, SE = 0.04). Species diversity was significantly higher in the mid marsh zone than in the pioneer marsh zone.

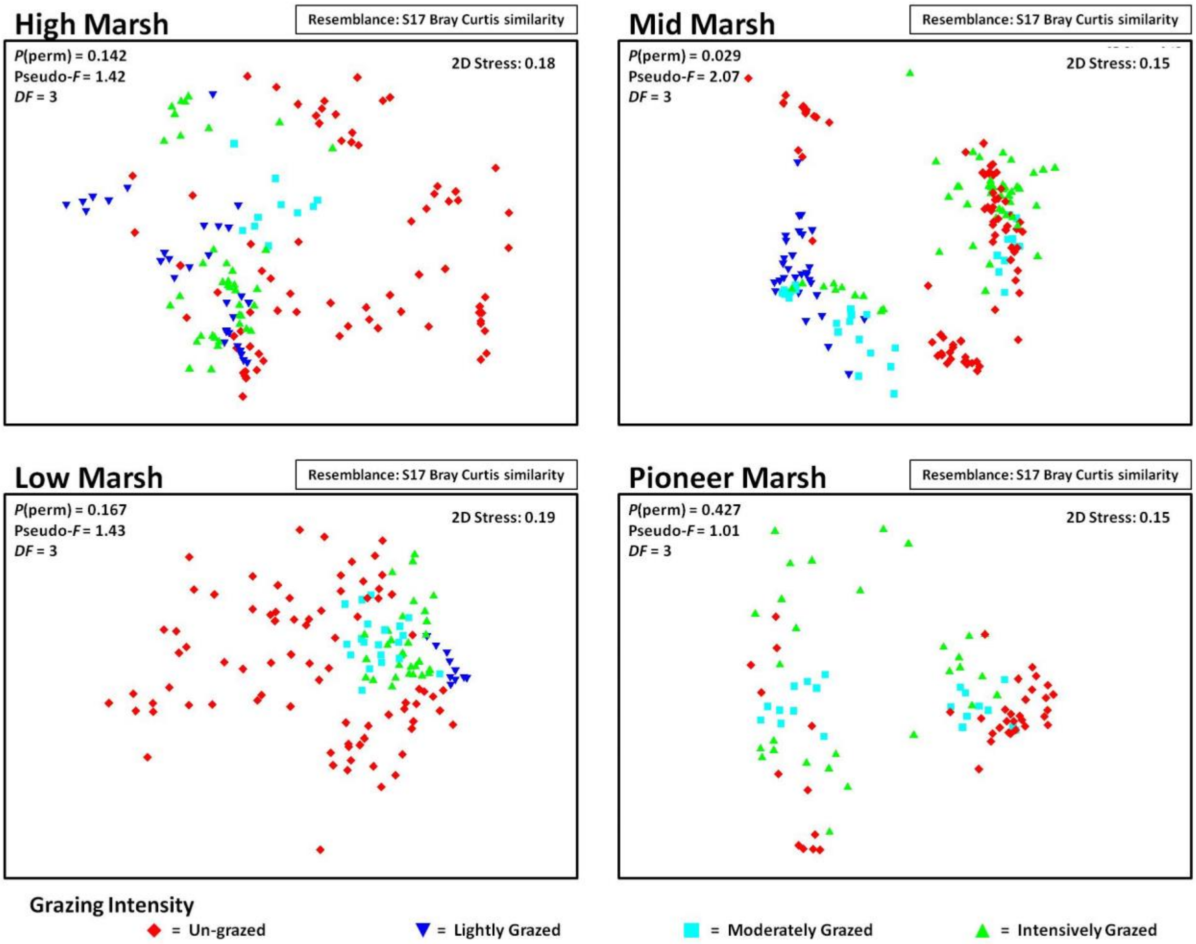


Figure 3.5 | MDS plots for each marsh zone with grouping by grazing intensity. Multi-dimensional scaling (MDS) representations of community compositions on each marsh zone based on a Bray-Curtis similarity matrix. Each of the four categorical grazing intensities are indicated: un-grazed (red diamonds), lightly grazed (dark blue triangles, point down), moderately grazed (light blue squares) and intensively grazed (green triangles, point up).

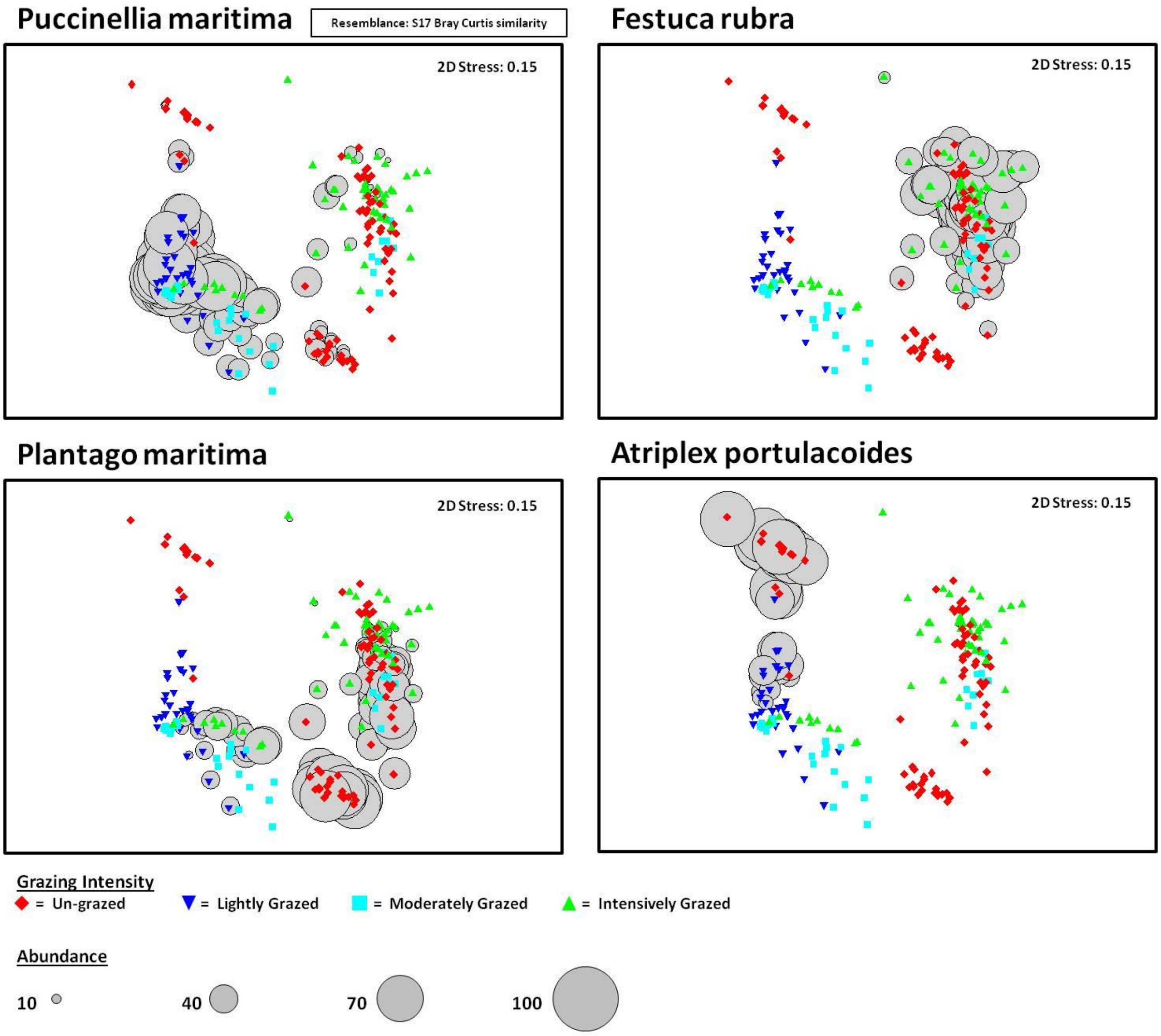


Figure 3.6 | MDS plots for the mid marsh zone showing distribution of key species. Multi-dimensional scaling (MDS) representations of community compositions on the mid marsh zone based on a Bray-Curtis similarity matrix with overlays of the four key species contributing to dissimilarities between plots. Each of the four categorical grazing intensities are indicated: un-grazed (red diamonds), lightly grazed (dark blue triangles, point down), moderately grazed (light blue squares) and intensively grazed (green triangles, point up). The abundance of each species is indicated by the size of each gray circle overlay.

Table 3.4 | Species contributing to dissimilarities between grazing intensity categories. Results of a SIMPER analysis showing the total dissimilarity between grazing intensities (groups: UG = un-grazed, LG = lightly grazed, MG = moderately grazed, IG = intensively grazed) per zone, and the species that contribute to the dissimilarities between grazing intensities within each zone. The average abundance is shown for each species for each grazing intensity category. The percent contribution of each species (Contr.) to the total dissimilarity between groups is also shown.

High Marsh Zone

Species	Average Abundance		Contr.
	UG	**LG**	
Festuca rubra	28.16	46.00	23.08
Juncus gerardii	7.11	23.97	14.14
Elymus repens	21.24	0.00	11.42
Atriplex prostrata	20.16	0.13	11.28
Average dissimilarity	79.73		
	UG	**MG**	
Festuca rubra	28.16	23.00	15.57
Plantago maritima	5.37	32.00	15.06
Juncus maritimum	16.46	28.70	14.40
Atriplex prostrata	20.16	8.60	11.31
Average dissimilarity	76.67		
	UG	**IG**	
Festuca rubra	28.16	46.88	22.10
Elymus repens	21.24	0.00	11.12
Atriplex prostrata	20.16	0.58	11.00
Glaux maritima	1.34	16.88	8.36
Average dissimilarity	79.92		
	LG	**MG**	
Festuca rubra	46.00	23.00	20.06
Plantago maritima	3.63	32.00	16.53
Juncus maritimum	0.00	28.70	16.23
Average dissimilarity	72.39		
	LG	**IG**	
Festuca rubra	46.00	46.88	27.38
Juncus gerardii	23.97	4.03	17.13
Puccinellia maritima	5.17	14.50	12.08
Average dissimilarity	61.19		
	MG	**IG**	
Festuca rubra	23.00	46.88	22.65
Juncus maritimum	28.00	3.95	17.12
Plantago maritima	32.00	11.58	14.78
Average dissimilarity	62.62		

Mid Marsh Zone

Species	Average Abundance		Contr.
	UG	**LG**	
Puccinellia maritima	2.94	69.67	34.03
Festuca rubra	31.06	0.00	15.61
Atriplex portulacoides	22.76	11.23	15.01
Average dissimilarity	90.03		
	UG	**MG**	
Festuca rubra	31.06	18.00	16.64
Puccinellia maritima	2.94	31.33	16.49
Plantago maritima	25.34	10.50	13.18
Atriplex portulacoides	22.76	0.00	12.48
Average dissimilarity	82.50		
	UG	**IG**	
Festuca rubra	31.06	46.20	25.75
Plantago maritima	25.34	7.46	15.93
Atriplex portulacoides	22.79	0.06	15.72
Average dissimilarity	73.52		
	LG	**MG**	
Puccinellia maritima	69.67	31.33	28.58
Festuca rubra	0.00	18.00	10.58
Salicornia europaea	0.27	16.30	10.24
Average dissimilarity	71.22		
	LG	**IG**	
Puccinellia maritima	69.67	15.16	35.25
Festuca rubra	0.00	46.20	26.89
Average dissimilarity	83.70		
	MG	**IG**	
Festuca rubra	18.00	46.20	25.66
Puccinellia maritima	31.33	15.16	21.08
Salicornia europaea	16.30	1.24	10.08
Average dissimilarity	74.71		

Low Marsh Zone

Species	Average Abundance		Contr.
	UG	**LG**	
Puccinellia maritima	28.00	87.50	38.54
Suaeda maritima	14.83	2.50	9.18
Spartina anglica	13.30	7.60	8.77
Average dissimilarity	69.07		
	UG	**MG**	
Puccinellia maritima	28.00	55.00	21.57
Spartina anglica	13.30	22.80	13.47
Suaeda maritima	14.83	2.45	9.98
Botrychia scorpioides	9.21	11.75	9.29
Average dissimilarity	59.19		
	UG	**IG**	
Puccinellia maritima	28.00	54.53	22.09
Spartina anglica	13.30	19.63	13.89
Suaeda maritima	14.83	1.70	10.39
Salicornia europaea	10.54	12.47	9.32
Average dissimilarity	63.50		
	LG	**MG**	
Puccinellia maritima	87.50	55.00	36.36
Spartina anglica	7.60	22.80	19.61
Average dissimilarity	38.69		
	LG	**IG**	
Puccinellia maritima	87.50	54.53	45.14
Spartina anglica	7.60	19.63	23.39
Average dissimilarity	38.69		
	MG	**IG**	
Spartina anglica	22.80	16.63	25.22
Puccinellia maritima	55.00	54.53	22.04
Botrychia scorpioides	11.75	3.37	14.27
Average dissimilarity	35.99		

Pioneer Marsh Zone

Species	Average Abundance		Contr.
No lightly grazed pioneer marsh zones			
	UG	**MG**	
Spartina anglica	42.08	24.70	41.68
Puccinellia maritima	6.85	19.90	21.03
Average dissimilarity	70.24		
	UG	**IG**	
Spartina anglica	42.08	13.53	58.79
Average dissimilarity	73.43		
No lightly grazed pioneer marsh zones			
No lightly grazed pioneer marsh zones			
	MG	**IG**	
Spartina anglica	24.70	13.53	31.41
Puccinellia maritima	19.90	0.87	23.89
Average dissimilarity	72.59		

Table 3.5 | Species contributing to dissimilarities between zones. Results of a SIMPER analysis showing the species associated with the pairwise dissimilarities between marsh zones. The average percent abundance of each species within each zone is recorded along with the percent contribution of each species to the total percent dissimilarity between the zones and the cumulative percent difference between zones. Only species contributing to the top 50% dissimilarity between groups are included. Total dissimilarity between zones is also recorded.

Species	Average Abundance		Contribution (%)	Cumulative %
	Pioneer	**Low**		
Puccinellia maritima	7.76	41.79	28.73	28.73
Spartina anglica	28.70	15.61	19.05	47.78
Salicornia europaea	6.53	10.67	7.89	55.67
Total dissimilarity between zones	78.87			
	Pioneer	**Mid**		
Festuca rubra	0.00	28.08	18.32	18.32
Spartina anglica	28.70	0.69	15.67	33.99
Puccinellia maritima	7.76	21.17	14.87	48.86
Plantago maritima	0.00	14.71	8.95	57.80
Total dissimilarity between zones	94.75			
	Pioneer	**High**		
Festuca rubra	0.00	36.37	21.23	21.23
Spartina anglica	28.70	0.01	14.33	35.55
Atriplex prostrata	0.00	10.16	6.19	41.74
Puccinellia maritima	7.76	5.47	6.02	47.76
Elymus repens	0.00	9.91	5.71	53.48
Total dissimilarity between zones	98.58			
	Low	**Mid**		
Puccinellia maritima	41.79	21.17	21.43	21.43
Festuca rubra	0.00	28.08	15.40	36.83
Plantago maritima	7.30	14.71	9.86	46.69
Spartina anglica	15.61	0.69	8.41	55.10
Total dissimilarity between zones	81.20			
	Low	**High**		
Puccinellia maritima	41.79	5.47	18.67	18.67
Festuca rubra	0.00	36.37	16.57	35.24
Spartina anglica	15.61	0.01	7.07	42.31
Plantago maritima	7.30	8.45	5.90	48.20
Atriplex prostrata	1.01	10.16	5.00	53.20
Total dissimilarity between zones	93.38			
	Mid	**High**		
Festuca rubra	28.08	36.37	20.86	20.86
Puccinellia maritima	21.17	5.47	12.83	33.69
Plantago maritima	14.71	8.45	9.10	42.79
Atriplex portulacoides	11.37	0.04	6.48	49.26
Atriplex prostrata	2.24	10.16	6.41	55.67
Total dissimilarity between zones	80.20			

3.3.7 The impact of grazing on the spread of the data

There was considerable spread in the data for each above-ground variable; however, there was no effect of grazing on the coefficients of variation (spread of the data around the mean) for vegetation height, plant biomass, or species diversity. Grazing did however significantly impact the coefficients of variance for litter biomass (ANOVA: $F_{3,24}$ = 2.95, p = 0.047, η_p^2 = 0.229) and percent vegetation cover (ANOVA: $F_{3,32}$ = 3.01, p = 0.042, η_p^2 = 0.327) with large effect sizes. The spread of data for litter biomass in moderately grazed marshes ($\bar{x}$ = 0.395, *SE* = 0.395) was significantly higher than those in un-grazed ($\bar{x}$ = 0.605, *SE* = 0.116), lightly grazed ($\bar{x}$ = 0.320, *SE* = 0.163), and intensively grazed marshes ($\bar{x}$ = 0.174, *SE* = 0.174) (*post hoc* Tukey HSD test). The spread of data for percentage vegetation cover in intensively grazed marshes ($\bar{x}$ = 0.172, *SE* = 0.053) was significantly higher than that in un-grazed marshes ($\bar{x}$ = 0.077, *SE* = 0.025) but neither significantly differed from that in lightly grazed ($\bar{x}$ = 0.101, *SE* = 0.041) or moderately grazed marshes ($\bar{x}$ = 0.074, *SE* = 0.020) (*post hoc* Tukey HSD test). When considering the zones separately, there was a significant effect of grazing on the coefficient of variation for average vegetation height in the low marsh (ANOVA: $F_{3,10}$ = 7.09, p = 0.008, η_p^2 = 0.680). The coefficient of variation for average vegetation height was significantly higher in moderately grazed marshes ($\bar{x}$ = 0.632, *SE* = 0.175) than in un-grazed marshes ($\bar{x}$ = 0.202, *SE* = 0.051) (*post hoc* Tukey HSD test).

Grazing also impacted the dispersions (a multivariate measure of the spread of the data) of community composition in the high (PERMDISP: $F_{2,146}$ = 37.32, p = 0.001), mid (PERMDISP: $F_{2,186}$ = 26.72, p = 0.001) and low (PERMDISP: $F_{2,136}$ = 121.25, p = 0.001) marsh zones but the pioneer zone showed no differences between the dispersions of each group (PERMDISP: $F_{2,87}$ = 2.78, p = 0.178). In the high marsh, un-grazed marshes ($\bar{x}$ = 56.58, *SE* = 0.87) showed a significantly greater dispersion than lightly grazed ($\bar{x}$ = 41.40, *SE* = 2.23), moderately grazed ($\bar{x}$ = 26.54, *SE* = 2.20) and intensively grazed ($\bar{x}$ = 40.01, *SE* = 2.44) marshes. Lightly grazed marshes also showed significantly greater dispersion than moderately grazed marshes. In the mid marsh, un-grazed marshes ($\bar{x}$ = 52.36, *SE* = 1.11) showed significantly greater dispersion than lightly grazed ($\bar{x}$ = 29.75, *SE* = 2.56) and intensively grazed ($\bar{x}$ = 43.81, *SE* = 2.16) marshes, and lightly grazed marshes showed significantly less dispersion than un-grazed, moderately grazed ($\bar{x}$ = 49.26, *SE* = 1.58) and intensively grazed marshes. In the low marsh, un-grazed marshes ($\bar{x}$ = 46.22, *SE* = 0.93) showed significantly greater dispersion than lightly grazed ($\bar{x}$ = 9.29, *SE* = 2.19), moderately grazed ($\bar{x}$ = 23.12, *SE* = 1.29) and intensively grazed ($\bar{x}$ = 25.15, *SE* = 1.46) marshes, and lightly grazed marshes showed significantly less dispersion than un-grazed, moderately grazed and intensively grazed marshes.

3.3.8 Changes in variation across the salt marsh zones

The coefficients of variation for percentage vegetation cover significantly differed between zones (ANOVA: $F_{3,32}$ = 17.61, p <0.001, η_p^2 = 0.775). The spread of data for percentage vegetation cover was significantly higher in the pioneer zone ($\bar{x}$ = 0.345, SE = 0.065) than in the high ($\bar{x}$ = 0.050, SE = 0.017), mid ($\bar{x}$ = 0.060, SE = 0.018) or low marsh zones ($\bar{x}$ = 0.057, SE = 0.012).

3.3.9 The impact of environmental variables

On the un-grazed marsh sites, community composition, soil grain size, tidal range, marsh geomorphology, marsh size and wave fetch (wave exposure) had significant associations with plant height, plant biomass, vegetation cover and species diversity, (Mixed effects model: Table 3.6a).

The community composition in the high marsh zones on un-grazed marshes was best explained by a combination of marsh size, marsh geomorphology, percent clay, and percent sand (DistLM: $AICc$ = 479.53, R^2 = 0.735). In the mid marsh, community composition was best explained by a combination of marsh size, tidal range, wave fetch, percent clay, and percent sand (DistLM: $AICc$ = 473.24, R^2 = 0.882). In the low marsh community composition was best explained by a combination of marsh size, tidal range, maximum fetch, marsh geomorphology, and percent sand (DistLM: $AICc$ = 482.18, R^2 = 0.786), and in the pioneer marsh zone, community composition was best explained by a combination of tidal range, wave fetch and marsh geomorphology (DistLM: $AICc$ = 265.14, R^2 = 0.710). Each environmental factor had a significant effect on community composition within each zone, and tidal range, percent sand, wave fetch, marsh geomorphology and marsh size explained the highest proportions of the variation in the community composition data (DistLM, Marginal tests; Table 3.6). A reduced model with additional environmental factors could not be run on the un-grazed marshes due to a low sample size of only 2 marshes.

On grazed marshes, in the higher marsh zones, stocking density explained a significant amount of the variation for both average plant height and species diversity (Mixed effect model: Table 3.6b). Marsh geomorphology, community composition, soil grain size, tidal range and wave fetch had significant associations with plant height, plant biomass, vegetation cover, and species diversity (Mixed effect model: Table 3.6b).

In the lower marsh zones on grazed marshes, stocking density (LSU) only explained a significant amount of the variation for maximum vegetation height (Mixed effects model: Table 3.6b). Community composition, soil grain size, marsh size, tidal range and wave fetch had significant associations with plant height, plant biomass, vegetation cover and species diversity (Mixed effect model: Table 3.6b).

The community composition in the high marsh was best explained by a combination of stocking density, tidal range, wave fetch, marsh geomorphology, and percent clay (*AICc* = 498.47, R^2 = 0.743). In the mid marsh, community composition was best explained by a combination of all the environmental factors and stocking density (*AICc* = 710.25, R^2 = 0.784). In the low marsh, community composition was best explained by stocking density, tidal range, wave fetch, marsh geomorphology, and percent sand (*AICc* = 353.67, R^2 = 0.569), and in the pioneer zone, community composition was best explained by tidal range, marsh geomorphology, percent clay, and percent sand (*AICc* = 319.65, R^2 = 0.755). Stocking density and all environmental factors had a significant effect on community composition, and tidal range, grain size, marsh size, marsh geomorphology and wave fetch explained the highest proportions of the variation in the community composition data (DistLM, Marginal tests; Table 3.6).

A reduced 7-marsh model with additional environmental factors showed that community composition in the high marsh was best explained by a combination of percent sand and water pH (DistLM; *AICc* = 498.47, R^2 = 0.743), in the mid marsh, community composition was best explained by percent clay (DistLM; AICc = 231.13, R^2 = 0.861), in the low marsh, community composition was best explained by percent clay and percent sand (DistLM; AICc = 120.67, R^2 = 0.360), and in the pioneer marsh, community composition was best explained by percent coarse sand (DistLM; AICc = 122.36, R^2 = 0.714). Stocking density and all environmental factors had a significant effect on community composition, and percent clay (Pseudo-F = 24.12, p = 0.001, $\propto$ = 0.463), water salinity (Pseudo-F = 21.33, p = 0.001, $\propto$ = 0.432) and wave fetch (Pseudo-F = 20.81, p = 0.001, $\propto$ = 0.426) explained the highest proportions of the variation in the community composition data in the high marsh. In the mid marsh, percent clay (Pseudo-F = 65.60, p = 0.001, $\propto$ = 0.633), dissolved orthophosphate (Pseudo-F = 64.72, p = 0.001, $\propto$ = 0.630) and dissolved inorganic nitrogen (Pseudo-F = 61.133, p = 0.001, $\propto$ = 0.617) explained the highest proportions of the variation in the community composition data. Due to the low number of pioneer and low marsh zones in the reduced model, marginal tests did not produce viable results.

Table 3.6a | Impacts of environmental factors on plant characteristics in un-grazed salt marshes. Results of a mixed effects model analyzing the impacts of environmental factors on above-ground variables across the marsh as a whole and in the lower (low and pioneer) and higher (mid and high) marsh zones on un-grazed salt marshes. Environmental variables that were included in the models are listed in the foremost column. Community composition (Comm. Comp.) and livestock stocking density (LSU) are also included. Significance level is indicated by *, where * = p<0.050, ** = p<0.010, and *** = p<0.001.

		Average Vegetation Height			Maximum Vegetation Height			Live Above-ground Plant Biomass			Percent Vegetation Cover			Species Diversity		
Effect	***df***	***F***	***p***		***F***	***p***		***F***	***p***		***F***	***p***		***F***	***p***	
								Un-grazed Marshes - Overall								
Marsh Size	1,3	4.15	0.134		7.16	0.075		21.38	**0.019**	*	0.24	0.658		0.04	0.856	
Tidal Range	1,3	119.88	**0.002**	**	153.80	**0.001**	**	163.50	**0.001**	**	3.87	0.144		7.48	0.072	
Wave Fetch	1,3	9.13	0.056		35.60	**0.009**	**	1.10	0.372		2.13	0.241		0.72	0.458	
Marsh Geomorphology	3,3	2.71	0.217		10.05	**0.045**	*	31.22	**0.009**	**	0.52	0.699		0.03	0.993	
Comm. Comp.	9,257	18.92	**<0.001**	***	20.51	**<0.001**	***	22.49	**<0.001**	***	37.81	**<0.001**	***	49.05	**<0.001**	***
Percent Clay	1,257	29.28	**<0.001**	***	6.77	**0.010**	*	0.42	0.516		3.39	0.067		28.43	**<0.001**	***
Percent Sand	1,257	0.63	0.427		15.20	**<0.001**	***	0.50	0.480		6.32	**0.013**	*	47.17	**<0.001**	***
								Un-grazed Marshes – Lower Marsh								
Marsh Size	1,4	14.41	**0.019**	*	13.27	**0.022**	*	3.14	0.151		1.02	0.369		2.39	0.197	
Tidal Range	1,4	50.66	**0.002**	**	52.00	**0.002**	**	11.87	**0.026**	*	0.61	0.478		0.65	0.464	
Wave Fetch	1,4	0.05	0.840		0.01	0.929		0.04	0.850		1.09	0.356		0.56	0.496	
Comm. Comp.	3,107	2.06	0.109		9.16	**<0.001**	***	3.64	**0.015**	*	36.76	**<0.001**	***	91.45	**<0.001**	***
Percent Clay	1,107	0.07	0.785		7.27	**0.008**	**	0.97	0.327		4.81	**0.031**	*	17.79	**<0.001**	***
Percent Sand	1,107	19.26	**<0.001**	***	22.99	**<0.001**	***	3.90	0.051		14.25	**<0.001**	***	23.08	**<0.001**	***
								Un-grazed Marshes – Higher Marsh								
Marsh Size	1,3	5.29	0.105		8.54	0.061		16.28	**0.027**	*	0.50	0.531		1.48	0.311	
Tidal Range	1,3	20.68	**0.020**	*	33.92	**0.010**	*	50.75	**0.006**	**	10.02	0.051		99.93	**0.002**	**
Wave Fetch	1,3	8.51	0.062		46.77	**0.006**	**	5.15	0.108		3.17	0.173		27.49	**0.013**	*
Marsh Geomorphology	3,3	4.23	0.133		0.91	0.530		55.23	**0.004**	**	23.52	**0.014**	*	15.53	**0.025**	*
Comm. Comp.	6,142	28.91	**<0.001**	***	17.94	**<0.001**	***	11.29	**<0.001**	***	13.59	**<0.001**	***	32.05	**<0.001**	***
Percent Clay	1,142	0.79	0.377		4.18	**0.043**	*	0.23	0.630		3.75	0.055		8.96	**0.003**	**
Percent Sand	1,142	0.26	0.609		0.21	0.650		1.60	0.209		12.75	**0.001**	**	30.40	**<0.001**	***

Table 3.6b | Impacts of environmental factors on plant characteristics in grazed salt marshes. Results of a mixed effects model analyzing the impacts of environmental factors on above-ground variables across the marsh as a whole and in the lower (low and pioneer) and higher (mid and high) marsh zones on grazed salt marshes. Environmental variables that were included in the models are listed in the foremost column. Community composition (Comm. Comp.) and livestock stocking density (LSU) are also included. Significance level is indicated by *, where * = p<0.050, ** = p<0.010, and *** = p<0.001.

		Average Vegetation Height			Maximum Vegetation Height			Live Above-ground Plant Biomass			Percent Vegetation Cover			Species Diversity		
Effect	***df***	***F***	***p***		***F***	***p***		***F***	***p***		***F***	***p***		***F***	***p***	
								Grazed Marshes – Overall								
Stocking Density (LSU)	1,5	1.49	0.874		0.23	0.806		2.06	0.211		2.37	0.184		3.56	0.118	
Marsh Size	1,5	0.03	0.277		0.07	0.654		0.53	0.501		0.44	0.539		4.18	0.096	
Tidal Range	1,5	0.62	0.465		0.31	0.603		15.41	**0.011**	*	0.59	0.478		35.95	**0.002**	**
Wave Fetch	1,5	0.36	0.572		3.24	0.132		14.53	**0.013**	*	0.04	0.856		2.68	0.163	
Marsh Geomorphology	4,5	5.25	**0.049**	*	3.95	0.082		34.05	**0.001**	**	0.55	0.706		9.83	**0.014**	*
Comm. Comp.	13,291	9.96	**<0.001**	***	12.48	**<0.001**	***	18.05	**<0.001**	***	40.15	**<0.001**	***	14.10	**<0.001**	***
Percent Clay	1,291	0.45	0.502		0.72	0.397		8.46	**0.004**	**	0.15	0.700		0.59	0.444	
Percent Sand	1,291	0.98	0.322		10.24	**0.002**	**	1.09	0.298		<0.01	0.984		22.22	**<0.001**	***
								Grazed Marshes – Lower Marsh								
Stocking Density (LSU)	1,2	14.06	0.064		25.07	**0.038**	*	5.47	0.144		9.67	0.090		3.12	0.220	
Marsh Size	1,2	2.64	0.246		105.02	**0.009**	**	43.35	**0.022**	*	7.20	0.115		55.08	**0.018**	*
Tidal Range	1,2	6.90	0.119		2.33	0.266		55.83	**0.017**	*	10.19	0.086		131.94	**0.008**	**
Wave Fetch	1,2	24.43	**0.039**	*	46.13	**0.021**	*	4.13	0.180		11.17	0.079		16.27	0.056	
Comm. Comp.	5,106	26.72	**<0.001**	***	41.51	**<0.001**	***	10.43	**<0.001**	***	211.47	**<0.001**	***	33.46	**<0.001**	***
Percent Clay	1,106	18.93	**<0.001**	***	6.67	**0.011**	*	11.13	**0.001**	**	275.34	**<0.001**	***	1.69	0.197	
Percent Sand	1,106	0.01	0.959		0.37	0.544		41.67	**<0.001**	***	3.13	0.080		1.06	0.305	
								Grazed Marshes – Higher Marsh								
Stocking Density (LSU)	1,5	9.63	**0.027**	*	5.12	0.073		3.11	0.138		4.62	0.084		6.87	**0.047**	*
Marsh Size	1,5	4.08	0.099		5.24	0.071		1.29	0.307		6.69	**0.049**	*	4.89	0.078	
Tidal Range	1,5	5.29	0.070		11.52	**0.019**	*	9.21	**0.029**	*	0.12	0.740		63.54	**0.001**	**
Wave Fetch	1,5	2.90	0.149		9.00	**0.030**	*	13.44	**0.015**	*	4.39	0.090		2.86	0.152	
Marsh Geomorphology	4,5	18.78	**0.003**	**	7.06	**0.027**	*	30.80	**0.001**	**	11.04	**0.012**	*	36.62	**0.001**	**
Comm. Comp.	9,175	4.91	**<0.001**	***	8.12	**<0.001**	***	13.68	**<0.001**	***	29.08	<0.001		16.90	**<0.001**	***
Percent Clay	1,175	2.08	0.151		8.23	**0.005**	**	4.67	**0.032**	*	0.06	0.808		13.65	**<0.001**	***
Percent Sand	1,175	1.27	0.261		0.04	0.836		3.05	0.082		2.16	0.143		16.17	**<0.001**	***

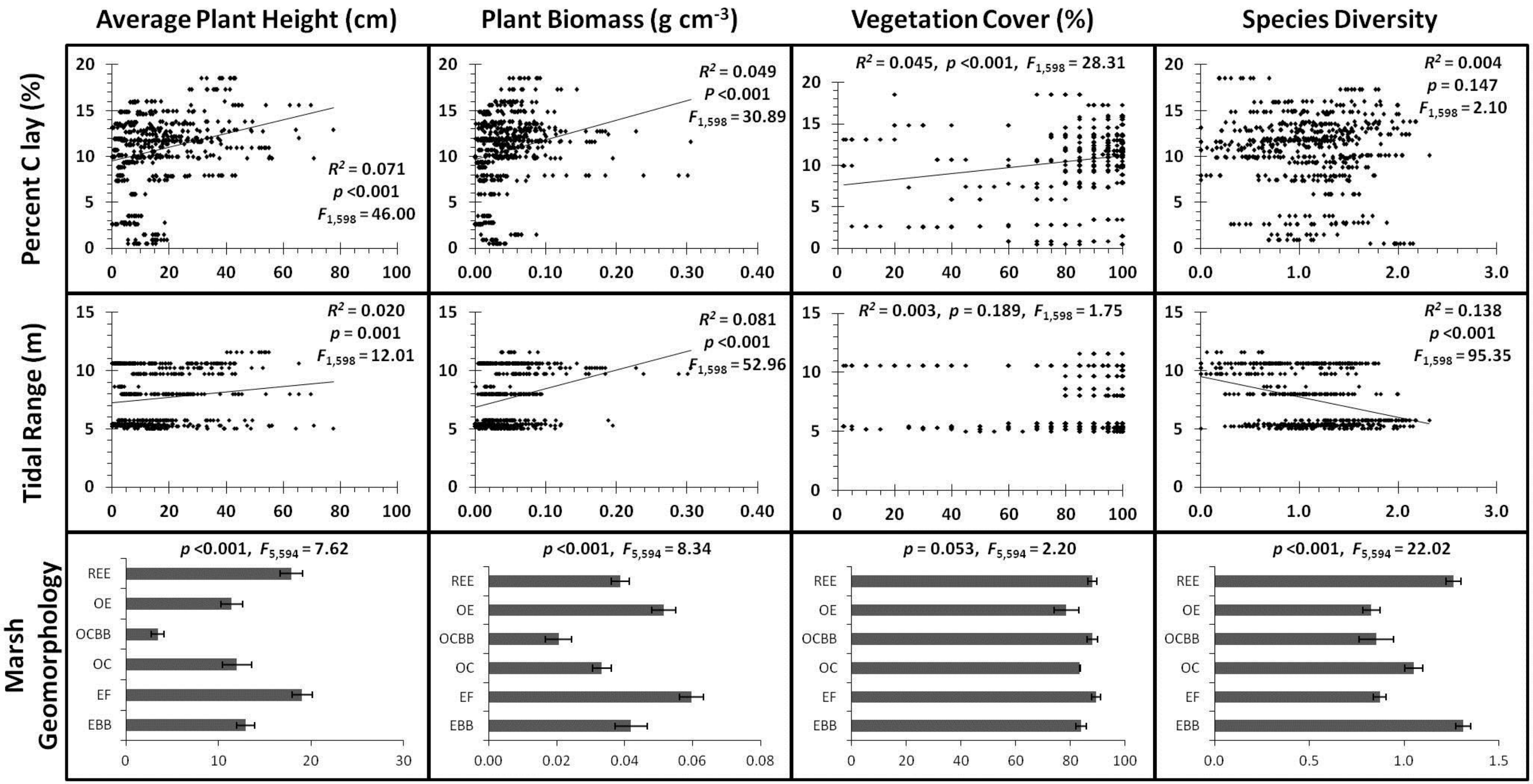


Figure 3.7 | Above-ground variables vs. environmental variables. Scatter and bar plots showing the relationships between the above-ground variables (plant height, plant biomass, percent vegetation cover, and species diversity) environmental variables (percent clay, tidal range, and marsh geomorphology). The marsh geomorphology codings represent the following: REE = restricted entrance embayment, OE = open embayment, OCBB = open coast back-barrier, OC = open coast, EF = estuarine fringing and EBB = estuarine back-barrier. The results (R^2, p and F) of associated regression and ANOVA tests are also shown.

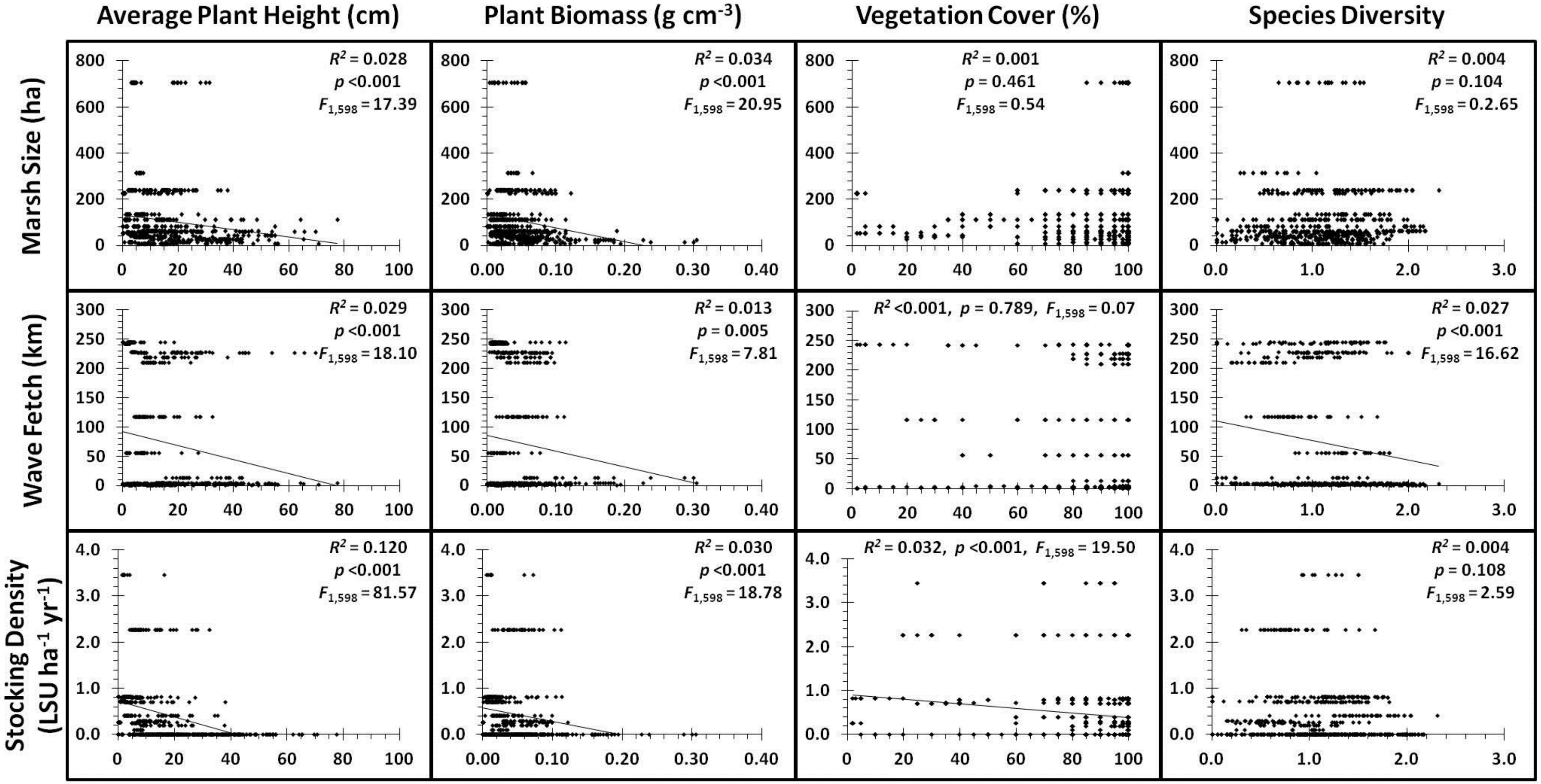


Figure 3.7 (cont) | Above-ground variables vs. environmental variables. Scatter plots showing the relationships between the above-ground variables (plant height, plant biomass, percent vegetation cover, and species diversity) environmental variables (marsh size, wave fetch and stocking density). The results (R^2, p and F) of associated regression analyses are also shown.

Table 3.7 | The impacts of environmental variables and grazing on community composition. Results of marginal tests from a DistLM analysis from un-grazed and grazed marshes for the overall data set and analysis per zone. Pseudo-F and associated p-values are shown for each environmental variable along with the proportion (∝) of the variation explained by that variable in the community composition data set.

	Un-grazed Marshes			Grazed Marshes		
Effect	**Pseudo-*F***	***p***	**∝**	**Pseudo-*F***	***p***	**∝**
Overall						
Stocking Density (LSU)	N/A	N/A	N/A	3.03	**0.016**	0.010
Zone	60.54	**0.001**	0.184	110.92	**0.001**	0.271
Marsh Size	6.18	**0.001**	0.023	3.32	**0.015**	0.011
Tidal Range	24.48	**0.001**	0.084	12.82	**0.001**	0.041
Wave Fetch	15.78	**0.001**	0.056	7.20	**0.001**	0.024
Marsh geomorphology	9.54	**0.001**	0.034	16.62	**0.001**	0.053
Percent Clay	8.35	**0.001**	0.030	15.59	**0.001**	0.050
Percent Sand	11.65	**0.001**	0.042	11.64	**0.001**	0.038
High						
Stocking Density (LSU)	N/A	N/A	N/A	7.06	**0.001**	0.083
Marsh Size	3.92	**0.008**	0.055	8.09	**0.001**	0.094
Tidal Range	21.60	**0.001**	0.241	19.56	**0.001**	0.200
Wave Fetch	12.47	**0.001**	0.154	9.14	**0.001**	0.105
Marsh geomorphology	3.18	**0.014**	0.045	9.38	**0.001**	0.107
Percent Clay	8.29	**0.001**	0.109	10.90	**0.001**	0.122
Percent Sand	21.61	**0.001**	0.241	7.62	**0.001**	0.089
Mid						
Stocking Density (LSU)	N/A	N/A	N/A	7.06	**0.001**	0.208
Marsh Size	9.39	**0.001**	0.107	8.09	**0.001**	0.074
Tidal Range	32.91	**0.001**	0.297	19.56	**0.001**	0.099
Wave Fetch	12.74	**0.001**	0.140	9.14	**0.001**	0.087
Marsh geomorphology	23.71	**0.001**	0.233	9.38	**0.001**	0.092
Percent Clay	3.44	**0.007**	0.024	10.90	**0.001**	0.062
Percent Sand	7.83	**0.002**	0.091	7.62	**0.001**	0.211
Low						
Stocking Density (LSU)	N/A	N/A	N/A	6.71	**0.001**	0.104
Marsh Size	4.61	**0.005**	0.056	10.47	**0.001**	0.153
Tidal Range	34.24	**0.001**	0.305	10.92	**0.001**	0.158
Wave Fetch	19.50	**0.001**	0.200	10.47	**0.001**	0.153
Marsh geomorphology	4.32	**0.004**	0.052	6.80	**0.001**	0.105
Percent Clay	17.86	**0.001**	0.186	7.87	**0.001**	0.120
Percent Sand	21.15	**0.001**	0.213	6.33	**0.001**	0.098
Pioneer						
Stocking Density (LSU)	N/A	N/A	N/A	6.34	**0.002**	0.117
Marsh Size	13.68	**0.001**	0.265	7.25	**0.001**	0.131
Tidal Range	5.38	**0.007**	0.124	13.30	**0.001**	0.217
Wave Fetch	4.90	**0.013**	0.114	11.22	**0.001**	0.190
Marsh geomorphology	5.52	**0.007**	0.127	12.28	**0.001**	0.204
Percent Clay	5.49	**0.010**	0.126	12.88	**0.001**	0.212
Percent Sand	5.94	**0.005**	0.135	14.06	**0.001**	0.227

3.4 Discussion

3.4.1 Grazing impacts plant community composition and structure

There were significant negative effects of grazing on plant height, live biomass, litter biomass and overall percentage cover in all marshes and all zones except the pioneer zone. The effects of grazing on vegetation in the higher marsh zones were expected and have been well documented throughout the salt marsh literature (Andresen et al., 1990; Jensen, 1985; Kiehl et al., 1996). However, this study found the broad-scale effects of grazing on vegetation diversity in salt marshes were inconsistent and weaker than expected from small-scale studies. Species diversity was expected to be highest under a lightly grazed regime, as documented by several terrestrial (Adler et al., 2001; J.P. Bakker et al., 1983; Jones, 2000) and small-scale saltmarsh studies (Andresen et al., 1990; J. P. Bakker, 1985; Kiehl et al., 1996). However, this study found no response of species diversity to grazing in the high and mid marsh zones. Community composition was also not affected by grazing in the high, low or pioneer zones, although grazing did show a significant effect on community composition in the mid marsh. Conversely, environmental variables such as tidal range, marsh geomorphology and grain size, were consistently good predictors of community composition and species diversity. The implications of this are that environmental context has an overridingly stronger impact on vegetation community composition and diversity than grazing intensity.

The effect of grazing on species diversity was also inconsistent between marsh zones; species diversity declined with increased stocking density in the low marsh, but rose with increased stocking density in the pioneer zone. The zones of salt marshes represent different stages of succession; the pioneer zone is the youngest part of the marsh, whereas the high marsh is the most mature part of the marsh, and the low and mid marsh zones are representative of intermediate successional stages (Adam, 1990b; Boorman, 2003; Davy et al., 2011; Krull & Craft, 2009; Packham & Liddle, 1970; D.S. Ranwell, 1964a). Grazing on salt marshes typically facilitates earlier successional species (Andresen et al., 1990; J. P. Bakker, 1978; Kuijper & Bakker, 2004a, 2004b). It is possible that, in the mid and high marsh zones, plant species that were lost due to increased grazing pressure were replaced by earlier successional plant species from the lower marsh zones that were resilient to physical disturbance; thus an increase in grazing pressure would not lead to a loss of species diversity, but merely a change in species composition. In the low marsh zone, reverse succession may occur to a certain extent. However, the low marsh is subject to harsher physical conditions than both the mid and high marsh zones (Adam, 1990a, 1990b; Langlois, Bonis, & Bouzille, 2003) and as few salt marsh plants can withstand both grazing pressure and physical disturbance (Adam, 1990a), there are few plant species to replace those lost in the low marsh as grazing pressure increases. Therefore an increase in grazing pressure is likely to cause a loss of species diversity in the low marsh, as observed here. Species diversity in the pioneer zone is lower than the other marsh zones and it is typically dominated by only a small number of highly resilient species (Adam, 1990a). If grazers can reach the pioneer zone, they could create more favourable conditions by compacting soil (Bezkorowajnyj, Gordon, & McBride, 1993) and introducing nutrients through defecation (Bhogal et al., 2010; Buschbacher, 1987; Sheldrick, Syers, & Linguard, 2003). It is possible that some species from the low marsh zone may colonise areas of the pioneer zone, where conditions would have previously been too harsh, and thus significantly increase species diversity. For example, *Puccinellia maritima* typically dominates the low marsh (Table 3.5) but this species contributes to the differences between the pioneer zones in moderately and un-grazed marshes, with a greater proportion of *Puccinellia maritima* in moderately grazed marshes (Table 3.4). This suggests that conditions in the pioneer zone under a moderately grazed regime may have facilitated for the colonisation of this low marsh species in the pioneer zone.

In the pioneer zone, vegetation height showed no significant response to grazing, and above-ground biomass showed a significant positive response to an increase in stocking density. The pioneer zone is subject to greater physical stresses than the higher marsh zones, and the substrate of the pioneer zone can be highly dynamic as it is exposed to greater wave and tidal disturbance than the higher marsh zones (Adam, 1990a, 1990b; Langlois et al., 2003). As grazers only minimally graze the pioneer zone due to the difficulty of access (Adam, 1990b; Kiehl et al., 1996), it is likely that the lack of a relationship between vegetation height and grazing is due to the relative influence of physical stress outweighing the impacts of livestock grazing in the pioneer marsh. However, as species diversity and above-ground biomass both increased with grazing, it is likely that grazing has some impact on the pioneer zone vegetation community. This suggests that grazing pressure in the pioneer zone is insufficient to reduce above-ground biomass, yet it is sufficient to facilitate favourable conditions for the plant community, similar to those created under a light grazing regime (Adler et al., 2001; J.P. Bakker et al., 1983; Jones, 2000).

The plant communities of un-grazed mid marsh zones were highly variable, but were dominated by one of three main community types: a *Festuca rubra* dominated community, an *Atriplex portulacoides* dominated community, or a diverse mixed sward dominated by *Plantago maritima*. Lightly and moderately grazed marshes were dominated by the low-marsh species *Puccinellia maritima*, suggesting that reverse succession occurred under these grazing regimes, as observed elsewhere (J. P. Bakker, 1978, 1985; Kiehl et al., 1996; Kuijper & Bakker, 2004a). The plant community in intensively grazed marshes, however, was dominated by *Festuca rubra*. *Festuca rubra* is particularly stress-tolerant and is normally found in the higher marsh zones where evaporation rates are high and tidal inundation is infrequent (Adam, 1990e). High evaporation rates in the high marsh result in highly saline conditions and low soil moisture leads to hard, compact soils (Pennings & Callaway, 1992). Intensive livestock grazing significantly compacts the soil (Bezkorowajnyj et al., 1993), and reduced vegetation biomass and cover is likely to increase evaporation rates, thus reducing soil moisture and increasing soil salinity (Shumway & Bertness, 1994). It is therefore feasible that an intensive grazing regime may create conditions in which *Festuca rubra* can out-compete resilient, but competitively inferior species from lower marsh zones, such as *Puccinellia maritima*.

3.4.2 Changes in plant community composition and structure across the zones

There were consistent patterns of above-ground plant characteristics with marsh zone: vegetation height, above-ground biomass, litter biomass, percent vegetation cover and species diversity were all greatest in the high marsh and lowest in the pioneer marsh. Physical stresses and disturbances are the main drivers of plant community characteristics in the lower marsh, which leads to a more sparse, low diversity sward in low marsh zones (Adam, 1990a; Huiskes et al., 1995; Pennings & Callaway, 1992). As the conditions become more favourable in the mid and high marsh zones, plants can grow larger and more extensively, and inter- and intraspecific competition become more dominant drivers of the plant community characteristics (Grime, 1974; Pennings & Callaway, 1992).

There was a clear differentiation between the community compositions of each zone, as expected (Adam, 1990e; Pennings & Bertness, 2001; Pennings & Callaway, 1992). The pioneer marsh was typically differentiated from the other zones by the presence and abundance of *Spartina anglica*, the low marsh was typically differentiated from the other zones by the presence and abundance of *Puccinellia maritima*, the mid marsh was typically differentiated from the other zones by the presence and abundance of *Plantago maritima*, and the high marsh was typically differentiated from the other zones by the presence and abundance of *Festuca rubra* or *Atriplex portulacoides*. *Spartina anglica* and *Puccinellia maritima* are tolerant of the saline and waterlogged conditions of the lower marsh zones but are competitively inferior species; as such *Spartina anglica* and *Puccinellia maritima* are found in high abundance in the lower marsh zones but not in the higher marsh zones, where inter- and intraspecific competition are dominant drivers of community competition (Adam, 1990e; Pennings & Bertness, 2001; Pennings & Callaway, 1992). *Plantago maritima* and *Festuca rubra*, while still tolerant of saline conditions, are less tolerant of prolonged waterlogged conditions and are thus found only in the higher marsh zones where tidal flooding is not frequent enough to facilitate prolonged waterlogged conditions (Adam, 1990e; Pennings & Bertness, 2001; Pennings & Callaway, 1992).

3.4.3 The influence of environmental context

The study area had considerable variation in environmental variables, and the contextual setting of each marsh site had a significant impact on all above-ground plant community characteristics across each marsh. Most of the variation in plant community characteristics across un-grazed marshes was explained by tidal range and a combination of other environmental stressors and contextual variables. On grazed marshes, the impact of livestock grazing was significant in both high and low marsh zones. However, the impacts of grazing did not outweigh the impacts of environmental factors in any zone. This suggests that the impact of environmental context on plant community characteristics, highlighted in the analysis on un-grazed marshes, was equal to or greater than the impact of livestock grazing.

The relative impacts of the environmental factors varied between the zones. The community compositions in the higher marsh zones were most strongly influenced by tidal range. Tidal range directly influences the extent of each zone and dictates physical stressors such as salinity, soil redox potential and soil moisture content across the marsh (Adam, 1990b; Allen, 2000; Boorman, 2003). Community composition and plant morphology are determined by the ability to tolerate or adapt to these physical stressors, thus it is unsurprising that tidal inundation is a major driver of plant community characteristics (Adam, 1990a, 1990d; Grime, 1974).

Marsh geomorphology and wave fetch were significant drivers of community composition and plant morphology across all marsh sites. The geomorphology of the marsh encompasses the physical setting of the marsh, such as whether a marsh is situated on an open coast, behind a land barrier, or along the edge of an estuary. The geomorphology can be influenced by a number of contextual parameters such as freshwater influence, nutrient availability and sediment regime (Allen, 2000). The geomorphology of a marsh also determines the relative wave exposure of a marsh; an open coast marsh is likely to have a higher exposure to waves than one situated behind a spit of land (Adam, 1990b; Allen, 2000). The wave exposure of a marsh is an indicator of the maximum wave disturbance that is likely to impact each marsh; the greater the fetch the greater the potential wave disturbance may be across the marsh (Burrows et al., 2008). Wave disturbance is a significant driver of plant community composition and morphology in the lower marsh zones and plant communities have to tolerate or adapt to high physical disturbance levels (Adam, 1990a, 1990d; Boorman, 2003). In the higher marsh, however, physical stress is typically not a significant driver of plant community characteristics, as wave and tidal energy dissipates in the lower marsh zones (Moeller & Spencer, 2002; Moeller et al., 1999; Spencer et al., 1995). Greater wave exposure may however increase the likelihood of flooding during storm events (Allen, 2000), which can result in increased salinity stress in the higher marsh zones; thus greater wave exposure may reduce plant growth rates in higher marsh zones (L. D. Clarke & Hannon, 1970; Howard & Mendelssohn, 1998; Pennings & Callaway, 1992). Grazing pressure could potentially alter the impacts of wave disturbance. In the lower marsh zones, compaction by livestock may stabilize the soil, creating a more favourable environment for the plant community. In the higher marsh zones, lower vegetation cover may increase evaporation rates and thus reduce the potential for waterlogged conditions (Pennings & Callaway, 1992; Shumway & Bertness, 1994), however, increased evaporation rates lead to higher soil salinities (Shumway & Bertness, 1994), which can significantly impair plant growth (C. L. Richards, Pennings, & Donovan, 2005).

The community compositions of the pioneer marsh zone on un-grazed marshes were most strongly influenced by marsh area. Marsh area also influenced community composition and morphology across all marsh sites, but had a stronger influence in the lower marsh zones than in the higher marsh zones. Tidal range is the main factor influencing marsh area; the larger the tidal range, the larger the marsh can potentially become (Allen, 2000). Wave exposure is a limiting factor in salt marsh formation; the greater the wave exposure, the greater the magnitude and frequency of erosion is across the marsh, particularly at the marsh seaward edge (Moeller & Spencer, 2002; Yang, Shi, Bouma, Ysebaert, & Luo, 2011). The presence of embankments at the landward edge and riverbanks at the seaward edge of a marsh also limit marsh size. Marsh area is therefore representative of a combination of contextual variables, and it may be this combination of variables that is describing plant community characteristics, rather than marsh area itself.

The community compositions of the pioneer and mid marsh zones on grazed marshes were most strongly influenced by soil grain size, although soil grain size also influenced plant community characteristics across all zones and marshes. Several soil properties, such as pore space, soil moisture, and soil organic content are directly correlated with soil grain size (Evans, Gill, & Robotham, 1990; Gupta & Larson, 1979; Juang & Holtz, 1986). A soil comprised mostly of clay typically has very small pore spaces, high moisture content and high nutrient retention due to the small particle sizes (Gupta & Larson, 1979). These conditions can be good for root growth but if the pore size is too small (i.e. the soil is too dense), root growth is reduced and above-ground plant growth can be stunted (Warnaars & Eavis, 1972). Furthermore, reduced pore size and increased moisture levels are more likely to lead to anaerobic conditions in the soil, leading to a community comprised only of species that can tolerate anaerobic conditions (Torbert & Wood, 2008). Conversely, a soil comprised mostly of sand typically has large pore spaces, low moisture content and low nutrient retention due to large particle sizes (Juang & Holtz, 1986). While the larger pore size favours root growth, sandy soils drain quickly, and due to the smaller surface area to volume ratio of the large particles, organic content of the soil is lower (Evans et al., 1990); this can create a stressful environment for the plants and reduce plant growth (Warnaars & Eavis, 1972). Furthermore, the large pore size makes sandy soils less stable, and in a physically disturbed environment, these soils can be very dynamic, resulting in a plant community dominated by species tolerant of, or adapted to, physical disturbance (Adam, 1990a). Intermediate soil grain sizes, such as those comprised mainly of silt, provide optimal growing conditions for plants (Adam, 1990a). It is possible that the impacts of soil grain size on plant community properties may conflict with or enhance the impacts of grazing. For example, in clay soils, soil compaction by livestock may further reduce pore size and thus create a more stressful environment for the plant community (Adam, 1990a; Armstrong, Justin, Beckett, & Lythe, 1991; Bezkorowajnyj et al., 1993; Warnaars & Eavis, 1972). Conversely, in sandy soils, soil compaction by livestock may be beneficial for the plant community as soil stability will increase and soil moisture loss will decrease as pore size decreases (Gupta & Larson, 1979).

Although livestock grazing has significant impacts on plant community characteristics, it is perhaps unsurprising that grazing impacts do not outweigh the impacts of environmental stressors in salt marshes. Salt marshes are naturally stressful environments, so conceivably, salt marsh plant communities can tolerate and adapt to stresses caused by grazing as well as the environmental stresses they naturally experience. As above-ground processes are likely to link to below-ground processes (Bardgett & Wardle, 2003; Bardgett, Wardle, & Yeates, 1998; Wardle et al., 2004), it is likely that grazers will influence below-ground carbon stocks. However, this study suggests the influence of grazers is likely to be, at best, equal to, or possibly less than, the impact of environmental contextual variables.

3.4.4 Study implications

This study was the first to examine the impact of grazing on above-ground vegetation on salt marshes in the context of wider environmental settings. Grazers have been used as a management tool on salt marshes for biodiversity protection and habitat provision for bird species such as redshank (Adam, 1990c; V. Bouchard et al., 2003; Gedan et al., 2009; Norris, Cook, O'Dowd, & Durdin, 1997). Previous grazing research in salt marshes has focused on relatively small scales, and not considered the influence of the large-scale geographical variation in environmental context that most governmental management schemes operate across. While this study supports small-scale studies in the observation that grazing significantly impacts plant height and biomass (Andresen et al., 1990; Jensen, 1985; Kiehl et al., 1996), it shows that the broad-scale impact of grazing on vegetation diversity is less consistent than that indicated by small-scale studies.

As this study was conducted over a large spatial scale, it is possible that the sample size was not sufficient to find strong effects of grazing due to the considerable natural variation across the study sites. While grazing effects were found, these effects were weaker than expected and the impact of grazing was equal to or weaker than the effects of several environmental drivers. Despite these limitations, this study is the first to look at above-ground grazing impacts on salt marshes in the context of wider environmental settings, and therefore it makes an important contribution to the literature. Further research into the broad-scale impacts of grazing would need to take into account the considerable impacts of environmental setting. By conducting more detailed studies over a range of marshes with known environmental influences, the interaction between livestock grazing and these environmental variables can be determined. This will benefit management schemes hoping to manage grazing to enhance carbon sequestration across several variable sites.

Chapter 4: To Graze or Not To Graze: The Impact of Livestock Grazing on Below-ground Salt Marsh Carbon Stocks

4.1 Introduction

4.1.1 Natural carbon capture and storage

Environmental policies and management seek to optimise natural carbon capture and storage (CCS) across exploited and near-pristine landscapes to mitigate climate change (K. R. Richards, 2004). Highly productive systems such as forests, peatlands and coastal wetlands have become the focal point for optimising natural CCS (Amundson, 2001; Chmura et al., 2003; Dalal & Allen, 2008; Lal, 2004). Ecosystem management and restoration provide relatively cheap ways of increasing natural carbon sequestration rates (Crooks, Herr, Tamelander, Laffoley, & Vandever, 2011; Jandl et al., 2007; Vasander et al., 2003). These natural systems are often exploited or disturbed by human activity, for example, deforestation, peat mining, or livestock grazing (Fearnside & Barbosa, 1998; Reid et al., 2008; Rodhe & Svensson, 1995). Effective management of CCS relies on understanding the nature of the relationship between CCS and intensity of exploitation, as well as the consistency of this relationship across environmentally variable landscapes.

4.1.2 The impact of grazers on carbon stocks

Globally, more than 40% of grasslands are grazed by livestock (Reid et al., 2008). Management of stocking density provides an opportunity to positively influence carbon sequestration (Tanentzap & Coomes, 2012). Grazers have a negative above-ground impact on vegetation (Chapter 3) that in turn provides a major input of carbon into the below-ground stores (Jobbagy & Jackson, 2000): grazing alters community composition, reduces vegetation biomass and minimizes litter production (Chapter 3; Figures 4.1a, 4.1b) (Facelli & Pickett, 1991; Jensen, 1985; Kiehl et al., 1996). Livestock can increase carbon inputs through manure (Bhogal et al., 2010; Sheldrick et al., 2003). This input, however, can be offset by significant carbon dioxide and methane emissions from livestock respiration, digestion, and faecal decomposition (Murray, Gill, Balsdon, & Jarvis, 2001; Pinares-Patino, D'Hpur, Jouany, & Martin, 2007). Livestock indirectly alter soil properties by trampling, which in turn reduces root growth and decomposition rates and increases gas effluxes from the soil (Cao et al., 2004; Ford, Garbutt, Jones, & Jones, 2012; McNaughton, Banyikwa, & McNaughton, 1998; Olofsson & Oksanen, 2002; Turner, 1987). The intensity of grazing dictates the direction and magnitude of these effects. For example, moderate grazing can result in a resilient, fast growing plant community, increased root growth and carbon allocation to the roots, whereas intense grazing results in stunted root growth, low species richness and minimal above-ground biomass (Jensen, 1985; Kiehl et al., 1996; McNaughton, 1979; Schuster, 1964).

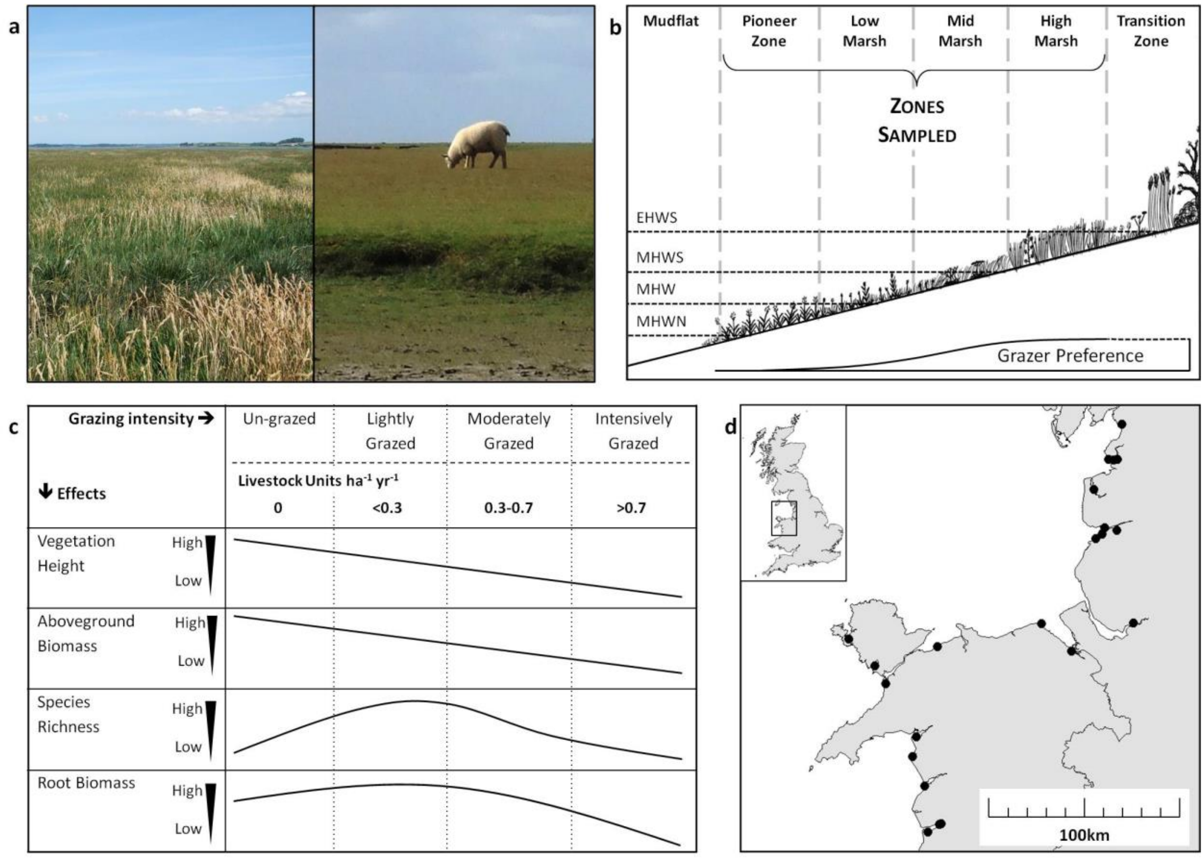


Figure 4.1 | Salt marsh ecology and impacts of grazing. a) The contrast between an un-grazed marsh (left) and an intensively grazed marsh (right). **b)** A diagrammatic representation of a salt marsh showing zonation according to tidal inundation: extreme high water spring (EHWS), mean high water spring (MHWS), mean high water (MHW) and mean high water neap (MHWN). Only the pioneer, low, mid and high zones were analysed in this study. Grazer preference is indicated showing decreased grazing activity in the lower zones. **c)** Predicted effects of a range of grazing intensities on vegetation height, above-ground biomass, species richness and root biomass according to the literature (Facelli & Pickett, 1991; Jensen, 1985; Kiehl et al., 1996; McNaughton et al., 1998; Stumpf, 1983). Grazing is shown as 'Grazing Intensity' category (un-grazed, lightly grazed, moderately grazed and intensively grazed) and Livestock Units per hectare per year (LSU ha^{-1} yr^{-1}). **d)** Location of the 22 study sites along the west coast of Wales and northwest England.

Grazing impacts on the above and below-ground vegetation are likely to link to changes in below-ground processes such as microbial activity, mineralization rates and decomposition rates (Bardgett & Wardle, 2003; Bardgett et al., 1998). Furthermore, the main input of carbon into the soil carbon stocks is organic matter (e.g. plant litter) (Elsey-Quirk, Seliskar, Sommerfield, & Gallagher, 2011), therefore it would be expected that an increase in stocking density will lead to a reduced input of organic matter, which may negatively impact below-ground soil carbon stocks. Conversely, plant compensatory responses to grazing, such as stimulated root growth (J. N. Holland et al., 1996; Schuster, 1964), may counter the above-ground impact of grazers on carbon storing and possibly impact below-ground carbon stocks (Tanentzap & Coomes, 2012). The few studies that have investigated the impacts of grazers on soil carbon stocks have focused at a local scale, on only a limited number of sites (R. T. Conant & Paustian, 2002; Klumpp et al., 2009; Schuman, Reeder, Manley, Hart, & Manley, 1999) and broad-scale empirical studies of carbon responses to variation in grazing intensity are lacking (Tanentzap & Coomes, 2012). As grazing management schemes tend to stipulate a range of grazing intensities, depending on the aim of the scheme, it is important to understand the impact of a range of stocking densities on soil organic carbon stocks, particularly in naturally carbon rich systems that are impacted by grazing.

4.1.3 Carbon capture and storage in coastal wetlands

Coastal wetlands, such as salt marshes, provide greater long-term carbon stores per-area than most terrestrial systems (Chmura, 2009; Chmura et al., 2003) due to high below-ground productivity (Adam, 1990f), high sedimentation rates (Stumpf, 1983), and slow decomposition rates in sulphurous, anaerobic sediments (Dalal & Allen, 2008; Freeman, Ostle, & Kang, 2001). Salt marshes are characterised by highly productive halophytic herbs, grasses and low shrubs that are periodically inundated with saline water (Adam, 1990b) (Figure 4.1b). Continuing salt marsh expansion and accretion results in distinct zonation according to elevation, each zone representing a different stage of salt marsh succession, with the most mature marsh at the highest elevations (Figure 4.1b) (Adam, 1990b; Armstrong, Wright, Lythe, & Gaynard, 1985; Bertness & Ellison, 1987). The presence and extent of each of these zones depends on the tidal range at the marsh (Adam, 1990b; Boorman, 2003; Chapman, 1940; Feagin et al., 2011; Weisbrod, 1964). All salt marshes are frequently inundated with saline water resulting in waterlogged soils with little oxygen, yet due to the nature of tidal cycles high marsh areas are flooded less frequently than lower marsh areas (Adam, 1990b); as a consequence the soils in high marsh areas are less waterlogged than low marsh soils (Adam, 1990b; Chapman, 1938; Pennings & Bertness, 2001).

Salt marsh carbon stocks vary considerably with marsh maturity, geomorphology and environmental setting (Sousa, Lillebo, Pardal, & Cacador, 2010). On un-grazed marshes the main inputs to soil carbon are sedimentation (Stumpf, 1983), degradation of root matter, and plant litter deposition (Saunders et al., 2006); the main losses of carbon are through gas emissions (Dalal & Allen, 2008; Freeman et al., 2001) and sediment loss from wave, and tidal erosion (Chalmers et al., 1985). Soil carbon stocks are likely to vary between the marsh zones; due to the nature of salt marsh growth and succession, the most mature high marsh zones will have accumulated carbon over a considerable period of time through growth and degradation of organic matter and accretion of sediment, while the youngest, pioneer marsh zones are unlikely to have accumulated large soil carbon stores (Adam, 1990b; Allen, 2000; Chmura, 2009; van der Wal, Pye, & Neal, 2002). However, sedimentation rates are highest in the pioneer marsh zones due to a higher tidal inundation frequency, so although large carbon stocks may not have accumulated, the rate of carbon accumulation is likely to be highest in the lowest marsh zones (Bartholdy, Bartholdy, & Kroon, 2010; Bricker-Urso, Nixon, Cochran, Hirschberg, & Hunt, 1989; de Groot, Veeneklaas, Kuijper, & Bakker, 2011; Shi, 1992; Stoddart, Reed, & French, 1983; Stumpf, 1983).

4.1.4 Grazing impacts on salt marsh carbon stocks

Salt marshes are natural grazing grounds (Koch et al., 1998) and globally, many salt marshes are grazed by livestock for agricultural production and conservation management purposes (Adam, 1990c). Grazing centres on mid and high marsh zones (Figure 4.2a) (Wallis De Vries et al., 1999) as access to the lower zones is cut off by creeks on high tides (Adam, 1990b). Introducing livestock is likely to have conflicting effects on salt marsh carbon stocks (Jensen, 1985; Kiehl et al., 1996; McNaughton et al., 1998; Schuster, 1964). For example, plant litter and above-ground biomass are likely to decrease under all grazing regimes (J. P. Bakker, 1985; Jensen, 1985; Kiehl et al., 1996) and consequently less sediment, and associated carbon, will be trapped by the vegetation during flooding (Neuhaus, Stelter, & Kiehl, 1999). Conversely, soil compaction by livestock reduces soil pore size and induces anaerobic conditions (Tanner & Mamaril, 1958). Anaerobic conditions result in slower decomposition rates and reduced carbon dioxide emissions (Freeman et al., 2001; Hussein & Rabenhorst, 2002; Scanlon & Moore, 2000). In terrestrial wetlands, the microbial communities associated with anaerobic conditions (methanogens) increase methane emissions (Wang et al., 1996). Methane is a potent greenhouse gas as it absorbs infra-red radiation ~25 times more effectively than carbon dioxide (Lelieveld et al., 1997). Consequently the greenhouse gas benefit of reduced carbon dioxide emissions in anaerobic terrestrial wetlands can be offset by an increase in methane production (Bridgham et al., 2006). This offset is less important in salt marshes, where abundant sulphates brought in by the tide inhibit methane production (Winfrey & Ward, 1983). Soil compaction by grazers might therefore boost carbon storage in salt marshes by lowering overall gas emissions. In summary, grazing is likely to reduce above-ground inputs of carbon through the removal of vegetation biomass and, as a consequence, reduce carbon input through sediment trapped by vegetation; however, plant compensation and induced anaerobic conditions through soil compaction might counter the above-ground effects of grazing on carbon accumulation.

4.1.5 The importance of environmental setting

Carbon management schemes are likely to encompass large geographical areas, which are subject to significant environmental variation (Laffoley & Grimsditch, 2009). Salt marshes are subject to a wide range of environmental stressors such as water salinity, wave exposure, and nutrient limitations (Adam, 1990a). Spatial variation in these stressors can lead to spatial variation in above-ground processes, which in turn may impact soil carbon stocks (Wardle et al., 2004). In Chapter 3 grazing was shown to have a strong effect on above-ground vegetation characteristics and assemblage composition acting in context with other environmental factors. The influence of environmental context on above-ground vegetation, such as root growth rates or degradation of plant litter, is likely to translate to below-ground carbon stocks (Elsey-Quirk et al., 2011). Thus it is probable that environmental context will play a role in carbon sequestration. The impact of livestock grazing on below-ground saltmarsh carbon stocks has only been studied on a small scale (Yu & Chmura, 2010) and it is unclear how environmental variability across a large area will interact with, or possibly compensate for, the effects of grazing on soil carbon. If ecosystems are to be managed effectively for CCS, broad-scale data is essential for assessing the continuity of trends and patterns found on a small scale, as scaling up from one or two sites can lead to considerable inaccuracies (Harvey, 2000; Jarvis, 2006).

4.1.6 Study aims

The overall aim of this chapter was to examine the broad-scale influence of livestock grazing on root biomass and below-ground soil carbon stocks. Root biomass was expected to peak under moderate grazing intensities as plants compensate for grazing pressure by increased growth rates, but significantly decrease under intensive grazing regimes due to high stress levels and highly compact soils (Kiehl et al., 1996; McNaughton, 1983; Schuster, 1964; Tanentzap & Coomes, 2012). Although root biomass is likely to increase under moderate grazing regimes (Kiehl et al., 1996; McNaughton, 1983; Schuster, 1964), litter biomass shows a significant negative response to an increase in stocking density (Chapter 3) and thus it is likely that the input of organic matter to soil carbon stocks will decrease with an increase of stocking density. Soil carbon stocks are therefore likely to show a significant negative response to increasing stocking density, as organic matter is a major input of carbon into the salt marsh soil carbon stock (Elsey-Quirk et al., 2011). Furthermore, live above-ground biomass of plants significantly decreases with an increase in stocking density, and thus it is likely that the amount of sediment trapped on a marsh will be reduced (Neuhaus et al., 1999; Stoddart et al., 1983; Stumpf, 1983). Marshes were sampled at all four intertidal, vegetated marsh zones (Figure 4.1b) to examine the influence of marsh zone on root biomass and soil organic carbon to reduce variation in the data set. Root biomass was expected to be lowest in the pioneer marsh zone, where physical stress and disturbance were greatest, and highest in the high marsh, where physical stress and disturbance were lowest (Adam, 1990b). Soil carbon was expected to be lowest in the pioneer marsh zone and greatest in the high marsh zones, as the zonation of a marsh represents the succession of a marsh: the higher the zone, the older it is, and therefore the more time it has had to accumulate carbon (Adam, 1990b; Allen, 2000; Chmura, 2009; van der Wal et al., 2002). The study also contrasted the influence of livestock grazing with the influence of environmental context on above-ground plant community characteristics. Tidal range, wave fetch and marsh geomorphology were expected to be significant drivers of carbon stocks as they dictate sedimentation rates on salt marshes (Allen, 2000; Stumpf, 1983) and can be significant drivers of above-ground plant characteristics (Chapter 3). Root biomass and soil organic carbon were analysed across a broad spatial scale (22 salt marshes) along the west coast of Wales and north-west England (Chapter 2), covering a range of livestock stocking densities and environmental stress gradients. A stratified sampling technique was used to differentiate between salt marsh zones where necessary on each site.

4.2 Materials and Methods

4.2.1 Site selection, determination of zones and quadrat selection

The study sites and sampling design are described in detail in Chapter 2. Twenty-two salt marshes were selected between the Dyfi Estuary, mid Wales, and Morecambe Bay, NW England (Chapter 2). Marshes varied in grazing intensity from un-grazed to intensively grazed (Chapter 2: Table 2.1). Marsh zones were determined using a combination of strand line position, marsh topography, and direct observations of tidal inundation (Chapter 2). Each zone was sampled by ten 2 x 2 metre plots that were randomly placed along a representative cross-shore 100m belt (Chapter 2).

4.2.2 Sampled response variables

One 46 cm deep, 4.6 cm diameter soil core was taken from four quadrats per zone using a split tube corer based on a smaller model design by Eijkelkamp (Figure 4.2 a, b). The cores were kept in labelled 46cm lengths of 4.6 diameter plastic tubing (inserted into the corer prior to sampling), and wrapped in tin foil to minimise damage and moisture loss prior to laboratory analysis (Figure 4.2). In the laboratory, the soil cores were cut in half lengthways; half of the core was used for root biomass analysis, the other for soil organic carbon and grain size analysis (Figure 4.2d). Three bulk density samples and soil strength measurements were taken from the surface surrounding the soil core (Figure 4.2e)

4.2.2.1 Root biomass: Root matter is one of the main inputs of carbon into the soil carbon stocks. The root biomass half-core was divided into 5cm depth segments down the entire length of the core (Figure 4.2d). These segments were washed free of sediment using a gentle flow of water from a showerhead over a 0.5mm meshed metal sieve to catch root and particulate organic matter. The root matter was then dried in pre-weighed, labelled paper bags at 80°C for 3 days and the dry weights were recorded for each depth.

4.2.2.2 Bulk density: Bulk density is a measurement of soil density; it is dependent on soil moisture content, soil grain size, organic matter content and soil compaction (Emmet et al., 2008). Bulk density can be used to calculate the concentration of soil components in terms of volume (Emmet et al., 2008). Samples were taken using 4.8 cm diameter, 2.5 cm deep metal rings (total volume = 42.24 cm^3) and placed in pre-weighed, labelled oven-proof bags (Figure 4.2e). The samples were taken from 2 cm depth to avoid the vegetation litter layer. Three bulk density samples per quadrat were pooled (total volume = 135.72 cm^3), homogenised and all root material was removed. The samples were heated in pre-weighed trays at 105°C for 16 hours to remove all moisture.

The samples were then weighed and bulk density was calculated as according to the Soils Manual of the Countryside Survey (Emmet et al., 2008):

$$\text{Bulk Density} = \frac{\text{Soil Dry Weight}}{\text{Total Volume}}$$

4.2.2.3 Soil organic carbon: The remaining soil organic carbon half-core was sampled at five depths: 0-2 cm, 5-7 cm, 11-13 cm, 22-24 cm and 44-46 cm depths (Figure 4.2d). Each sample was homogenised, root material was removed and an approximately ten gram sample was used to determine the soil organic carbon content by using loss on ignition techniques based on Ball (1964) and Schumacher (2002). Percentage soil organic matter was calculated using methods outlined in the Soils Manual of the Countryside Survey (Emmet et al., 2008):

$$\text{Organic Matter Concentration (OMC)} = 100 \times \frac{(\text{Dry Soil Weight} - \text{Combusted Soil Weight})}{(\text{Dry Soil Weight} - \text{Crucible Weight})}$$

Carbon density is normally used in the CCS literature (Chmura, 2009; Chmura et al., 2003), but it is affected by soil compaction by livestock, and thus can mask a reduction in carbon deposition. Percentage soil organic carbon (soil organic carbon concentration) is not impacted by soil bulk density, however, it does not give an absolute value for soil carbon content. Both carbon concentration and carbon density measures were used in this study. Organic carbon concentration was estimated using a conversion formula devised by Craft, Seneca, and Broome (1991):

$$\text{Soil Organic Carbon Concentration} = (0.4 \times \text{OMC}) + (0.0025 \times \text{OMC}^2)$$

This formula was used because Craft found that a quadratic equation best described the relationship between organic carbon and organic matter, rather than the linear relationship that is used in other literature. Soil organic carbon concentration was then converted into soil organic carbon (SOC) per volume (soil organic carbon density) using bulk density.

$$\text{SOC (g cm}^{-3}\text{)} = \text{Bulk Density} \times \frac{\text{Soil Organic Carbon Concentration}}{100}$$

4.2.2.4 Soil strength and compaction: To measure the impact of livestock on soil compaction, three surface soil compaction measurements were taken per plot using a hand held penetrometer and three sub-surface soil strength measurements were taken per plot using a soil shear vane (Figure 4.3).

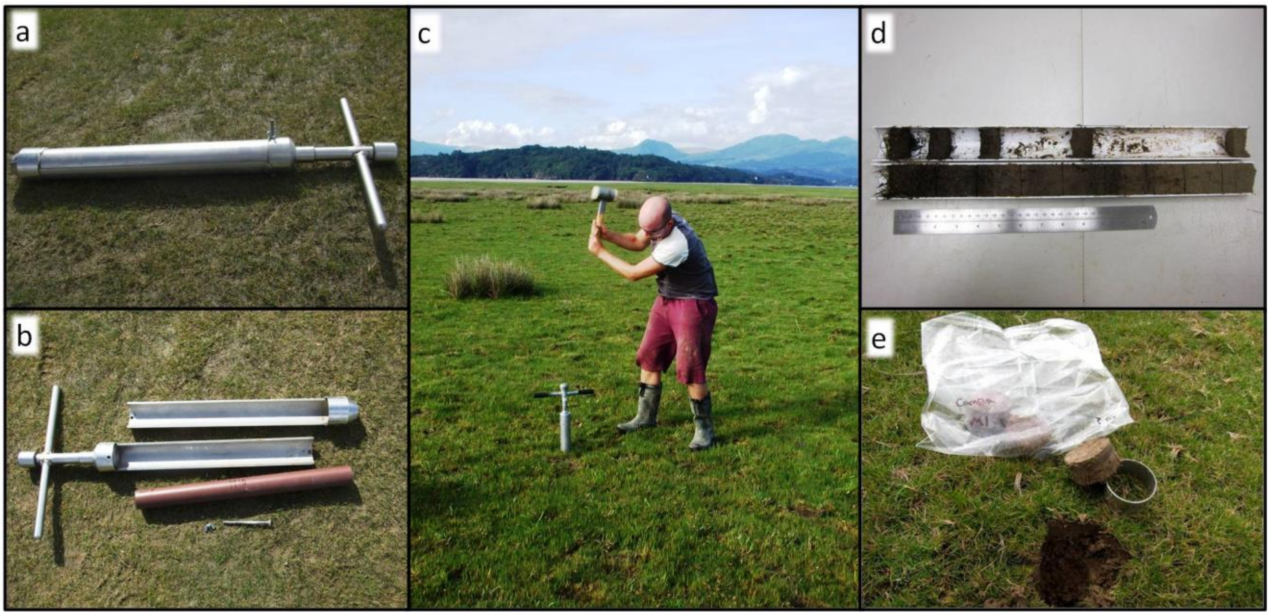


Figure 4.2 | Soil coring and the soil corer. **a)** The soil corer used in this study. Based on a model by Eijkelkamp, this split tube corer has an internal length of 46cm and an internal diameter of 4.6cm. **b)** The corer components: the main corer is split in two and held together by a pin. The plastic piping fits inside the corer and can be labelled. **c)** The Eijkelkamp corer in use at Morfa Harlech. A lump hammer had to be used in most cases, particularly in heavily compacted or sandy marshes. **d)** The division of the core for root biomass and soil organic carbon analysis. Soil organic carbon samples (top half) were taken at 0-2cm, 5-7cm, 11-13cm, 22-24cm and 44-46cm, while root biomass samples were taken from 5cm depth block down the length of the core. **e)** Bulk density samples were taken using a 4.8cm diameter, 2.5cm deep metal ring. Three samples were taken per plot and pooled. Samples were placed in pre-weighed, labelled oven-proof plastic bags, ready for drying in the laboratory.

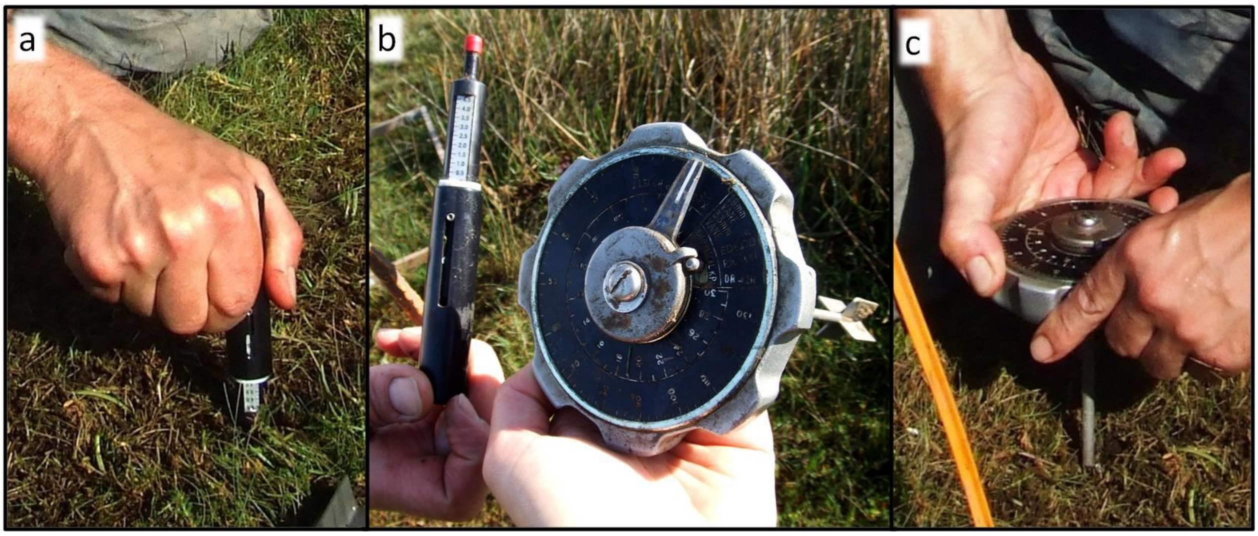


Figure 4.3 | Soil strength and compaction. **a)** Measuring surface soil compaction using a hand held penetrometer. The top of the penetrometer is pushed down until the red tip on the end of the penetrometer is pushed fully into the soil. The white ring then remains at the recorded value on the scale. **b)** The penetrometer (left) and the soil shear vane (right). **c)** Measuring sub-surface soil strength using a soil shear vane. The vane is inserted into the soil to approximately 10cm depth. The dial is then turned clockwise on a spring mechanism until the soil gives way and the vane snaps around. There are two different sizes of vane; a wide vane is for measurement in soft soils and a narrow vane is for use in hard, compact soils.

4.2.3 Determination of stocking density and contextual environmental variables

The stocking density of each marsh was calculated as livestock units (Woodend, 2010) per hectare per year (LSU ha^{-1} yr^{-1}) (Chapter 2). The marshes were then categorised into four grazing intensities: un-grazed, lightly grazed, moderately grazed and intensively grazed, to conform with local management schemes and grazing intensities in other studies (Chapter 2). A series of contextual environmental variables were analysed as indicators of contextual drivers of salt marsh productivity and carbon storing processes (Chapter 2).

4.2.4 Statistical analysis

Based on regional records of sediment accumulation rates, the top 6-15 cm of soil represents approximately the last 30 years of salt marsh accumulation, for which grazing intensity was well documented (Appendix 3: Accretion Rates in Other Studies). As such, evaluation of grazer-carbon relationships took into consideration three depth layers in the soil: 0-2 cm, 0-10 cm and 0-50 cm. The top soil depth profile (0-2 cm) was regarded to be indicative of the present flux of material from above-ground biomass (e.g. litter) to the below-ground carbon pool. This top layer was expected to show a strong relationship between above and below-ground processes, and to be representative of the current grazing regime. The middle depth profile (0-10 cm) included most of the root biomass and was used to analyse more long-term grazing impacts on the organic layer of the soil (including the 0-2 cm depth profile), as this depth reflected the 30-year time scale for which there was reliable grazing data. It was expected that this depth profile would be less representative of the current above-ground processes than the 0-2 cm depth profile but still show a weak coupling between above and below-ground processes. The deepest profile (0-50 cm) was considered an integrator of the broader contextual influences. This holistic approach enabled comparison of current and past (last 30 years) grazing regimes with the deeper, older layers associated with past environmental settings. Due to the considerable differences between saltmarsh zones, an analysis including all zones would invariably add variance to the data set, which could over-ride any effects of grazing; therefore, separate analyses were used for each zone as well as the for overall data set (all zones combined).

As management schemes stipulate grazing pressure by categorizing sites into a range of grazing intensities, the data were analysed with grazing as both a continuous variable (LSU) and as an ordinal categorical variable (four categories of grazing intensity). LSU is a continuous measurement of stocking density; however, it does not lend itself to factorial-type analyses such as ANOVA. Grazing intensity categories are arbitrary and somewhat subjective classifications of grazing regime. It was included in this analysis to relate to current management schemes that use these categories. The data analysis was divided into three parts:

i) Regression analyses with grazing intensity as a continuous variable (LSU ha^{-1} yr^{-1}) for a continuous determination of grazing impacts on below-ground measures (Section 4.2.4.1).

ii) Factorial analyses with categorical levels of grazing intensity (un-grazed, lightly grazed, moderately grazed, or intensely grazed), as stipulated by management schemes, using ANOVA (Section 4.2.4.2), PERMANOVA (Section 4.2.4.3), and ANCOVA (Section 4.2.4.4).

iii) Analyses of the impacts of grazing in relation to a series of environmental variables (3.2.4.5 DistLM; 4.2.4.6 Mixed effects model).

4.2.4.1 Regression: A series of regression analyses investigated the effect of livestock density (LSU ha^{-1} yr^{-1}) on root biomass and soil organic carbon. Analyses were run for the overall data set (all zones) and separately for each zone (high, mid, low or pioneer). False discovery rate (FDR) control *p*-values were calculated to compensate for the large number of tests (Verhoeven et al., 2004). Partial eta squared effect size (η_p^2) was calculated for each test where ≥0.0099 was a small effect, ≥0.0588 was a medium effect, and ≥0.1379 was a large effect (Cohen, 1988; Richardson, 2011). Square root and $\log_{10}$ transformations were used when necessary to meet test assumptions.

3.2.4.2 ANOVA: A series of analyses of variance (ANOVAs) were run alongside the regression analyses to investigate the impact of categorical levels of grazing intensity on the below-ground response (soil organic carbon, root biomass, root depth, and soil compaction) variables and their coefficients of variation (spread in the data). To analyse the impact of grazing on soil organic carbon and root biomass in the overall data set, a three-way, between-group factorial ANOVA was run with the model *Grazing Intensity | Zone + Marsh(Grazing Intensity)*. This model determined both independent effects of grazing, zone and marsh, as well as interaction effects of grazing and zone. Marsh a random factor and was nested within grazing intensity so no interaction terms could be determined for marsh. To analyse the impact of grazing on soil organic carbon and root biomass within each zone, a 2-way ANOVA was run for each zone (high, mid, low and pioneer) with the model *Grazing Intensity + Marsh(Grazing Intensity)*. This model determined the independent effects of grazing and marsh within each zone. Tukey HSD *post hoc* tests were used to determine where any between-group significant differences lay. False discovery rate control p-values were calculated for the main factor, 'Grazing', to compensate for the large number of analyses. Partial *eta* squared effect size was calculated for each test

4.2.4.3 PERMANOVA: A permutational analysis of variance (PERMANOVA) (Anderson, 2005) was used to analyse the effects of grazing on soil organic carbon, and root biomass. The PERMANOVA design included the factors:

i) Grazing intensity (GI): Fixed factor; 4 levels (un-grazed, lightly grazed, moderately grazed, intensively grazed)
ii) Marsh: Random factor; 22 marshes; nested in GI
iii) Zone: Fixed factor; up to 4 levels per marsh (pioneer, low, mid, high)

The PERMANOVA was run with 9999 permutations on a log transformed Bray-Curtis similarity matrix.

4.2.4.4 ANCOVA: An analysis of covariates (ANCOVA) was run on both root biomass and soil organic carbon (SOC) with depth as a covariate. This was to analyse the impact of grazing intensity (four categorical levels: un-grazed, lightly grazed, moderately grazed, intensively grazed) on the depth profile of both root biomass and soil carbon.

4.2.4.5 Mixed Effects Model: A mixed effects model was used to analyse the impact of multiple environmental and contextual factors (including LSU) on both root biomass and soil organic carbon. The model was run on the overall data set, the combined high zone and mid zone data (zones most likely to be influenced by grazers), and the combined low zone and pioneer zone data (zones least likely to be influenced by grazers).

4.3 Results

Grazing had no single or interactive effects on below-ground soil organic carbon (SOC) (PERMANOVA Factor: Grazing – Pseudo F = 1.18, P(perm) = 0.327) or root biomass (PERMANOVA Factor: Grazing – Pseudo F = 1.35, P(perm) = 0.235) for any of the sediment depths analysed (Tables 4.1 & 4.2; Figures 4.4 & 4.5). SOC did decrease significantly with soil depth (ANCOVA: $F_{1,1093}$ = 219.96, p <0.001, η_p^2 = 0.166). The rate of SOC decrease with depth did not, however, vary significantly between grazing intensities (ANCOVA: $F_{3,1093}$ = 0.64, p = 0.597, η_p^2 = 0.009) (Figure 4.6). This finding was unaffected by whether carbon content was expressed in units of carbon density (g(C) cm^{-3}) or in units of percent carbon concentration (g(C) g(soil)$^{-1}$ (%)). Despite no overall (all zones) significant relationship between root biomass and stocking density, livestock grazing had a significant positive impact on root biomass in the surface soil of the high marsh (Table 4.1; Figure 4.5).

Soil organic carbon (PERMANOVA Factor: Zone – Pseudo F = 5.19, P(perm) = 0.001) and root biomass (PERMANOVA Factor: Zone – Pseudo F = 4.60, P(perm) = 0.002) did differ between marsh zones Table 4.2). SOC in the top 10 cm for both the pioneer ($\bar{x}$ = 0.009, SD = 0.007) and low ($\bar{x}$ = 0.014, SD = 0.008) marsh zones were significantly lower than in the mid ($\bar{x}$ = 0.019, SD = 0.008) and high ($\bar{x}$ = 0.017, SD = 0.008) zones (Tukey HSD *post hoc* tests). Overall SOC (0-50 cm) in the pioneer zone ($\bar{x}$ = 0.007, SD = 0.005) was significantly lower than in the other three zones (low: $\bar{x}$ = 0.012, SD = 0.007; mid: $\bar{x}$ = 0.014, SD = 0.005; high: $\bar{x}$ = 0.012, SD = 0.005) (Tukey HSD *post hoc* tests). A similar pattern was found for root biomass. Root biomass in the top 10 cm for the pioneer zone ($\bar{x}$ = 0.003, SD = 0.005) was significantly lower than in the low ($\bar{x}$ = 0.011, SD = 0.007) and mid ($\bar{x}$ = 0.015, SD = 0.011) zones. Root biomass in the top 10 cm for the high marsh ($\bar{x}$ = 0.021, SD = 0.015) was also significantly higher than in the other three zones.

There were consistent significant between-marsh differences in SOC (ANOVA factor: Marsh – $F_{3,18}$ = 7.95, p <0.001, η_p^2 = 0.315) and root biomass (ANOVA factor: Marsh – $F_{3,18}$ = 7.14, p <0.001, η_p^2 = 0.392). Several contextual and environmental variables explained more variation in the data than did grazing. Plant community composition was found to have a significant impact on SOC in the surface layers, but this generally did not translate to the deeper soil profiles (Mixed effects model: Table 4.3). Tidal range, wave fetch and marsh geomorphology were significant drivers of SOC in the deeper soil profiles in the higher zones, while grain size was a significant driver of SOC in the deeper profiles in the lower marsh zones (Table 4.3). Stocking density had no overall effect when all zones were considered together, but considered separately stocking density had a significant impact on SOC in deepest soil profile of the higher marsh zones and the shallowest soil profile in the lower zones (Table 4.3).

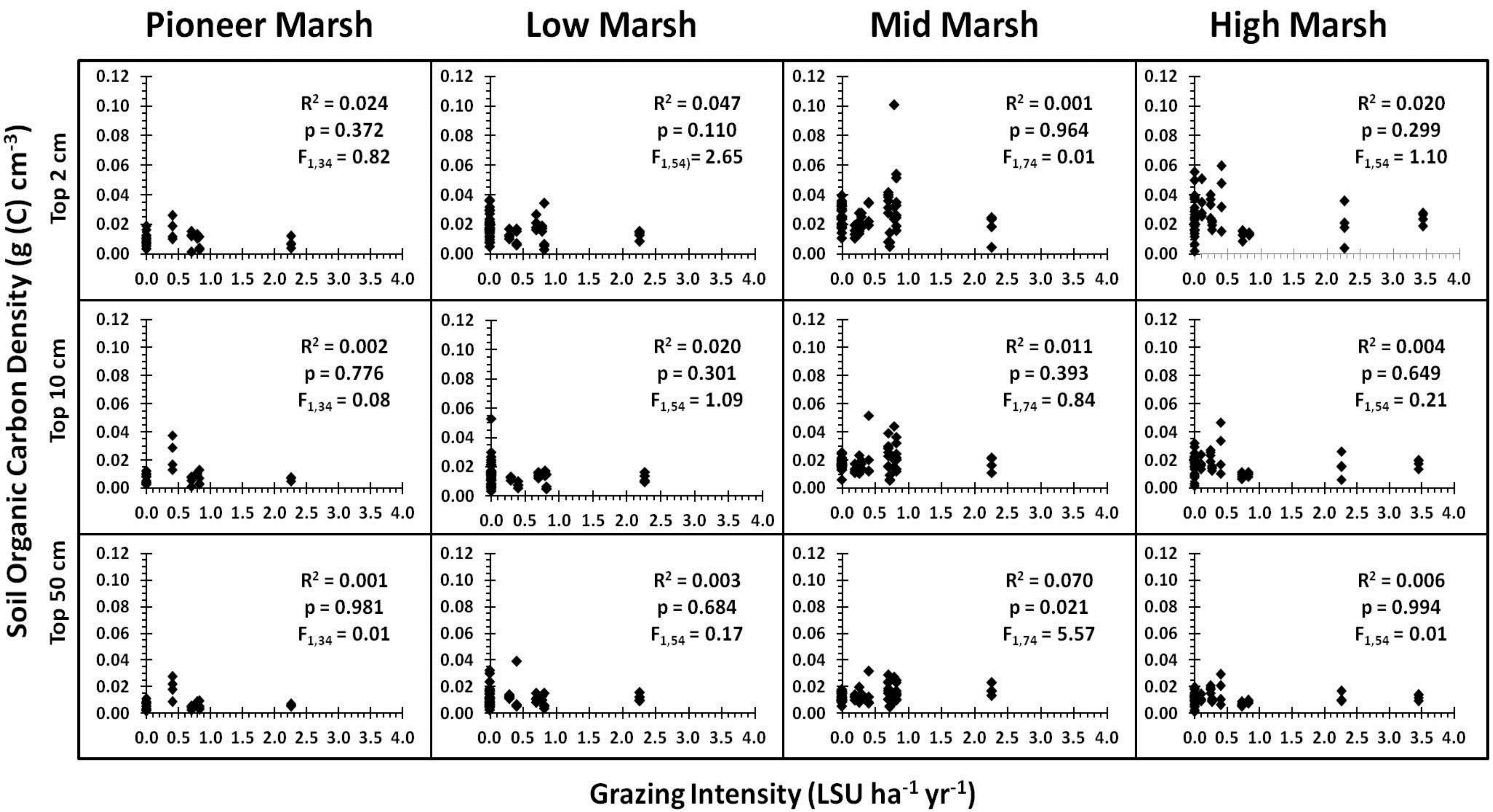


Figure 4.4 | Soil organic carbon vs. grazing intensity by zone for three soil depth profiles. Scatter plots showing the relationship between soil organic carbon (carbon density: g (C) cm^{-3}) and grazing intensity (LSU ha^{-1} yr^{-1}) for each zone and for each of the depth profiles analysed: top 2cm, top 10cm and top 50cm.

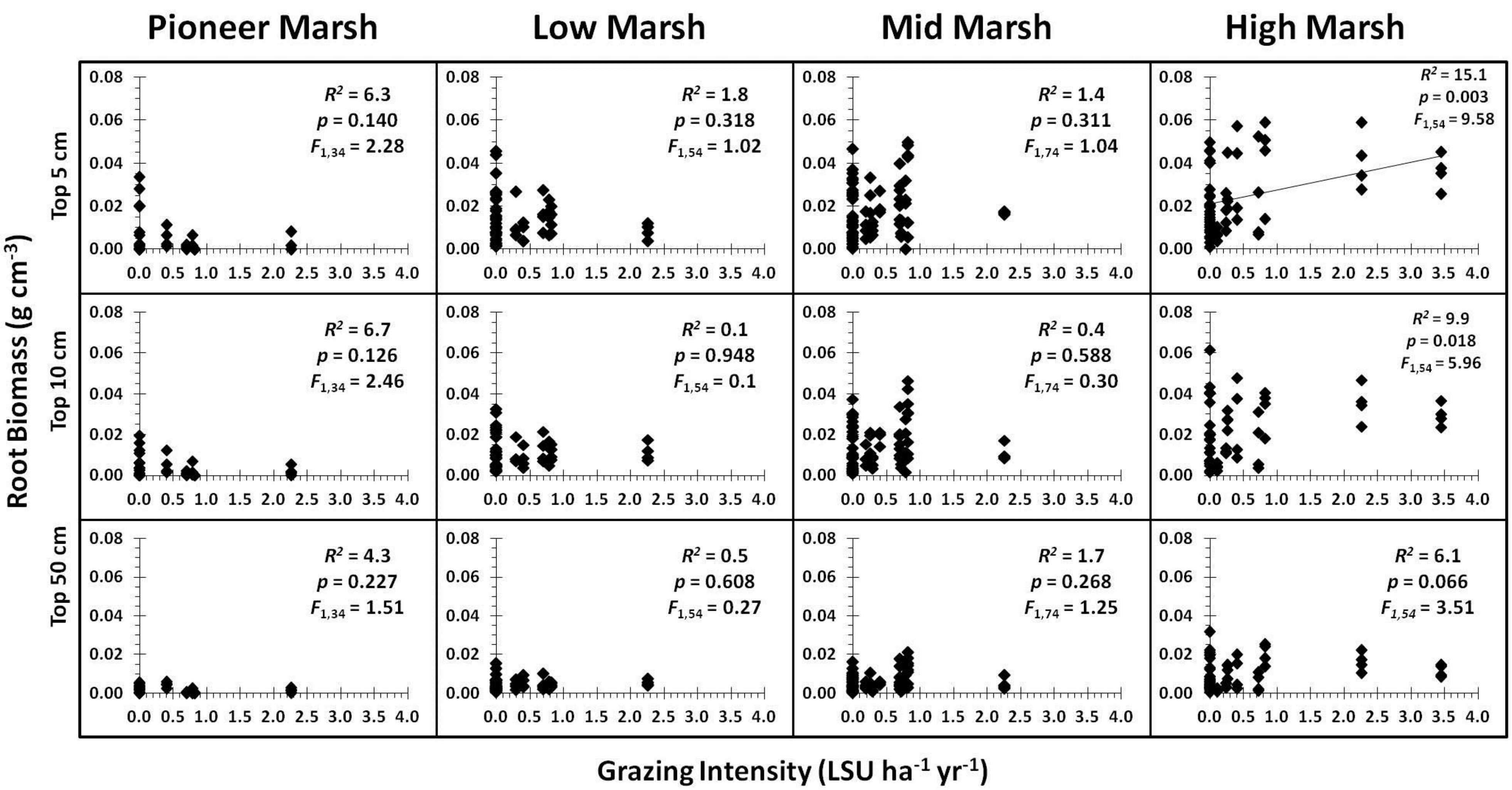


Figure 4.5 | Root biomass vs. grazing intensity by zone for three soil depth profiles. Scatter plots showing the relationship between root biomass (g cm^{-3}) and grazing intensity (LSU ha^{-1} yr^{-1}) for each zone and for each of the depth profiles analysed: top 5cm, top 10cm and top 50cm.

Table 4.1 | Regression analyses for below-ground variables against LSU. Results of regression analyses for each predictor variable vs. LSU ha^{-1} yr^{-1} for overall data set followed by analysis by zone (high, mid, low and pioneer). Results of ANOVA (*df*, *F* and *p*) are shown along with FDR *p*-value thresholds ($p_{(i)}$). An emboldened *p*-value denotes a significant effect. The results of the regression are shown in the last three columns: R^2, Intercept (*b*) and Slope (*m*).

Predictor Variable	*df*	*F*	*p*	$p_{(i)}$	R^2	*b*	*m*
Overall							
Root Biomass (Top 5cm) (g cm^{-3})	1, 222	5.19	0.024	0.018	0.023		
Root Biomass (Top 10cm) (g cm^{-3})	1, 222	4.80	0.029	0.023	0.021		
Root Biomass (Top 50cm) (g cm^{-3})	1, 222	5.86	0.016	0.014	0.026		
Maximum Root Depth (cm)	1, 222	4.30	0.039	0.032	0.019		
Soil Organic Carbon Density (Top 2cm) (g cm^{-3})	1, 222	1.78	0.183	0.041	0.008		
Soil Organic Carbon Density (Top 10cm) (g cm^{-3})	1, 222	0.34	0.562	0.045	0.002		
Soil Organic Carbon Density (Top 50cm) (g cm^{-3})	1, 222	0.10	0.750	0.050	0.000		
Soil Organic Carbon Concentration (Top 2cm) (%)	1, 222	6.55	0.011	0.009	0.029		
Soil Organic Carbon Concentration (Top 10cm) (%)	1, 222	4.83	0.029	0.027	0.021		
Soil Organic Carbon Concentration (Top 50cm) (%)	1, 222	3.77	0.053	0.036	0.017		
Soil Shear Strength	1, 222	40.07	**<0.001**	0.005	0.153	24.200	8.440
High Marsh							
Root Biomass (Top 5cm) (g cm^{-3})	1,54	9.58	**0.003**	0.009	0.151	0.021	0.007
Root Biomass (Top 10cm) (g cm^{-3})	1,54	5.96	0.018	0.018	0.099		
Root Biomass (Top 50cm) (g cm^{-3})	1,54	3.51	0.066	0.032	0.061		
Maximum Root Depth (cm)	1,54	14.02	**<0.001**	0.005	0.206	32.300	3.950
Soil Organic Carbon Density (Top 2cm) (g cm^{-3})	1,54	1.10	0.299	0.041	0.020		
Soil Organic Carbon Density (Top 10cm) (g cm^{-3})	1,54	0.21	0.649	0.045	0.004		
Soil Organic Carbon Density (Top 50cm) (g cm^{-3})	1,54	0.00	0.994	0.050	0.000		
Soil Organic Carbon Concentration (Top 2cm) (%)	1,54	3.60	0.063	0.027	0.062		
Soil Organic Carbon Concentration (Top 10cm) (%)	1,54	2.09	0.154	0.032	0.037		
Soil Organic Carbon Concentration (Top 50cm) (%)	1,54	1.64	0.205	0.036	0.030		
Soil Shear Strength	1,54	8.09	**0.006**	0.014	0.130	31.600	6.320
Mid Marsh							
Root Biomass (Top 5cm) (g cm^{-3})	1, 74	1.04	0.311	0.032	0.014		
Root Biomass (Top 10cm) (g cm^{-3})	1, 74	0.30	0.588	0.045	0.004		
Root Biomass (Top 50cm) (g cm^{-3})	1, 74	1.25	0.268	0.023	0.017		
Maximum Root Depth (cm)	1, 74	0.36	0.551	0.041	0.005		
Soil Organic Carbon Density (Top 2cm) (g cm^{-3})	1, 74	0.00	0.964	0.050	0.000		
Soil Organic Carbon Density (Top 10cm) (g cm^{-3})	1, 74	0.84	0.363	0.036	0.011		
Soil Organic Carbon Density (Top 50cm) (g cm^{-3})	1, 74	5.57	0.021	0.009	0.070		
Soil Organic Carbon Concentration (Top 2cm) (%)	1, 74	3.10	0.083	0.014	0.040		
Soil Organic Carbon Concentration (Top 10cm) (%)	1, 74	2.26	0.137	0.018	0.030		
Soil Organic Carbon Concentration (Top 50cm) (%)	1, 74	1.07	0.305	0.027	0.014		
Soil Shear Strength	1, 74	31.35	**<0.001**	0.005	0.298	25.100	14.700
Low Marsh							
Root Biomass (Top 5cm) (g cm^{-3})	1, 54	1.02	0.318	0.032	0.018		
Root Biomass (Top 10cm) (g cm^{-3})	1, 54	0.00	0.948	0.050	0.000		
Root Biomass (Top 50cm) (g cm^{-3})	1, 54	0.27	0.608	0.036	0.005		
Maximum Root Depth (cm)	1, 54	0.25	0.621	0.041	0.005		
Soil Organic Carbon Density (Top 2cm) (g cm^{-3})	1, 54	2.65	0.110	0.018	0.047		
Soil Organic Carbon Density (Top 10cm) (g cm^{-3})	1, 54	1.09	0.301	0.027	0.020		
Soil Organic Carbon Density (Top 50cm) (g cm^{-3})	1, 54	0.17	0.684	0.045	0.003		
Soil Organic Carbon Concentration (Top 2cm) (%)	1, 54	4.86	0.032	0.009	0.083		
Soil Organic Carbon Concentration (Top 10cm) (%)	1, 54	2.75	0.103	0.014	0.048		
Soil Organic Carbon Concentration (Top 50cm) (%)	1, 54	2.26	0.138	0.023	0.040		
Soil Shear Strength	1, 54	15.62	**<0.001**	0.005	0.224	21.200	10.500

Table 4.1 (Cont.) | Regression analyses for below-ground variables on LSU.

Predictor Variable	*df*	*F*	*p*	$p_{(i)}$	R^2	*b*	*m*
Pioneer Marsh							
Root Biomass (Top 5cm) (g cm^{-3})	1, 34	2.28	0.140	0.023	0.063		
Root Biomass (Top 10cm) (g cm^{-3})	1, 34	2.46	0.126	0.018	0.067		
Root Biomass (Top 50cm) (g cm^{-3})	1, 34	1.51	0.227	0.032	0.043		
Maximum Root Depth (cm)	1, 34	0.61	0.440	0.045	0.018		
Soil Organic Carbon Density (Top 2cm) (g cm^{-3})	1, 34	0.82	0.372	0.041	0.024		
Soil Organic Carbon Density (Top 10cm) (g cm^{-3})	1, 34	0.08	0.776	0.045	0.002		
Soil Organic Carbon Density (Top 50cm) (g cm^{-3})	1, 34	0.00	0.981	0.050	0.000		
Soil Organic Carbon Concentration (Top 2cm) (%)	1, 34	3.84	0.058	0.014	0.101		
Soil Organic Carbon Concentration (Top 10cm) (%)	1, 34	1.73	0.197	0.027	0.048		
Soil Organic Carbon Concentration (Top 50cm) (%)	1, 34	1.17	0.287	0.036	0.033		
Soil Shear Strength	1, 34	17.86	**<0.001**	0.009	0.344	12.700	4.680

Table 4.2 | ANOVA table of below-ground variables by grazing intensity. Results of a factorial ANOVA for the overall data set ('Overall') with the model: Grazing Intensity | Zone + Marsh(Grazing Intensity), and a 2-way ANOVA for each zone ('High', 'Mid', 'Low', and 'Pioneer') with the model: Grazing Intensity + Marsh(Gr)(Grazing Intensity). Column headers depict degrees of freedom (df: numerator, denominator), F-values (F), p-values (p), False Discovery Rate control thresholds (FDR $p_{(i)}$). An emboldened p-value denotes a significant effect. Means ($\bar{x}$) and Standard Error (SE) are shown by Grazing Intensity for each predictor variable.

		ANOVA					Un-grazed		Light		Moderate		Intensive	
Predictor Variable		***df***	***F***	***p***	**FDR *$p_{(i)}$***	***η_p^2***	***$\bar{x}$***	***SE***	***$\bar{x}$***	***SE***	***$\bar{x}$***	***SE***	***$\bar{x}$***	***SE***
					Overall									
Root Biomass (Top 5cm) (g cm^{-3})	Grazing	3, 18	1.96	0.152	0.018	0.112	0.016	0.001	0.015	0.002	0.016	0.002	0.020	0.002
	Marsh(Gr)	18, 18	5.48	**<0.001**	0.036	0.332								
	Zone	3, 18	32.80	**<0.001**	0.036	0.326								
Root Biomass (Top 10cm) (g cm^{-3})	Grazing	3, 18	1.62	0.218	0.036	0.131	0.013	0.001	0.012	0.002	0.014	0.002	0.016	0.002
	Marsh(Gr)	18, 18	8.03	**<0.001**	0.014	0.421								
	Zone	3, 18	45.57	**<0.001**	0.014	0.390								
Root Biomass (Top 50cm) (gcm^{-3})	Grazing	3, 18	1.86	0.170	0.027	0.134	0.005	0.001	0.005	0.001	0.006	0.001	0.007	0.001
	Marsh(Gr)	18, 18	7.14	**<0.001**	0.032	0.392								
	Zone	3, 18	41.47	**<0.001**	0.018	0.365								
Maximum Root Depth (cm)	Grazing	3, 18	0.44	0.725	0.050	0.020	29.110	1.040	31.070	1.630	30.340	1.850	30.850	1.710
	Marsh(Gr)	18, 18	3.81	**<0.001**	0.045	0.256								
	Zone	3, 18	39.10	**<0.001**	0.027	0.387								
Soil Organic Carbon Density (Top 2cm) (g cm^{-3})	Grazing	3, 18	0.52	0.672	0.045	0.021	0.021	0.001	0.023	0.002	0.024	0.002	0.018	0.002
	Marsh(Gr)	18, 18	3.40	**<0.001**	0.050	0.235								
	Zone	3, 18	26.61	**<0.001**	0.041	0.298								
Soil Organic Carbon Density (Top 10cm) (g cm^{-3})	Grazing	3, 18	1.82	0.173	0.032	0.080	0.015	0.001	0.016	0.001	0.019	0.002	0.014	0.001
	Marsh(Gr)	18, 18	3.92	**<0.001**	0.041	0.262								
	Zone	3, 18	13.91	**<0.001**	0.045	0.221								
Soil Organic Carbon Density (Top 50cm) (g cm^{-3})	Grazing	3, 18	1.59	0.221	0.041	0.088	0.011	0.001	0.013	0.001	0.015	0.001	0.011	0.001
	Marsh(Gr)	18, 18	9.17	**<0.001**	0.005	0.315								
	Zone	3, 18	5.09	**<0.001**	0.050	0.193								
Soil Organic Carbon Concentration (Top 2cm) (%)	Grazing	3, 18	1.93	0.158	0.023	0.157	6.514	0.596	4.860	0.529	5.400	1.080	3.256	0.528
	Marsh(Gr)	18, 18	8.35	**<0.001**	0.009	0.430								
	Zone	3, 18	54.64	**<0.001**	0.005	0.426								
Soil Organic Carbon Concentration (Top 10cm) (%)	Grazing	3, 18	2.18	0.123	0.009	0.167	4.504	0.427	3.363	0.278	3.970	0.782	2.301	0.287
	Marsh(Gr)	18, 18	7.94	**<0.001**	0.023	0.418								
	Zone	3, 18	41.30	**<0.001**	0.023	0.360								
Soil Organic Carbon Concentration (Top 50cm) (%)	Grazing	3, 18	2.03	0.143	0.014	0.157	3.042	0.271	2.554	0.182	2.892	0.509	1.708	0.180
	Marsh(Gr)	18, 18	7.95	**<0.001**	0.018	0.418								
	Zone	3, 18	38.53	**<0.001**	0.032	0.339								
Soil Shear Strength (Pa)	Grazing	3, 18	6.39	**0.003**	0.005	0.355	20.056	0.780	27.200	1.580	33.820	2.910	39.780	2.470
	Marsh(Gr)	18, 18	7.41	**<0.001**	0.027	0.401								
	Zone	3, 18	49.24	**<0.001**	0.009	0.424								

Table 4.2 (Cont.) | ANOVA table of below-ground variables by grazing intensity

		ANOVA					Un-grazed		Light		Moderate		Intensive	
Predictor Variable		***df***	***F***	***p***	**FDR $p_{(i)}$**	**η_p^2**	**$\bar{x}$**	***SE***	**$\bar{x}$**	***SE***	**$\bar{x}$**	***SE***	**$\bar{x}$**	***SE***
High Marsh														
Root Biomass (Top 5cm) (g cm^{-3})	Grazing	3, 10	2.73	0.100	0.014	0.317	0.020	0.003	0.017	0.003	0.034	0.010	0.036	0.004
	Marsh(Gr)	10, 10	2.38	**0.025**	0.045	0.362								
Root Biomass (Top 10cm) (g cm^{-3})	Grazing	3, 10	0.81	0.517	0.045	0.275	0.020	0.003	0.014	0.003	0.027	0.009	0.028	0.003
	Marsh(Gr)	10, 10	6.56	**<0.001**	0.027	0.610								
Root Biomass (Top 50cm) (g cm^{-3})	Grazing	3, 10	0.76	0.544	0.050	0.304	0.009	0.002	0.006	0.001	0.011	0.004	0.013	0.002
	Marsh(Gr)	10, 10	8.10	**<0.001**	0.018	0.658								
Maximum Root Depth (cm)	Grazing	3, 10	5.13	0.021	0.005	0.528	30.460	1.510	30.830	2.520	41.000	2.350	42.000	1.200
	Marsh(Gr)	10, 10	3.06	**0.005**	0.036	0.421								
Soil Organic Carbon Density (Top 2cm) (g cm^{-3})	Grazing	3, 10	2.57	0.113	0.018	0.283	0.025	0.003	0.030	0.003	0.039	0.010	0.018	0.002
	Marsh(Gr)	10, 10	2.16	**0.041**	0.050	0.339								
Soil Organic Carbon Density (Top 10cm) (g cm^{-3})	Grazing	3, 10	2.02	0.175	0.023	0.277	0.017	0.002	0.019	0.001	0.027	0.008	0.013	0.001
	Marsh(Gr)	10, 10	2.66	**0.013**	0.041	0.388								
Soil Organic Carbon Density (Top 50cm) (g cm^{-3})	Grazing	3, 10	1.17	0.369	0.036	0.219	0.011	0.001	0.013	0.001	0.017	0.005	0.010	0.001
	Marsh(Gr)	10, 10	3.35	**0.003**	0.032	0.444								
Soil Organic Carbon Concentration (Top 2cm) (%)	Grazing	3, 10	1.95	0.185	0.027	0.518	11.160	1.440	7.593	0.485	14.050	4.190	4.166	0.939
	Marsh(Gr)	10, 10	7.69	**<0.001**	0.023	0.647								
Soil Organic Carbon Concentration (Top 10cm) (%)	Grazing	3, 10	1.28	0.332	0.032	0.509	7.700	1.140	4.735	0.245	9.560	3.370	3.100	0.694
	Marsh(Gr)	10, 10	11.31	**<0.001**	0.009	0.729								
Soil Organic Carbon Concentration (Top 50cm) (%)	Grazing	3, 10	1.00	0.431	0.041	0.447	4.998	0.771	3.291	0.220	5.910	2.100	2.227	0.418
	Marsh(Gr)	10, 10	11.26	**<0.001**	0.014	0.728								
Soil Shear Strength (Pa)	Grazing	3, 10	4.04	0.040	0.009	0.856	24.160	2.160	30.970	1.830	50.750	1.300	51.560	4.700
	Marsh(Gr)	10, 10	20.66	**<0.001**	0.005	0.831								
Mid Marsh														
Root Biomass (Top 5cm) (g cm^{-3})	Grazing	3, 15	0.58	0.637	0.041	0.138	0.017	0.002	0.013	0.002	0.022	0.002	0.022	0.004
	Marsh(Gr)	15, 15	5.24	**<0.001**	0.036	0.580								
Root Biomass (Top 10cm) (g cm^{-3})	Grazing	3, 15	0.57	0.645	0.045	0.175	0.014	0.002	0.010	0.002	0.018	0.002	0.018	0.003
	Marsh(Gr)	15, 15	7.11	**<0.001**	0.014	0.652								
Root Biomass (Top 50cm) (g cm^{-3})	Grazing	3, 15	0.64	0.600	0.036	0.192	0.005	0.001	0.004	0.001	0.007	0.001	0.007	0.001
	Marsh(Gr)	15, 15	7.02	**<0.001**	0.018	0.649								
Maximum Root Depth (cm)	Grazing	3, 15	0.05	0.985	0.050	0.019	33.220	1.520	33.830	1.840	31.830	1.750	32.750	1.670
	Marsh(Gr)	15, 15	7.37	**<0.001**	0.009	0.660								
Soil Organic Carbon Density(Top 2cm) (g cm^{-3})	Grazing	3, 15	0.98	0.427	0.032	0.113	0.026	0.001	0.019	0.002	0.031	0.003	0.027	0.005
	Marsh(Gr)	15, 15	2.46	**0.008**	0.045	0.393								
Soil Organic Carbon Density(Top 10cm) (g cm^{-3})	Grazing	3, 15	2.14	0.138	0.009	0.215	0.018	0.001	0.015	0.001	0.025	0.003	0.019	0.002
	Marsh(Gr)	15, 15	2.43	**0.008**	0.050	0.390								

Table 4.2 (Cont.) | ANOVA table of below-ground variables by grazing intensity

Predictor Variable		ANOVA					Un-grazed		Light		Moderate		Intensive	
		df	*F*	*p*	FDR $p_{(i)}$	η_p^2	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*
Mid Marsh														
Soil Organic Carbon Density(Top 50cm) (g cm^{-3})	Grazing	3, 15	1.18	0.351	0.027	0.182	0.012	0.001	0.013	0.001	0.017	0.002	0.014	0.001
	Marsh(Gr)	15, 15	3.58	**<0.001**	0.041	0.485								
Soil Organic Carbon Concentration (Top 2cm) (%)	Grazing	3, 15	1.24	0.330	0.023	0.291	8.280	0.944	2.912	0.417	7.310	1.720	5.060	1.230
	Marsh(Gr)	15, 15	6.29	**<0.001**	0.023	0.623								
Soil Organic Carbon Concentration (Top 10cm) (%)	Grazing	3, 15	1.60	0.230	0.014	0.320	5.106	0.499	2.292	0.288	5.440	1.260	3.184	0.527
	Marsh(Gr)	15, 15	5.75	**<0.001**	0.032	0.594								
Soil Organic Carbon Concentration (Top 50cm) (%)	Grazing	3, 15	1.41	0.279	0.018	0.317	3.420	0.283	1.835	0.193	3.642	0.773	2.335	0.315
	Marsh(Gr)	15, 15	6.27	**<0.001**	0.027	0.623								
Soil Shear Strength (Pa)	Grazing	3, 15	4.61	0.018	0.005	0.799	21.710	1.280	28.180	1.660	38.750	3.800	44.040	3.780
	Marsh(Gr)	15, 15	16.41	**<0.001**	0.005	0.812								
Low Marsh														
Root Biomass (Top 5cm) (g cm^{-3})	Grazing	3, 10	0.08	0.972	0.045	0.034	0.015	0.002	0.013	0.005	0.012	0.003	0.013	0.002
	Marsh(Gr)	10, 10	6.50	**<0.001**	0.018	0.608								
Root Biomass (Top 10cm) (g cm^{-3})	Grazing	3, 10	0.02	0.995	0.050	0.011	0.012	0.002	0.010	0.003	0.011	0.002	0.012	0.001
	Marsh(Gr)	10, 10	6.75	**<0.001**	0.014	0.617								
Root Biomass (Top 50cm) (g cm^{-3})	Grazing	3, 10	0.08	0.971	0.041	0.019	0.004	0.001	0.004	0.001	0.005	0.001	0.005	<0.001
	Marsh(Gr)	10, 10	3.53	**0.002**	0.041	0.457								
Maximum Root Depth (cm)	Grazing	3, 10	0.56	0.651	0.014	0.098	30.840	1.480	23.500	5.780	30.250	1.660	29.920	1.220
	Marsh(Gr)	10, 10	2.69	**0.012**	0.050	0.390								
Soil Organic Carbon Density (Top 2cm) (g cm^{-3})	Grazing	3, 10	0.63	0.611	0.009	0.166	0.019	0.001	0.013	0.001	0.016	0.002	0.014	0.002
	Marsh(Gr)	10, 10	4.42	**<0.001**	0.036	0.513								
Soil Organic Carbon Density (Top 10cm) (g cm^{-3})	Grazing	3, 10	0.36	0.780	0.032	0.099	0.016	0.002	0.013	0.001	0.011	0.001	0.012	0.001
	Marsh(Gr)	10, 10	6.43	**<0.001**	0.023	0.500								
Soil Organic Carbon Density (Top 50cm) (g cm^{-3})	Grazing	3, 10	0.11	0.953	0.036	0.021	0.012	0.002	0.012	0.001	0.013	0.004	0.010	0.001
	Marsh(Gr)	10, 10	2.78	**0.010**	0.045	0.399								
Soil Organic Carbon Concentration (Top 2cm) (%)	Grazing	3, 10	0.55	0.660	0.018	0.422	3.900	0.632	2.503	0.192	2.542	0.313	1.501	0.233
	Marsh(Gr)	10, 10	18.59	**<0.001**	0.005	0.816								
Soil Organic Carbon Concentration (Top 10cm) (%)	Grazing	3, 10	0.41	0.749	0.023	0.198	3.277	0.696	2.459	0.049	1.774	0.176	1.318	0.169
	Marsh(Gr)	10, 10	8.42	**<0.001**	0.009	0.667								
Soil Organic Carbon Concentration (Top 50cm) (%)	Grazing	3, 10	0.39	0.761	0.027	0.131	2.361	0.425	2.504	0.306	2.242	0.879	1.103	0.127
	Marsh(Gr)	10, 10	5.37	**<0.001**	0.027	0.561								
Soil Shear Strength (Pa)	Grazing	3, 10	5.45	0.018	0.005	0.673	19.146	0.774	12.920	2.640	34.380	7.080	39.180	3.670
	Marsh(Gr)	10, 10	5.29	**<0.001**	0.032	0.557								

Table 4.2 (Cont.) | ANOVA table of below-ground variables by grazing intensity

Predictor Variable		ANOVA					Un-grazed		Light		Moderate		Intensive	
		df	*F*	*p*	FDR $p_{(i)}$	η_p^2	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*
Pioneer Marsh														
Root Biomass (Top 5cm) (g cm^{-3})	Grazing	2, 6	0.99	0.426	0.027	0.169	0.008	0.003	-	-	0.003	0.001	0.002	0.001
	Marsh(Gr)	6, 6	2.79	**0.030**	0.041	0.383								
Root Biomass (Top 10cm) (g cm^{-3})	Grazing	2, 6	1.05	0.406	0.023	0.159	0.005	0.002	-	-	0.003	0.001	0.001	0.001
	Marsh(Gr)	6, 6	2.42	0.053	0.045	0.350								
Root Biomass (Top 50cm) (g cm^{-3})	Grazing	2, 6	0.70	0.535	0.032	0.249	0.002	0.001	-	-	0.002	0.001	0.001	<0.001
	Marsh(Gr)	6, 6	6.41	**<0.001**	0.032	0.588								
Maximum Root Depth (cm)	Grazing	2, 6	0.27	0.773	0.045	0.167	15.380	2.940	-	-	22.880	5.710	13.750	4.880
	Marsh(Gr)	6, 6	10.05	**<0.001**	0.009	0.691								
Soil Organic Carbon Density (Top 2cm) (g cm^{-3})	Grazing	2, 6	1.90	0.230	0.005	0.195	0.010	0.001	-	-	0.014	0.003	0.008	0.001
	Marsh(Gr)	6, 6	1.73	0.153	0.050	0.278								
Soil Organic Carbon Density (Top 10cm) (g cm^{-3})	Grazing	2, 6	1.30	0.341	0.014	0.397	0.007	0.001	-	-	0.015	0.004	0.008	0.001
	Marsh(Gr)	6, 6	6.85	**<0.001**	0.027	0.603								
Soil Organic Carbon Density (Top 50cm) (g cm^{-3})	Grazing	2, 6	1.31	0.338	0.009	0.489	0.005	0.001	-	-	0.012	0.003	0.006	0.001
	Marsh(Gr)	6, 6	9.88	**<0.001**	0.014	0.687								
Soil Organic Carbon Concentration (Top 2cm) (%)	Grazing	2, 6	0.61	0.575	0.036	0.173	1.241	0.197	-	-	1.072	0.196	0.787	0.133
	Marsh(Gr)	6, 6	4.65	**0.002**	0.036	0.508								
Soil Organic Carbon Concentration (Top 10cm) (%)	Grazing	2, 6	0.26	0.782	0.050	0.141	0.953	0.168	-	-	1.160	0.337	0.749	0.109
	Marsh(Gr)	6, 6	8.66	**<0.001**	0.023	0.658								
Soil Organic Carbon Concentration (Top 50cm) (%)	Grazing	2, 6	0.28	0.769	0.041	0.202	0.714	0.128	-	-	0.908	0.254	0.574	0.057
	Marsh(Gr)	6, 6	12.44	**<0.001**	0.005	0.734								
Soil Shear Strength (Pa)	Grazing	2, 6	1.18	0.370	0.018	0.457	12.410	1.050	-	-	17.420	1.280	17.570	1.960
	Marsh(Gr)	6, 6	9.63	**<0.001**	0.018	0.682								

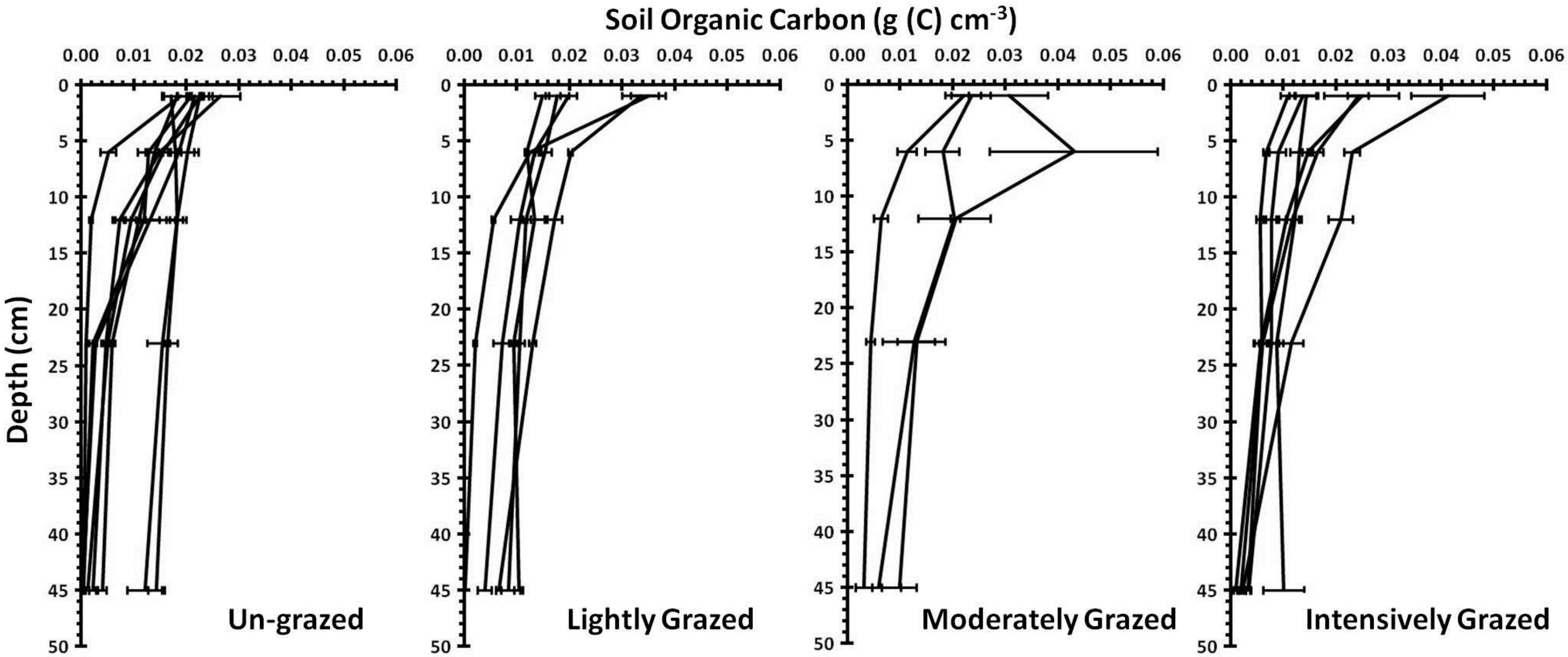


Figure 4.6 | Soil organic carbon density vs. depth for four different grazing intensities. The mean soil organic carbon (carbon density: g C cm^{-3}) ± standard error vs. soil depth for each marsh within each 'Grazing Intensity' category classified according to a Welsh Assembly Grazing Management Scheme: un-grazed (n=8), lightly grazed (n=5), moderately grazed (n=3) and intensively grazed (n=6). Each line represents one salt marsh.

Table 4.3 | Results of mixed effects models for below-ground parameters. Results of a mixed effects model with soil organic carbon as a response variable and zone, grazing and several environmental variables as predictor variables. Column headers depict the effect, degrees of freedom (df: numerator, denominator), F-values (F) and p-values (p). Significant results are indicated by a series of asterisks, where * denotes p<0.05, ** denotes p<0.01 and *** denotes p<0.001.

		0-2cm depth			0-10cm depth			0-50cm depth		
Effect	***df***	***F***	***p***	***m***	***F***	***p***	***m***	***F***	***p***	**m**
Overall										
Carbon Density (gC cm^{-3})										
Zone	3,181	28.11	**<0.001**	***	23.58	**<0.001**	***	8.77	**<0.001**	***
Grazing (LSU)	1,181	2.78	0.097		0.44	0.505		0.04	0.851	
Marsh Area (ha)	1,12	9.52	**0.010**	*	2.94	0.112		1.99	0.184	
Tidal Range (m)	1,12	12.00	**0.005**	**	1.80	0.204		5.58	**0.036**	*
Wave Fetch (m)	1,12	0.68	0.426		10.15	**0.008**	**	11.56	**0.005**	**
Marsh geomorphology	5,12	1.61	0.231		2.99	0.056		2.38	0.101	
Community Composition	16,181	3.10	**<0.001**	***	1.67	0.057		1.17	0.292	
Percent Clay	1,181	2.28	0.133		2.64	0.106		<0.01	0.984	
Percent Coarse Sand	1,181	2.52	0.114		0.07	0.798		4.95	**0.027**	*
High and Mid Zones										
Carbon Density (gC cm^{-3})										
Grazing (LSU)	1, 96	0.29	0.592		0.87	0.353		5.51	**0.021**	*
Zone	1, 96	1.02	0.315		0.29	0.592		0.06	0.800	
Marsh Area (ha)	1, 12	8.73	**0.012**	*	4.75	0.050		2.88	0.115	
Tidal Range (m)	1, 12	7.20	**0.020**	*	2.40	0.147		11.86	**0.005**	**
Maximum Fetch (m)	1, 12	0.29	0.602		10.71	**0.007**	**	21.69	**0.001**	**
Marsh geomorphology	5, 12	2.42	0.098		3.34	**0.040**	*	3.92	**0.024**	*
Community Composition	11, 96	4.15	**<0.001**	***	3.02	**0.002**	**	2.18	**0.021**	*
Percent Clay	1, 96	0.01	0.935		2.26	0.136		0.11	0.740	
Percent Coarse Sand	1, 96	5.05	**0.027**	*	0.71	0.402		4.95	**0.029**	*
Low and Pioneer Zones										
Carbon Density (gC cm^{-3})										
Zone	1, 69	26.83	**<0.001**	***	20.81	**<0.001**	***	35.17	**<0.001**	***
Grazing (LSU)	1, 5	6.97	**0.046**	*	1.91	0.225		0.07	0.799	
Marsh Area (ha)	1, 5	0.20	0.674		0.05	0.825		0.37	0.570	
Tidal Range (m)	1, 5	8.50	**0.033**	*	2.48	0.176		13.53	**0.014**	*
Maximum Fetch (m)	1, 5	0.11	0.725		3.00	0.144		11.27	**0.020**	*
Marsh geomorphology	4, 5	3.21	0.117		4.34	0.069		14.77	**0.006**	**
Community Composition	6, 69	3.90	**0.002**	**	1.55	0.175		1.42	0.219	
Percent Clay	1, 69	2.24	0.139		4.45	**0.038**	*	4.88	**0.031**	*
Percent Coarse Sand	1, 69	5.53	**0.022**	*	27.38	**<0.001**	***	19.26	**<0.001**	***

4.4 Discussion

Significant effects of grazing on soil organic carbon (SOC) and root biomass were expected, as there were marked above-ground effects on plant characteristics (Chapter 3: Tables 3.3 & 3.4). Instead the study found no single or interacting impacts of grazing on either SOC or root biomass. The study did find significant effects of 'Zone' and 'Marsh', and the mixed effects model showed significant impacts of several environmental drivers. This suggests that both micro- and macro-environmental variation are important drivers of SOC and root biomass. Salt and tidal stress increases down the marsh and the vegetation community strongly reflects this stress gradient (Adam, 1990a). As SOC and root biomass in the top layers of the soil depend strongly on the above-ground plant community composition (Table 4.3), it is understandable that there is a significant effect of zone on both SOC and root biomass. However, this does not translate to the deeper layers of soil, which were influenced predominantly by the broader environmental setting of the marsh (Table 4.3). Salt marshes are at the interface between terrestrial and marine environments (Adam, 1990b) and are subjected to greater variation in environmental conditions than many grazed terrestrial grasslands (Adam, 1990a). Environmental context determines external carbon inputs on salt marshes; for instance, sedimentation rates are linked to the local tidal regime (Stumpf, 1983). Arguably, the impact of grazing on carbon in salt marshes is comparatively weak relative to the influence of sharp background environmental gradients (Grime, 1974). Therefore, the assumption that CCS benefits from management of grazing is tenuous in naturally variable and disturbed systems, such as salt marshes.

A strong coupling between above and below-ground processes was anticipated. However, grazing has complex influences on system abiotic and biotic conditions that influence CCS. As a result, an increase in stocking density can initiate compensatory responses by the vegetation community, such as increased root growth or carbon allocation to the roots, although only some studies have shown this (J. N. Holland et al., 1996; McNaughton, 1983; J. H. Richards, 1984; Tanentzap & Coomes, 2012; Wardle et al., 2004). It is possible that these compensatory responses counter any impact of grazing on soil organic carbon stocks. A recent meta-data analysis of grazer exclusion studies found that after a small reduction of soil carbon storing in the early years after grazer addition, soil carbon stocks recovered when study systems had sufficient time to develop compensatory responses to herbivory (Tanentzap & Coomes, 2012). The study found that livestock grazing weakly stimulated root content in soils (Table 4.1; Figure 4.5). This suggests that there is some compensation by the vegetation community, which may have mitigated any negative impact of grazing on carbon stocks. In salt marshes, above-ground plant adaptation to grazing occurs within a few years to a decade (Kuijper & Bakker, 2004a). This study could not detect any mean effect across marshes and soil depths of any carbon loss associated with the early periods of grazer introduction to sites. The study sites had been grazed at the observed levels for a minimum of 20 years, so it is likely that soil carbon stocks would have fully recovered, or that grazer introduction might have occurred in soil layers that were older (deeper) than the ~100 year top layer we sampled. The study does not dismiss that grazers might have diminished annual carbon storing at some point. However, over long time scales this early impact on soil carbon stocks is likely to have been diluted into insignificance by decades of compensation by the whole plant community (Tanentzap & Coomes, 2012).

The expectations of negative impacts on soil carbon by grazing were based on a combination of single-site studies on salt marshes that showed little variation in environmental context (Ford et al., 2012; Yu & Chmura, 2010), meta-data analyses showing carbon loss from complete habitat loss (Chmura et al., 2003), and small-scale studies from terrestrial grasslands (J. N. Holland et al., 1996; Klumpp et al., 2009; Schuster, 1964). None of these studies incorporated a full range of stocking densities, as was done here, nor did they contrast the influence of grazing with the influence of natural contextual variation. The present study does not dismiss the idea that grazing can have an effect on carbon stocks; rather it shows that the effect of grazing is insufficiently strong to be detectable above the influence of environmental variation and vegetation compensation on the broad-scale. The work demonstrates that a grazing management scheme involving multiple sites is unlikely to enhance CCS in a predictable manner. There are, however, still many other reasons to manage grazing on salt marshes for conservation purposes (Norris et al., 1997), and to enhance other services they provide, such as meat production and coastal defense (Adam, 1990c; Moeller et al., 2001).

Finally, this study did not explore any fluxes of carbon, only carbon stocks. Grazers may feasibly alter carbon fluxes but only have minimal impact on carbon stocks if both carbon inputs and losses are influenced at an equal rate. For example, grazers reduce carbon inputs through vegetation litter (J. P. Bakker, 1985; Jensen, 1985; Kiehl et al., 1996) but this may be countered by the reduction of carbon loss through gas effluxes (Scanlon & Moore, 2000; Tanner & Mamaril, 1958; Winfrey & Ward, 1983). However, livestock contribute significantly to the total carbon emissions from a salt marsh through respiration, digestion, and faecal decomposition (Murray et al., 2001; Pinares-Patino et al., 2007). These emissions are only indirectly linked to carbon already assimilated in below-ground soil carbon stocks (Byrne, Kiely, & Leahy, 2007). To fully understand the nature and magnitude of grazing effects on salt marsh carbon, a more holistic approach needs to be taken to incorporate the various pathways of carbon sequestration and loss in the salt marsh environment.

PART 3: INVESTIGATING CARBON PATHWAYS IN A SALT MARSH ENVIRONMENT

Chapter 5: Determining the Main Drivers of Carbon Sequestration on Un-grazed Salt Marshes

5.1 Introduction

It has been established that carbon sequestration into the soil carbon sink is a reliable means of trapping atmospheric carbon (Lal, 2004). Highly productive natural systems, such as salt marshes, are a focal point for the management of carbon sequestration as they are generally thought to be long-term carbon sinks (Amundson, 2001; Chmura et al., 2003; Kalaugher, 2011; Laffoley & Grimsditch, 2009). Models have shown, however, that an increase in global temperatures is likely to lead to a global loss of soil carbon back into the atmosphere through increased soil respiration (Jenkinson, Adams, & Wild, 1991; Kirschbaum, 1995; Schimel, Braswell, & Holland, 1994). It is therefore important to understand the impacts of environmental variation on carbon sequestration rates in natural systems, and to establish current trends in carbon sequestration rates to predict what might happen to these natural carbon stocks in the future, considering potential changes in climate.

There are two approaches to determine carbon sequestration over time: chronosequences measure soil carbon stocks in soils of different ages (i.e. different depths) to determine changes over time, using isotope analysis or deep core analysis. Mass balance approaches or carbon budget models measure carbon cycling rates and can provide data on soil responses to environmental changes (Amundson, 2001). In salt marshes, chronosequence approaches have been conducted using radioisotope analyses in shallow soils (up to 1 m depth) (DeLaune, Patrick, & Buresh, 1978; Fox, Johnson, Jones, Leah, & Copplestone, 1999; Marshall et al., 2007). Deep core analyses do not work well on salt marshes, as it is difficult to determine the true depth of the salt marsh. Since salt marshes develop over sand or mud flats rather than over bedrock and salt marsh formation can be patchy, it is difficult to tell where the mudflats ends and the salt marsh starts (Adam, 1990b; Allen, 2000; Davy, 2002; van de Koppel et al., 2005). The mass balance approach is perhaps more appropriate for salt marshes; but while some studies investigate one component of a carbon budget such as gas effluxes (Ford et al., 2012; Lipshultz, 1981; Magenheimer et al., 1996; Morris & Whiting, 1986) or sediment accretion (Allen & Rae, 1988; Andersen, Svinth, & Prejrup, 2010; Bricker-Urso et al., 1989; Harrison & Bloom, 1977), no study has delivered a 'total carbon budget' of a salt marsh – investigating all of the carbon fluxes into and out of the soil carbon stocks – or how the contributions of different carbon budget components might vary between seasons and locations. Furthermore, no study has used a mass balance approach to predict future carbon stocks on salt marshes.

5.1.1 Salt marsh carbon fluxes

The main inputs of carbon into salt marsh soil carbon stocks are degradation of organic matter (degraded plant litter and root matter) (Coûteaux, Bottner, & Berg, 1995; Sollins, Homann, & Caldwell, 1996; Trumbore, 1997) and marine sediment trapped by plants (Connor et al., 2001; Flessa et al., 1977; Stumpf, 1983), while the main outputs of carbon are soil respiration and erosion (Morris & Whiting, 1986) (Figure 5.1). These carbon fluxes are all influenced by, or directly related to other carbon stocks and flows in the carbon budget (Figure 5.1). Litter production and root biomass are directly linked to plant productivity (Facelli & Pickett, 1991; Valiela et al., 1985), which in turn is driven by the plant community composition (Naeem, Hakansson, Lawton, Crawley, & Thompson, 1996; Wardle et al., 2004) and soil characteristics such as soil compaction, nutrient availability, and soil moisture (Bedford, Walbridge, & Aldous, 1999; Davidson, 1969; Gomez, Powers, Singer, & Horwath, 2002). The degradation of plant litter has been extensively studied in the literature (Coûteaux et al., 1995; Giese et al., 2009; Olofsson & Oksanen, 2002; Valiela et al., 1985), however, the degradation of root matter has not been studied to the same extent. Litter degradation has two components: (1) the breakdown (mineralization and humification) of cellulose, lignin and other compounds by a succession of microorganisms; (2) the leaching downward in the soil of soluble compounds (Coûteaux et al., 1995). Decomposition is impacted by soil temperature; enzyme and metabolic activity increase with increasing temperature and rapidly falls if the temperature rises above a critical level (Coûteaux et al., 1995). Metabolic activity also increases with soil moisture until the soil becomes anaerobic, at which point the decomposition of biological compounds is reduced or completely suppressed (Coûteaux et al., 1995; Freeman et al., 2001; Freeman, Ostle, Fenner, & Kang, 2004).

On an accreting salt marsh, sedimentation can be a major input of carbon, particularly if there is a high plant biomass to trap incoming sediment (Allen & Rae, 1988; Huckle, Marrs, & Potter, 2004; F. J. Richards, 1934; Shi, 1992; Stumpf, 1983). When erosion is greater than accretion, large amounts of carbon can be lost from a salt marsh (Cooper, Cooper, & Burd, 2001; Greensmith & Tucker, 1965; Ravens, Thomas, Roberts, & Santchi, 2009). The accretion/erosion rate on a salt marsh depends on the environmental setting of the marsh where wave exposure, marsh size, marsh geomorphology and tidal range are significant drivers (Adam, 1990b; Allen, 2000). Extreme events such as large storms also play a significant role in the accretion or erosion of a marsh (Boorman, 2003), although they are very difficult to predict (Elsner & Kocher, 2000; Hecht, 2007; G. J. Holland & Webster, 2007; Kim, Cairns, & Bartholdy, 2011; Schuerch, Rapaglia, Liebetrau, Vafeidis, & Reise, 2012), so large scale erosion can by hard to quantify. A large-scale erosion event (the loss of large blocks of soil or the movement of large creeks) would be a mass export of carbon from the salt marsh environment to the marine environment, which is considered another long-term carbon sink, so although carbon is lost from the soil carbon sink, it is still considered to be sequestered (Lal, 2008).

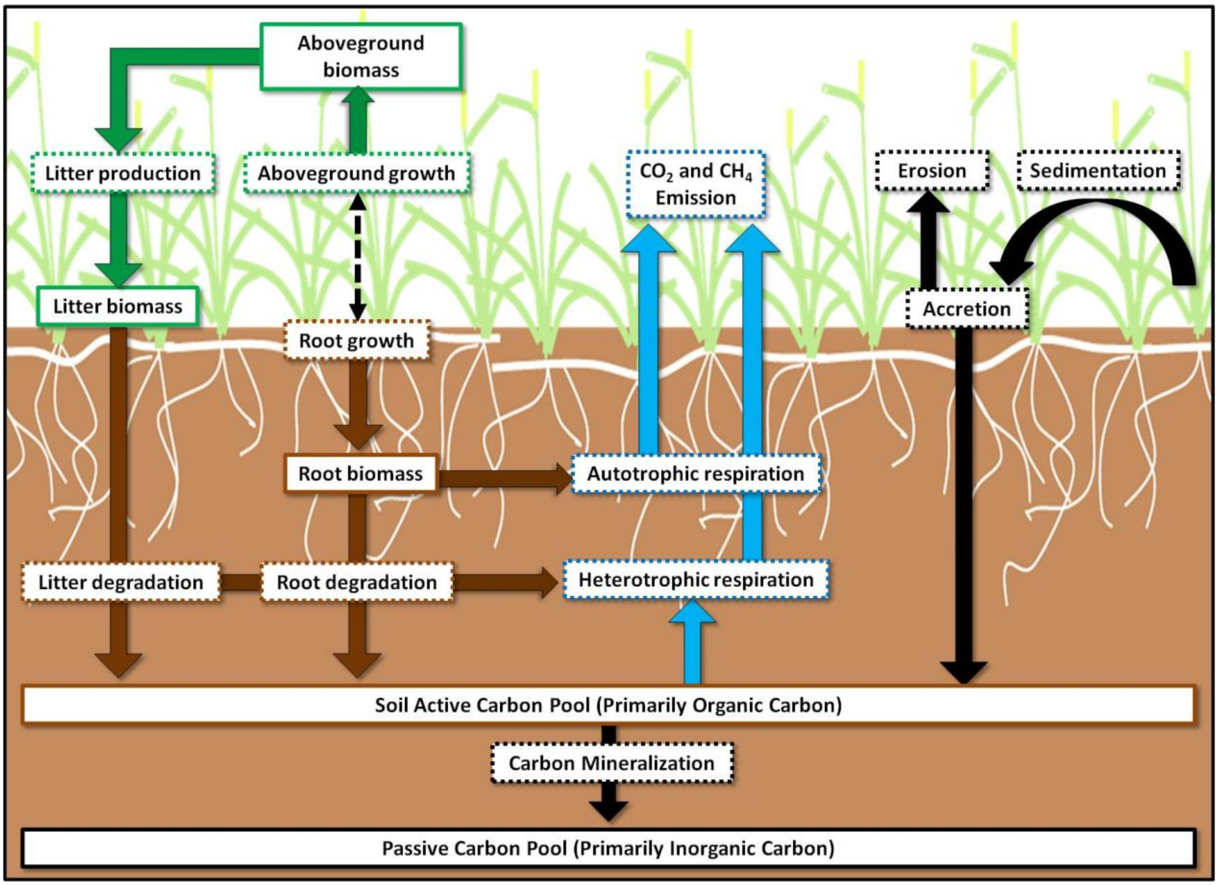


Figure 5.1 | A salt marsh carbon budget model for an un-grazed salt marsh. The main carbon stocks (solid outlines) and fluxes (dashed outlines) on a salt marsh and the links between them. The main inputs of carbon into the soil carbon stock are organic matter (litter and root material) and sedimentation, and the main output of carbon from the soil carbon stock is heterotrophic respiration (Coûteaux et al., 1995; Morris & Whiting, 1986; Sollins et al., 1996; Stumpf, 1983).

Gas efflux can be a significant output of carbon from salt marsh soils (Ford et al., 2012; Magenheimer et al., 1996). Methane (CH_4) and carbon dioxide (CO_2) are the most significant gases produced by natural systems (Dalal & Allen, 2008) and the mean methane emissions in the northern hemisphere are 5-6% higher than in the southern hemisphere due to the 3 times larger methane source strength in the northern hemisphere (Lelieveld et al., 1997). Methane is produced in many natural wetlands due to anaerobic conditions, which facilitate for methanogenic microorganisms that are capable of producing methane gas (Lai, 2009). In salt marshes, abundant sulphates brought in by the tide can inhibit methane production (Winfrey & Ward, 1983), so methane emissions are likely to be minimal. Carbon dioxide effluxes are derived from root respiration (autotrophic respiration) and the aerobic decomposition of soil carbon by microorganisms (heterotrophic respiration) (Pendall et al., 2004). Carbon dioxide produced through autotrophic respiration comes directly from the roots of plants and the organisms directly associated with the rhizosphere and is therefore not associated with the soil carbon stock (Bond-Lamberty, Wang, & Gower, 2004; Hanson, Edwards, Garten, & Andrews, 2000). Carbon dioxide produced through heterotrophic respiration comes from the soil microbial communities, which are actively breaking down the soil carbon stock and are therefore directly contributing to the loss of carbon through respiration (Bond-Lamberty et al., 2004; Hanson et al., 2000). Soil respiration varies with soil temperature and soil moisture, as well as the nature of the carbon pool, which has active, slow-turnover and passive components (Amundson, 2001; Pendall et al., 2004); the active carbon pool receives inputs from the roots and plant litter and has a turnover time of up to a few years, the slow turnover soil carbon pool receives inputs from the active pool and has a turn over time of decades or centuries, and the passive carbon pool consists of very stable organo-mineral complexes with a turn over time of millennia (Amundson, 2001; Pendall et al., 2004).

5.1.2 The effects of seasonality

It is assumed that salt marsh carbon accumulation by high plant productivity and sedimentation outweigh carbon losses through erosion and gas effluxes, and therefore salt marshes generally accumulate carbon (Chmura, 2009; Chmura et al., 2003; Kalaugher, 2011). However, the anaerobic conditions that inhibit carbon dioxide production (Pendall et al., 2004) may also slow decomposition rates and therefore reduce the input of carbon through decomposition of organic matter (Coûteaux et al., 1995). Soil conditions may vary between seasons and lead to seasonal fluctuations in carbon flux rates. In the winter months, it is likely that soil moisture will be high, soil temperatures will be low and anaerobic conditions will dominate. Therefore, gas emissions will be lower (Pendall et al., 2004), and degradation rates of some biological components, such as lignin, are likely to be slower during winter than during summer (Coûteaux et al., 1995; Freeman et al., 2004). Storms, and affiliated erosion events, are more likely during autumn and winter than during spring and summer (Hurrell & Deser, 2009). Because both output of carbon through gas efflux and input of carbon through organic matter follow the same pattern (low in winter, high in summer), the overall carbon sequestration rate could feasibly remain constant over the year. Nevertheless, there may still be a significant difference between winter and summer months. This seasonal change may not be important if looking just at soil carbon stocks, but if a carbon flux was being used as a proxy for total soil carbon stock estimations or predictions, seasonality may result in significant errors.

5.1.3 Study aims

The overall aim of this chapter was to determine which of the main carbon fluxes best determines the soil carbon stock on an un-grazed salt marsh by constructing a carbon budget model for an un-grazed salt marsh using annual averages of several carbon fluxes calculated from field measurements taken over the course of 1 year. Organic matter degradation and sedimentation were expected to be large inputs of carbon into the soil carbon stocks, while gas efflux was expected to be a small output of carbon. As the study area was along the west coast of the UK, where salt marshes are generally accreting (Adam, 1990b; Boorman, 2003) sedimentation on the mid marsh was expected to be greatest in the winter and autumn months when storm surges were more likely. Degradation of organic matter was expected to be lowest in winter when anaerobic conditions were likely to prevail and input of fresh organic matter was likely to be minimal. Gas effluxes were expected to be greatest in the summer when aerobic conditions and warmer soil temperatures would facilitate greater CO_2 production.

Un-grazed salt marshes were used to investigate the role of environmental drivers and contextual setting on natural carbon sequestration rates in a system with minimal anthropogenic disturbance. The impacts of several environmental and abiotic soil parameters on the carbon stocks and fluxes were measured each month to investigate the effect of seasonal changes and environmental variability on the carbon stocks and fluxes. Soil moisture and soil temperature were expected to be significant drivers of organic matter degradation and gas efflux. Marsh setting, tidal range and wave exposure were expected to be significant drivers of carbon accretion rates. Carbon stocks and fluxes were measured monthly and seasonally across three un-grazed salt marshes along the west coast of Wales and north-west England (Chapter 2) over the course of 13 months.

5.2 Materials and Methods

5.2.1 Empirical study

5.2.1.1 Site selection, determination of zones and quadrat selection: Within the study area, three un-grazed marshes were selected for sampling empirical data (carbon parameters and environmental variables) (Chapter 2). The three sites were Y Foryd, Malltraeth and Crossens (see Chapter 2 for full site details). These sites were selected from the nine un-grazed marshes in the study area as they represented the three main community types of un-grazed marshes in the area (Chapter 3), and exhibited a wide range of sediment and tidal regimes. Y Foryd, was chosen for a more detailed analysis of the salt marsh carbon budget. Y Foryd was an un-grazed marsh that was easily accessible from Bangor, Gwynedd. Soil redox potential and gas emissions were measured on Y Foryd at high frequency (4 measurements per month). At other sites, measurements were only taken seasonally due to logistical constraints (travel time, sample processing time, and difficulty of transporting equipment over long distances and difficult terrain). Sediment deposition patterns over a tidal cycle, autotrophic-heterotrophic respiration ratios, and litter degradation rates were only measured at Y Foryd as time constraints made these measurements impossible across all sites. The study focused on the mid marsh exclusively. The mid marsh was considered representative of the whole marsh; it was not subject to the extreme wave and tidal disturbance of the pioneer zone or the terrestrial influences of the high marsh, yet it was still subject to regular tidal flooding and it is colonized by halophytic plants from across all the marsh zones (Adam, 1990b). Observations per site were made in the same four 2 x 2 metre 'below-ground plots' used in the broad-scale study (Chapters 2 & 4).

5.2.2 Carbon response variables

Samples were taken in four plots per sample site either at monthly, seasonal (every 3 months) or annual (one-off measurement) frequency between November 2011 and November 2012. Sampling frequency depended on growth and degradation rates, ease of sampling technique, and logistical constraints (ability to take field equipment to the plots). All carbon stocks were converted into metric tonnes of carbon per hectare (t (C) ha^{-1}) and all rates were converted into metric tonnes of carbon per hectare per year (t (C) ha^{-1} yr^{-1}). The following were sampled.

5.2.2.1 Above-ground live and litter biomass: Above-ground biomass and litter biomass were measured using a 25 x 50cm quadrat placed in a representative area of each plot. Any vegetation litter within the 25 x 50cm quadrat was collected and put in a labelled plastic bag. Above-ground biomass and litter biomass were sampled in a 25 x 50cm quadrat placed in a representative area of each plot. Vegetation litter was collected and bagged before the living vegetation (above-ground biomass) was cut down to the soil. Samples were dried in the laboratory at 80°C for 3 days, and weighed. The carbon content of the above-ground vegetation was derived using loss on ignition techniques based on Ball (1964): dry samples were weighed, ashed at 550°C for 5 hours and weighed again. The organic content was calculated by subtracting the ashed weight from the dry weight and converted to organic carbon content using using a conversion formula devised by Craft et al. (1991):

$$\text{Soil Organic Carbon Concentration} = (0.4 \times \text{OMC}) + (0.0025 \times \text{OMC}^2)$$

This formula was used because Craft found that a quadratic equation best described the relationship between organic carbon and organic matter, rather than the linear relationship that is used in other literature.

5.2.2.2 Above-ground plant growth rates: Above-ground plant growth was measured throughout the 2012 growing season (March to September). Vegetation was clipped and re-clipped from two 25 x 50cm quadrats in each plot; one for seasonal growth measurements and one for overall growth measurements. The overall growth quadrats were initially clipped only in February, before the start of the growing season, and re-clipped in September, at the end of the growing season. This was to account for the production rates of species sensitive to clipping, as well as total community growth rates. The seasonal measurements were re-clipped every three months throughout the growing season (March, June and September); vegetation was cut down to the soil. This was to account for seasonal changes in community growth rates. The differences between each seasonal clipping were used to calculate an average growth rate per month during the growing season, and the differences between overall growth quadrats were used as the annual growth rate.

5.2.2.3 Litter production rates: In the literature, litter production rates are sampled using litter traps placed on the marsh surface and emptied weekly to prevent litter decay (V. Bouchard & Lefeuvre, 2000). Weekly sampling was beyond the scope of this study due the distance between sites. Instead, litter production rates were predicted from the above-ground live biomass based on litter fall rates calculated by V. Bouchard and Lefeuvre (2000): it was assumed that 55% of the above-ground live plant biomass per year would fall as litter and approximately 15% of the live plant biomass per year would be washed off the marsh as detritus.

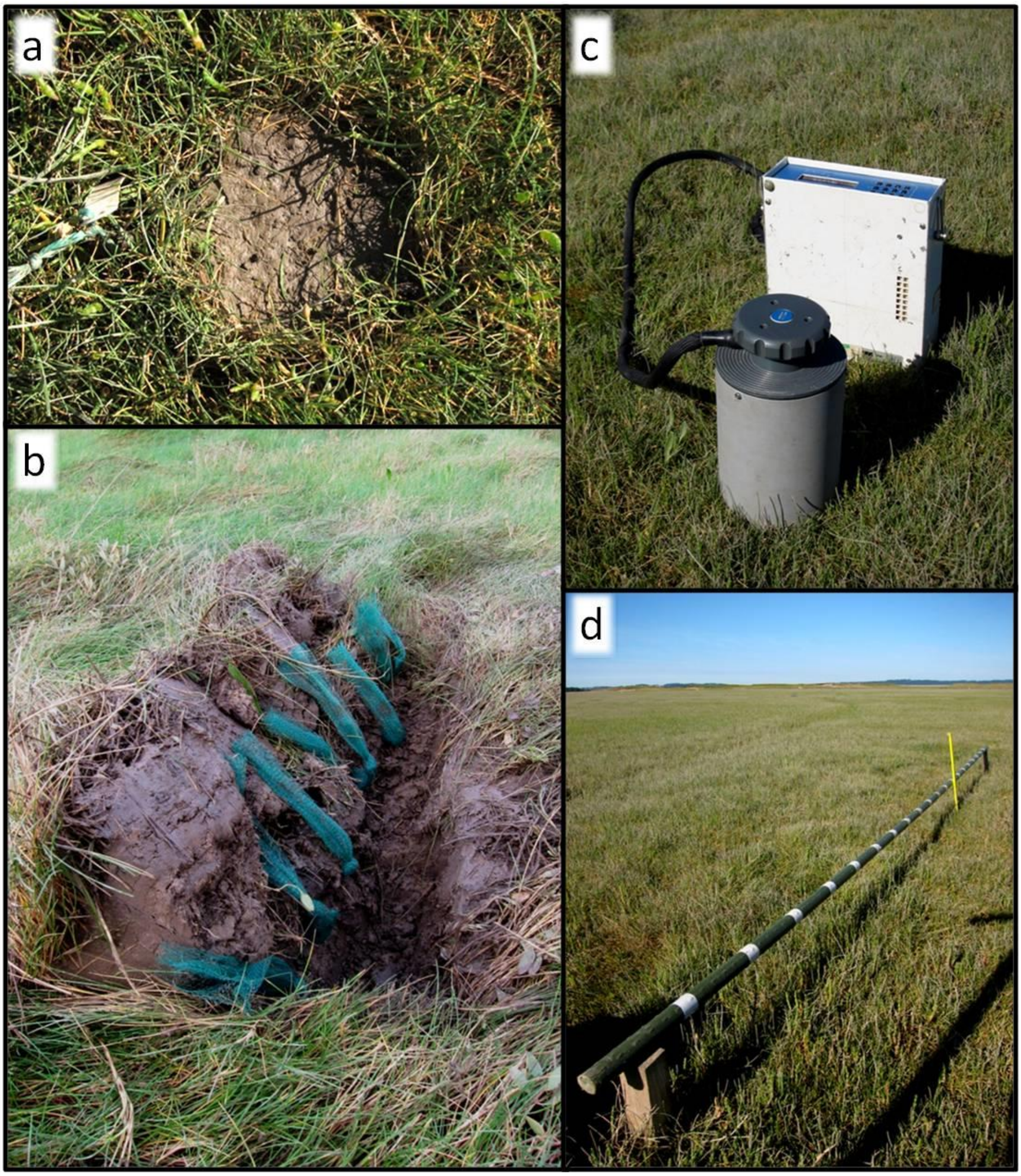


Figure 5.2 | The monthly and seasonal measurements. **a)** The root growth core before re-sampling. The core has had all root matter removed and the remaining sediment was placed back into the core hole to re-create a natural and realistic substrate for new root growth. **b)** Inserting the root bags into the sidewall of a 20cm deep trench. The soil clods were then placed back into the trench and the root bags were sampled seasonally. **c)** Using the EGM-4 infrared gas analyser to measure soil carbon dioxide flux rates. **d)** Measuring monthly accretion rates using two permanently placed wooden posts and a 2m garden pole marked at 10cm increments. The distance from the pole to the soil surface was measured at each white marker.

5.2.2.4 Root biomass: A 25cm deep, 4.6cm diameter soil core was taken from each plot in October 2011 using a split tube corer based on a smaller model by Eijkelkamp. The core was divided into 5cm depth segments down the entire length of the core. Live roots were removed from the core segments by hand dry weights were expressed per volume of soil. Root carbon content was derived after loss on ignition at 550°C for 5 hours using techniques based on Ball (1964). The organic content was the ashed weight subtracted from the dry weight.

5.2.2.5 Root growth rates: Root growth rates were measured in each plot seasonally (every 3 months) in January, April, July and October 2012 using methods based on in-growth cores in Steingrobe, Schmid, and Claassen (2000). A 15cm deep 4.6cm diameter sediment core was taken in each plot and all root material was removed. Root-free sediment was then replaced into the hole left by the corer and marked (Figure 5.2a). Although this method was time consuming, this provided a natural and realistic substrate for new root growth. The core was then re-sampled after 3 months to assess the root growth rate over the season. The core was washed free of sediment over a 0.5mm meshed metal sieve. Root matter was then dried at 80°C for 3 days and the dry weights were recorded.

5.2.2.6 Litter and root degradation: Litter and root degradation rates were sampled based on litter bag methods in Olofsson and Oksanen (2002). Litter material was collected from a strand line on Warton Bank marsh on the Ribble Estuary, and root material was collected from the high marsh zone on Malltraeth marsh in August 2011. The same litter and root material was used on each marsh to enable reliable comparisons between marshes. Both root and litter material was washed free of sediment and dried at 80°C for 5 days. Litter and root samples were placed in 5mm mesh, plastic Netlon bird feeder bags. The dry weight of each sample was recorded on waterproof paper and placed in the sample bag with the sample. Eight root bags were then buried at each plot in October 2011 by digging a 20cm deep trench and using a knife to insert the sample bag into a narrow hole in the side wall of the trench approximately 10cm from the top of the trench (Figure 5.2b). The dry weight and position of each sample was recorded as the samples were buried. The ends of the sample bags were then left protruding from the trench wall and soil clods were returned to the trench to cover the bags fully. Litter bags were only buried on Y Foryd due to logistical restraints. To account for potential loss of litter and root matter, 20 dummy root bags and ten dummy litter bags were buried in using the method described above. These bags were then immediately removed and the average percent weight loss was calculated; this was used to account for any matter lost while deploying and retrieving the experimental litter and root bags. Twelve litter bags and twelve root bags were buried at each plot on Y Foryd and eight root bags were buried per marsh on the other marsh sites. Root and litter bags were retrieved seasonally in January, April, July and October 2012; three litter bags and three root bags were retrieved per plot on Y Foryd, and two root bags were retrieved from each plot from the other marsh sites. The root and litter material was washed free of sediment and new roots that had grown into the samples were removed. The samples were then dried at 80°C for 3 days and the dry weights were recorded and compared to the original dry weights to determine seasonal rates of decomposition.

5.2.2.7 Carbon dioxide emissions and heterotrophic respiration: Total carbon dioxide emission rates from the soil were measured at each plot using an EGM-4 infra red gas analyser (PP-Systems, 2010) (Figure 5.2c). Measurements were taken monthly at Y Foryd and seasonally (February, May, August and November 2012) on the other study sites. The total carbon dioxide emitted from the soil surface is a combination of carbon dioxide derived from both autotrophic respiration and heterotrophic respiration (Bond-Lamberty et al., 2004). The autotrophic-heterotrophic respiration ratio was determined in the mid marsh zone on Y Foryd in July 2012 based on Carbone and Trumbore (2007). A paired experimental design was used to test the difference between carbon dioxide emissions in ten 20 x 20cm clipped and ten 20 x 20cm un-clipped plots. Plots were clipped one week prior to the experiment to avoid any immediate disturbance effects of the clipping. The EGM-4 was used to measure carbon dioxide emission rates from both clipped and un-clipped plots and the soil temperature and moisture were measured within each plot. From the total and heterotrophic gas measurements, carbon dioxide produced from autotrophic respiration was estimated and the percentage contribution of heterotrophic and autotrophic respiration to the total soil carbon dioxide efflux was calculated.

5.2.2.8 Accretion rate: Accretion rates were sampled using the a method based on sediment poles used in Stock (2011). Two permanent wooden posts were inserted into the marsh approximately 2m apart at each plot in October 2011 and the height of each post was recorded. Sediment accretion rates were the measured monthly at each plot on each marsh using a 2.2m garden pole marked at 10cm increments (Figure 5.2d). The distance between the pole and the marsh surface was measured at each marker along the pole except the two markers closest to each post; this was to avoid any micro sedimentation patterns caused by the posts. The accretion rate readings were compared with the base line data taken in November 2011 to determine the annual accretion rate and monthly readings were used to determine monthly and seasonal variations in accretion rates. Accretion rates were converted from centimeters per year to grams per square centimetre using bulk density measurements:

$$\text{Accretion rate (g cm}^{-3}\text{ yr}^{-3}\text{)} = \text{Accretion rate (cm yr}^{-1}\text{)} \times \text{Bulk density (g (soil) cm}^{-3}\text{)}$$

This was then converted in to tones of sediment per hectare per year by multiplying by 100, and organic carbon content was calculated from loss on ignition analysis of suspended sediment (see 5.2.2.9).

5.2.2.9 Whole-marsh particulate organic matter fluxes: Salt marshes along the west coast of the UK are generally accreting and it is therefore assumed that small scale erosion during large tidal cycles is outweighed by sediment deposition (Adam, 1990b; Boorman, 2003). This assumption was tested on Y Foryd during an equinoctial spring tide in September 2012. It is difficult to test for small-scale erosion or sediment movement within each zone as it is likely that particulate organic matter (POM) moves between zones before leaving the marsh (Stock, 2011; Stumpf, 1983). As such, a whole-marsh approach was more insightful: measurements of suspended matter in the water column before it reached the marsh were compared to measurements of suspended matter in the water column as it left the marsh to determine if there was a net gain (erosion) or loss (sedimentation) of sediment from the water column as the water passed over the marsh. This was refined by measuring suspended matter in the water column over each zone to determine where on the marsh suspended matter was deposited or picked up. The suspended sediment in the water column was measured on the mudflat (before and after it passed over the marsh) and on each marsh zone both on the incoming tide and the outgoing tide. Water samples were collected in plastic bottles attached to the end of a 2m pole to reduce disturbance of the marsh surface near the sample collection point. Five water samples were collected above each of the mudflat and the four marsh zones (pioneer, low, mid and high) on the incoming tide as it flooded the marsh, and a further five water samples were collected from each zone and from the mudflat on the ebb tide. In the laboratory, the water samples were filtered through pre-sterilized filter papers of a known weight to collect any suspended matter. The samples were then dried at 105°C for three hours and weighed to determine the weight of suspended matter. The samples were then ashed at 550°C for three hours to remove any organic matter, and weighed again to determine the weight of organic matter in each sample. The weight of organic matter was then converted into organic carbon content using the formula from Craft et al. (1991):

$$\text{Sample Organic Carbon Content} = (0.4 \times \text{Organic Matter}) + (0.0025 \times \text{Organic Matter}^2)$$

A 2-way ANOVA (Factor: tide, with two levels: flood and ebb; Factor: zone, with five levels: mudflat, pioneer, low, mid and high) with *post hoc* Tukey HSD tests was used to determine the difference in suspended particulate organic carbon (POC) between the flooding and the ebbing tides. If suspended POC was greater on the flow tide than the ebb tide, it was assumed that accretion was occurring, and if suspended POC was greater on the ebb tide than the flow tide, it was assumed that erosion was occurring.

To determine sediment deposition rates in the mid marsh relative to the other marsh zones, the pattern of sedimentation across the marsh was also measured. Prior to tidal flooding, sediment traps were laid out in the mud flat and within each zone. The traps were laid out nearby the sample plots from chapters 3 and 4 to ensure they were in a representative area of each zone. Pre-weighed, labeled filter papers were used to trap any sediment deposited on the marsh surface; the filter papers were held off the marsh surface using an upside down petri dish and held in place using tent pegs (Figure 5.3). Nine sediment traps were deployed on the mudflat and in each marsh zone in a 3 x 3 grid covering an approximately 3 x 3m area. The sediment traps were left over the course of one spring equinox tide and re-sampled at low tide. In the laboratory, the filter papers were dried at 105°c for 24 hours and re-weighed to determine the weight of sediment deposited by area within each zone. A one-way ANOVA (Factor: 'Zone' with five levels: mudflat, pioneer, low, mid and high) with *post hoc* Tukey HSD tests was used to determine the difference in sediment deposition between zones.

Figure 5.3 | The sediment trap. Filter papers were used to trap any sediment deposited on the marsh surface. The filter papers were held off the marsh surface using an upside down petri dish and held in place using tent pegs.

5.2.2.10 Soil organic carbon: A 25 x 4.6cm soil core was taken from each plot in November 2011 using a split tube corer based on a smaller model by Eijkelkamp. The core was divided into 5cm depth segments down the entire length of the core. Each segment was homogenised, root material was removed and an approximately ten gram sample was used to determine the soil organic carbon content by using loss on ignition techniques described in Ball (1964). The percentage soil organic matter content was calculated using methods outlined in the Soils Manual of the Countryside Survey (Emmet et al., 2008):

$$\text{Organic Matter Concentration (OMC)} = \frac{100 \times (\text{Dry Soil Weight} - \text{Combusted Soil Weight})}{(\text{Dry Soil Weight} - \text{Crucible Weight})}$$

The percentage of soil organic carbon (soil organic carbon concentration) was estimated using a conversion formula (Craft et al., 1991):

$$\text{Soil Organic Carbon Concentration} = (0.4 \times \text{OMC}) + 0.0025 \times \text{OMC}^2)$$

This was then converted into soil organic carbon (SOC) per volume (soil organic carbon density) using bulk density figures from summer 2011:

$$\text{SOC (g cm}^{-3}\text{)} = \frac{\text{Bulk Density} \times \text{Soil Organic Carbon Concentration}}{100}$$

To determine the actual change in soil organic carbon over the course of a year, a second 25 x 4.6cm soil core was taken from each plot on each marsh in November 2012 and soil organic carbon content was calculated using the above technique.

5.2.2.11 Soil inorganic carbon and nitrogen content: A sub-set of soil samples was used to determine the total carbon and nitrogen content of the soil (CN analysis). Soil nitrogen is an important driver of plant productivity and may explain some patterns in plant growth rates. Soil samples from a depth of 5-10 cm were taken from the same core as the organic carbon samples, and soil samples from 0-5, 10-15, 15-20 and 20-25 cm depths were taken from one representative core per marsh. The soil samples were dried at 105°C for 16 hours and ground up using a pestle and mortar. Between 0.1 and 0.2 grams of soil was used for the CN analysis. Combustion CN analysis was run using a Leco Instruments, Truspec CN analyser; carbon content was detected using infrared sensors, and nitrogen content was detected using thermal conductivity. EDTA and blank standards were run alongside the sample soils. Soil inorganic carbon content was then calculated by subtracting the soil organic carbon content from the total carbon content of each sample.

5.2.2.12 Carbon mineralization: Carbon mineralization is the conversion of organic carbon to inorganic carbon and represents carbon moving from the active carbon pool to the slow turn over carbon pool (Pendall *et al*. 2004). This was not directly measured in this study but a conservative estimate of carbon mineralization rate of 10% of soil organic stocks was used as a rate constant based on measurements by Howes, Dacey, and Teal (1985).

5.2.3 Abiotic contextual variables

In order to investigate the influence of soil conditions and environmental variation on the carbon budget, a series of abiotic factors were measured monthly or seasonally at each plot on each marsh.

These abiotic variables, collectively, were assumed to be the predominant variables that affect the measured carbon fluxes, as outlined in the introduction.

5.2.3.1 Soil temperature: A digital thermometer was used to measure soil temperature monthly at a depth of 10cm at one point per plot per marsh. In addition air temperature was recorded at each site once a month.

5.2.3.2 Soil moisture and water table depth: A theta probe was used to measure surface soil moisture content monthly at each plot per marsh. As theta probes measure moisture using electrical resistance, saline soils can cause inaccuracies in soil moisture readings (Miller & Gaskin, 1999). For this reason, water table depth was also recorded as proxy for soil water content. Water table depth was recorded using water-permeable dip wells (50 cm deep, 5 cm diameter, water-porous PVC cores) inserted into the marsh to a depth of approximately 45 cm.

5.2.3.3 Soil pH and salinity: Soil samples were taken monthly for pH and salinity analyses from a depth of 7-10 cm using a 2 cm diameter half corer. In the laboratory, soil pH was measured within 24 hours of sampling using an IQ soil pH meter. Soil salinity was measured using ten gram of each homogenized soil sample. The samples were diluted to a 1 to 2.5 ratio using 10g of each sample with 25ml of deionised water; samples were then well mixed and allowed to settle. The electrical conductivity of the supernatant of each sample and the temperature at time of sampling were then measured using a Jenway Conductivity Meter 4320 and the conductivity of each sample was calculated using the dilution ratio. Salinity was then calculated as practical salinity units (S) (Lewis, 1980) using an online calculator (Tomczak, 2000).

5.2.3.4 Soil redox: To determine potential methane production levels from soil microbial communities, an Eijkelkamp Ag 3 mol/l KCl combination glass electrode was used to measure soil redox (anaerobic state) at each plot monthly at Y Foryd and seasonally (November 2011, February, May, August and November 2012) on other marsh sites. Measurements were taken at depths of 2.5, 7.5, 12.5, 17.5, 22.5 and 27.5 cm using a 2 cm diameter half corer. Soil temperature readings were taken at each depth alongside each redox reading. The standard measurement of redox (mV) is that measured by a standard hydrogen electrode (Eh) (Eijkelkamp, 2009). Standard hydrogen electrodes are difficult to use in the field, and several alternative redox electrodes can be used; however, field readings from these alternative electrodes must be converted back to standard readings (mV) (Eijkelkamp, 2009). This study used an Ag 3 mol/l KCl electrode (Em) so a conversion factor (Eref) was used to convert field redox readings (Em) to standard redox measurements:

Standard measurement (Eh) = Field measurement (Em) + Eref

Eref depends on the reference electrode used in the field and the soil temperature at the time of the field reading (Eijkelkamp, 2009) (Table 5.1).

Table 5.1 | Eref values for redox conversion. Eref values for different temperatures for the Ag 3 mol/l KCl reference electrode.

Temperature (°C)	Eref
0	224
5	221
10	217
15	215
20	211
25	207
30	200

Once calculated, the standard redox potential measurement (Eh) was used to determine the anaerobic state of the soil. Below 250 mV, soil begins to become anaerobic as nitrogen is reduced (Table 5.2) (Mitsch & Gosselink, 2000). The redox potential has to reach less than -200mV before carbon dioxide can be reduced to methane (Table 5.2) (Mitsch & Gosselink, 2000).

Table 5.2 | Oxidised and reduced forms of elements. The oxidised and reduced forms for elements in the anaerobic chain against the standard redox potential (mV). Adapted from Mitsch and Gosselink (2000).

Element	Oxidised Form	Reduced Form	Redox Potential Required for Transformation (mV)
Oxygen	O_2 (Oxygen)	H_2O (Water)	+400 → +600
Nitrogen	NO_3^- (Nitrate)	N_2O, N_2, NH_4^+ (Nitrous Oxide, Nitrogen, Ammonium)	+225 → +250
Manganese	Mn^{4+} (Manganic)	Mn^{2+} (Manganous)	+100 → +225
Iron	Fe^{3+} (Ferric)	$Fe2^+$ (Ferrous)	-100 → +100
Sulphur	SO_4^{2-} (Sulphate)	S^{2-} (Sulphide)	-200 → -100
Carbon	CO_2 (Carbon dioxide)	CH_4 (Methane)	Below -200

5.2.3.5 Daily tidal height: Predicted times and heights of low and high tides were derived from Tideplotter (BelfieldSoftware, 2011). The tidal height at the time of sampling, the time and height of the last high tide, and the date and height of the last spring tide were also recorded monthly for each site.

5.2.3.6 Daily weather: Observations of air temperature, wind speed, atmospheric pressure and rain fall near each site were derived from local weather stations using the Weather Underground database (Steremberg, 2010). The weather conditions and air temperature at each site were also recorded during monthly sampling.

5.2.3.7 Broader contextual environmental variables: A series of contextual environmental variables were analysed as indicators of contextual drivers of salt marsh productivity and carbon storing processes (Chapter 2) including tidal range, marsh geomorphology and wave fetch (exposure).

5.2.4 Statistical analysis

The following analyses were run to determine which factors were the main drivers of soil carbon stocks in an un-grazed salt marsh:

5.2.4.1 Determining the relative differences between carbon fluxes: Kruskal-Wallis Multiple Comparisons tests were used to evaluate the relative differences between salt marsh carbon input (litter degradation, root degradation and sediment accretion) and output (heterotrophic respiration) fluxes. The *post hoc* comparisons and the group medians and interquartile ranges indicated the comparative size of each carbon flux. From this, the relative size of carbon inputs could be compared to the relative size of carbon outputs to indicate whether salt marshes were likely to be long-term carbon sinks or sources. Analyses were run separately for the annual dataset and for each season in turn to determine seasonal differences in carbon flux relationships. Kruskal-Wallis multiple comparisons tests were used in place of ANOVA because some of the data (litter degradation, sediment accretion and heterotrophic respiration) did not meet ANOVA test assumptions.

5.2.4.2 Determining carbon flux influences on empirical soil carbon stocks: A series of distance-based linear models (DistLM's) and regression analyses were used to determine the possible relationships between empirically measured carbon fluxes with empirically measured soil carbon stocks. Analyses were run for both soil organic carbon and soil inorganic carbon over three depth profiles (0-5 cm, 0-10 cm and 0-25 cm). Based on regional records of sediment accretion rates, the top 6-15 cm of soil was assumed to represent approximately the last 30 years of salt marsh accretion (Appendix 3: Accretion Rates in Other Studies). As with the previous study (Chapter 4), the top soil depth profile (0-5 cm) was regarded to be indicative of the present flux of material from above-ground biomass (e.g. litter) to the below-ground carbon pool, the middle depth profile (0-10 cm) included most of the root biomass and was used to analyse more long-term processes relating to soil carbon stocks, and the deepest profile (0-25 cm) was considered an integrator of the broader contextual influences.

5.2.4.3 Carbon flux relations with contextual variables: A series of mixed effects models were run to determine which environmental variables and abiotic soil variables were the best predictors of soil carbon stock. ANOVA's with *post hoc* Tukey HSD tests, and Kruskal-Wallis Multiple Comparisons tests were used to test the effect for season (4 levels) on the environmental and abiotic soil variables to determine the variation of these parameters over the seasons. These analyses were done on empirical data collected over the year-long study period.

5.2.4.4 Constructing a carbon budget: A carbon budget was constructed using modeling software to predict possible future changes in carbon stocks and to determine the validity of the annual measurements of carbon stocks and fluxes. The annual means ± standard errors were calculated for each carbon flux and stock component. A carbon budget model based on the mean values was then constructed using the Simile v5.96 program. The model was constructed using the carbon stocks and fluxes shown in Figure 5.1. In this case, the stocks were carbon stocks such as soil carbon stock, plant biomass or root biomass, and the flows were carbon fluxes such as litter degradation, plant growth rates and soil respiration. The stocks were used as an initial starting figure for the model (i.e. year 0), and the fluxes indicated changes to these stocks. For example the above-ground biomass stock may start at 1.9 t C ha^{-1} in year 0. The plant growth flux would add 2.4 t C ha^{-1} y^{-1}, and the litter production flux would take away 1.1 t C ha^{-1} yr^{-1}, so after year 1, the above-ground biomass stock would be 2.4-1.9+1.1 = 3.2 t C ha^{-1}. The Simile uses a graphical interface to build up a model diagram consisting of stocks and flows, and can calculate future stocks given the relationships between all the fluxes and stocks in the diagram. To determine the confidence limits for the mean carbon stock predictions, the model was re-run to determine the lowest possible carbon stock predictions according to the data means ($\bar{x}$ − 1 *SE* for inputs; $\bar{x} + 1$ *SE* for outputs) and the highest possible carbon stock predictions according to the data means ($\bar{x} + 1$ *SE* for inputs; $\bar{x} - 1$ *SE* for outputs). The model was then run for a 1-year, and a 50-year time scale to predict future carbon stocks on an un-grazed salt marsh.

5.2.4.5 Comparing model predictions to empirical data: The results from the modeling were compared to empirical data taken from the field to test the predicting power of the carbon budget model. A soil core from each experimental plot was collected in November 2011; the plots were then re-sampled a year later in 2012. The soil organic carbon content for each core was calculated using loss on ignition techniques and a paired t-test was used to determine the *in situ* changes in soil carbon stocks over the course of one year. The model created in Simile was then run for one year and compared to the empirical soil carbon data results from the paired T-test on the two soil core samples.

5.3 Results

5.3.1 The empirical carbon budget

Figure 5.4 shows the patterns of the measured carbon fluxes over time and the related change in carbon stock over the course of one year for each site. There were significant differences in fluxes over the seasons. Of the main carbon fluxes, sedimentation, soil respiration and root growth significantly varied over the seasons (Table 5.3). Sediment accretion was significantly highest in the winter and significantly lowest in the autumn when the marshes generally eroded (Kruskal-Wallis multiple comparisons: Table 5.3). Soil respiration was significantly higher in the summer than in the winter and significantly lower in the autumn than in the spring (Table 5.3). Root growth was significantly lower in the winter than in the summer and autumn (Table 5.3).

Table 5.3 | Differences between seasons for the main carbon fluxes. Results of Kruskal-Wallis multiple comparisons tests for the main carbon fluxes comparing between seasons. Emboldened *p*-values indicate a significant effect. Medians ($\tilde{x}$) and Interquartile Range (*IQR*) are shown by season for each predictor variable. Significant differences between variables within each season are indicated by superscript numbers: variables that share a number are significantly different. Units for each variable are tons of carbon per hectare per year.

Carbon Flux	Kruskal-Wallis			Winter		Spring		Summer		Autumn	
	df	*H*	*p*	$\tilde{x}$	IQR	$\tilde{x}$	IQR	$\tilde{x}$	IQR	$\tilde{x}$	IQR
Litter Degradation	3	0.14	0.987	0.00	0.20	0.00	0.24	0.00	0.24	0.00	0.27
Root Degradation	3	2.97	0.397	0.06	0.07	0.06	0.08	0.05	0.06	0.09	0.09
Sediment Accretion	3	11.77	**0.008**	6.34	17.56 ^{12}	3.36	5.63 ^{3}	2.02	13.51 ^{1}	-5.07	6.20 ^{23}
Soil Respiration	3	22.41	**<0.001**	3.23	7.06 ^{1}	6.11	5.91 ^{2}	11.00	5.35 ^{13}	2.47	2.10 ^{23}
Root Growth	3	11.33	**0.010**	0.01	0.01 ^{12}	0.02	0.02	0.03	0.04 ^{1}	0.03	0.09 ^{2}

Over the year, losses of carbon through heterotrophic soil respiration and carbon input through sediment accretion were significantly greater than carbon inputs through litter and root degradation (Kruskal-Wallis Multiple Comparisons: Table 5.4). This pattern was consistent throughout the winter and spring (Table 5.4), however, in the summer and autumn, loss of carbon through heterotrophic soil respiration was greater than carbon inputs through sediment accretion, litter degradation and root degradation, and sediment accretion rates did not significantly differ from carbon inputs through litter and root degradation (Table 5.4). It is therefore suggested that salt marshes generally accrete carbon during the winter and spring, but may lose carbon during the summer and autumn when soil respiration rates outweigh sediment accretion rates.

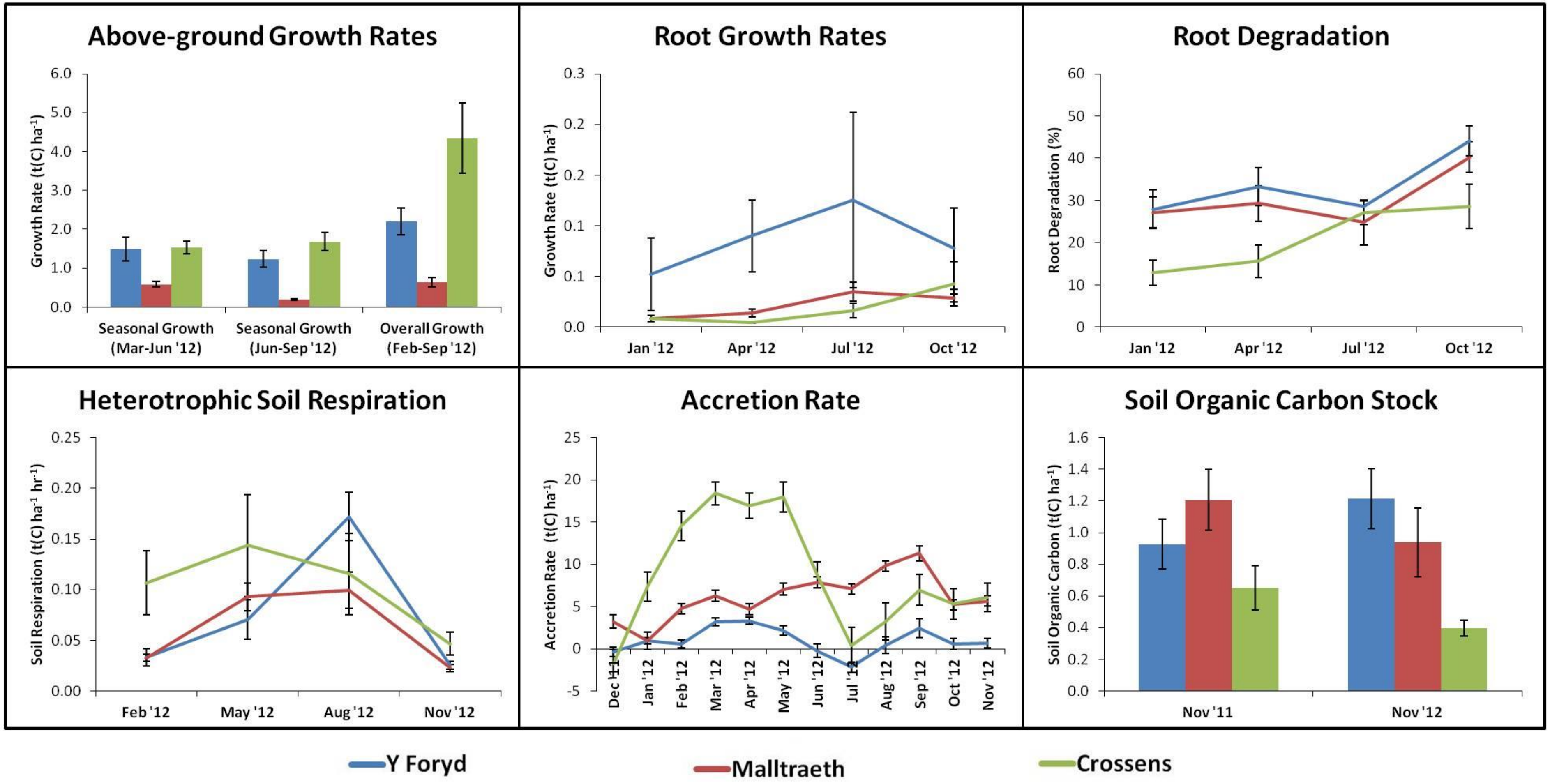


Figure 5.4 | Patterns of measured carbon fluxes over time by marsh. Bar and line charts showing the patterns of the measured carbon fluxes (above-ground growth, root growth, root degradation, soil respiration and accretion rate) alongside the empirical measurements of soil organic carbon in November 2011 and November 2012 for the three un-grazed salt marshes (Y Foryd, Malltraeth and Crossens). Data is presented as tonnes of carbon per hectare, except for root degradation, which is recorded as a percentage loss of mass.

Table 5.4 | Differences between carbon inputs and outputs by season. Results of Kruskal-Wallis multiple comparisons tests for annual data set and by season comparing the main inputs and outputs of carbon, averaged over the three marshes, (t (C) ha^{-1} yr^{-1}) according to the salt marsh carbon budget model (Figure 5.1). Emboldened *p*-values indicate a significant effect. Medians ($\tilde{x}$) and Interquartile Range (*IQR*) are shown by season for each predictor variable. Significant differences between variables within each season are indicated by superscript numbers: variables that share a number are significantly different.

	Kruskal-Wallis			Litter Degradation		Root Degradation		Sediment Accretion		Heterotrophic Soil Respiration	
Season	***df***	***H***	***p***	$\tilde{x}$	**IQR**	$\tilde{x}$	**IQR**	$\tilde{x}$	**IQR**	$\tilde{x}$	**IQR**
Annual	3	99.88	**<0.001**	0.00	0.23 [12]	0.06	0.22 [34]	4.61	12.00 [13]	6.61	2.28 [24]
Winter	3	29.90	**<0.001**	0.00	0.20 [12]	0.06	0.07 [34]	6.34	17.56 [13]	3.23	7.06 [24]
Spring	3	30.82	**<0.001**	0.00	0.24 [12]	0.06	0.08 [34]	3.36	5.63 [13]	6.11	5.91 [24]
Summer	3	25.08	**<0.001**	0.00	0.24 [1]	0.05	0.06 [2]	2.02	13.51 [3]	11.00	5.35 [123]
Autumn	3	23.00	**<0.001**	0.00	0.27 [1]	0.09	0.09 [2]	-5.07	6.20 [3]	2.47	2.10 [123]

Salt marsh study sites were assumed to be generally accreting, with minimal erosion during large spring tidal cycles. Sampling at Y Foryd marsh showed that there was a significant difference in the amount of suspended organic carbon in incoming water (flooding) and outgoing water (ebbing) (ANOVA: $F_{1,40}$ = 70.02, p < 0.001, η_p^2 = 0.637); Tukey HSD tests showed that the there was more suspended organic carbon on the flooding tide ($\bar{x}$ = 0.0032, *SD* = 0.0011 (g (C) cm^{-3})) than on the ebbing tide ($\bar{x}$ = 0.0022, *SD* = 0.0004 (g (C) cm^{-3})). Suspended organic carbon in the water column also varied between marsh zones (ANOVA: $F_{4,40}$ = 21.39, p < 0.001, η_p^2 = 0.682); Tukey HSD test showed that there was significantly more suspended organic carbon over the pioneer zone ($\bar{x}$ = 0.0034, *SD* = 0.0013) than over the mudflat ($\bar{x}$ = 0.0027, *SD* = 0.0007), the mid marsh ($\bar{x}$ = 0.0026, *SD* = 0.0005) or the high marsh ($\bar{x}$ = 0.0017, *SD* = 0.0004), and there was significantly less suspended organic carbon over the high marsh than the other zones. There was a significant difference in the amount of sediment deposited on the deployed sediment traps between the marsh zones (ANOVA: $F_{4,40}$ = 29.17, p < 0.001, η_p^2 = 0.745). A Tukey HSD test showed that sediment deposition on the pioneer zone ($\bar{x}$ = 0.0034, *SD* = 0.0012) was higher than on the mudflat ($\bar{x}$ = 0.0021, *SD* = 0.0003), the low marsh ($\bar{x}$ = 0.0015, *SD* = 0.0001), the mid marsh ($\bar{x}$ = 0.0012, *SD* = 0.0001), and the high marsh ($\bar{x}$ = 0.0007, *SD* = 0.0003). Sediment deposition on the mudflat was significantly greater than in the mid and high marsh zones, and sediment deposition in the low marsh zone was greater than in the high marsh zone.

5.3.2 The main carbon flux predictors of soil organic and inorganic carbon

A combination of root growth rates, litter degradation rates and heterotrophic soil respiration best described the spatial variation in soil organic carbon in un-grazed marshes (DistLM: AICc = 55.10, R^2 = 0.840). Soil organic carbon stocks at 0-5 cm depth had a significant negative relationship with vegetation growth rate, and significant positive relationships with both litter and root degradation rates (Regression: Table 5.5). Soil organic carbon stocks at 0-15cm depth showed a significant negative relationship with both vegetation growth rate and litter degradation rate, and a significant positive relationship with root degradation rate (Table 5.5). When considering the core as a whole (0-25cm depth), soil organic carbon stocks had a significant positive relationship with both root growth and root degradation rates (Table 5.5).

A combination of sediment accretion, and vegetation and root growth rates best described the variation in soil inorganic carbon (DistLM: AICc = 65.97, R^2 = 0.673). Soil inorganic carbon stocks at 0-5 cm and 0-15 cm depth had a significant positive relationship with root growth rate (Regression: Table 5.6). When considering the core as a whole (0-25 cm depth), soil organic carbon stocks had no significant relationship with any individual carbon flux variable (Table 5.6).

Table 5.5 | Regression analysis for carbon fluxes against soil organic carbon. Regression analyses were made for three different depth profiles (0-5cm, 0-10cm and 0-25cm). An emboldened p-value denotes a significant effect. R2, Intercept (b) and Slope (m) values for regression lines are shown.

Predictor Variable	*df*	*F*	*p*	R^2	*b*	*m*
Soil Organic Carbon (t (C) ha^{-1} yr^{-1}) – 0-5cm Depth Layer						
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,10	12.22	**0.006**	0.550	2.900	-0.395
Litter Degradation (t (C) ha^{-1} yr^{-1})	1,10	18.76	**0.001**	0.652	2.510	5.620
Root Growth (t (C) ha^{-1} yr^{-1})	1,10	2.62	0.137	0.207		
Root Degradation (t (C) ha^{-1} yr^{-1})	1,10	8.17	**0.017**	0.450	1.390	5.210
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,10	0.29	0.601	0.028		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,10	2.38	0.154	0.192		
Soil Organic Carbon (t (C) ha^{-1} yr^{-1}) – 0-15cm Depth Layer						
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,10	10.14	**0.010**	0.504	1.740	-0.218
Litter Degradation	1,10	13.60	**0.004**	0.576	1.520	-3.050
Root Growth (t (C) ha^{-1} yr^{-1})	1,10	4.35	0.064	0.303		
Root Degradation (t (C) ha^{-1} yr^{-1})	1,10	9.76	**0.011**	0.494	0.878	3.150
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,10	0.22	0.647	0.022		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,10	2.93	0.118	0.226		
Soil Organic Carbon (t (C) ha^{-1} yr^{-1}) – 0-25cm Depth Layer						
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,10	6.37	0.030	0.389		
Litter Degradation	1,10	8.07	0.018	0.447		
Root Growth (t (C) ha^{-1} yr^{-1})	1,10	6.17	**0.032**	0.382	0.636	5.560
Root Degradation (t (C) ha^{-1} yr^{-1})	1,10	11.64	**0.007**	0.538	0.617	2.13
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,10	0.43	0.525	0.042		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,10	2.62	0.137	0.179		

Table 5.6 | Regression analysis for carbon fluxes against soil inorganic carbon. Regression analyses were made for three different depth profiles (0-5cm, 0-10cm and 0-25cm). An emboldened p-value denotes a significant effect. R2, Intercept (b) and Slope (m) values for regression lines are shown.

Predictor Variable	*df*	*F*	*p*	$p_{(i)}$	R^2	*b*	*m*
Soil Inorganic Carbon (t (C) ha^{-1} yr^{-1}) – 0-5cm Depth Layer							
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,10	<0.01	0.954	0.050	<0.001		
Litter Degradation (t (C) ha^{-1} yr^{-1})	1,10	0.35	0.566	0.029	0.034		
Root Growth (t (C) ha^{-1} yr^{-1})	1,10	55.71	**<0.001**	0.007	0.848	0.239	9.86
Root Degradation (t (C) ha^{-1} yr^{-1})	1,10	3.41	0.094	0.014	0.255		
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,10	0.45	0.517	0.021	0.043		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,10	0.16	0.694	0.036	0.016		
C Mineralization (t (C) ha^{-1} yr^{-1})	1,10	0.08	0.787	0.043	0.008		
Soil Inorganic Carbon (t (C) ha^{-1} yr^{-1}) – 0-15cm Depth Layer							
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,10	<0.01	0.971	0.050	<0.001		
Litter Degradation	1,10	0.14	0.720	0.029	0.013		
Root Growth (t (C) ha^{-1} yr^{-1})	1,10	23.04	**0.001**	0.007	0.697	0.322	4.32
Root Degradation (t (C) ha^{-1} yr^{-1})	1,10	1.02	0.337	0.014	0.092		
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,10	0.01	0.940	0.043	0.001		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,10	0.16	0.700	0.021	0.016		
C Mineralization (t (C) ha^{-1} yr^{-1})	1,10	0.13	0.722	0.036	0.013		
Soil Inorganic Carbon (t (C) ha^{-1} yr^{-1}) – 0-25cm Depth Layer							
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,10	3.04	0.112	0.014	0.233		
Litter Degradation	1,10	1.92	0.196	0.029	0.161		
Root Growth (t (C) ha^{-1} yr^{-1})	1,10	3.58	0.088	0.007	0.264		
Root Degradation (t (C) ha^{-1} yr^{-1})	1,10	0.14	0.715	0.050	0.014		
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,10	0.46	0.511	0.043	0.044		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,10	0.50	0.497	0.036	0.047		
C Mineralization (t (C) ha^{-1} yr^{-1})	1,10	2.61	0.137	0.021	0.207		

5.3.4 The influence of environmental setting and soil parameters carbon fluxes

Table 5.7 shows the results of several mixed effects models testing for associations of environmental and soil parameters with each of the main carbon flux parameters identified in previous sections as being main drivers of soil carbon stocks. Soil temperature was a significant predictor of litter in the winter, root degradation in the winter, spring and autumn, and soil respiration in the autumn. Soil moisture was a significant predictor of litter degradation in the winter, and soil respiration in the winter and autumn. Water table depth was a significant predictor of root degradation in the winter and soil respiration in the winter. Generally, the measured environmental variables were more likely to be predictors of carbon fluxes in the winter and autumn months than in the spring and summer months, particularly when considering soil heterotrophic respiration.

Several environmental and abiotic soil parameters varied between seasons (Tables 5.8, 5.9). Soil moisture was significantly higher in the winter and spring than it was in summer, soil temperature significantly differed between each season with the lowest temperatures in winter and the highest in the summer, and soil salinity was significantly higher in the spring and summer than in the autumn (ANOVA; Table 5.8). Tidal height when sampling was higher in the autumn than in the winter, the air temperature was significantly higher in the summer than in winter, spring and autumn, and the wind speed was higher in the winter and autumn than the spring and summer (Kruskal-Wallis multiple comparisons; Table 5.9)

Table 5.7 | Variation in carbon fluxes with variation in environmental and soil parameters. Results of mixed effects models comparing testing for association of variation in the main (identified from the DistLM and regression analyses) carbon fluxes (vegetation growth, litter degradation, root growth, root degradation, heterotrophic soil respiration and sediment accretion) with variation in environmental and abiotic soil parameters. Column headers depict the effect, degrees of freedom (df: numerator, denominator), F-values (F), p-values (p) and slopes of linear relationships (m).

		Winter			**Spring**			**Summer**			**Autumn**		
Predictor Variable	***df***	***F***	***p***	***m***	***F***	***p***	***m***	***F***	***p***	***m***	***F***	***p***	***m***
Vegetation Growth													
Soil Moisture (θ)	1,2	-	-		5.21	0.150		12.34	0.072		-	-	
Soil Temperature (°C)	1,2	-	-		4.14	0.179		4.70	0.162		-	-	
Water Table Depth (cm)	1,2	-	-		16.22	0.057		7.23	0.115		-	-	
Soil pH	1,2	-	-		4.89	0.158		1.81	0.311		-	-	
Soil Salinity (S)	1,2	-	-		0.03	0.883		0.17	0.722		-	-	
Soil Redox Potential (mV)	1,2	-	-		0.14	0.742		0.68	0.496		-	-	
Community Composition (NVC)	1,1	-	-		3.44	0.315		0.06	0.847		-	-	
Soil Nitrogen (t (N) ha^{-1} yr^{-1})	1,2	-	-		3.13	0.219		0.20	0.698		-	-	
Litter Degradation													
Soil Moisture (θ)	1,3	14.57	**0.032**	-0.019	1.71	0.283		1.95	0.257		0.74	0.452	
Soil Temperature (°C)	1,3	11.20	**0.044**	0.082	1.67	0.286		1.30	0.338		3.26	0.169	
Water Table Depth (cm)	1,3	2.05	0.248		4.86	0.115		1.14	0.364		2.77	0.195	
Soil pH	1,3	2.68	0.200		1.35	0.329		2.14	0.240		0.21	0.679	
Soil Salinity (S)	1,3	2.06	0.246		0.17	0.705		0.15	0.725		0.54	0.516	
Soil Redox Potential (mV)	1,3	0.69	0.466		0.95	0.402		0.02	0.896		0.17	0.707	
Root Growth													
Soil Moisture (θ)	1,1	0.04	0.871		4.13	0.291		0.02	0.905		1.75	0.412	
Soil Temperature (°C)	1,1	0.38	0.649		10.77	0.188		0.01	0.973		2.04	0.389	
Water Table Depth (cm)	1,1	11.59	0.182		1.96	0.395		0.08	0.825		0.32	0.673	
Soil pH	1,1	0.22	0.722		0.05	0.866		1.35	0.452		1.63	0.423	
Soil Salinity (S)	1,1	1.25	0.465		1.07	0.490		0.03	0.893		2.46	0.361	
Soil Compaction (pa)	1,1	0.03	0.889		1.39	0.448		0.05	0.856		0.06	0.846	
Percent Clay	1,1	0.01	0.950		0.19	0.741		0.07	0.834		0.23	0.714	
Community Composition (NVC)	1,1	0.06	0.848		0.63	0.573		0.33	0.668		0.69	0.559	
Soil Nitrogen (t (N) ha^{-1} yr^{-1})	1,1	0.06	0.842		0.50	0.609		0.10	0.804		0.04	0.880	

Table 5.7 (Cont.) | Variation in carbon fluxes with variation in environmental and soil parameters.

		Winter			Spring			Summer			Autumn		
Predictor Variable	***df***	***F***	***P***	***m***	***F***	***p***	***m***	***F***	***p***	***m***	***F***	***p***	***m***
Root Degradation													
Soil Moisture (θ)	1,3	0.01	0.933		4.96	0.112		0.11	0.766		5.71	0.097	
Soil Temperature (°C)	1,3	48.84	**0.006**	-7.359	13.64	**0.034**	4.615	1.45	0.315		75.04	**0.003**	4.356
Water Table Depth (cm)	1,3	19.29	**0.022**	3.302	0.60	0.497		1.77	0.275		4.94	0.113	
Soil pH	1,3	0.04	0.861		2.32	0.226		4.09	0.136		0.20	0.688	
Soil Salinity (S)	1,3	3.71	0.150		1.07	0.380		1.28	0.340		1.41	0.320	
Soil Redox Potential (mV)	1,3	0.03	0.873		<0.01	0.985		0.67	0.473		0.07	0.808	
Heterotrophic Soil Respiration													
Soil Moisture (θ)	1,2	28.31	**0.034**	0.318	1.61	0.332		4.34	0.173		263.13	**0.039**	0.043
Soil Temperature (°C)	1,2	14.44	0.063		3.91	0.187		12.82	0.070		177.58	**0.048**	1.230
Water Table Depth (cm)	1,2	87.03	**0.011**	1.419	1.71	0.321		0.79	0.469		6.53	0.238	
Soil pH	1,2	232.54	**0.004**	41.466	0.09	0.793		6.92	0.119		57.07	0.084	
Soil Salinity (S)	1,2	81.83	**0.012**	-2.125	0.20	0.700		1.09	0.407		1.32	0.456	
Soil Redox Potential (mV)	1,2	12.02	0.074		3.36	0.208		1.85	0.307		583.94	**0.026**	-0.017
Soil Organic Carbon (t (C) ha^{-1} yr^{-1})	1,2	45.52	**0.021**	9.495	1.68	0.325		3.09	0.221		53.27	0.087	
Tidal Height	1,1	767.44	**0.023**	-1.464	1.86	0.403		4.56	0.279		1494.82	**0.012**	2.383
Air Temperature	1,1	58.13	0.083		0.16	0.758		13.66	0.168		89.76	0.067	
Sediment Accretion													
Tidal Range (m)	1,1	35.68	0.106		0.75	0.546		8.91	0.206		0.92	0.513	
Wind Speed (Gust) (kmph)	1,1	2.77	0.344		0.04	0.874		2.05	0.388		0.51	0.605	
Percent Clay	1,4	0.07	0.801		3.99	0.102		0.01	0.947		0.39	0.558	
Soil Compaction (pa)	1,4	1.69	0.250		13.90	**0.014**	-11.491	1.08	0.347		3.51	0.120	
Vegetation Height (cm)	1,4	0.31	0.601		1.31	0.305		1.89	0.228		2.71	0.161	
Vegetation Cover (%)	1,4	5.54	0.065		0.60	0.475		0.25	0.638		0.09	0.781	

Table 5.8 | ANOVA analysis of seasonal differences in soil properties. Results of 1-way ANOVA's showing differences between seasons for several soil properties. Column headers depict degrees of freedom (df: numerator, denominator), F-values (F), p-values (p) and partial eta squared effect size (ηp2). An emboldened p-value denotes a significant effect. Means ($\bar{x}$) and Standard Error (SE) are shown by season for each predictor variable. Significant differences between variables within each season are indicated by superscript numbers: variables that share a number are significantly different.

	ANOVA				Winter		Spring		Summer		Autumn	
Variable	***df***	***F***	***p***	η_p^2	$\bar{x}$	***SD***	$\bar{x}$	***SD***	$\bar{x}$	***SD***	$\bar{x}$	***SD***
Soil Moisture (θ)	3,44	7.69	**<0.001**	0.344	973.17	4.98 [1]	972.72	6.83 [2]	956.08	17.45 [12]	965.63	4.84
Soil Temperature (°C)	3,44	268.51	**<0.001**	0.948	4.74	1.01 [123]	9.17	0.39 [145]	16.28	1.44 [246]	10.53	0.83 [356]
Water Table Depth (cm)	3,44	1.60	0.204	0.098	8.59	8.36	13.12	9.11	14.80	5.53	11.03	5.76
Soil pH	3,44	0.45	0.716	0.030	6.62	0.21	6.62	0.35	6.53	0.18	6.63	0.23
Soil Salinity (S)	3,44	8.25	**<0.001**	0.360	8.94	2.28	11.24	2.46 [1]	11.47	2.95 [2]	7.12	2.19 [12]
Soil Redox (mV)	3,44	1.64	0.194	0.101	292.2	110.6	260.0	126.9	206.1	87.6	272.0	60.3

Table 5.9 | Kruskal-Wallis multiple comparisons tests of seasonal differences in soil properties. Results of Kruskal-Wallis multiple comparisons tests showing differences between seasons for several environmental parameters. Column headers depict degrees of freedom (df), H-values (H) and p-values (p). An emboldened p-value denotes a significant effect. Medians ($\tilde{x}$) and Interquartile Range (IQR) are shown by season for each predictor variable. Significant differences between variables within each season are indicated by superscript numbers: variables that share a number are significantly different.

	Kruskal-Wallis			Winter		Spring		Summer		Autumn	
Variable	***df***	***H***	***p***	$\tilde{x}$	***IQR***	$\tilde{x}$	***IQR***	$\tilde{x}$	***IQR***	$\tilde{x}$	***IQR***
Tidal Height when Sampling (m)	3	9.69	**0.021**	2.60	2.97 [1]	2.65	3.26	3.31	2.03	4.29	1.36 [1]
Air Temperature (°C)	3	42.34	**<0.001**	3.60	3.37 [123]	12.57	1.20 [14]	21.80	4.93 [245]	14.10	2.70 [35]
Wind Speed (Gust) (kmph)	3	21.01	**<0.001**	17.66	14.71 [12]	15.74	13.67 [1]	5.58	10.67 [23]	16.01	14.00 [3]

5.3.3 Comparing the model predictions to observed soil carbon stocks

There was no significant gain or loss of soil organic carbon over the course of 1 year in any of the soil depths sampled when comparing 2011 and 2012 data (t-test: Table 5.10). This was compared to predictions of future carbon stocks based on the changes in, and relationships between, the measured carbon stocks and fluxes using a carbon budget model. This carbon budget model was constructed based on overall averages and standard errors calculated from the empirical carbon flux and stock data shown in Figure 5.5. The model predicted that soil organic carbon for the 0-25 cm depth profile would decrease slightly over one year, although any significant difference between Time 0 and Time 1 (1 year) was unlikely to be significant due to large error margins (Table 5.10, Figure 5.6). This indicates that the model is unsuitable for predictions in its current state.

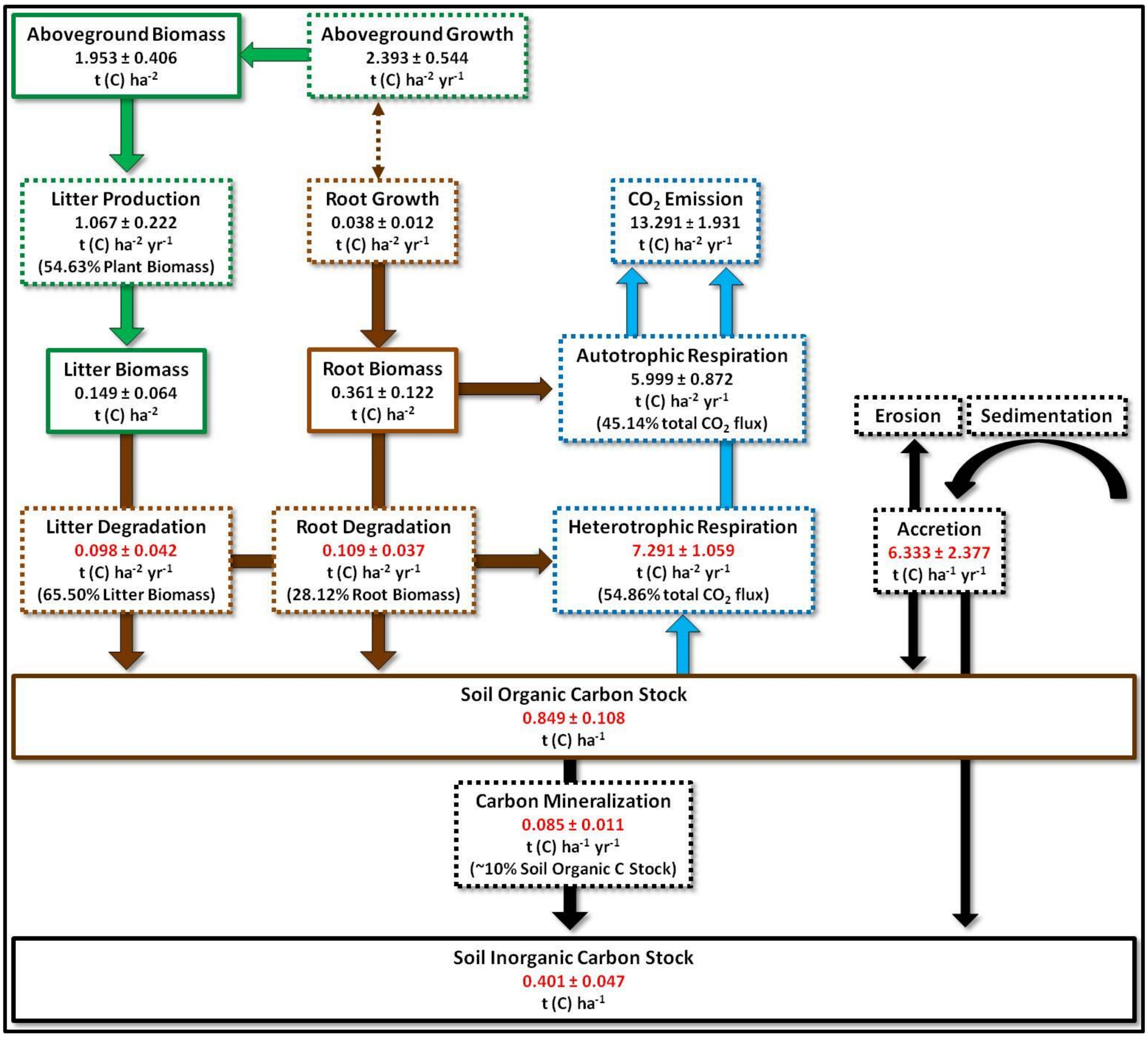


Figure 5.5 | A calculated carbon budget for an un-grazed salt marsh. Annual means ± one standard error are shown for each carbon stock (solid boarder) and flux (dashed boarder) variable based on empirical observations from three un-grazed salt marshes. Carbon flow rates recorded as tonnes of carbon per hectare per year (t (C) ha^{-1} yr^{-1}) and carbon stocks are recorded as tonnes of carbon per hectare (t (C) ha^{-1} yr^{-1}). Figures in red are principal stocks, inputs or outputs of soil organic carbon or soil inorganic carbon based.

Table 5.10 | Comparison between soil organic carbon content in 2011 and 2012. Results of a two-sample t-test comparing the soil organic content of November 2011 with November 2012 for soil depths 0-5cm, 0-10cm and 0-25cm. Means and standard errors are shown after the test results.

	T-Test			2011		2012	
Depth Profile	***N***	***T***	***p***	$\bar{x}$	***SE***	$\bar{x}$	***SE***
0-5cm	12	-1.35	0.205	1.710	0.260	1.957	0.289
0-15cm	12	0.12	0.907	1.243	0.172	1.223	0.167
0-25cm	12	0.58	0.574	0.923	0.125	0.849	0.108
Model Predictions	-	-	-	0.849	0.108	0.400	3.400

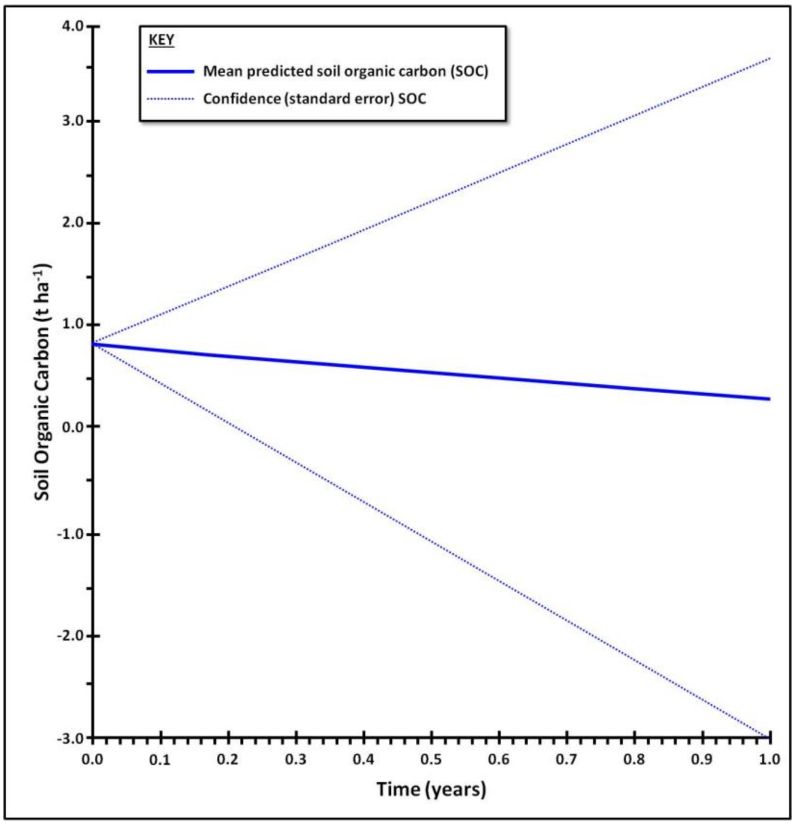


Figure 5.6 | Model predictions for soil organic carbon stocks over 1 year. Model outputs of an un-grazed salt marsh carbon budget model showing results for soil organic carbon stocks for a 1-year prediction showing mean and upper and lower confidence intervals (based on standard error).

Longer term (50-year) model predictions of soil organic carbon showed that mean soil organic and inorganic carbon were likely to increase with time although the confidence in this prediction reduced considerably with time (Figure 5.7). Carbon mineralization is a constant; over time soil organic carbon is mineralized. Thus, after an initial increase, soil organic plateaus off and the increase in soil carbon stocks is shown more in the soil inorganic carbon stocks.

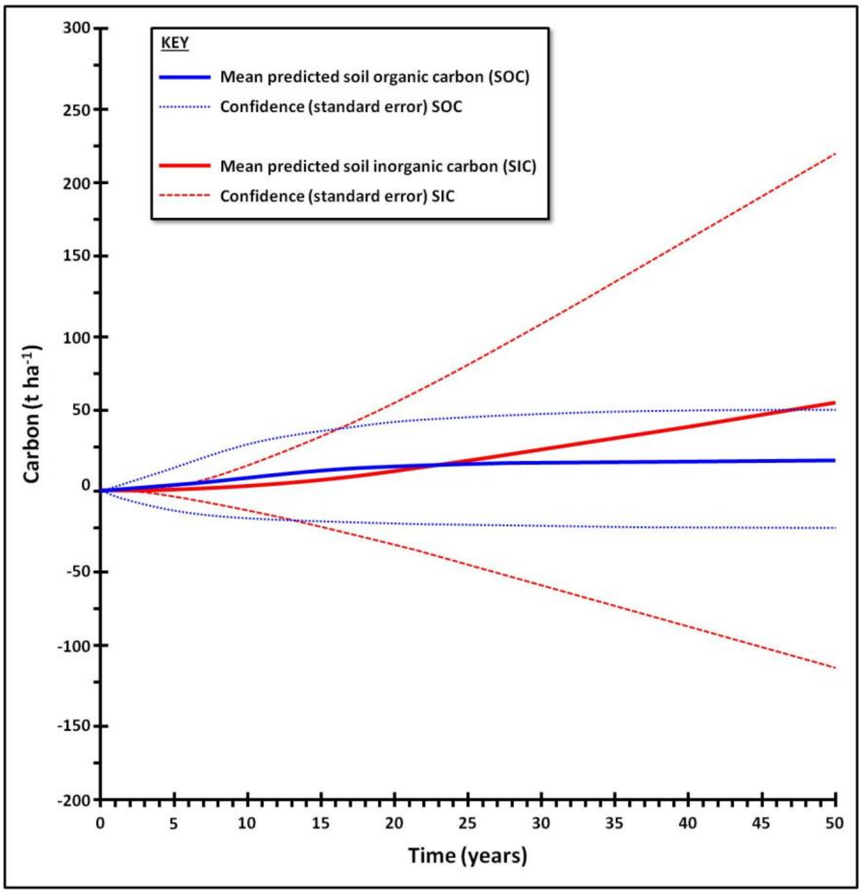


Figure 5.7 | Model predictions of future carbon SOC and SIC for an un-grazed salt marsh. Model outputs of an un-grazed salt marsh carbon budget showing results for soil organic (blue) and inorganic carbon (red) stocks for a 50-year prediction. The means and upper and lower confidence intervals (based on standard error) are shown for both soil organic and inorganic carbon stocks.

5.4 Discussion

5.4.1 Comparing the carbon fluxes

It was expected that inputs of carbon through sedimentation and the degradation of organic matter would be greater than the outputs of carbon through soil heterotrophic respiration. This was not the case, as heterotrophic respiration rates were consistently higher than litter and root degradation rates. Sedimentation rates were variable between seasons; during the winter and spring, sedimentation rates were equal to soil respiration rates but during the summer and autumn, soil respiration rates were greater than sedimentation rates. However, on average over the year, sedimentation rates balanced out soil respiration. It is perhaps not surprising that soil respiration is greater than inputs of carbon through degradation of organic matter: organic matter is broken down by the soil microbial community (Coûteaux et al., 1995), which respire and can emit considerable amounts of carbon dioxide (W. H. Schlesinger & J. Andrews, 1999).

Litter degradation rates, soil respiration, and root growth rates were important predictors of empirical soil organic and inorganic carbon data collected in November 2011. Litter degradation showed a positive relationship with soil organic carbon stocks in the shallow soil profile, and root degradation showed a positive relationship with soil organic carbon stocks in the deeper soil profiles. This implies that inputs through organic matter were important for soil carbon storing, despite their apparently small contribution. With the balance between sedimentation rates and soil respiration, it is feasible that the small inputs of organic matter through litter and root degradation may lead to an increase in soil carbon stocks over a long period of time.

5.4.2 Seasonal changes in carbon fluxes

It was predicted that degradation rates would be lower in the winter than in the summer due to waterlogged conditions and low temperatures in winter. However, litter and root degradation rates did not differ between the seasons. Soil redox potential has to be below 250mV for nitrogen to be reduced and aerobic conditions to prevail (Mitsch & Gosselink, 2000). The average redox potential of the study sites remained above this threshold, except in the summer when the average redox potential was 206.1mV. So, although soil moisture was higher in winter and spring than in summer, it was not low enough for anaerobic conditions to prevail. As degradation rates increase with an increase in soil moisture and temperature (Coûteaux et al., 1995), it is likely that degradation rates remained relatively high in the winter due to high moisture levels, despite low soil temperatures, and also remained high in the summer due to high soil temperatures.

Sediment accretion varied between the seasons; accretion was greatest in the winter and low in the spring and summer, as expected. Erosion generally occurred in the autumn. This seasonal pattern in sedimentation has been found in previous studies (Adam, 1990b; Frostick & McCave, 1979; D.S. Ranwell, 1964b). During the autumn, equinox tides coupled with more frequent storms result in a transport of sediment away from both high and low areas of the marsh (Adam, 1990b; Frostick & McCave, 1979; D.S. Ranwell, 1964b). During winter, the tides are not great enough to cover the whole marsh, so storms wash sediment up from the lower marsh zones to the higher marsh zones, resulting in high sedimentation rates in the higher marsh zones (D.S. Ranwell, 1964b). Here, wind gusts were greatest in the winter and autumn, suggesting a greater frequency of storms. As this study was situated on the mid marsh, it is likely that sediment was washed up the marsh during the winter storms. During the spring and summer, algal mats and vegetation growth stabilize the sediment so less is lost to large tides and storms, but also less is transported up the marsh to the higher marsh zones (Frostick & McCave, 1979; D.S. Ranwell, 1964b) where this study was situated.

Soil heterotrophic respiration also varied between seasons: respiration rates were high in the summer and spring, and low in the autumn and winter, as predicted. Aerobic soil respiration increases with soil temperature and soil moisture (Pendall et al., 2004). It is likely that soil respiration rates increased in the summer due to higher soil temperatures. Soil moisture, however, may not have an effect on soil respiration in the salt marsh environment. Previous studies on the mechanisms of soil respiration have been conducted in terrestrial systems where soil moisture is generally much lower (Cao et al., 2004; Dalal & Allen, 2008; Pendall et al., 2004). In the salt marsh environment, soil moisture is always relatively high due to frequent tidal flooding (Adam, 1990b); therefore soil moisture is unlikely to become low enough to reduce soil respiration rates. Despite high soil moisture levels, the soils were generally not anaerobic: the high soil redox potential indicated that soils were mostly aerobic and that methane production was unlikely, as carbon is reduced at a redox potential of less than -200mV (Lai, 2009; Mitsch & Gosselink, 2000).

5.4.3 The impact of environmental variables on carbon sequestration

Soil moisture, temperature, pH and salinity were predictors of degradation rates and soil respiration during the winter and autumn, but during the summer, the main carbon fluxes were not affected by any of the measured soil or environmental variables. It is possible that during the spring and summer, the increased plant cover and higher temperatures facilitate for a larger soil microbial community than in the winter. Bardgett, Leemans, Cook, and Hobbs (1997) and Bardgett, Lovell, Hobbs, and Jarvis (1999) found that across several managed and un-managed grasslands, microbial biomass showed consistent summer maxima and winter minima. If this is the case in salt marshes, perhaps in the summer soil microbial communities may be large enough to remain active regardless of small changes in temperature and moisture, whereas in the winter soil microbial communities are small enough to react to small changes in soil conditions. As such, soil respiration and degradation rates could correlate with soil conditions during the winter but not during the summer.

5.4.4 Predictions of future carbon stocks

There was no significant change in carbon stocks over the course of one study year when looking at carbon stocks measured in November 2011 and November 2012. This is perhaps unsurprising as there is a general balance between the two largest inputs and outputs of carbon (sediment accretion and soil respiration), and inputs through organic carbon were very low in comparison. It is also possible that the two cores taken a year apart were not entirely comparable. The cores sampled a set depth below the marsh surface; yet, the marsh surface elevation can change over the course of the year due to marsh accretion, erosion, or soil compaction (Stock, 2011). It is possible that one core may consist of a different layer of sediment than the other. Although this is unlikely to have let to any considerable inaccuracies over the course of just one year, it highlights the problems associated with carbon sequestration predictions based on shallow cores.

The model predictions were used as a 'first-look' at modeling techniques for salt marsh soil carbon stocks. When run for one year, the model predicted a slight decrease in soil carbon stocks. However, this prediction lacked statistical confidence and it conflicted with the no-change empirical observations from the two soil cores taken a year apart. The error associated with the model predictions after just one year was too great to make the model useful for predicting carbon stocks in its present state. Prediction error was amplified when the model was run over a 50-year time scale, although there was a slight increase in mean soil carbon, as expected.

5.4.5 Study implications

Modelling techniques have been used extensively throughout climate-change science as means to predict future scenarios based on current trends and predictions of environmental drivers (Moss et al., 2010). In light of the uncertain future of soil carbon stocks, modelling can prove a useful tool to examine how carbon sequestration rates may change in the future (Jenkinson et al., 1991; Kirschbaum, 1995; Schimel et al., 1994). This study was the first to take a mass balance approach to measure salt marsh carbon sequestration rates over a broad-scale. As such, the model forms a useful starting point for future modelling of salt marsh carbon stocks. Further research into salt marsh carbon stocks would need to take into account seasonal and spatial variation, and ideally studies would be run over several years to build up a reliable long-term data set. With time, carbon budget models may be able to more accurately determine likely impacts of climate change on soil carbon stocks in natural, carbon-rich systems

Chapter 6: Carbon Sequestration on a Grazed Salt Marsh: Does Grazing Really Matter?

6.1 Introduction

The previous three chapters have established that salt marshes are highly variable systems subject to a range of environmental disturbances and stresses. Grazing is a common disturbance in salt marshes; 64% of the study marshes in Chapters 3 and 4 were grazed by livestock for management or farming purposes. Although Chapters 3 and 4 showed that the effects of grazing can be outweighed by the effects of several environmental contextual variables, grazing-carbon relationships in salt marshes are still important to investigate, given that grazing management is considered a promising route to enhance grassland carbon sequestration (V. Bouchard et al., 2003; R. Conant et al., 2000; Gedan et al., 2009). Chapter 5 took a 'mass balance' approach (Amundson, 2001) to construct a carbon budget model for un-grazed salt marshes; the purpose was to identify the most important sources of carbon fluxes in the carbon budget in the absence of grazing. Grazing might not affect soil carbon stocks in the long-term (Tanentzap & Coomes, 2012; Yu & Chmura, 2010) (Chapter 4). However, grazing may influence several carbon fluxes associated with carbon sequestration, such as soil respiration, input of organic matter and sedimentation rates, and these effects need to be considered when using livestock grazing as a management tool. In order to examine how grazing might influence the relative partitioning between carbon budget components, this study builds on the model created in Chapter 5 by investigating grazer influences on carbon fluxes and soil abiotic factors that drive them.

6.1.1 Carbon fluxes on grazed salt marshes

As with un-grazed marshes, the main inputs of carbon into soil carbon stocks on grazed salt marshes are sedimentation and degradation of organic matter (Coûteaux et al., 1995; Flessa et al., 1977; Stumpf, 1983; Trumbore, 1997), and the main output from the soil carbon stock is heterotrophic respiration (Morris & Whiting, 1986; Pendall et al., 2004) (Figure 6.1). In grazed marshes, however, the above ground biomass is removed and vegetation changes to a more robust, earlier successional community (Chapter 3) (J. P. Bakker, 1978; Jensen, 1985; Jones, 2000; Kiehl et al., 1996). Loss of above ground biomass and plant community changes are likely to influence several carbon fluxes; litter production will dramatically decrease, as plant biomass is consumed rather than being left to degrade (Chapter 3) (Jensen, 1985). Sedimentation may decrease as there is less plant biomass to trap sediment (Neuhaus et al., 1999; Stumpf, 1983), and soil properties may change due to the opening up of the sward and changes in plant carbon allocations (Bardgett et al., 1998; Holt, 1997;

Ingram et al., 2007). Grazers will also create a new input of carbon into the soil carbon stocks through production of faeces and its subsequent degradation that can act as a plant fertilizer and alter the nutrient regime (Bhogal et al., 2010; Sheldrick et al., 2003). As a result, grazers may enhance plant productivity, although this will depend on the response and sensitivity of the vegetation community to grazing (Hilbert, Swift, Detling, & Dyer, 1981; McNaughton, 1979; J. H. Richards, 1984). Under an intensive grazing regime, grazers are likely to reduce plant productivity regardless of plant resilience, thereby reducing the input of carbon through the root system (McNaughton, 1979; Schuster, 1964). Although grazing is likely to alter the amount of organic material available for degradation, it is unlikely that grazing will alter actual decomposition rates, as these are governed more by seasonal changes in soil parameters, particularly soil moisture (Chapter 5) (Giese et al., 2009). Similarly, grazing does not seem to have an impact on soil carbon dioxide and methane effluxes, which depend on soil moisture, soil temperature and the presence of certain plant species that form aerenchyma tissue (Ford et al., 2012; Ma, Wang, Wang, Jiang, & Nyren, 2010). It can be argued, however, that grazers alter soil conditions by trampling and removal of vegetation (J. P. Bakker, 1985), and thus may indirectly impact soil gas effluxes.

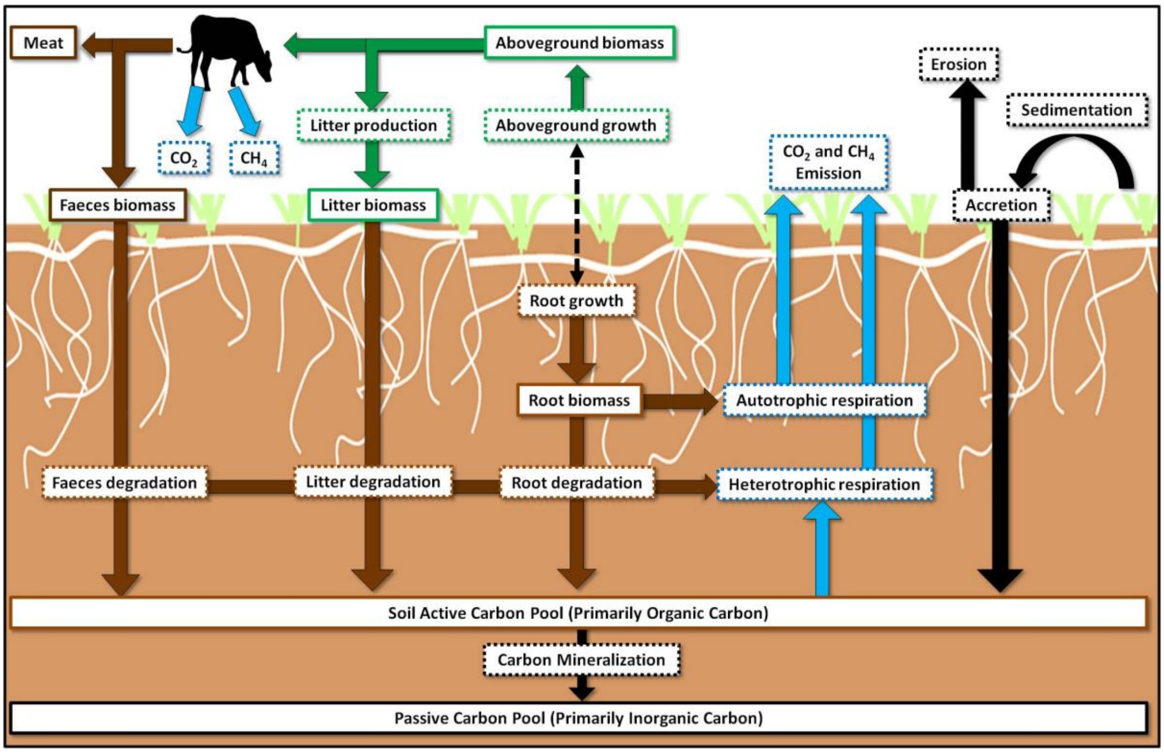


Figure 6.1 | A salt marsh carbon budget model for a grazed salt marsh. The main carbon stocks (solid outlines) and flows (dashed outlines) on a salt marsh and the links between them. The main inputs of carbon into the soil carbon stock are organic matter (litter, root and faecal material) and sedimentation, and the main output of carbon from the soil carbon stock is heterotrophic respiration, although gas efflux from the livestock is also likely to be a significant output of carbon from the system (Coûteaux et al., 1995; Morris & Whiting, 1986; Sollins et al., 1996; Stumpf, 1983).

6.1.2 The impact of grazers on salt marsh carbon balances

It is likely that grazers may increase the inputs of carbon through the degradation of organic matter. Although the input of carbon through litter degradation is reduced (Kiehl et al., 1996), the input through degradation of faeces may be substantial enough to compensate for this (Bhogal et al., 2010). An increase in plant productivity under light and moderate grazing regimes (Hilbert et al., 1981; J. H. Richards, 1984) may also result in greater root biomass and, although the proportion of root matter degraded will not change (Giese et al., 2009), the total carbon input through root degradation may increase. Conversely, grazers are likely to reduce the input of carbon through sedimentation by diminishing the above ground biomass of particle trapping vegetation; this effect would be particularly important in the winter months when sedimentation is highest (Chapter 5) (Havaren, 1983; Neuhaus et al., 1999; Stumpf, 1983). Given the observed no grazing effect on soil carbon stocks (Chapter 4) (Tanentzap & Coomes, 2012; Yu & Chmura, 2010), perhaps the increased input of carbon through organic matter may be sufficient to counter the lower sedimentation rates. While livestock grazing is not expected to impact overall soil carbon stocks, direct production of carbon dioxide and methane by grazers (Johnson & Johnson, 1995; Murray et al., 2001; Pinares-Patino et al., 2007) might constitute a substantial enough output of carbon from the salt marsh system to tip the overall saltmarsh carbon balance from a sink to a source.

6.1.3 Study aims

The overall aim of this chapter was to explore the influence of grazing on the carbon stocks and fluxes over an annual cycle, relative to the influence of environmental contextual variables. Empirical data consisted of carbon stocks and fluxes measured monthly and seasonally across nine grazed marshes along the coast of west Wales and north-west England (Chapter 2) over the course of 13 months. Input of carbon through sedimentation was expected to be lower in grazed than in un-grazed marshes. The output of carbon through gas emissions was not expected to differ between grazed and un-grazed marshes. Seasonal patterns in carbon fluxes and stocks in the modelled grazed marshes were expected to be similar to those in un-grazed marshes (Chapter 5). Stocking density was expected to impact sedimentation rates, but not degradation rates or gas effluxes.

6.2 Materials and Methods

6.2.1 Empirical Study

6.2.1.1 Site selection, determination of zones and quadrat selection: Within the study area, nine salt marshes were selected for sampling empirical data (carbon parameters and environmental variables) (Chapter 2). The nine sites were selected to incorporate a wide range of grazing intensities and contextual environmental variables as part of a balanced experimental design (Chapter 2). Measurements were only taken seasonally due to logistical constraints. The study focused on the mid marsh exclusively. The mid marsh was considered representative of the whole marsh; it is not subject to the extremes of wave and tidal disturbance of the pioneer zone or the terrestrial influences of the high marsh, yet it is still subject to regular tidal flooding and it is colonized by halophytic plants from across the marsh (Adam, 1990b). Observations per site were made in the same four 2 x 2 metre 'below-ground plots' used in the broad-scale study (Chapters 2 & 4).

6.2.2 Carbon response variables

Samples were taken in four plots per sample site either at monthly, seasonal (every 3 months) or annual (one-off measurement) frequency between November 2011 and November 2012. Sampling frequency depended on growth and degradation rates, ease of sampling technique, and logistical constraints (ability to take field equipment to the plots). All carbon stocks were converted into metric tonnes of carbon per hectare (t (C) ha^{-1}) and all rates were converted into metric tonnes of carbon per hectare per year (t (C) ha^{-1} yr^{-1}). The following were sampled.

6.2.2.1 Above ground live and litter biomass: Above ground live and litter biomass were measured both in summer 2010 and in winter 2011-12 to determine the difference between summer and winter live biomass and litter biomass. Aboveground biomass and litter biomass were sampled in a 25 x 50cm quadrat placed in a representative area of each plot. Vegetation litter was collected and bagged before the living vegetation (above ground biomass) was cut down to the soil. Samples were dried in the laboratory at 80°C for 3 days, and weighed. The carbon content of the aboveground vegetation was derived using loss on ignition techniques based on Ball (1964): dry samples were weighed, ashed at 550°c for 5 hours and weighed again. The organic content was calculated by subtracting the ashed weight from the dry weight.

6.2.2.2 Aboveground plant growth rates: Aboveground plant growth was measured throughout the 2012 growing season (March to September). Vegetation was clipped from two sample areas in each plot; one for seasonal growth measurements and one for overall growth measurements. The samples were taken from either a 39.5cm diameter or 34cm diameter circular area (Figure 6.2a). These circular sample areas were then covered with upside down hanging baskets to protect the vegetation from the grazers. The overall measurements were clipped only in February, before the start of the growing season, and in September, at the end of the growing season. This was to account for the production rates of species sensitive to clipping, as well as total community growth rates. The seasonal measurements were taken every three months throughout the growing season (March, June and September); vegetation was cut down to the soil. This was to account for seasonal changes in community growth rates. Samples were dried at 80°C for 3 days and the total dry weight (g cm^{-2}) was determined.

6.2.2.3 Litter production rates: Litter production rates are usually sampled using litter traps placed on the marsh surface and emptied weekly to prevent litter decay (V. Bouchard & Lefeuvre, 2000). Weekly sampling throughout the study period was beyond the scope of this study due to the distance between sites. Instead, litter production rates were predicted from the above ground live biomass based on litter fall rates calculated by V. Bouchard and Lefeuvre (2000): it was assumed that 55% of the above ground live plant biomass per year would fall as litter and approximately 15% of the live plant biomass per year would be washed off the marsh as detritus.

6.2.2.4 Root biomass: A 25cm deep, 4.6cm diameter soil core was taken from each plot in October 2011 using a split tube corer based on a smaller model by Eijkelkamp. The core was divided into 5cm depth segments down the entire length of the core. Live roots were removed from the core segments by hand and dry weights were expressed per volume of soil. Root carbon content was derived after loss on ignition at 550°c for 5 hours using techniques based on Ball (1964). The organic content was the ashed weight subtracted from the dry weight.

6.2.2.5 Root growth rates: Root growth rates were measured in each plot seasonally (every 3 months) in January, April, July and October 2012, using approaches based on Steingrobe et al. (2000). A 15cm deep 4.6cm diameter sediment core was taken in each plot and all root material was removed. Root-free sediment was then replaced into the hole left by the corer and marked. Although this method was time consuming, this provided a natural and realistic substrate for new root growth. The core was then re-sampled after 3 months to assess the root growth rate over the season. The core was washed free of sediment over a 0.5mm meshed metal sieve. Root matter was then dried at 80°C for 3 days and the dry weights were recorded.

6.2.2.6 Litter and root degradation: Litter and root degradation rates were sampled based on methods by Olofsson and Oksanen (2002). Litter material was collected from a strand line on Warton Bank Marsh and root material was collected from the high marsh zone on Malltraeth Marsh in August 2011. The same litter and root material was used on each marsh to enable reliable comparisons between marshes. Both root and litter material was washed free of sediment and dried at 80°C for 5 days. Litter and root samples were placed in 5mm mesh, plastic Netlon bird feeder bags. The dry weight of each sample was recorded on waterproof paper and placed in the sample bag with the sample. Eight root bags were then buried at each plot in October 2011 by digging a 20cm deep trench and using a knife to insert the sample bag into a narrow hole in the side wall of the trench approximately 10cm from the top of the trench (Figure 6.2b). The dry weight and position of each sample was recorded as the samples were buried. The ends of the sample bags were then left protruding from the trench wall and soil clods were returned to the trench to cover the bags fully. To account for potential loss of litter and root matter, 20 dummy root bags were buried in using the method described above. These bags were then immediately removed and the average percent weight loss was calculated; this was then used to account for any matter lost while deploying and retrieving the experimental root bags. Litter bags were only buried on Y Foryd, an un-grazed marsh, due to logistical constraints (Chapter 5) and litter degradation rates were extrapolated from y Foryd. Two root bags were retrieved seasonally from each plot in January, April, July and October 2012 from each plot at each marsh. The root material was washed free of sediment and new roots that had grown into the samples were removed. The samples were then dried at 80°C for 3 days and the dry weights were recorded and compared to the original dry weights to determine seasonal rates of decomposition:

$$\text{Percent degradation} = 100 \times \frac{\text{Mass at time 2 (re-sample)}}{\text{Mass at time 1 (deployment)}}$$

6.2.2.7 Faeces biomass, defecation rate, and degradation: Faeces were counted in each plot and in four 10 x 10 m areas within each zone. The diameters of ten samples of each sheep, cow and goose faeces were measured; samples were then dried at 80°C for 3 days and dry weight was determined before organic carbon content of each faeces type was determined using loss on ignition techniques. The total faeces carbon stock per marsh was scaled up from the faeces count, the dry weight and the organic carbon content. Faeces defecation rates were calculated from Rollins, Bryant, and Montandon (1984) and Buschbacher (1987). A defecation rate of 7.5 times per day was used for sheep (Rollins et al., 1984). This was converted in to grams per day using average faeces biomass. A defecation rate of 23.43 grams per animal per day was used for cattle (Buschbacher, 1987). Total faeces defecation rates per year were calculated using the stocking density of each marsh. Faeces degradation rates were determined from the faeces carbon stock using figures calculated in Allard et al. (2004).

6.2.2.8 Carbon loss through gas emissions from livestock: Carbon dioxide and methane emissions per head of livestock (kg per head) were obtained from (Kupfer & Karimanziara, 2007). Carbon dioxide emissions per head were 238 kg per year for sheep and 1697 kg per year for cattle (Kupfer & Karimanziara, 2007). Methane emissions per head were 8 kg per year for sheep and 57 kg per year for cattle (Kupfer & Karimanziara, 2007). Kilograms of carbon dioxide and methane emissions per hectare per year were calculated using livestock numbers per hectare per year:

$$\text{Total gas } (CO_2 \text{ or } CH_4) \text{ emissions (kg ha}^{-1}\text{ yr}^{-1}) = \text{Number of livestock (ha}^{-1}\text{ yr}^{-1}) \times \text{Gas emissions per head (kg)}$$

Total carbon release from livestock gas emissions were calculated using the atomic weight of each compound compared to the atomic weight of carbon:

$$\text{Atomic weight of C} = 12$$

$$\text{Atomic weight of } CO_2 = 44 \qquad \text{Ratio of } CO_2 \text{ to C} = 12/44 = 0.25$$
$$\text{Atomic weight of } CH_4 = 16 \qquad \text{Ratio of } CH_4 \text{ to C} = 12/16 = 0.75$$

$$\text{Total C release through } CO_2 \text{ (kg ha}^{-1}\text{ yr}^{-1}) = \text{Total } CO_2 \text{ emissions (kg ha}^{-1}\text{ yr}^{-1}) \times 0.25$$
$$\text{Total C release through } CH_4 \text{ (kg ha}^{-1}\text{ yr}^{-1}) = \text{Total } CH_4 \text{ emissions (kg ha}^{-1}\text{ yr}^{-1}) \times 0.75$$

This was then up-scaled to tonnes of carbon per hectare per year by multiplying by 0.001.

6.2.2.9 Carbon dioxide emissions and heterotrophic respiration: Total carbon dioxide emission rates from the soil were measured at each plot using an EGM-4 infra red gas analyser (PP-Systems, 2010) (Figure 6.2c). Measurements were taken seasonally (February, May, August and November 2012). The total carbon dioxide emitted from the soil surface is a combination of carbon dioxide derived from both autotrophic respiration and heterotrophic respiration (Bond-Lamberty et al., 2004). Carbon dioxide produced through autotrophic respiration can account for up to 80% of the total carbon dioxide flux in some systems and comes directly from the roots of plants and the organisms directly associated with the rhizosphere (Bond-Lamberty et al., 2004; Hanson et al., 2000). Therefore, carbon released from the system through the autotrophic pathway is not associated with the soil carbon stock (Bond-Lamberty et al., 2004; Hanson et al., 2000). Carbon dioxide produced through heterotrophic respiration comes from the soil microbial communities, which are actively breaking down the soil carbon stock and are therefore directly contributing to the loss of carbon through respiration (Bond-Lamberty et al., 2004; Hanson et al., 2000). The autotrophic-heterotrophic respiration ratio was determined in the mid marsh zone on Y Foryd in July 2012 based on Carbone and Trumbore (2007). A quasi-experimental design was used to test the difference between carbon dioxide emissions in ten 20 x 20cm clipped and ten 20 x 20cm un-clipped plots. Plots were clipped one week prior to the experiment to avoid any immediate disturbance effects of the clipping. The EGM-4 was then used to measure carbon dioxide emission rates from both clipped and un-clipped plots, and the soil temperature and moisture was measured within each plot. The autotrophic-heterotrophic respiration ratio was determined from the averages of clipped (heterotrophic respiration) and unclipped plots (total respiration). The respiration in un-clipped plots was assumed to represent only heterotrophic respiration and respiration in un-clipped plots was assumed to represent both autotrophic and heterotrophic respiration (Carbone & Trumbore, 2007).

Total carbon release from soil respiration was calculated using the atomic weight of each compound compared to the atomic weight of carbon. This was then up-scaled to tonnes of carbon per hectare per year by multiplying by 0.001.

6.2.2.10 Accretion rate: Accretion rates were sampled using methods based on Stock (2011). Two permanent wooden posts were inserted approximately two metres apart at each plot into the marsh in October 2011 and the height of each post was recorded. Sediment accretion rates were the measured monthly at each plot on each marsh using a 2.2m garden pole marked at 10cm increments (Figure 6.2d). The distance between the pole and the marsh surface was measured at each marker along the pole except the two markers closest to each post; this was to avoid any micro sedimentation patterns caused by the posts. The accretion rate readings were compared with the base line data taken in November 2011 to determine annual accretion rates and monthly readings were used to determine monthly and seasonal variations in accretion rates.

6.2.2.11 Whole-marsh particulate organic matter fluxes: Salt marshes along the west coast of the UK are generally accreting and it is therefore assumed that small scale erosion during large tidal cycles is outweighed by sediment deposition (Adam, 1990b; Boorman, 2003). This assumption was tested on Y Foryd during an equinoctial spring tide in September 2012. It is difficult to test for small-scale erosion or sediment movement within each zone as it is likely that particulate organic matter (POM) moves between zones before leaving the marsh (Stock, 2011; Stumpf, 1983). As such, a whole-marsh approach is more insightful: measurements of suspended matter in the water column before it reaches the marsh can be compared to measurements of suspended matter in the water column as it leaves the marsh to determine if there is a net gain (erosion) or loss (sedimentation) of sediment as the water passes over the marsh. This can be refined by measuring suspended matter in the water column over each zone to determine where on the marsh suspended matter is deposited or picked up. The suspended sediment in the water column was measured on the mudflat (before and after it passed over the marsh) and on each marsh zone both on the incoming tide and the outgoing tide. This was to determine if the marsh was generally accreting or losing sediment; if the amount of suspended matter was greater on the incoming tide than the outgoing tide, it was assumed that the marsh was accreting sediment. Water samples were collected in plastic bottles attached to the end of a 2m pole to reduce disturbance of the marsh surface near the sample collection point. Five water samples were collected above each of the mudflat and the four marsh zones (pioneer, low, mid and high) on the incoming tide as it flooded the marsh, and a further five water samples were collected from each zone and from the mudflat on the ebb tide. In the laboratory, the water samples were filtered through pre-sterilized filter papers of a known weight to collect any suspended matter. The samples were then dried at 105°C for three hours and weighed to determine the weight of suspended matter. The samples were then ashed at 550°C for three hours to remove any organic matter, and weighed again to determine the weight of organic matter in each sample. The weight of organic matter was then converted into organic carbon content using the formula from Craft et al. (1991):

$$\text{Sample Organic Carbon Content} = (0.4 \times \text{Organic Matter}) + (0.0025 \times \text{Organic Matter}^2)$$

To determine sediment deposition rates in the mid marsh relative to the other marsh zones, the pattern of sedimentation across the marsh was also measured. Prior to tidal flooding, sediment traps were laid out in the mud flat and within each zone. Pre-weighed, labeled filter papers were used to trap any sediment deposited on the marsh surface; the filter papers were held off the marsh surface using an upside down petri dish and held in place using tent pegs. Nine sediment traps were deployed on the mudflat and in each marsh zone in a 3×3 grid covering an approximately 3×3m area. The sediment traps were left over the course of one spring equinox tide and re-sampled at low tide. In the laboratory, the filter papers were dried at 105°c for 24 hours and re-weighed to determine the weight of sediment deposited by area within each zone.

6.2.2.12 Soil organic carbon: A 25×4.6cm soil core was taken from each plot in November 2011 using a split tube corer based on a smaller model by Eijkelkamp. The core was divided into 5cm depth segments down the entire length of the core. Each segment was homogenised, root material was removed and an approximately 10g sample was used to determine the soil organic carbon content by using loss on ignition techniques based on Ball (1964). The percentage soil organic matter content was calculated using methods outlined in the Soils Manual of the Countryside Survey (Emmet et al., 2008):

$$\text{Organic Matter Concentration (OMC)} = 100 \times \frac{(\text{Dry Soil Weight} - \text{Combusted Soil Weight})}{(\text{Dry Soil Weight} - \text{Crucible Weight})}$$

The percentage of soil organic carbon (soil organic carbon concentration) was estimated using a conversion formula (Craft et al., 1991):

$$\text{Soil Organic Carbon Concentration} = (0.4 \times \text{OMC}) + 0.0025 \times \text{OMC2})$$

This was then converted into soil organic carbon (SOC) per volume (soil organic carbon density) using bulk density figures from summer 2011:

$$\text{SOC (g cm}^{-3}) = \text{Bulk Density} \times \frac{\text{Soil Organic Carbon Concentration}}{100}$$

To determine the actual change in soil organic carbon over the course of a year, a second 25×4.6cm soil core was taken from each plot on each marsh in November 2012 and soil organic carbon content was calculated using the above technique.

6.2.2.13 Soil inorganic carbon and nitrogen content: A sub-set of soil samples was used to determine the total carbon and nitrogen content of the soil (CN analysis). Soil samples from a depth of 5-10cm were taken from the same core as the organic carbon samples, and soil samples from 0-5, 10-15, 15-20 and 20-25cm depths were taken from one representative core per marsh. The soil samples were dried at 105°C for 16 hours and ground up using a pestle and mortar. Between 0.1 and 0.2g of soil was used for the CN analysis. Combustion CN analysis was run using a Leco Instruments, Truspec CN analyser; carbon content was detected using infra red and nitrogen content was detected using thermal conductivity. EDTA and blank standards were run alongside the sample soils. Soil inorganic carbon content was then calculated by subtracting the soil organic carbon content from the total carbon content of each sample.

6.2.2.14 Carbon mineralization: Carbon mineralization is the conversion of organic carbon to inorganic carbon and represents carbon moving from the active carbon pool to the slow turn over carbon pool (Pendall *et al*. 2004). This was not directly measured in this study but a conservative estimate of carbon mineralization rate of 10% of soil organic stocks was used as a rate constant based on measurements by Howes et al. (1985).

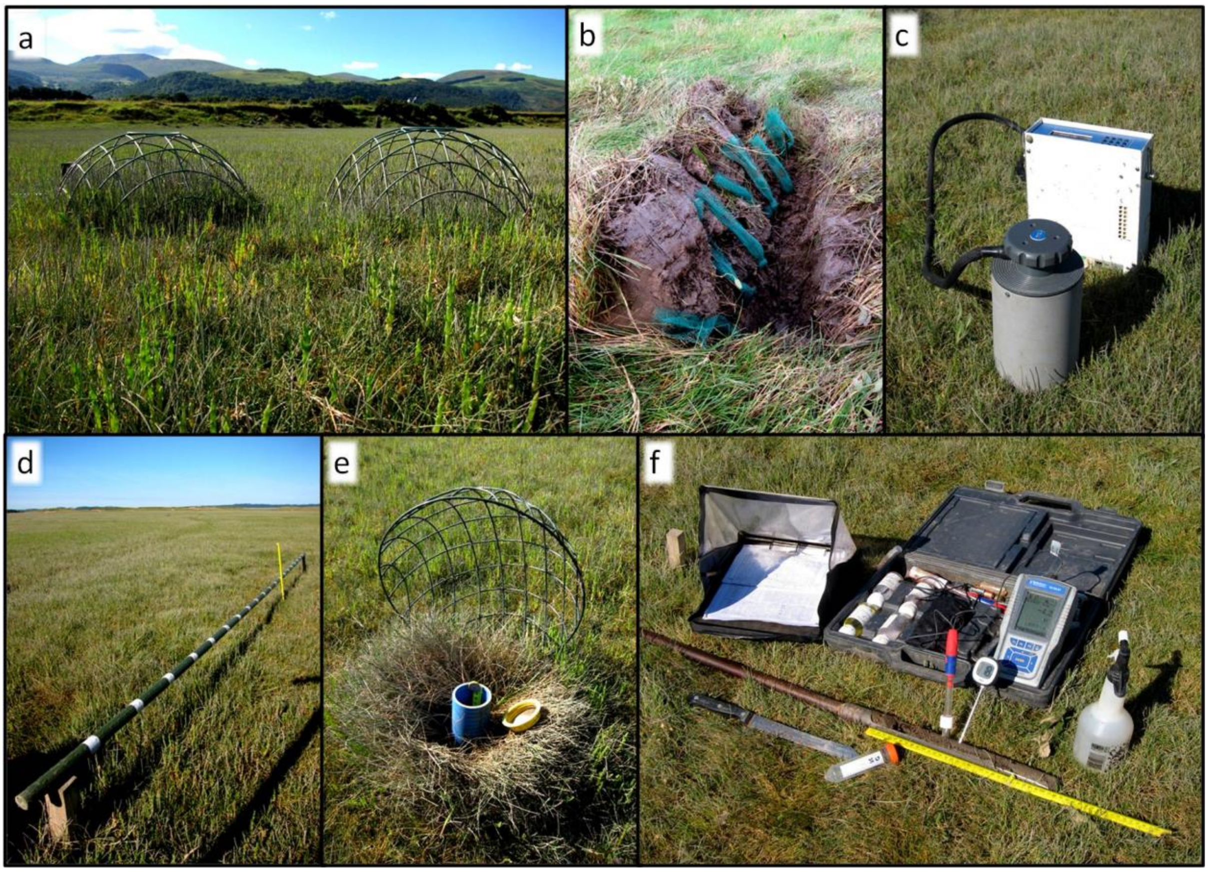


Figure 6.2 | The monthly and seasonal measurements. a) The overall (left) and seasonal (right) vegetation growth plots on a grazed marsh. **b)** Inserting the root bags into the side wall of a 20cm deep trench. The soil clods were then placed back into the trench and the root bags were sampled seasonally. **c)** Using the EGM-4 infra red gas analyser to measure soil carbon dioxide flux rates. **d)** Measuring monthly accretion rates using two permanently placed wooden posts and a 2m garden pole marked at 10cm increments. The distance from the pole to the soil surface was measured at each white marker. **e)** Measuring the water table depth using a 50cm deep dip well. Hanging baskets were used to protect the dip well from grazers. **f)** Measuring soil redox potential at different depths using a narrow half corer. Soil temperature was measured alongside each redox reading. A soil sample was also taken from the core in a centrifuge pot for soil pH and salinity measurements.

6.2.3 Abiotic contextual variables

In order to investigate the influence of soil conditions and environmental variation on the carbon budget, a series of abiotic factors were measured monthly or seasonally at each plot on each marsh. These abiotic variables, collectively, were the predominant variables that affect the measured carbon fluxes, as outlined in the introduction.

6.2.3.1 Soil temperature: A digital thermometer was used to measure surface soil temperature monthly at one point per plot per marsh. In addition air temperature was recorded once monthly at each site.

6.2.3.2 Soil moisture and water table depth: A theta probe was used to measure surface soil moisture content monthly at each plot per marsh. As theta probes measure moisture using electrical resistance, saline soils can cause inaccuracies in soil moisture readings (Miller & Gaskin, 1999). For this reason, water table depth was also recorded as proxy for soil water content. Water table depth was recorded using water-permeable dip wells (50cm deep, 5cm diameter, water-porous PVC cores) inserted into the marsh to a depth of ~45cm (Figure 6.2e). The distance from the top of the dip well tube to the water surface within the tube was measured and actual water table depth was calculated by subtracting the measured water depth from the height of the tube protruding from the marsh surface.

6.2.3.3 Soil pH and salinity: Soil samples were taken monthly for pH and salinity analyses from a depth of 7-10cm using a 2cm diameter half corer (Figure 6.2f). In the laboratory, soil pH was measured within 24 hours of sampling using an IQ soil pH meter. Soil salinity was measured using 10g of each homogenized soil sample. The samples were diluted to a 1:2.5 ratio using 10g of each sample with 25ml of deionised water; samples were then well mixed and allowed to settle. The electrical conductivity of the supernatant of each sample and the temperature at time of sampling were then measured using a Jenway Conductivity Meter 4320 and the conductivity of each sample was calculated using the dilution ratio:

$$\text{Sample Conductivity (mS)} = \frac{\text{Supernatant Conductivity (mS)}}{2.5}$$

Salinity was then calculated as practical salinity units (S) (Lewis, 1980) using an online calculator (Tomczak, 2000).

6.2.3.4 Soil redox: To determine potential methane production levels from soil microbial communities, an Eijkelkamp Ag 3 mol/l KCl combination glass electrode was used to measure soil redox (anaerobic state) at each plot monthly at Y Foryd and seasonally (November 2011, February, May, August and November 2012) on other marsh sites. Measurements were taken at depths of 2.5, 7.5, 12.5, 17.5, 22.5 and 27.5cm using a 2cm diameter half corer (Figure 6.2f). Soil temperature readings were taken at each depth alongside each redox reading (Figure 6.2f). The standard measurement of redox (mV) is that measured by a standard hydrogen electrode (Eh) (Eijkelkamp, 2009). Standard hydrogen electrodes are difficult to use in the field, and several alternative redox electrodes can be used; however, field readings from these alternative electrodes must be converted back to standard readings (mV) (Eijkelkamp, 2009). This study used an Ag 3 mol/l KCl electrode (Em) so a conversion factor (Eref) was used to convert field redox readings (Em) to standard redox measurements:

Standard measurement (Eh) = Field measurement (Em) + Eref

Eref depends on the reference electrode used in the field and the soil temperature at the time of the field reading (Eijkelkamp, 2009); the appropriate conversion (Eref) was used to convert the field measurements into standard measurements.

Once calculated, the standard redox potential measurement (Eh) was used to determine the anaerobic state of the soil. Below 250 mV, soil begins to become anaerobic as nitrogen is reduced (Table 6.1) (Mitsch & Gosselink, 2000). The redox potential has to reach less than -200mV before carbon dioxide is reduced to methane (Table 6.1) (Mitsch & Gosselink, 2000).

Table 6.1 | Oxidised and reduced forms of elements. The oxidised and reduced forms for elements in the anaerobic chain against the standard redox potential (mV). Adapted from Mitsch and Gosselink (2000).

Element	Oxidised Form	Reduced Form	Redox Potential Required for Transformation (mV)
Oxygen	O_2 (Oxygen)	H_2O (Water)	+400 → +600
Nitrogen	NO_3^- (Nitrate)	N_2O, N_2, NH_4^+ (Nitrous Oxide, Nitrogen, Ammonium)	+225 → +250
Manganese	Mn^{4+} (Manganic)	Mn^{2+} (Manganous)	+100 → +225
Iron	Fe^{3+} (Ferric)	Fe2$^+$ (Ferrous)	-100 → +100
Sulphur	SO_4^{2-} (Sulphate)	S^{2-} (Sulphide)	-200 → -100
Carbon	CO_2 (Carbon dioxide)	CH_4 (Methane)	Below -200

6.2.3.5 Daily tidal height: Predicted times and heights of low and high tides were derived from using Tideplotter Belfield Software (BelfieldSoftware, 2011). The tidal height at the time of sampling, the time and height of the last high tide, and the date and height of the last spring tide were also recorded monthly for each site.

6.2.3.6 Daily weather: Observations of air temperature, wind speed, atmospheric pressure and rain fall near each site were derived from local weather stations using the Weather Underground database (Steremberg, 2010). The weather conditions and air temperature at each site were also recorded during monthly sampling.

6.2.4 Modelling components and statistical analysis

The following analyses were run to determine which factors were the main drivers of soil carbon stocks in a grazed salt marsh and whether salt marshes were likely to be a carbon sink or source:

6.2.4.1 Determining the relative differences between carbon fluxes: Kruskal-Wallis Multiple Comparisons tests were used to evaluate the relative differences between salt marsh carbon input (litter degradation, root degradation and sediment accretion) and output (heterotrophic respiration) fluxes. The *post hoc* comparisons and the group medians and interquartile ranges indicated the comparative size of each carbon flux. From this, the relative size of carbon inputs could be compared to the relative size of carbon outputs to indicate whether salt marshes were likely to be long-term carbon sinks or sources. Analyses were run separately for the annual dataset and for each season in turn to determine seasonal differences in carbon flux relationships. Kruskal-Wallis multiple comparisons tests were used in place of ANOVA because some of the data (litter degradation, sediment accretion and heterotrophic respiration) did not meet ANOVA test assumptions.

6.2.4.2 Determining carbon flux influences on empirical soil carbon stocks: A series of distance-based linear models and regression analyses were used to determine the possible relationships between empirically measured carbon fluxes and empirically measured soil carbon stocks. Analyses were run for both soil organic carbon and soil inorganic carbon over three depth profiles (0-5 cm, 0-10 cm and 0-25 cm). Based on regional records of sediment accretion rates, the top 6-15 cm of soil was assumed to represent approximately the last 30 years of salt marsh accretion (Appendix 3: Accretion Rates in Other Studies). As with the previous study (Chapter 4), the top soil depth profile (0-5 cm) was regarded to be indicative of the present flux of material from above ground biomass (e.g. litter) to the below ground carbon pool, the middle depth profile (0-10 cm) included most of the root biomass and was used to analyse more long-term processes relating to soil carbon stocks, and the deepest profile (0-25 cm) was considered an integrator of the broader contextual influences.

6.2.4.3 Carbon flux relations with contextual variables: A series of mixed effects models were run to determine which environmental variables and abiotic soil variables were the best predictors of soil carbon stock. ANOVA's with *post hoc* Tukey HSD tests, and Kruskal-Wallis Multiple Comparisons tests were used to test the effect for season (4 levels) on the environmental and abiotic soil variables to determine the variation of these parameters over the seasons. These analyses were done on empirical data collected over the year-long study period.

6.2.4.4 Constructing the carbon budget model: The annual means ± standard errors were calculated for each carbon flux and stock component. A carbon budget model based on the mean values was then constructed using the Simile v5.96 program. The model was parameterised using the terms shown in Figure 5.1. Simile uses a graphical interface to build up a model diagram consisting of stocks, flows and influences. In this case, the stocks were carbon stocks such as soil carbon stock, plant biomass or root biomass, and the flows were carbon fluxes such as litter degradation, plant growth rates and soil respiration. The influences were other carbon stocks; for example a certain percentage of root biomass was broken down each year (root degradation) but the actual amount of carbon degraded depended on how much root biomass there was, and thus root biomass had an influence on root degradation. To determine the confidence limits for the mean carbon stock predictions, the model was re-run to determine the lowest possible carbon stock predictions according to the data means ($\bar{x}$ − 1 *SE* for inputs; $\bar{x} + 1$ *SE* for outputs) and the highest possible carbon stock predictions according to the data means ($\bar{x} + 1$ *SE* for inputs; $\bar{x} - 1$ *SE* for outputs). The model was then run for a 1-year, and a 50-year time scale to predict future carbon stocks on an un-grazed salt marsh.

6.2.4.5 Comparing model predictions to empirical data: A soil core from each experimental plot was collected in November 2011; the plots were then re-sampled a year later in 2012. The soil organic carbon content for each core was calculated using loss on ignition techniques. A paired t-test was used to determine the *in situ* changes in soil carbon stocks over the course of one year. The model created in Simile was then tested by running it for one year and comparing the results to the empirical soil carbon data results from the paired T-test on the two soil core samples.

6.2.4.6 Comparisons with un-grazed salt marshes: A Mann-Whitney U test was used to compare the main carbon flux components of grazed marshes with those of un-grazed marshes. The model prediction outputs from Simile were similarly compared to that from un-grazed marshes.

6.3 Results

6.3.1 The empirical carbon budget

Figure 6.4 shows the patterns of the measured carbon fluxes over time and the related change in carbon stock over the course of one year for each site. There were significant differences in fluxes over the seasons. Of the main carbon fluxes, sedimentation, soil respiration and root growth significantly varied over the seasons (Table 6.2). Sediment accretion was significantly highest in the winter, and significantly lowest in the autumn when the marshes generally eroded (Kruskal-Wallis multiple comparisons: Table 6.2). Soil respiration was significantly higher in the summer and spring than in the autumn and winter (Table 6.2). Root growth was significantly lower in the winter than in the other seasons and higher in the summer and autumn than in the spring (Table 6.2).

Table 6.2 | Differences between seasons for the main carbon fluxes. Results of Kruskal-Wallis multiple comparisons tests for the main carbon fluxes comparing between seasons. Emboldened *p*-values indicate a significant effect. Medians ($\tilde{x}$) and Interquartile Range (*IQR*) are shown by season for each predictor variable. Significant differences between variables within each season are indicated by superscript numbers: variables that share a number are significantly different.

Carbon Flux	**Kruskal-Wallis**			**Winter**		**Spring**		**Summer**		**Autumn**	
	df	***H***	***p***	$\tilde{x}$	***IQR***	$\tilde{x}$	***IQR***	$\tilde{x}$	***IQR***	$\tilde{x}$	***IQR***
Faeces Degradation	3	3.94	0.268	0.06	0.08	0.08	0.10	0.09	0.07	0.09	0.11
Root Degradation	3	4.78	0.189	0.04	0.13	0.05	0.11	0.06	0.14	0.13	0.19
Sediment Accretion	3	17.32	**0.001**	7.23	9.87 ^{12}	2.63	6.01	2.73	5.81 ^{1}	-2.35	14.59 ^{2}
Soil Respiration	3	73.64	**<0.001**	1.84	1.86 ^{12}	6.09	3.54 ^{13}	8.92	6.43 ^{24}	2.24	2.45 ^{34}
Root Growth	3	39.93	**<0.001**	0.01	0.01 ^{123}	0.02	0.03 ^{145}	0.03	0.06 ^{24}	0.04	0.08 ^{35}

Over the year, loss of carbon through heterotrophic soil respiration and carbon input through sediment accretion were significantly greater than carbon inputs through faeces, litter and root degradation (Kruskal-Wallis Multiple Comparisons; Table 6.3a,b). This pattern was consistent throughout the winter and spring (Table 6.3b), but in the summer and autumn, loss of carbon through heterotrophic soil respiration was greater than carbon inputs through sediment accretion, faeces degradation, litter degradation and root degradation, and sediment accretion rates did not significantly differ from carbon inputs through faeces and root degradation (Table 6.3b). Litter degradation rates were consistently significantly lower than any other carbon flux (Table 6.3b). It is therefore suggested that salt marshes generally accrete carbon during the winter and spring, but may lose carbon during the summer and autumn when soil respiration rates outweigh sediment accretion rates.

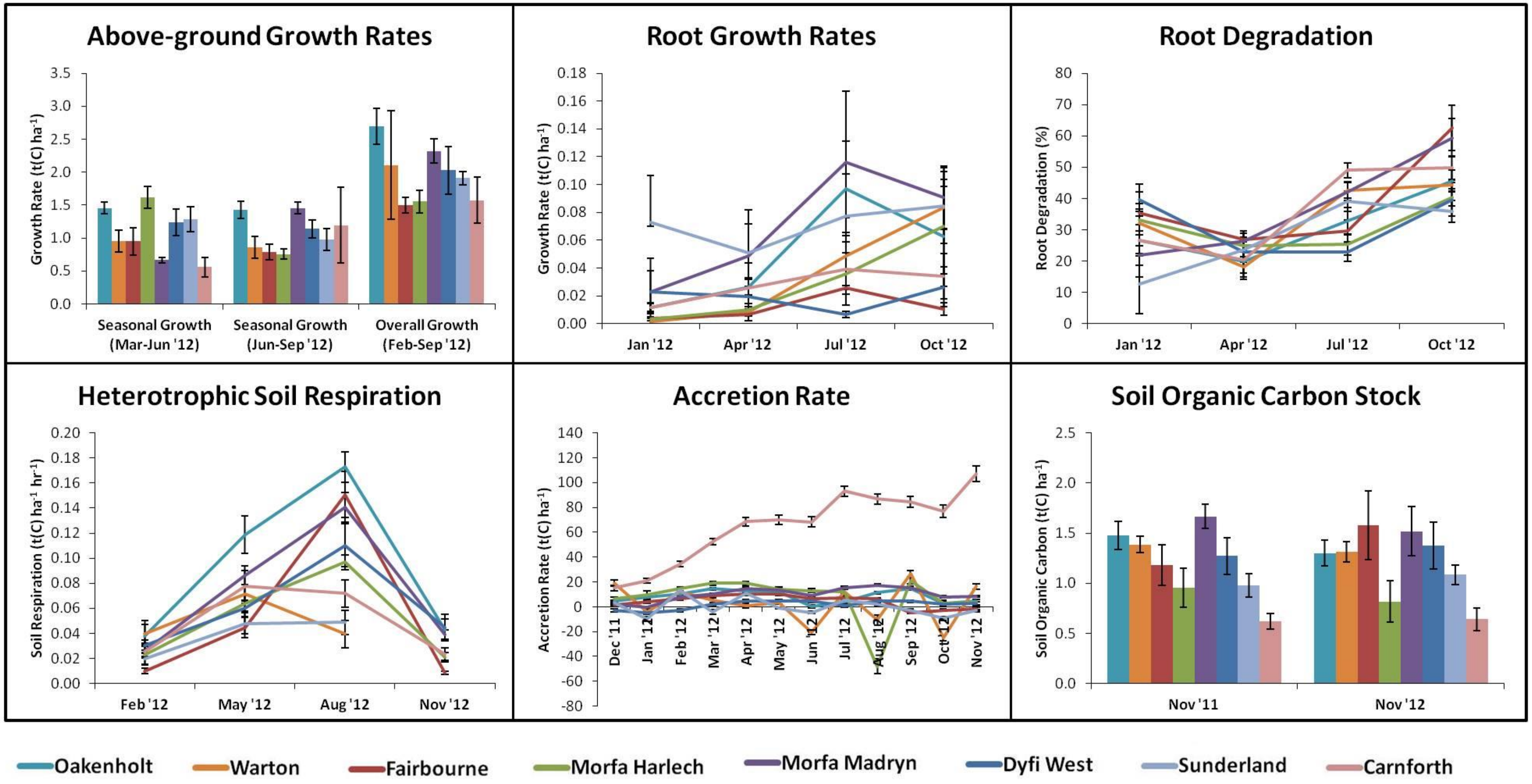


Figure 6.3 | Patterns of measured carbon fluxes over time by marsh. Bar and line charts showing the patterns of the measured carbon fluxes (above-ground growth, root growth, root degradation, soil respiration and accretion rate) alongside the empirical measurements of soil organic carbon in November 2011 and November 2012 for the eight grazed salt marshes (Oakenholt, Warton, Fairbourne, Morfa Harlech, Morfa Madryn, Dyfi West, Sunderland and Carnforth). Data is presented as tonnes of carbon per hectare, except for root degradation, which is recorded as a percentage loss of mass.

Table 6.3a | Kruskal-Wallis multiple comparisons comparing the main carbon fluxes. Results of Kruskal-Wallis multiple comparisons tests for annual data set and by season, comparing the main inputs and outputs of carbon (t (C) ha^{-1} yr^{-1}) according to the salt marsh carbon budget model. Emboldened *p*-values indicate a significant effect.

	Kruskal Wallis		
Season	***df***	***H***	***p***
Annual	4	102.17	**<0.001**
Winter	4	100.68	**<0.001**
Spring	4	120.38	**<0.001**
Summer	4	101.76	**<0.001**
Autumn	4	59.25	**<0.001**

Table 6.3b | Descriptive statistics and statistical grouping of main inputs and outputs of carbon. Medians ($\tilde{x}$) and Interquartile Range (*IQR*) are shown by season for each predictor variable. Significant differences between variables within each season are indicated by superscript numbers: variables that share a number are significantly different.

	Faeces Degradation		**Litter Degradation**		**Root Degradation**		**Sediment Accretion**		**Heterotrophic Soil Respiration**	
Season	$\tilde{x}$	**IQR**	$\tilde{x}$	**IQR**	$\tilde{x}$	**IQR**	$\tilde{x}$	**IQR**	$\tilde{x}$	**IQR**
Annual	0.03	0.04 ^{123}	0.00	0.00 ^{1456}	0.06	0.12 ^{478}	6.67	14.77 ^{257}	5.13	2.77 ^{368}
Winter	0.06	0.08 ^{123}	0.00	0.00 ^{1456}	0.04	0.13 ^{478}	7.23	9.87 ^{257}	1.84	1.86 ^{368}
Spring	0.08	0.10 ^{123}	0.00	0.00 ^{1456}	0.05	0.11 ^{478}	2.63	6.01 ^{257}	6.09	3.54 ^{368}
Summer	0.09	0.07 ^{12}	0.00	0.00 ^{1345}	0.06	0.14 ^{36}	2.73	5.81 ^{47}	8.92	6.43 ^{2567}
Autumn	0.09	0.11 ^{12}	0.00	0.00 ^{1345}	0.13	0.19 ^{36}	-2.35	14.59 ^{47}	2.24	2.45 ^{2567}

6.3.2 The main carbon flux predictors of soil organic and inorganic carbon

A combination of sediment accretion, vegetation growth and heterotrophic soil respiration best described the variation of soil organic carbon in un-grazed marshes (DistLM: AICc = 165.72, R^2 = 0.281). Soil organic carbon stocks at 0-5cm and 0-15 depth showed significant a negative relationship with sediment accretion rates (Regression: Table 6.4). When considering the core as a whole (all depths pooled: 0-25cm depth), soil organic carbon stocks had no significant relationship with any of the measured carbon fluxes (Table 6.4).

A combination of faeces degradation, litter production and sediment accretion rates best described the variation in soil inorganic carbon in un-grazed marshes (DistLM: AICc = 206.68, R^2 = 0.289). Soil inorganic stocks in the top 5cm soil profile showed a significant positive relationship with faeces degradation rate, but in the deeper soil profiles (0-15cm and 0-25cm), soil inorganic carbon stocks showed no significant response to any individual carbon flux (Regressions: Table 6.5).

Table 6.4 | Regression analysis of empirical measurements of carbon fluxes vs. SOC. Regression analyses were made for three different depth profiles (0-5cm, 0-10cm and 0-25cm). An emboldened *p*-value denotes a significant effect. R^2, Intercept (*b*) and Slope (*m*) values for regression lines are shown.

Predictor Variable	***df***	***F***	***p***	R^2	***b***	***m***
Soil Organic Carbon (t (C) ha^{-1} yr^{-1}) – 0-5cm Depth Layer						
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,34	1.76	0.194	0.049		
Litter Degradation (t (C) ha^{-1} yr^{-1})	1,34	0.42	0.522	0.012		
Faeces Degradation (t (C) ha^{-1} yr^{-1})	1,34	<0.01	0.981	<0.001		
Root Growth (t (C) ha^{-1} yr^{-1})	1,34	0.34	0.565	0.010		
Root Degradation (t (C) ha^{-1} yr^{-1})	1,34	0.13	0.721	0.004		
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,34	11.73	**0.002**	0.257	2.190	-0.017
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,34	0.16	0.689	0.005		
Soil Organic Carbon (t (C) ha^{-1} yr^{-1}) – 0-15cm Depth Layer						
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,34	0.39	0.537	0.011		
Litter Degradation	1,34	2.24	0.144	0.062		
Faeces Degradation (t (C) ha^{-1} yr^{-1})	1,34	0.02	0.899	<0.001		
Root Growth (t (C) ha^{-1} yr^{-1})	1,34	0.77	0.387	0.022		
Root Degradation (t (C) ha^{-1} yr^{-1})	1,34	1.58	0.217	0.044		
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,34	4.20	**0.048**	0.110	1.63	-0.008
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,34	0.11	0.744	0.003		
Soil Organic Carbon (t (C) ha^{-1} yr^{-1}) – 0-25cm Depth Layer						
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,34	0.40	0.531	0.012		
Litter Degradation	1,34	2.64	0.114	0.072		
Faeces Degradation (t (C) ha^{-1} yr^{-1})	1,34	<0.01	0.970	<0.001		
Root Growth (t (C) ha^{-1} yr^{-1})	1,34	0.06	0.804	0.002		
Root Degradation (t (C) ha^{-1} yr^{-1})	1,34	0.79	0.382	0.023		
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,34	3.81	0.059	0.101		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,34	0.95	0.337	0.027		

Table 6.5 | Regression analysis of empirical measurements of carbon fluxes vs. SIC. Regression analyses were made for three different depth profiles (0-5cm, 0-10cm and 0-25cm). An emboldened *p*-value denotes a significant effect. R^2, Intercept (*b*) and Slope (*m*) values for regression lines are shown.

Predictor Variable	*df*	*F*	*p*	R^2	*b*	*m*
Soil Inorganic Carbon (t (C) ha^{-1} yr^{-1}) – 0-5cm Depth Layer						
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,34	0.62	0.437	0.020		
Litter Degradation (t (C) ha^{-1} yr^{-1})	1,34	0.35	0.559	0.011		
Faeces Degradation (t (C) ha^{-1} yr^{-1})	1,34	21.67	**<0.001**	0.417	0.388	22.800
Root Growth (t (C) ha^{-1} yr^{-1})	1,34	0.79	0.381	0.026		
Root Degradation (t (C) ha^{-1} yr^{-1})	1,34	0.51	0.482	0.017		
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,34	1.47	0.236	0.047		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,34	0.75	0.393	0.024		
C Mineralization (t (C) ha^{-1} yr^{-1})	1,34	0.66	0.424	0.021		
Soil Inorganic Carbon (t (C) ha^{-1} yr^{-1}) – 0-15cm Depth Layer						
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,34	0.85	0.365	0.027		
Litter Degradation	1,34	0.54	0.466	0.018		
Faeces Degradation (t (C) ha^{-1} yr^{-1})	1,34	0.23	0.636	0.008		
Root Growth (t (C) ha^{-1} yr^{-1})	1,34	0.15	0.703	0.005		
Root Degradation (t (C) ha^{-1} yr^{-1})	1,34	2.48	0.126	0.076		
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,34	<0.01	0.987	<0.001		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,34	0.64	0.431	0.021		
C Mineralization (t (C) ha^{-1} yr^{-1})	1,34	0.60	0.443	0.020		
Soil Inorganic Carbon (t (C) ha^{-1} yr^{-1}) – 0-25cm Depth Layer						
Vegetation Growth (t (C) ha^{-1} yr^{-1})	1,34	0.63	0.4.35	0.020		
Litter Degradation	1,34	0.40	0.533	0.013		
Faeces Degradation (t (C) ha^{-1} yr^{-1})	1,34	0.09	0.767	0.003		
Root Growth (t (C) ha^{-1} yr^{-1})	1,34	0.10	0.749	0.003		
Root Degradation (t (C) ha^{-1} yr^{-1})	1,34	3.86	0.059	0.114		
Sediment Accretion (t (C) ha^{-1} yr^{-1})	1,34	0.59	0.447	0.019		
Heterotrophic Soil Respiration (t (C) ha^{-1} yr^{-1})	1,34	0.41	0.529	0.013		
C Mineralization (t (C) ha^{-1} yr^{-1})	1,34	0.36	0.554	0.012		

6.3.5 The impacts of abiotic factors on carbon budget parameters

Table 6.8 shows the results of several mixed effects models analyzing the impact of environmental and soil parameters with each of the main carbon fluxes identified in previous sections as being main drivers of soil carbon stocks. Water table depth was a significant predictor of litter and root degradation in the spring, and soil respiration in the summer and autumn. Soil salinity was a significant predictor of root degradation in the spring and soil respiration in the spring and summer. Soil redox was a significant predictor of litter degradation in the spring and soil respiration in the summer. Generally, the measured environmental variables were more likely to be predictors of carbon fluxes in the spring and summer months than in the winter and autumn months, particularly when considering soil heterotrophic respiration.

Several environmental and abiotic soil parameters changed between seasons (Tables 6.6, 6.7). Soil salinity was significantly higher in the spring and summer than in the autumn and winter (ANOVA; Table 6.6). Soil moisture was significantly lower in the autumn than it was in winter and spring, soil and air temperatures were lowest in winter and highest in the summer, water table depth was significantly higher in the autumn than in the winter, soil redox potential was significantly higher in the winter than in summer and autumn, and wind gust speeds were significantly higher in the winter and autumn than in the spring and summer (Kruskal-Wallis multiple comparisons; Table 6.7).

Stocking density had a significant relationship with some of these soil variables; soil moisture showed a significant positive response to an increase in stocking density in summer, soil temperature showed a significant positive response to increased stocking density in the winter, water table depth showed a significant negative response to stocking density sin the winter, spring and autumn, soil pH showed a significant negative response in the winter, summer and autumn but a significant positive response in the spring, and soil salinity showed a significant positive response throughout the year (Regression; Table 6.8).

Table 6.6 | Comparing environmental and soil parameters with main carbon fluxes. Results of mixed effects models comparing testing for association of variation in the main (identified from the DistLM and regression analyses) carbon fluxes (litter degradation, root degradation, heterotrophic soil respiration and sediment accretion) with variation in environmental and abiotic soil parameters. Column headers depict the effect, degrees of freedom (*df*: numerator, denominator), *F*-values (*F*), *p*-values (*p*) and slopes of linear relationships (*m*).

		Winter			Spring			Summer			Autumn		
Predictor Variable	***df***	***F***	***p***	***m***	***F***	***p***	***m***	***F***	***p***	***m***	***F***	***p***	***m***
Litter Degradation													
Stocking Density (LSU ha^{-1} yr^{-1})	1,6	0.55	0.489		0.50	0.501		0.73	0.421		0.54	0.492	
Soil Moisture (θ)	1,18	0.15	0.701		22.96	**<0.001**	-0.001	1.89	0.183		0.67	0.424	
Soil Temperature (°C)	1,18	<0.01	0.953		0.15	0.707		0.42	0.520		3.01	0.100	
Water Table Depth (cm)	1,18	3.71	0.070		10.92	**0.004**	-0.001	1.11	0.304		0.88	0.359	
Soil pH	1,18	3.71	0.070		15.59	**0.001**	-0.046	6.66	**0.017**	-3.019	2.91	0.105	
Soil Salinity (S)	1,18	0.02	0.896		0.05	0.822		<0.01	0.976		0.10	0.758	
Soil Redox Potential (mV)	1,18	3.58	0.075		8.28	**0.010**	-0.001	0.01	0.927		2.95	0.103	
Root Degradation													
Stocking Density (LSU ha^{-1} yr^{-1})	1,6	0.57	0.480		0.15	0.709		0.60	0.463		0.03	0.858	
Soil Moisture (θ)	1,18	0.58	0.457		0.01	0.919		0.05	0.824		0.71	0.411	
Soil Temperature (°C)	1,18	0.16	0.695		0.07	0.801		2.81	0.109		0.18	0.677	
Water Table Depth (cm)	1,18	0.02	0.886		6.11	**0.024**	-0.001	1.40	0.250		0.22	0.642	
Soil pH	1,18	0.45	0.512		3.05	0.098		0.11	0.744		1.88	0.187	
Soil Salinity (S)	1,18	0.45	0.511		5.88	**0.026**	-0.014	1.32	0.264		0.37	0.552	
Soil Redox Potential (mV)	1,18	0.87	0.363		0.97	0.338		0.13	0.721		0.18	0.678	
Heterotrophic Soil Respiration													
Stocking Density (LSU ha^{-1} yr^{-1})	1,4	2.53	0.187		1.12	0.350		32.91	**0.002**	0.725	1.43	0.318	
Soil Moisture (θ)	1,17	0.10	0.756		0.40	0.534		2.38	0.140		1.27	0.284	
Soil Temperature (°C)	1,17	1.47	0.241		6.07	**0.025**	0.752	14.16	**0.001**	-0.431	0.07	0.801	
Water Table Depth (cm)	1,17	0.24	0.631		3.58	0.076		9.22	**0.007**	0.098	14.61	**0.003**	-0.045
Soil pH	1,17	0.53	0.477		0.45	0.512		4.32	0.051		0.07	0.796	
Soil Salinity (S)	1,17	0.02	0.903		17.73	**0.001**	0.676	5.62	**0.028**	1.115	1.46	0.252	
Soil Redox Potential (mV)	1,17	0.06	0.815		<0.01	0.990		5.95	**0.024**	0.017	0.83	0.382	
Soil Organic Carbon (g (C) ha^{-1} yr^{-1})	1,17	0.42	0.528		0.06	0.814		5.40	**0.031**	0.564	8.55	**0.014**	3.122
Tidal Height (m)	1,4	0.19	0.688		5.49	0.079		4.57	0.086		1.87	0.265	
Air Temperature (°C)	1,4	1.20	0.335		0.75	0.435		22.59	**0.005**	-1.810	0.34	0.601	

Table 6.6 (Cont.) | Comparing environmental and soil parameters with main carbon fluxes.

		Winter			Spring			Summer			Autumn		
Predictor Variable	***df***	***F***	***p***	***m***	***F***	***p***	***m***	***F***	***p***	***m***	***F***	***p***	***m***
						Sediment Accretion							
Stocking Density (LSU ha^{-1} yr^{-1})	1,2	5.15	0.151		0.30	0.638		0.29	0.629		0.67	0.499	
Tidal Range (m)	1,2	0.79	0.467		10.86	0.081		0.35	0.594		3.26	0.213	
Wind Speed (Gust) (kmph)	1,2	2.93	0.229		0.15	0.740		0.30	0.623		0.02	0.907	
Percent Clay	1,2	1.02	0.419		2.07	0.286		0.37	0.587		5.79	0.138	
Soil Compaction (pa)	1,2	2.96	0.227		14.85	0.061		0.67	0.473		0.01	0.945	
Vegetation Height (cm)	1,22	5.84	**0.024**	-0.333	1.66	0.211		0.19	0.667		0.05	0.818	
Vegetation Cover (%)	1,22	9.81	**0.005**	-0.257	13.43	**0.001**	-0.333	0.14	0.713		10.48	**0.004**	-1.338

Table 6.7 | ANOVA analysis of seasonal differences in soil properties. Results of 1-way ANOVA's showing differences between seasons for several soil properties. Column headers depict degrees of freedom (*df*: numerator, denominator), *F*-values (*F*), *p*-values (*p*) and partial eta squared effect size (η_p^2). An emboldened *p*-value denotes a significant effect. Means ($\bar{x}$) and Standard Error (*SE*) are shown by season for each predictor variable. Significant differences between variables within each season are indicated by superscript numbers: variables that share a number are significantly different.

	ANOVA				Winter		Spring		Summer		Autumn	
Variable	***df***	***F***	***p***	η_p^2	$\bar{x}$	***SD***	$\bar{x}$	***SD***	$\bar{x}$	***SD***	$\bar{x}$	***SD***
Soil pH	3,168	2.53	0.059	0.043	7.02	0.05	6.80	0.06	6.83	0.05	6.90	0.06
Soil Salinity (S)	3,168	17.76	**<0.001**	0.241	5.29	0.46 [12]	8.89	0.40 [13]	8.70	0.49 [24]	6.03	0.39 [34]

Table 6.8 | Kruskal-Wallis multiple comparisons tests of seasonal differences in soil properties. Results of Kruskal-Wallis multiple comparisons tests showing differences between seasons for several environmental parameters. Column headers depict degrees of freedom (*df*), *H*-values (*H*) and *p*-values (*p*). An emboldened *p*-value denotes a significant effect. Medians ($\tilde{x}$) and Interquartile Range (*IQR*) are shown by season for each predictor variable. Significant differences between variables within each season are indicated by superscript numbers: variables that share a number are significantly different.

	Kruskal-Wallis			Winter		Spring		Summer		Autumn	
Variable	***df***	***H***	***p***	$\tilde{x}$	***IQR***	$\tilde{x}$	***IQR***	$\tilde{x}$	***IQR***	$\tilde{x}$	***IQR***
Soil Moisture (θ)	3	11.50	**0.009**	964.33	39.25 [12]	959.83	37.58 [3]	951.00	38.25 [1]	942.00	36.25 [23]
Soil Temperature (°C)	3	121.35	**<0.001**	5.33	1.76 [123]	9.55	0.97 [145]	16.18	1.71 [246]	10.66	0.91 [356]
Water Table Depth (cm)	3	8.28	**0.041**	24.47	17.80 [1]	26.85	19.21	26.12	12.65	31.69	12.68 [1]
Soil Redox (mV)	3	9.63	**0.022**	403.20	140.10 [12]	368.50	120.90	336.30	61.90 [1]	343.90	91.10 [2]
Air Temperature (°C)	3	115.78	**<0.001**	7.13	0.68 [123]	11.32	1.33 [14]	17.93	2.37 [245]	12.50	1.17 [35]
Tidal Height when Sampling (m)	3	3.23	0.357	4.24	2.22	3.49	2.43	3.20	0.63	2.96	1.70
Wind Speed (Gust) (kmph)	3	24.87	**<0.001**	30.27	8.22 [12]	22.90	5.63 [1]	20.58	6.41 [23]	29.32	8.61 [3]

6.3.3 Comparing model predictions to observed soil carbon stocks

There was no significant gain or loss of carbon over the course of one year in any of the soil depths samples when comparing 2011 and 2012 data (t-test: Table 6.9). This was compared to predictions of future carbon stocks based on the changes in, and relationships between, the measured carbon stocks and fluxes using a carbon budget model. This carbon budget model was constructed based on overall averages and standard errors calculated from the empirical carbon flux and stock data shown in Figure 6.4. In contrast to the empirical observations, the model predicted that soil organic carbon for the 0-25cm depth would increase considerably over one year, despite large error margins (Figure 6.5). The large error margins, coupled with the mismatch with empirical observations, indicate that the model is unsuitable for predictions in its current state.

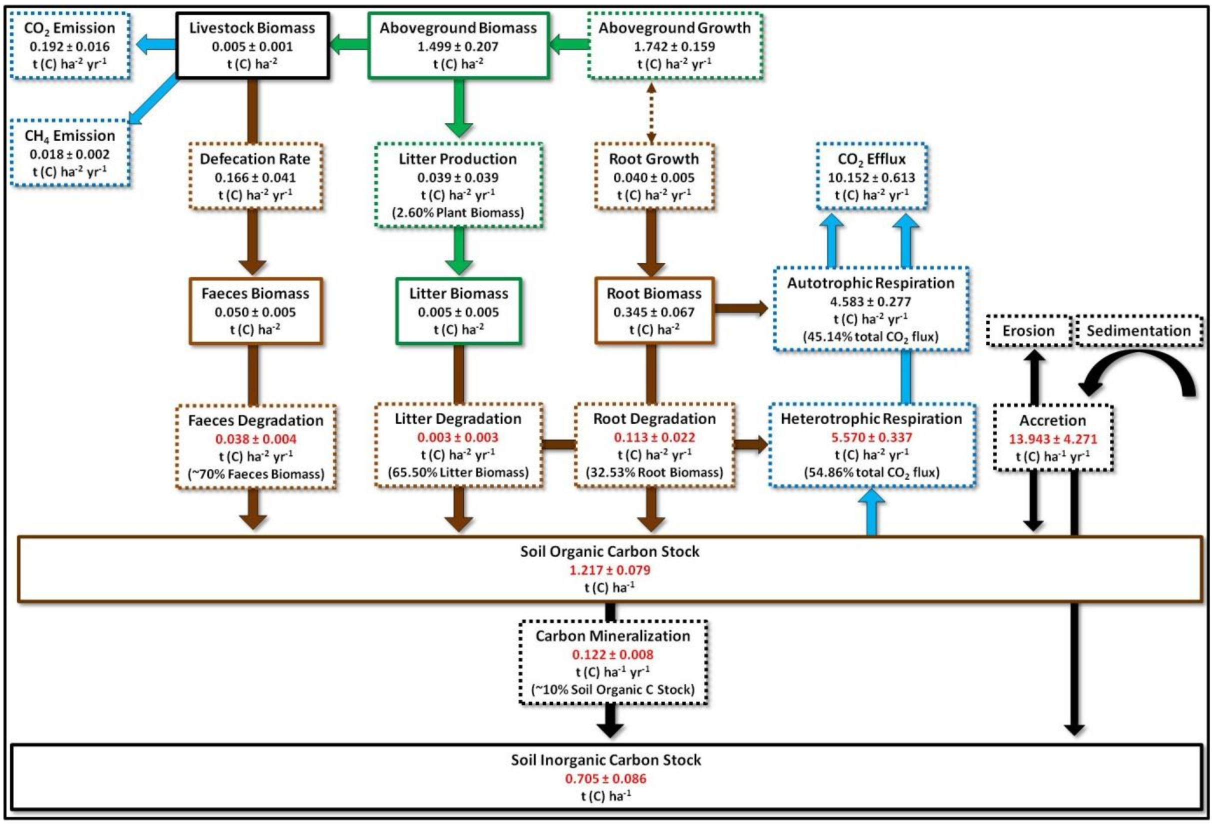


Figure 6.4 | A calculated carbon budget for a grazed salt marsh. Annual means ± one standard error are shown for each carbon flux variable based on empirical evidence from nine grazed salt marshes. Figures in red are principal stocks, inputs or outputs of soil organic carbon or soil inorganic carbon.

Table 6.9 | Comparison between empirical soil organic carbon content in 2011 and 2012. Results of a two-sample t-test comparing between November 2011 and November 2012 for soil depths 0-5cm, 0-10cm and 0-25cm. Means and standard errors are shown after the test results.

	T-Test			2011		2012	
Depth Profile	***N***	***T***	***p***	$\bar{x}$	***SE***	$\bar{x}$	***SD***
0-5cm	44	0.79	0.435	2.001	0.115	1.911	0.128
0-15cm	44	0.45	0.657	1.455	0.078	1.415	0.087
0-25cm	44	0.38	0.705	1.125	0.062	0.101	0.070
Model Predictions	-	-	-	1.217	0.079	9.400	4.600

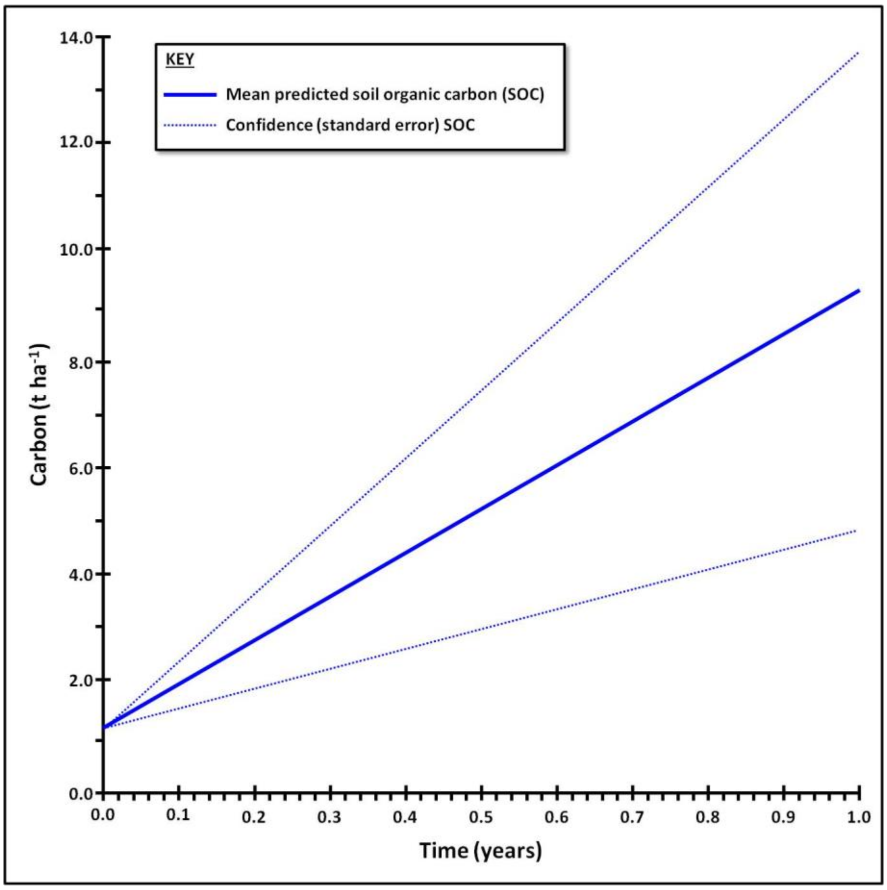


Figure 6.5 | Model predictions for soil organic carbon stocks over 1 year. Model outputs of a grazed salt marsh carbon budget model showing results for soil organic carbon stocks for a 1-year prediction showing mean and upper and lower confidence intervals (based on standard error).

6.3.4 Comparing grazed with un-grazed

Litter degradation rates were significantly lower on grazed marshes than on un-grazed marshes, and faeces degradation rates were significantly higher on grazed marshes than on un-grazed marshes (Mann-Whitney U: Table 6.10). Root degradation rates, sediment accretion rates and soil respiration rates did not differ between grazed and un-grazed marshes (Table 6.10). Carbon input through litter degradation in un-grazed marshes did not significantly differ from carbon inputs through faeces degradation in grazed marshes (Mann-Whitney U: $W = 258.0$, $p = 0.398$).

Table 6.10 | The differences between grazed and un-grazed empirical salt marsh carbon fluxes. Results of Mann-Whitney U tests for the main carbon fluxes associated with soil carbon stocks, comparing between grazed and un-grazed salt marshes. Column headers depict the test results (*W*) and associated *p*-value (*p*), followed by the sample size (*n*), median ($\tilde{x}$) and interquartile range (*IQR*) for both grazed and un-grazed salt marshes. Units for each variable are tons of carbon per hectare per year.

Carbon Flux	Mann-Whitney		Grazed			Un-grazed		
	W	*p*	*n*	$\tilde{x}$	*IQR*	*n*	$\tilde{x}$	*IQR*
Faeces Degradation	1098.0	**<0.001**	36	0.03	0.04	12	0.00	<0.01
Litter Degradation	797.5	**0.046**	36	0.00	<0.01	12	0.00	0.23
Root Degradation	926.0	0.300	36	0.06	0.12	12	0.06	0.22
Sediment Accretion	920.5	0.366	36	6.67	14.77	12	4.61	12.00
Soil Respiration	800.0	0.052	36	5.13	2.77	12	6.61	2.28

Carbon dioxide emissions from livestock were significantly lower than outputs of carbon through heterotrophic soil respiration, but significantly higher than carbon inputs through faeces and litter degradation. Methane emissions from livestock were significantly lower than carbon input by sediment accretion and carbon loss through soil respiration, but significantly higher than carbon inputs through litter degradation. Methane emissions were significantly lower than carbon dioxide emissions (Kruskal-Wallis multiple comparison: $df = 6$, $H = 158.64$, $p < 0.001$) (Table 6.11).

Table 6.11 | Statistical grouping of livestock gas effluxes and the main carbon fluxes. Descriptive statistics and grouping according to Kruskal-Wallis multiple comparisions tests for empirical livestock gas emissions and empirical carbon fluxes. Medians ($\tilde{x}$) and Interquartile Range (*IQR*) are shown for each variable. Significant differences between variables within each season are indicated by 'Grouping': variables that share a number are significantly different. Units for each variable are tons of carbon per hectare per year.

	$\tilde{x}$	IQR	Grouping
CO_2 Emissions (t(C) ha^{-1} yr^{-1})	0.166	0.177	1, 2, 3, 4
CH_4 emissions (t(C) ha^{-1} yr^{-1})	0.011	0.019	1, 5, 6, 7
Faeces Degradation (t(C) ha^{-1} yr^{-1})	0.035	0.028	2, 8, 7, 10, 11, 12
Litter Degradation (t(C) ha^{-1} yr^{-1})	0.000	0.000	3, 5, 8, 10, 13, 14, 15
Root Degradation (t(C) ha^{-1} yr^{-1})	0.060	0.119	13, 16, 17
Sediment Accretion (t(C) ha^{-1} yr^{-1})	6.670	14.770	6, 9, 11, 14
Soil Respiration (t(C) ha^{-1} yr^{-1})	5.130	2.773	4, 7, 12, 15

Livestock grazing had significant impacts on several abiotic soil characteristics, although the influence of grazers varied between seasons (Table 6.12).

Table 6.12 | Regression analysis of soil parameters vs. stocking density. Results of a regression analysis for each measured soil parameter vs. stocking density (LSU) for each season. Results of ANOVA (*df*, *F* and *p*) are shown. An emboldened *p*-value denotes a significant effect. The results of the regression are shown in the last three columns: R^2, Intercept (*b*) and Slope (*m*).

Predictor Variable	*df*	*F*	*p*	R^2	*b*	*m*
Winter						
Soil Moisture (θ)	1,30	2.68	0.112	0.082		
Soil Temperature (°C)	1,30	20.11	**<0.001**	0.461	4.370	1.910
Water Table Depth (cm)	1,30	8.41	**0.007**	0.219	28.700	-14.200
Soil pH	1,30	6.62	**0.015**	0.181	7.190	-0.370
Soil Salinity (S)	1,30	5.67	**0.024**	0.159	3.900	2.980
Soil Redox (mV)	1,30	0.15	0.700	0.005		
Spring						
Soil Moisture (θ)	1,30	1.49	0.231	0.047		
Soil Temperature (°C)	1,30	1.76	0.194	0.056		
Water Table Depth (cm)	1,30	7.93	**0.009**	0.209	31.200	-14.500
Soil pH	1,30	7.19	**0.012**	0.193	7.080	0.461
Soil Salinity (S)	1,30	9.50	**0.004**	0.241	6.600	3.030
Soil Redox (mV)	1,30	4.14	0.051	0.121		
Summer						
Soil Moisture (θ)	1,30	8.48	**0.006**	0.200	930.000	32.400
Soil Temperature (°C)	1,30	0.36	0.554	0.010		
Water Table Depth (cm)	1,30	0.47	0.498	0.014		
Soil pH	1,30	11.50	**0.002**	0.253	7.140	-0.523
Soil Salinity (S)	1,30	11.24	**0.002**	0.248	6.280	3.620
Soil Redox (mV)	1,30	0.84	0.366	0.250		
Autumn						
Soil Moisture (θ)	1,30	3.59	0.067	0.096		
Soil Temperature (°C)	1,30	2.49	0.124	0.068		
Water Table Depth (cm)	1,30	11.49	**0.002**	0.253	34.500	-14.000
Soil pH	1,30	11.13	**0.002**	0.247	7.210	-0.544
Soil Salinity (S)	1,30	11.83	**0.002**	0.258	4.010	3.980
Soil Redox (mV)	1,30	0.64	0.429	0.021		

6.4 Discussion

6.4.1 Grazing influence on the mass balance of carbon

A mass balance carbon budget based on empirical data showed grazing had little impact on the total carbon balance in salt marshes, although it did affect the relative contributions by different budget components. As on un-grazed marshes, sedimentation and soil respiration were higher than inputs through organic matter, and sedimentation and soil respiration did not differ between grazed and un-grazed marshes. Input of carbon through the degradation of litter matter in grazed marshes was approximately zero, due to the fact there was no litter present. Carbon input through faeces degradation in grazed marshes was not significantly different from carbon inputs through litter degradation in un-grazed marshes. In terms of the overall carbon balance, therefore, carbon input in grazed marshes through degradation of faeces compensated for the loss of litter-derived inputs in un-grazed marshes. As overall degradation rates did not differ between grazed and un-grazed marshes, it is perhaps unsurprising that soil respiration also did not differ between grazed and un-grazed marshes. Ford, Rousk, Garbutt, Jones, and Jones (2013) found that, although grazing had small effects on the composition of the soil microbial community, the total microbial biomass was not affected by grazing, and therefore, grazing is unlikely to affect soil respiration rates (Ford et al., 2012; Ma et al., 2010). It was expected that, as grazers reduce above ground biomass, less sediment would be accreted on grazed marshes. However, French and Spencer (1993) found that sedimentation across a marsh depended more on direct settling rather than the retention of sediment on plant surfaces. The present results suggest that the above ground plant biomass had little to do with the process of sedimentation in mid marsh, and instead sedimentation across the study plots was more likely due to direct settling from the water column.

Gas emissions from livestock were lower than soil respiration rates and sedimentation rates, but higher than inputs of carbon through faeces degradation; they did not differ from root degradation rates. It is therefore likely, that carbon dioxide and methane gas emissions from livestock do not result in salt marshes becoming a net source of carbon, but instead slightly offset salt marsh carbon storing.

Sediment accretion was an important predictor of empirical soil organic carbon stock. Sediment accretion showed a negative relationship with soil organic carbon in the top two soil profiles (0-5 and 0-15 cm depth). If sedimentation was chiefly by means of direct settlement, rather than being trapped by plants (French & Spencer, 1993), the constant high sedimentation rates coupled with a loss in plant biomass (Chapter 3) could lead to a change in inorganic to organic carbon ratio in the soil carbon stock with an increase in grazing and thus lead to a relative decrease in soil organic carbon stocks. Livestock grazing showed a positive relationship with heterotrophic soil respiration in the summer. An increase in grazing leads to a decrease in vegetation cover (Chapter 3), which is likely to lead to higher soil temperatures (Oliver, Oliver, Wallace, & Roberts, 1987), and therefore higher soil respiration rates (Amundson, 2001; Pendall et al., 2004). Livestock grazing did alter soil properties; grazing showed a positive relationship with soil temperatures in the winter but this relationship was not evident in the other seasons, suggesting that grazing impact on soil temperature may be minor. Furthermore, soil compaction by livestock leads to higher soil moisture levels (Jensen, 1985), as observed here, which increases soil respiration rates (Amundson, 2001; Pendall et al., 2004).

6.4.2 Seasonal changes in carbon fluxes

Grazing did not affect the seasonal patterns of salt marsh carbon fluxes. As with un-grazed marshes, there were no seasonal patterns with degradation of organic matter (faeces and roots), and soil respiration was greatest in the summer and lowest in the winter. Sediment accretion was greatest in the winter, lower in the spring and summer, and again erosion generally occurred in the autumn.

6.4.3 The impact of environmental variables on carbon sequestration

As predicted, soil moisture and temperature were significant predictors of degradation rates and soil respiration. However, unlike on un-grazed marshes, which showed stronger effects of soil characteristics in the winter, the effects of soil moisture and temperature were significant only in the summer. Soil temperature showed a negative relationship with soil respiration in the summer, while soil moisture parameters showed a positive relationship with soil respiration in the summer. Although it has been established that both grazed and un-grazed grasslands show a summer maxima and a winter minima of microbial biomass (Bardgett et al., 1997), there is no difference in microbial biomass or fungi:bacteria ratios between grazed and un-grazed salt marshes (Ford et al., 2013). The difference in seasonal effects of soil conditions is therefore unlikely to be due to differences between grazed and un-grazed microbial communities. Instead, it is possible that grazers alter soil abiotic factors indirectly by removing above ground vegetation, which has knock-on effects on degradation rates and respiration rates. For example, elevated soil temperatures in the summer may reach a threshold point and inhibit soil respiration (Couteaux et al 1995). Furthermore, soil moisture showed a positive relationship with grazing during the summer; on intensively grazed marshes where soil compaction was greatest (Chapter 4), soil moisture, and therefore soil respiration was high (Amundson, 2001; Jensen, 1985; Pendall et al., 2004). No seasonal changes in degradation rates or soil respiration rates were recorded in this study, however, so seasonal changes in soil abiotic parameters are likely only to have marginal impacts on carbon fluxes.

6.4.4 Predictions of future carbon stocks

As with the un-grazed marshes, there was no significant change over the course of one year when looking at actual carbon stocks from 2011 vs. 2012. This observation was expected, as Chapter 4 showed that there was no difference in the carbon stocks of grazed and un-grazed marshes. When comparing one year of data with a one year model prediction, however, the model showed a large increase in carbon (just less than 6 tonnes of carbon per hectare), and the confidence intervals seemed to show that this was a significant increase. This implies that the model is not a good predictor of future carbon stocks, as it overestimated carbon flux increases and showed large error margins.

6.4.5 Study implications

Livestock grazing does not impact the overall carbon budget model, but it does alter some of the carbon fluxes both directly and indirectly. Management schemes need to keep in mind that loss of litter and above ground biomass by grazing can result in changes in soil conditions, which will alter some carbon fluxes. Soil respiration is a considerable output of carbon from salt marshes, and grazers could enhance this output during the summer months. This may add to concerns of rising soil temperatures and loss of soil carbon in the future (Jenkinson et al., 1991; Kirschbaum, 1995; Schimel et al., 1994). Furthermore, although gas effluxes from livestock were smaller than soil respiration and sedimentation fluxes, they are another carbon output from salt marshes, which cannot be ignored when looking at a total mass balance of salt marsh carbon.

As livestock grazing is a common use of salt marshes, it is important to consider both grazed and un-grazed salt marshes when studying carbon sequestration over a large spatial area. This study showed that, on the whole, grazing does not impact the total carbon budget on a salt marsh. However, future studies will need to take into account the small differences between grazed and un-grazed marshes when investigating carbon sequestration on salt marshes, particularly as there is a definite shift between carbon inputs through litter and faeces degradation. Management schemes wishing to focus on the mechanisms of carbon sequestration on salt marshes should therefore consider the impacts of livestock grazing.

PART 4: CONCLUSIONS

Chapter 7: General Discussion

7.1 Overall Conclusions

There were clear effects of grazing on above ground plant communities in salt marshes, which also related to some carbon fluxes: there was a direct effect of grazing on litter, and perhaps indirect effects of grazing on degradation rates and soil respiration. However, the effects of grazing did not translate to effects on below ground soil carbon stocks, as predicted in small-scale studies. This disconnection between above and below ground processes was corroborated by Chapters 5 and 6, where carbon budget models showed that there was no overall effect of grazing on the salt marsh carbon budget. Environmental and seasonal variation generally influenced above and below ground processes to a greater extent than grazing, suggesting that environmental setting is the most important predictor of salt marsh carbon capture and storage processes.

The disconnection between above and below ground processes may be a question of relative time scales. Below ground turnover of carbon stocks occurs on the decadal, century or even millennial scale (Pendall et al., 2004), while above ground changes occur within a few years (Bos et al., 2002; Kuijper et al., 2004). Furthermore, grassland systems are known to adapt to grazing disturbance over the course of decades through plant compensation techniques (Tanentzap & Coomes, 2012), so any impact of grazing is perhaps unlikely to reflect in the soil carbon stores.

The below ground soil profile is a collective history of several decades, intertwined in current physical and above ground processes; all layers, as they are laid down, are a product of present processes, such as root growth, mixed with past conditions (Parton, Schimel, Cole, & Ojima, 1987). If soil builds up approximately 0.4 cm a year in salt marshes (Appendix 2) and the top layer of soil is affected by current above ground processes, then this top layer of soil is a product of both past conditions and current processes (Parton et al., 1987). This mixing of current and past conditions is likely to obscure any impact of the current above ground status on the below ground environment.

7.2 Study Limitations

Another possible explanation for the disconnection between above and below ground processes is that sample size may not have been big enough to detect an effect. The effect of grazing on below ground carbon stocks was expected to be large (Chapter 2: Table 2.3), but the effect of grazing may have been smaller than expected. *A priori* power analyses showed that a minimum sample size of 36 was needed to detect the expected large effect of grazing (Chapter 2: Table 3.2); the minimum sample size would have been larger if a small effect was expected (Cohen, 1988). Sample size in un-grazed (n=112) and intensively grazed (n=60) may have been large enough to detect an effect of grazing, but sample sizes in lightly grazed (n=32) and moderately grazed (n=32) would have been too small to detect an effect. If grazing had a small impact on soil carbon stocks, it is likely that the effects of grazing would have been outweighed by the larger impacts of environmental factors.

Over such a large spatial scale, the variation between sites was greater than any grazing impacts (Chapters 3 and 4). This problem may have been solved by taking more replicates and measuring more environmental parameters at each site, for example nutrient balances. However, this quickly becomes logistically impossible without considerable and frequent sampling efforts from several research groups across the study area. Another alternative would have been to reduce the number of sites for detailed measurements, such as in Chapters 5 and 6, but much of the environmental variation would then have been lost, reducing the value of the broad-scale aspect of the study. The effects of grazing on salt marsh carbon stocks have not been studied in the context of broader-scale contextual variables in the past, so this data set, although not detailed, provides a good baseline data set upon which to build.

The model predictions in Chapters 5 and 6 showed considerable error when predicting future carbon stocks. This variation was perhaps inevitable, as the models were based on annual means. As the data were collected over the course of just one year, seasonal variation would have contributed to a significant amount of variation in the model. If this project had the scope to do so, data would have been collected over the course of several years in order to reduce this variation.

One of the main outputs of carbon from the soil stocks was heterotrophic respiration. The ratio of heterotrophic respiration to autotrophic respiration was measured in July 2012 on Y Foryd, an un-grazed marsh. Autotrophic respiration rates increase with increased plant productivity (Bond-Lamberty et al., 2004) and, as productivity rates in spring and summer are high, it is likely that autotrophic respiration rates are higher in the summer than in the winter. As the heterotrophic to autotrophic respiration ratio was calculated from summer readings, it is possible that autotrophic respiration contributed more to the total gas efflux than readings taken during the winter would have done. This may have led to an underestimation of soil heterotrophic respiration rates during the winter. However, heterotrophic respiration depends on the soil microbial community, which was likely to show a summer maxima and a winter minima (Bardgett et al., 1997; Bardgett et al., 1999). Although this study did not have the scope to investigate soil microbial communities, Chapter 5 and 6 showed seasonal changes in soil respiration rates, which supports the theory that soil microbial biomass showed a summer maxima and a winter minima. It is therefore possible that, alongside autotrophic respiration rates, heterotrophic rates may also have been lower in the winter, and thus the autotrophic to heterotrophic ratio would have remained unchanged.

Faeces biomass was a small input of carbon on grazed marshes, and was thought to compensate for the loss of litter-derived inputs found in un-grazed marshes. However, it can be problematical measuring faeces degradation in the salt marsh environment, as faecal matter is moved around or lost from the marsh due to tidal water movements. As such, faeces degradation rates were estimated from figures calculated in the terrestrial literature (Allard et al., 2004), which may not bear accurate comparisons to the salt marsh environment. Although this is unlikely to impact the results of this study, future studies may wish to explore the process of faeces degradation on salt marshes further.

7.3 Study Implications

In the past, livestock grazing on salt marshes has been used as a management tool for several ecosystem services. The most frequent uses for livestock grazing on salt marshes are meat production, biodiversity protection, and habitat provision for wetland bird species such as redshank (Adam, 1990c; Kuijper et al., 2004; Norris et al., 1997). The use of livestock grazing as a management tool for carbon sequestration is a relatively new concept and has generally been used only in terrestrial systems (Bhogal et al., 2010; Ma et al., 2010; Reeder & Schuman, 2002; Schuman et al., 1999). A recent study on salt marshes in Canada has now shown that livestock grazing can boost carbon stocks on salt marshes, and livestock can be used on marshes to benefit both meat production and carbon storing services (Yu & Chmura, 2010).

While this study does not discount the fact that grazing may affect soil carbon stocks on the small-scale, or after initial introduction, it shows that grazing impacts are insignificant next to broader contextual factors on marshes with well-established grazing regimes. The drivers of soil carbon stocks are difficult to differentiate in a complex and environmentally variable system, such as salt marshes. Therefore, it is perhaps naive to assume a constant effect of grazing on below ground, or even above ground variables. This will have an impact on grazing management schemes that employ a broad-sweep policy over a large area; these schemes would need to take into account environmental variables, plant community responses, and seasonality effects as well as grazing.

7.4 Possible Directions for Future Studies

This study has provided a good baseline data set upon which to build. In the future, salt marsh carbon stocks and fluxes can be better understood through more detailed, empirical, broad-scale studies. For example, to fully investigate the relative importance of grazing in relation to environmental factors, several paired experiments could be set up on a range of different marshes. Grazers could be introduced to small areas of un-grazed marshes, or exclosures could be set up on currently grazed sites, as in previous studies in The Netherlands (J. P. Bakker, 1978; Kuijper & Bakker, 2004a; Kuijper et al., 2004). These studies would have to be run over a period of several years to account for initial ecosystem responses to a change in disturbance levels (Dormaar, Smoliak, & Willms, 1989; Tanentzap & Coomes, 2012). Grazer introduction studies would be useful to investigate initial changes in soil carbon stocks within the few years of grazing, and a broad-scale aspect would inform on the relative importance of these initial changes in relation to the broader contextual setting of each site.

To fully understand the broad-scale processes relating to carbon sequestration on salt marshes, and to build more reliable carbon budget models, further data needs to be collected over the course of several years. Although a broad-scale study adds substantial variation to a data set, it is important to keep the broad-scale aspect to fully understand the importance of marsh environmental setting, and to better inform management schemes over a large spatial scale. Further understanding of the salt marsh carbon budget may lead to easier holistic approaches in the future, and eventually, more accurate calculations of carbon stocks and carbon sequestration rates in naturally carbon rich environments.

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PART 6: APPENDICES

Appendix 1: Grazing Intensities in Other Studies

The grazing intensity thresholds in this study are adapted from Tir Gofal, a Welsh Assembly Government guideline: light grazing <0.3 Livestock Unit (LSU) hectare^{-1} year^{-1} (ha^{-1} yr^{-1}), moderate grazing = 0.3-0.7 LSU ha^{-1} yr^{-1} and intensive grazing >0.7 LSU ha^{-1} yr^{-1}, where 1 LSU = 1 cow, 6.6 sheep or 22 geese (Woodend, 2010). This table shows how the grazing intensities in this study compare with those in studies from salt marshes and terrestrial ecosystems. For the most part the grazing intensities of our sites are comparable to other salt marsh studies and many non-salt marsh studies. Some of our intensively grazed marshes show considerably higher grazing intensities than other salt marsh studies (although, the thresholds remain the same). We believe this is due to the fact that many salt marshes are grazed purely for management purposes (particularly in mainland Europe) and thus such high grazing intensities are deemed un-necessary, while many of our study sites are extensions to farm land with no stocking density restrictions in place.

Table A1.1 | Grazing intensities in other studies. Grazing intensity for salt marsh and terrestrial studies showing system type, study location, grazing intensity categories, number and type of grazing animal per hectare per year (ha^{-1} yr^{-1}), calculated Livestock Units (LSU) per ha^{-1} yr^{-1}, and reference details.

System	Location	Grazing Information: Grazing Intensity	Animals (ha^{-1} yr^{-1})	LSU (ha^{-1} yr^{-1})	Reference
		Salt Marsh			
Salt marsh	German Wadden Sea	Intensive grazing	10 sheep	>1.5	(Stock, 2011)
Salt marsh	German Wadden Sea	Moderate grazing Intensive grazing	0.75-1.5 sheep 10 sheep	0.1-0.2 >1.5	(Kiehl et al., 2007)
Salt marsh	Marais Poitevin, Western France	Extensive grazing	0.6-1.3 cattle/horses	0.6-1.3	(Loucougaray et al., 2004)
Salt marsh	Schiermonnikoog (NL), Skallingen (DK) and Terschelling (NL)		0.08-0.5 cattle/sheep	0.08-0.5	(Bos et al., 2002)
Salt marsh	Schleswig-Holstein, Northern Germany	Un-grazed Moderate grazing Intensive grazing	- 3 sheep 10 sheep	0 0.45 1.5	(Neuhaus et al., 1999)
Salt marsh	German Wadden Sea	Un-grazed Moderate grazing Intensive grazing	- 1.5-4.5 sheep 10 sheep	0 0.2-0.7 1.5	(Berg, Esselink, Groeneweg, & Kiehl, 1997)
Salt marsh	German Wadden Sea	Un-grazed Moderate grazing Intensive grazing	- 1.5-4.5 sheep 10 sheep	0 0.2-0.7 1.5	(Kiehl et al., 1996)
Salt marsh	Leybucht, Niedersachsen, Northern Germany	Un-grazed Lightly grazing Moderate grazing Intensively grazing	- 0.5 cattle 1 cow 2 cattle	0 0.5 1 2	(Andresen et al., 1990)
Salt marsh	Schiermonnikoog, The Netherlands	Intensive grazing	1.3-1.7 cattle, June - October	1.3-1.7	(J. P. Bakker, 1985)
Salt marsh	Westerholt, The Netherlands		3 sheep	0.45	(J. P. Bakker et al., 1984)
Salt marsh	Schiermonnikoog, The Netherlands	Intensive grazing	1.3-1.7 cattle, June - October	1.3-1.7	(J. P. Bakker, 1978)

Table A1.1 (cont) | Grazing intensities in other studies.

System	Location	Grazing Information: Grazing Intensity	Animals (ha^{-1} yr^{-1})	LSU (ha^{-1} yr^{-1})	Reference
		Non-Salt Marsh			
Grassland	Patagonian Steppe	Moderate grazing	0.2 sheep	0.03	(Graff et al., 2007)
		Intensive grazing	0.4 sheep	0.06	
Grassland	Eastern Inner Mongolia	Light grazing	0.5 sheep	0.08	(Y. Zhao et al., 2007)
		Moderate grazing	1.2 sheep	0.18	
		Intensive grazing	2 sheep	0.30	
Grassland	Great Plain, Hungary	Light grazing	0.5 cattle	0.5	(Baldi et al., 2005)
		Intensive grazing	1 cattle	1	
Meadow	Fussingø manor, Denmark	Light grazing	4.5 sheep	0.68	(Schmidt et al., 2005)
		Intensive grazing	4.8 cattle	4.8	
Grassland	Northern Chinese steppe	Light grazing	0.5 sheep	0.08	(Xie & Wittig, 2004)
		Moderate grazing	0.5-1 sheep	0.08-0.15	
		Intensive grazing	>1 sheep	>0.15	
Grassland	Tibetan Plateau	Light grazing	2.55 sheep	0.38	(Cao et al., 2004)
		Intensive grazing	5.35 sheep	0.81	
Grassland	Schleswig-Holstein, North Germany	Light grazing	1.4 ± 0.1 cattle	1.4 ± 0.1	(Kruess & Tscharntke, 2002)
		Intensive grazing	5.5 ± 1.4 cattle	5.5 ± 1.4	
Grassland	Kansas Prairie	Light grazing	0.26 cattle	0.26	(Hickman & Hartnett, 2000)
		Moderate grazing	0.36 cattle	0.36	
		Intensive grazing	0.56 cattle	0.56	
Woodland	Haweswater, Cumbria, UK	Light grazing	0.6-1.2 sheep	0.09-0.18	(Hester, Mitchell, & Kirby, 1996)
		Moderate grazing	1.2-2 sheep	0.18-0.30	
		Intensive grazing	2.1-3.8 sheep	0.32-0.58	
Grassland	Great Plains, Montana	Light grazing	0.32 cattle	0.32	(Olson, White, & Sindelar, 1985)
		Moderate grazing	0.43 cattle	0.43	
		Intensive grazing	0.53 cattle	0.53	
Grassland	Great Plains, Colorado	Light grazing	0.25 cattle	0.25	(Havaren, 1983)
		Moderate grazing	0.32 cattle	0.32	
		Intensive grazing	0.56 cattle	0.56	
Grassland	Great Plains, Colorado	Light grazing	0.24 cattle	0.24	(Bement, 1968)
		Moderate grazing	0.32 cattle	0.32	
		Intensive grazing	0.56 cattle	0.56	
Grassland	Kansas Rangeland	Light grazing	0.20 cattle	0.20	(Launchbaugh, 1967)
		Moderate grazing	0.29 cattle	0.29	
		Intensive grazing	0.50 cattle	0.50	
Grassland	South Dakota Rangeland	Light grazing	0.31 cattle	0.31	(Rauzi & Hanson, 1966)
		Moderate grazing	0.41 cattle	0.41	
		Intensive grazing	0.74 cattle	0.74	

Appendix 2: Accretion Rates in Other Studies.

The accretion rate on salt marshes is an important component in understanding past carbon dynamics. The deeper the soil, the older it is, and thus soil at a certain depth will reflect the conditions and grazing regime at one particular time. The accretion rate can be used to estimate this, so for example if there was grazing 30 years ago and the accretion rate is on average 0.5 centimetres per year; one would have to sample soil at 15 centimetres (30 yr x 0.5 cm) depth to take soil from that period. Due to the short term nature of the broad-scale study (Chapters 3 & 4), it was impossible to estimate accretion rates for each site so an extensive literature study was used to estimate likely accretion rates for (a) the study sites, (b) other UK sites, (c) other European sites and (d) American sites. Accretion rates can vary considerably over one marsh, depending on tidal inundation frequency and marsh geomorphology (Adam, 1990b). The lower, younger zones are inundated frequently and sedimentation rates can be much greater than higher, more mature zones that are flooded only a few times a year. This is evident when looking at the two studies from the Dyfi Estuary: the earlier study (1934) finds high accretion rates (2.1-7.8 cm yr^{-1}) while a later study on the same marsh finds much lower accretion rates (1-1.15cm yr^{-1}). The initial high accretion rates on the lower marsh zones elevated the marsh surface, creating higher, more mature zones that are seldom inundated and show lower accretion rates. When estimating an average accretion rate for our sites, we placed more emphasis on recent studies and ignored studies looking only at the lower marsh zones. We estimated a conservative average accretion rate of 0.4cm per year for our study sites.

Table A2.1 | Accretion rates in different regions. Sedimentation rates for study sites (a), other UK marshes (b), other European marshes (c) and American marshes (d) showing marsh location, accretion rate in cm per year, methods used to collect the data, and the reference details.

Marsh Location	Accretion Rate (cm/yr)	Method Used	Reference
		(a) Study Sites	
Ribble Estuary	0.5	Historical mapping	(van der Wal et al., 2002)
Mersey Estuary:		Isotope analysis	(Fox et al., 1999)
• Widnes Warth	0.6		
• Ince Bank	0.8-3		
Dyfi Estuary	1.00-1.15	Marker layer + X-ray laminae counts	(Shi, 1992)
Dyfi Estuary	2.1-7.8	Marker layer	(F. J. Richards, 1934)

Table A3.1 (cont) | Accretion rates in different regions

Marsh Location	Accretion Rate (cm/yr)	Method Used	Reference
		(b) Other UK	
Blackwater Estuary, Essex	0.4	Modelling	(Shepherd et al., 2007)
Southampton, Hampshire	0.4-0.5	Isotope analysis	(Cundy & Croudace, 1996)
North Norfolk coast	0.1-0.8 (mean=0.39)	Marker layer	(French & Spencer, 1993)
The Wash, Essex	0.5	Sediment poles	(Reed, 1988)
North Norfolk coast	0.21-0.51	Marker layer	(Stoddart et al., 1983)
Somerset and Poole, Dorset	2.6-10.2	Marker layer and bamboo canes	(D.S. Ranwell, 1964b)
		(c) Other Europe	
Sylt, Germany	0.1-1.6	Pb-210 dating Cs-137 dating aerial photographs	(Schuerch et al., 2012)
Skallingen, Denmark	0.34	Cs-137 dating	(Andersen et al., 2010)
Hamburger Hallig, Schleswig-Holstein, Northern Germany	0.62	Sedimentation erosion table	(Stock, 2011)
Schleswig-Holstein, Northern Germany	1.2-2.1	Sedimentation erosion table	(Neuhaus et al., 1999)
Leybucht, Niedersachsen, Germany	1.7-2.3	Sediment plates	(Andresen et al., 1990)
		(d) America	
Orleans and Eastham, Massachusetts	0.22-2.4 0.38-0.45 0.26-0.42	Marker layer Cs-137 dating Pb-210 dating C-14 dating	(Roman, Peck, Allen, King, & Appleby, 1997)
Narragansett Bay, Rhode Island	0.15-0.60	Pb-210 dating	(Bricker-Urso et al., 1989)
Mississippi River Delta, Louisiana	0.59-0.94	Cs-137 dating	(Hatton, DeLaune, & Patrick, 1983)
Lewes, Delaware	0.5		(Stumpf, 1983)
Sapelo Island, Georgia	0.2-0.65		(Letzsch & Frey, 1980)
Louisiana	0.75-1.35	Cs-137 dating	(DeLaune et al., 1978)
Long Island Sound, Connecticut	0.20-0.66		(Harrison & Bloom, 1977)
Long Island Sound, Connecticut	0.47-0.64	Pb-210 dating	(Armentano & Woodwell, 1975)
Long Island Sound, Connecticut	0.15	Radiocarbon in peat	(Bloom, 1964)
Lewes, Delaware	0.6	Marker layer	(Stearns & MacCreary, 1957)