

Title:

The effects of elevated CO₂ and eutrophication on surface elevation gain in a European saltmarsh

Running head:

High CO₂ boosts saltmarsh resilience to SLR

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Abstract:

Saltmarshes can play a vital role in mitigating the effects of global environmental change by dissipating incident storm wave energy and, through accretion, tracking increasing water depths consequent upon sea level rise. Atmospheric CO₂ concentrations and nutrient availability are two key variables that can affect the biological processes that contribute to marsh surface elevation gain. We measured the effects of CO₂ concentrations and nutrient availability on surface elevation change in intact mixed-species blocks of UK saltmarsh using six open-top chambers receiving CO₂ enriched (800 ppm) or ambient (400 ppm) air. We found more rapid surface elevation gain in elevated CO₂ conditions: an average increase of 3.4 mm over the growing season relative to ambient CO₂. Boosted regression analysis to determine the relative influence of different parameters on elevation change identified that a 10% reduction in microbial activity in elevated CO₂ grown blocks had a positive influence on elevation. The biomass of *Puccinellia maritima* also had a positive influence on elevation, while other saltmarsh species (e.g. *Suaeda maritima*) had no influence or a negative impact on elevation. Reduced rates of water use by the vegetation in the high CO₂ treatment could be contributing to elevation gain, either directly through reduced soil shrinkage or indirectly by decreasing microbial respiration rates due to lower redox levels in the soil. Eutrophication did not influence elevation change in either CO₂ treatment despite doubling above ground biomass. The role of below ground processes (transpiration, root growth and decomposition) in the vertical adjustment of European saltmarshes, which are primarily minerogenic in composition, could increase as atmospheric CO₂ concentrations rise and should be considered in future wetland models for the region. Elevated CO₂ conditions could enhance resilience in vulnerable systems such as those with low mineral sediment supply or where migration upwards within the tidal frame is constrained.

Introduction:

The combination of chronic (a rising base level of accelerating sea level rise) and acute (increased magnitude and frequency of storm surges) environmental change are predicted to have severe impacts for many shorelines around the world (Wong *et al.*, 2014). Saltmarshes are the primary vegetated intertidal habitat in many temperate and subtropical regions, and are widely distributed along the European coastline (Dijkema, 1987). They can play a vital role in mitigating the effects of sea level rise and in coastal risk reduction through dissipating wave energy, promoting nearshore sediment retention and/or reducing surface erosion and sediment transport (Spalding *et al.*, 2014a, Spalding *et al.*, 2014b). Furthermore, unlike engineered structures, such systems have the potential, through surface vertical accretion, to track sea level rise and thus provide continued natural coastal protection over time (McIvor *et al.*, 2013). Geological evidence from the Holocene, when sea levels rose quickly, suggests that saltmarshes were able to keep pace with sea level rise when sediment supply was sufficiently high, thereby protecting inland habitats from inundation and maintaining the niche saltmarshes occupy within the intertidal zone (Allen, 2000, Kirwan & Temmerman, 2009). Modelling of contemporary changes in surface elevation in saltmarshes also suggests that some saltmarshes' vertical accretion could keep up with, or even outpace, near-future sea level rise (French, 2006, Kirwan *et al.*, 2016, Spencer *et al.*, 2016). A knowledge of the rates of, and controls on, surface accretion on saltmarsh surfaces is, therefore, of considerable interest and significance.

Vertical near-surface accretion rates in vegetated coastal habitats are the result of complex interactions between geomorphological (e.g. shallow subsidence, autocompaction and sedimentation rates (French, 2006)) and biological processes (e.g. root growth and organic matter accumulation (Cahoon *et al.*, 2000)). In micro-tidal

systems, remarkably minor (± 1 mm) changes in surface elevation can alter the inundation frequency and duration of inundation on marsh surfaces (Reed, 1990); thus even small changes in the processes contributing to vertical accretion gains, or losses, may be critical in determining the resilience of the ecosystem to sea level rise. It has been argued (Ford *et al.*, 2016, Shepard *et al.*, 2011) that saltmarsh vegetation characteristics are an important driver of changes in the rate of vertical accretion, through variation in productivity (and thus organic matter production contributions to sediments) and sediment retention. However, and unlike the information base on physical processes, the paucity of quantitative information on the role of biological processes, especially belowground production of roots, has been identified as a factor requiring further work in order to improve confidence in saltmarsh elevation models, particularly in European settings (Fagherazzi *et al.*, 2012, Shepard *et al.*, 2011).

Atmospheric CO₂ concentrations and nutrient availability are two key variables that can affect the biological processes that contribute to the vertical accretion of saltmarshes.

The steady rise in atmospheric CO₂ concentrations since the late 1800s is having a pronounced effect on plant growth and physiology of both terrestrial (Ainsworth & Long, 2005) and tidal wetland plants (Langley *et al.*, 2013, Reef & Lovelock, 2014), often leading to enhancement in root biomass. Similarly, increases in nutrient availability are also likely to lead to changes in plant growth and biomass allocation (Reef *et al.*, 2010), species composition and rates of decomposition of belowground biomass (Deegan *et al.*, 2012). All these factors may influence rates of vertical accretion in saltmarshes.

Evidence from North American saltmarshes suggests that for some saltmarsh species, elevated CO₂ could lead to positive effects on vertical accretion due to enhanced root growth (Langley *et al.*, 2009, Langley *et al.*, 2013; McKee, 2012; Ratliff, 2015, McKee *et al.*, 2012, Ratliff *et al.*, 2015). Generality of the CO₂ response over all biogeographic regions, however, cannot be assumed. This is largely due to the fundamental differences

between European and North American saltmarshes in species composition and diversity (e.g. the dominance of C4 photosynthesis species in North America compared to C3 species in the more floristically diverse European saltmarshes), minerogenic sediment supply and the saltmarsh position within the tidal frame (Mitsch, 1994).

Coastal habitats in Europe are affected by both atmospheric nitrogen deposition due to air pollution and widespread coastal eutrophication (Vermaat *et al.*, 2008). Under nutrient limiting conditions, plants allocate more biomass to below ground growth to increase exploration of the soil volume and the root surface area for nutrient absorption, as was shown experimentally for a number of wetland plants (Darby & Turner, 2008). Eutrophication can thus result in a reduction in the allocation of carbon to below ground biomass, which can lead to elevation loss on saltmarsh surfaces. Furthermore, eutrophication can lead to changes to plant tissue elemental stoichiometry and biochemistry that can enhance its decomposition rate (Wigand *et al.*, 2015), promoting further surface elevation loss. Multifactorial studies in North American marshes have shown contrasting effects of eutrophication in combination with elevated CO₂ on root production responses, finding either a synergistic effect on root production which has a positive effect on surface elevation in a mesocosm study (Langley *et al.*, 2013) or a negative effect on root production in a field study (Langley *et al.*, 2009), making the synergistic effects of elevated CO₂ and eutrophication on surface elevation gain due to organic contributions difficult to predict.

In this study we i) measured the effect of CO₂ and nutrient concentration on the below ground components contributing to vertical near-surface accretion in a UK saltmarsh using a mesocosm approach and ii) modelled the relative importance of biotic and abiotic factors on vertical accretion rate, measured through monitoring surface elevation change. By isolating the mixed-species saltmarsh community and its soil from

tidal influence within mesocosms, we removed the role of minerogenic sediment supply and focused on the role of biological influences (e.g. root biomass and microbial respiration) on the vertical adjustment of saltmarsh surfaces. We hypothesised that i) elevated CO₂ would have a positive effect on surface elevation gain due to increased plant growth rates and lower root decomposition rates associated with changes in tissue quality and ii) elevated nutrients would have a negative influence on elevation gain due to higher rates of microbial decomposition of root matter. We also hypothesised that iii) changes to CO₂ and nutrient concentrations would alter plant community structure.

Materials and Methods:

Saltmarsh blocks were collected from a saltmarsh along the Dengie Peninsula, Essex (N 051° 41' 38" / E 000° 56' 20") on 22 May 2015. We collected the blocks from a mid-marsh elevation of 2.4 m above mean sea level (MSL), 300 m from the seaward saltmarsh edge. Within this zone, we identified nine sites from which we carved out four 30 x 40 cm blocks of saltmarsh soil to a depth of 30 cm, which comprises most of the rooting depth in this location (Ford *et al.*, 2016), keeping the vegetation and root systems intact (n=36). By nesting the treatments within sites we controlled for spatial variations in plant composition and sediment characteristics. Analysis of short (10 cm) sediment cores from the collection site found the sediment to be predominantly clay and fine silts with a bulk density of 0.74 g cm⁻³ and total organic matter of 7.7% of the soil dry mass. The individual blocks were placed in plastic crates lined with geotextile. This allowed for the flow of water and nutrients but prevented root matter or sediment from exiting the crate. The blocks were immediately transported to the Cambridge University Botanic Gardens research plot.

Each crate was placed in a larger tray filled with 6.5 L of artificial seawater (Seachem Marine Salt, Seachem Laboratories, GA, USA) with a salinity of 35 ppt (the pore water salinity measured at the collection site), which covered the drainage holes to a depth of 7 cm. From 4 June 2015 nutrients were added to the saline solution according to the Hoagland liquid solution recipe (Hoagland & Arnon, 1950). The Hoagland solution provides all the nutrients necessary for plant growth and has a nitrogen (N), phosphorous (P) to potassium (K) ratio of 81:1.2:1. The stock solution was diluted in the saline water surrounding the crate to give either a low (1.5 mg l⁻¹ N, 0.02 mg l⁻¹ P) nutrient concentration or high (5 mg l⁻¹ N, 0.07 mg l⁻¹ P) concentration. The low nutrient concentration treatments were chosen to represent ambient conditions at the Dengie Peninsula (Parr *et al.*, 1999), while the high nutrient treatment was similar to annual mean nutrient concentrations for the eutrophic threshold in English estuaries (Painting *et al.*, 2007). The solutions were replaced every 10 days and additional replacements conducted following extreme rain events, which caused the solution in the tray to overflow. The rate of evaporation in the Cambridge region is low, and combined with regular rainfall, we found through visual inspection of the water level in the crates that solutions remained similar between changes. Apart from rainfall, irrigation was not applied to the soil or plant surface.

High and low nutrient saltmarsh blocks were then allocated among CO₂ treatments within open top chambers that were either ambient air or air enriched with CO₂ to a level of ca. 800 ppm (N=3; Table 1). Each of the four nutrient/CO₂ treatment combinations was replicated nine times, so that all nine collection sites were represented in each treatment. Six blocks were placed in each of six open top chamber. Of these, three received high nutrient and three low nutrient solutions. The positions of the blocks within each chamber were changed regularly. The experiment was conducted between 4 June 2015 until the harvest of the experiment on 4 November 2015.

We constructed 6 octagonal open top chambers from PVC pipe and clear greenhouse plastic sheet (Fig. 1a,b) on the research plots of the Cambridge University Botanic Gardens. A flexible pipe ($d = 15$ cm) with a fan unit was inserted into each chamber to provide ventilation. In three of the six chambers, CO₂ concentrations were elevated by injecting CO₂ gas from cylinders into the ventilation pipe. A CO₂ concentration control unit was placed at the centre of the chamber, at canopy height, and set to 800 ppm (DDAC-1 Digital Atmosphere Controller, Xiamen Superpro Technology Co., Xiamen, Fujian, China). When concentrations in the chamber fell below 750 ppm, the monitoring unit switched on a solenoid valve on the CO₂ cylinder regulator to inject CO₂ into the air stream. We elevated CO₂ concentrations in the chambers only during daylight hours (Fig. S1) which are long at this location during the boreal summer (ranging from 10 h to 16.5 h over the experimental period). Although there is growing evidence for an effect of elevated CO₂ on night time respiration rates, the effect of night time CO₂ enrichment on the growth parameters measured here such as root/shoot ratios, root biomass, total biomass or specific leaf area was not found to be significant (Griffin *et al.*, 1999). We monitored CO₂ concentration, temperature and humidity in all chambers using data loggers. The Cambridge University Botanic Gardens weather station was 10 m north of the research plot and provided additional meteorological data (Table 1, Fig. S1).

Surface Elevation Change:

Surface elevation change was measured using a custom made modification of the Surface Elevation Table (SET, Cahoon *et al.*, 2002), which is a device designed to measure at intervals the elevation of a sediment surface with a high degree of accuracy (± 1 mm). The custom table was made of a 28 x 28 cm measuring plate, supported by four aluminium legs raising the measuring plate 50 cm above the crate (Fig. 1c). A consistent height of the removable reference plate during each measurement time was

achieved by fixing the table to four notches on each crate during measurements. Nine holes in the measuring plate, with stainless steel collars, guided 1 m long fiberglass pins to the surface at sampling points, which remained fixed for all subsequent measurements. An initial (baseline) measurement was made on 29 June 2015, allowing for five weeks of settlement of the sediments in each crate following field collection. Changes to the height of the pins above the measuring plate in subsequent measurements indicated changes in surface elevation. The surface elevation change of each block was defined as the average change of the 9 pins per block relative to the baseline measurement.

Vegetation analysis

The saltmarsh blocks were removed from the field and continued to grow during the experiment with the mixed community vegetation intact. We identified seven species of saltmarsh plants (all C3 photosynthesis species) in the blocks during the growing season: the woody shrub *Atriplex portulacoides* (occurred in 100% of the blocks); the herbaceous annuals *Suaeda maritima* (95%) and *Salicornia* sp. (5%, for a few weeks); the herbaceous perennials *Puccinellia maritima* (72%); *Aster tripolium* (30%); *Cochlearia anglica* (22%); and *Limonium binervosum* (15%). During the cooler months (the time of collection) the UK saltmarsh perennial vegetation does not grow and annual species are yet to germinate; thus, the biomass present in the blocks at the final harvest developed during the experiment, but may have been influenced by variation in the initial biomass of perennial species. By comparing the effect of the treatment on blocks from the same site, and replicating this for nine sites, we constrained some of the spatial variability in plant communities and soil seed banks. In order to account for differences in the plant community, we conducted surveys of above ground vegetation cover within each treatment block at the start of the experiment and at monthly intervals. Species

composition and ground cover were estimated from photographs by sampling 100 computer generated random points per image.

The plants were harvested at the end of the growing season (4 November 2015) and above ground biomass separated by species. For the perennial woody shrub *Atriplex portulacoides*, we also separated leaf from stem biomass. Belowground biomass was removed from the sediment by sieving the mud through a 1000 μm stainless steel mesh using water pressure. Due to the high clay content in the soil, high water pressure was necessary for separating the roots from the soil leading to breakage of the root systems; thus it was not possible to separate the roots by species. Plant material was dried at 80°C for three days and weighed. Leaf area of *A. portulacoides* was measured prior to drying using the image analysis software, Image J (Rasband, 1997). Specific leaf area (SLA) was calculated as leaf area divided by dry weight.

Samples for root nutrient concentrations and isotopic composition were taken from finely ground roots from each block. All roots from each block were pooled before grinding. Samples were analysed for percentage carbon (by mass) and percentage nitrogen (by mass), at the Cambridge University Department of Earth Sciences using a Costech Elemental Analyser attached to a Thermo DELTA V mass spectrometer in continuous flow mode. The dried samples were carefully weighed into tin capsules, sealed and loaded into the auto-sampler. Phosphorous (P) tissue concentrations were measured for dry ground root samples using ICP-OES (Perkin-Elmer) at the Cambridge University Department of Geography.

The effect of the CO₂ and nutrient treatments on the measured parameters was determined using linear mixed-effect models with the block as the sampling unit and the

collection site as a random effect. Linear mixed effect models were performed using the *lme* function in the R package *nlme*.

Microbial community and activity

Physiological activity and functional diversity of the microbial communities in the saltmarsh soil was measured using BIOLOG ECOplates (Biolog, Hayward, CA, USA). Sediment cores were taken from the centre of each block by removing 1 ml of soil from the top horizon, avoiding fresh litter, using a brass volumetric soil sampler. The sediment cores were placed in 50 ml tubes and resuspended in 50 ml of sterile (0.2 µm filtered) 35 ppt salinity artificial seawater (Seachem Marine Salt, Seachem Laboratories, GA, USA). The tubes were left on a shaker at room temperature for 4 h to disperse the sediment core, and then removed from the shaker and left to settle overnight. The supernatant was then inoculated to BIOLOG ECOplates. The Ecoplate is a 96 well microplate that contains (in triplicate) 31 different carbon sources and a well with no substrate as a blank. A redox sensitive tetrazolium dye, which is not metabolized by fungi, is incorporated into each well. When a carbon source is utilised by the microbial community, the tetrazolium dye is reduced and this is indicated by purple colour development. To quantify colour development, we measured optical density at 595 nm using an iMark microplate reader (Bio-Rad Laboratories Ltd., Hercules, CA, USA) immediately following inoculation (0 h) and at 24 h, 48 h, 72 h and 96 h following inoculation. Between measurements, plates were kept at room temperature under low light conditions and exposed to ambient air.

The variety of carbon sources used by the microbial community from each soil core provided the community-level physiological profile (CLPP) (Garland & Mills, 1991) for each saltmarsh block. The average well colour development (AWCD) for each soil

sample at each time point was used to calculate the relative average metabolic rate (AMR). The AWCD data were fitted to a Weibull sigmoid growth curve and the rate parameter k (henceforth represented by AMR) was derived from the fitted kinetic equation and compared among treatments using a linear mixed effect model as described above. CLPP was analysed using non-metric multidimensional scaling of a Jaccard dissimilarity matrix among saltmarsh blocks based on presence/absence data (carbon source use or non-use) of the 31 carbon sources. The multivariate analysis was done in R package *vegan*.

Boosted Regression Tree analysis

We used predictive statistical modelling to determine the factors influencing surface elevation change in the saltmarsh blocks over the measurement period. The changes in surface elevation over the 5 month period in the 36 salt marsh blocks were modelled against nine predictor variables (Table 2) using boosted regression trees (BRT), a machine learning decision tree method reviewed in Elith *et al.* (2008). We used CV deviance and standard error (se) as the measure of model performance. The BRT gradient boosted model with gaussian loss function was run using *gbm.step* in the R package *dismo* (Elith *et al.*, 2008). 4050 iterations were performed, with a tree complexity of 4, a learning rate of 0.001 and bag fraction of 0.7. The final model includes 9 predictors, all of which had non-zero influence. The above ground biomass of species with low contributions (<5%) to aboveground biomass (*A. tripolium*, *C. anglica*, *L. binervosum*), initially included in the model, were found to have no influence on surface accretion and removed during model optimization. Root phosphorus (P) concentration was not included in the model since our experiment indicated plant growth was N, rather than P, limited. A test for collinearity among the predictors (*gbm.interaction*) revealed no significant interactions among the predictors in the final model.

Results

Elevated CO₂ concentrations led to a significant increase in surface elevation of saltmarsh blocks during the growing season (Linear mixed effect model, $F_{(1,25)} = 4.54$, $p = 0.04$, Fig. 2), which gained on average 2 mm of surface elevation by the end of the growing season (over 5 months). Under ambient CO₂ conditions, both high and low nutrient blocks showed a decrease in elevation over time. Nutrient levels had no significant effect on surface elevation gains at either CO₂ concentration.

The BRT model fitted to the data had an estimated CV deviance of 0.061 (± 0.01 SE). Although there were 9 variables included in the final model, surface elevation change was largely predicted by two factors (together contributing more than 60% to explaining surface elevation change in this study). These were the microbial respiration rate (relative influence of 33.5%) and the aboveground biomass of the perennial grass *Puccinellia maritima* (27.2%, Fig. 3, Table 3). Similar to the univariate analysis, which showed a significant increase in surface elevation under elevated CO₂ conditions, CO₂ concentration was also found to exert a positive influence (8.1%) on surface elevation gains in the BRT model (Fig. 3). Moreover, consistent with the univariate analysis, nutrient concentrations did not influence surface elevation gain in our model (Relative influence = 0.75%).

Predictors that had a negative influence on surface elevation gain were microbial respiration rate (relative influence 33.5%); the above ground biomass of the annual *Suaeda maritima* (8.8%); and the % cover of non-vegetated surfaces (6.73%, Fig. 3). Positive influences on surface elevation included the above ground biomass of *P. maritima* (27.2%); CO₂ concentration (8.1%); the concentration of nitrogen in root

material (5.7%); and belowground biomass (4.2%, Fig. 3). The effect of the CO₂ and nutrient treatment on these variables is provided in Table 3.

Microbial respiration rates in soil samples from elevated CO₂ blocks under aerobic conditions were significantly lower than from soil collected in the ambient CO₂ treatment ($F_{(1,24)} = 7.2$, $p = 0.01$, Fig. 4). Nutrient availability had no significant effect on average microbial respiration rates ($p=0.32$). Other parameters measured in this study did not significantly influence microbial activity measured in the BIOLOG ECOplates. To assess changes in the microbial community level physiological profile (CLPP), we created a Jaccard dissimilarity matrix based on presence/absence data for colour development in wells of the different carbon sources. We found no significant differences among treatments in the microbial community composition (Permutational ANOVA, 999 permutations, $F_{(1,35)} = 0.47$, $p = 0.88$ and $F_{(1,35)} = 0.95$, $p = 0.54$ for nutrient and CO₂ respectively).

Using photographic images, the vegetation community of the saltmarsh blocks was analysed in early June at the start of the experiment, and the % cover of the different species analysed using non-metric multidimensional scaling (NMDS). We found no significant differences among treatments in community composition or cover at the start of the experiment (Permutational ANOVA on Bray-Curits dissimilarity matrix, 999 permutations, $F_{(1,35)} = 0.02$, $p = 0.96$ and $F_{(1,35)} = 0.46$, $p = 0.67$ for nutrient and CO₂ respectively). Plant cover at this time of year was low, averaging 65% of the surface cover (increasing to >85% by the end of the experiment). Root N:P ratios (Table 3) were within the low range for northwest European saltmarshes. Root N:P ratios reported for mixed community European saltmarsh collected over a range of nutrient availability and inundation conditions averaged 6.7 (± 33.7 SD) (Minden & Kleyer, 2014), suggesting that in our experiment plant growth was limited by N rather than P availability.

Discussion

Surface elevation in the saltmarsh blocks showed a significant positive gain of more than 2 mm over the measurement period of 5 months in the elevated CO₂ treatments due to sub-surface expansion. In contrast, a loss of elevation (sub-surface compaction) was observed in the ambient CO₂ treatment over this time. In field and mesocosm studies in North-eastern USA elevated CO₂ also led to an increase in surface elevation over the growing season (Cherry *et al.*, 2009, Langley *et al.*, 2009), which was attributed to increases in below ground productivity. Nutrient addition did not lead to a significant change in surface elevation in either CO₂ treatment despite a doubling of above ground biomass.

There was no single factor that we could identify that led to the observed enhancement of surface elevation gain under elevated CO₂. Mean root biomass was slightly higher under elevated CO₂ (Fig. S2) and higher rates of surface elevation gain in this treatment coincided with the period of peak growth for UK saltmarshes (Boorman & Ashton, 1997) suggesting a role for enhanced plant growth in elevation gain; decomposition may have been lower as indicated by the lower microbial respiration in the BIOLOG plate assay.

Additional to these factors for which we have evidence for a contribution, elevated CO₂ may also have influenced the physical environment of the sediment, e.g. by decreasing redox potential (Davy *et al.*, 2011, Megonigal & Schlesinger, 1997), and thereby inhibiting organic matter decomposition. Moreover, changes in root structure have been observed for plants growing under elevated CO₂ (Reef *et al.*, 2015), which could also influence surface elevation non-linearly with root biomass. This could be due to

potential variation in specific root length (volume per biomass, Ostonen *et al.*, 2007) and variation in contribution of different species that respond differentially to elevated CO₂ (Jastrow *et al.*, 2005). The proportion of bare sediment surface was lower under elevated CO₂ which may have protected the marsh from erosion during rainfall events (although the high clay content of the soil suggests significant erosion is unlikely even on bare sediments, and we did not observe noticeable amounts of sediment in the trays during solution replacements).

We measured 2.2 mm of elevation loss in our ambient CO₂, nutrient enriched blocks over the summer period. Sediment shrinkage during the summer months is commonly observed in European marshes (Oenema & DeLaune, 1988, Spencer *et al.*, 2012, Stock, 2011) and is a reversible pattern suggested to be caused by physical desiccation, shrinkage and enhanced vegetation transpiration rates (Spencer *et al.*, 2012). The role of desiccation in surface elevation dynamics may suggest that the higher elevation gain we observed in the CO₂ enriched blocks could be linked to lower rates of desiccation.

Desiccation in NW European marshes, which are generally situated high in the tidal frame, is commonly observed in the summer months as a result of lower spring tides and higher water deficit conditions (Smith *et al.*, 1998). Intrinsic water use efficiency (WUE), measured using gas exchange (Fig. S3) showed a significant increase in WUE and a reduction in calculated intrinsic total canopy water use for *A. portulacoides* in the blocks under elevated CO₂ conditions, in line with accepted theory that elevated CO₂ reduces C3 plant transpiration (Morison, 1985, Polley *et al.*, 1993). Increased water use efficiency is a plant response to rising atmospheric CO₂ concentration that persists over decades (Keenan *et al.*, 2013, Peñuelas *et al.*, 2011), suggesting that this short term enhancement (one growing season) of water use efficiency is likely to continue over time, as has been shown for saltmarshes in N America that have been growing under elevated CO₂ conditions for 12 years (Li *et al.*, 2010). This could have led to reduced

rates of desiccation and thus lower rates of shrinkage, contributing to higher elevation gains under elevated CO₂ conditions during the growing season. Desiccation in ambient CO₂ blocks could have also influenced soil redox, by improving entry of oxygen into the blocks thereby increasing microbial respiration (carbon mineralisation) rates (D'Angelo & Reddy, 1999), which is supported by our aerobic respiration data.

The presence and biomass of *Puccinellia maritima* had a positive influence on surface elevation gain. The importance of this species in stabilising and trapping sediments has been highlighted in field (Langlois *et al.*, 2003), flume (Spencer *et al.*, 2015) and glasshouse (Langlois *et al.*, 2001) studies. Here we were able to isolate the biogenic contribution of *P. maritima* to surface elevation changes due to there being no sediment input to the mesocosms, and thus provide evidence for the significant role the *P. maritima* root system plays in determining marsh topography. *Puccinellia maritima* is a perennial grass with a creeping, fibrous rooting system. In addition to the primary roots, it can produce many tillers from which adventitious roots form, making it an important contributor to shallow marsh root biomass (Gray & Scott, 1977).

The remarkable role of this species in surface elevation gain, both through biogenic and sediment trapping processes (e.g. Langlois *et al.*, 2003), indicates that changes to the abundance of this species could have significant impacts on marsh topography and resilience to sea level rise. Grazing can have a significant positive effect on the presence and dominance of this species (Bos *et al.*, 2002, Kiehl *et al.*, 1996) although there are concerns that, primarily on grazed saltmarshes, *P. maritima* from the mid and low marsh is being replaced by *Elymus athericus*, a native invasive clonal grass with an original distribution confined to the high marsh (Valéry *et al.*, 2004). Changes to *P. maritima* distribution could also be caused by climate change. Experimental work on *P. maritima* grown in pots suggests that the growth response of *P. maritima* to elevated

CO₂ is small and that biomass allocation to shoots and roots remains similar under different CO₂ concentrations (Lenssen *et al.*, 1995). Our study also finds that the growth of this species is not likely to be affected by increases in atmospheric CO₂ concentrations. However, species distribution modelling predicts a loss of suitable habitat for *P. maritima* under future climate scenarios, driven by increasing water deficits that could lead to a loss of this species from saltmarshes throughout the British Isles but especially in East and South England by 2050 (Berry *et al.*, 2002). The importance of *P. maritima* for surface elevation gains, along with the *P. maritima* distribution modelling suggest that climate change may lead to significant topographic effects and elevation deficit in UK marshes.

Unlike in many North American marshes, the surface elevation gain in European marshes is primarily due to mineral sediment deposition (Allen, 2000, French, 2006), thus saltmarsh models used for the prediction of saltmarsh evolution and sustainability with sea level rise in this region have so far not incorporated below ground processes (e.g. Schuerch *et al.*, 2013, Temmerman *et al.*, 2004). Our experimental data suggests that the role of below ground processes in European saltmarshes, whilst not currently key to surface elevation gain, is likely to become more significant as atmospheric CO₂ concentrations rise. We show here that under elevated CO₂ conditions, the capacity for maintenance of elevation in European marshes through biological processes becomes considerable, potentially enhancing resilience in vulnerable systems such as those with low mineral sediment supply. European saltmarsh models should thus include below ground processes in future predictions.

Higher rates of biologically controlled surface elevation gain can afford resilience to saltmarshes where mineral sediment supply is not sufficient for surface accretion to keep up with rising sea levels (Spencer *et al.*, 2016). Under elevated CO₂ conditions, such

as those predicted by the IPCC (Myhre *et al.*, 2013), biologically controlled surface elevation gain will be significantly enhanced and could alleviate some of the pressures exerted upon salt marsh ecosystems by an increase in sea level. However, the species composition of the saltmarsh has a significant effect on surface elevation gain as well and the differential response of individual species to climate change could further confound predictions of the response of temperate saltmarshes to such change.

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Tables:

Table 1: Mean (SD) of temperature (T), relative humidity (RH) and [CO₂] conditions in the six open top chambers between 2 June and 4 November 2015. Measurements were taken every 2 minutes (Fig. S1). N/A indicates missing data. Total rainfall for this period was 195 mm. There were no air frost days. Temperature and relative humidity (RH) were not significantly different among chambers. Differences in CO₂ concentrations between chambers of the same CO₂ treatment were not statistically significant.

Chamber	Daytime (10:00-16:00 GMT)			Night-time (00:00-03:00 GMT)		
	T °C	RH %	CO ₂ ppm	T °C	RH %	CO ₂ ppm
1-ElevatedCO ₂	22.4 (6.8)	69.8 (20)	798 (213)	12.2 (3.2)	91.9 (40)	389.3 (4)
2-Elevated CO ₂	21.9 (6.4)	69.1 (19)	798 (210)	11.8 (3.4)	91.2 (40)	413.1 (33)
3-Ambient CO ₂	21.9 (6.4)	N/A	389 (23)	12.3 (3.5)	N/A	403.2 (5)
4-Ambient CO ₂	20.6 (5.9)	71.4 (21)	N/A	12.5 (3.4)	94 (9)	N/A
5-Elevated CO ₂	22.0 (6.4)	67.1 (18)	798 (270)	11.7 (3.3)	88.2 (34)	395.5 (11)
6-Ambient CO ₂	22.6 (4.2)	N/A	387 (17)	13.2 (2.3)	N/A	400.1 (6)

Table 2: Factors (both continuous and categorical) included in the final boosted regression tree model to predict surface accretion rates in the saltmarsh blocks, along with their minimum, maximum and mean values.

Factor	Type	Min	Max	Mean
[CO ₂] ppm	Categorical	400	800	n/a
[Nutrient]	Categorical	Low	High	n/a
<i>A. portulacoides</i> biomass (g)	Continuous	1	129.2	44.8
Microbial metabolic rate (AMR)	Continuous	0.009	0.021	0.015
Non-vegetated area (%)	Continuous	3	38	15.3
<i>P. maritima</i> biomass (g)	Continuous	0	83.3	11.5
Belowground biomass (g)	Continuous	64.6	376.2	144.5
Root %N	Continuous	0.75	1.76	1.26
<i>S. maritima</i> biomass (g)	Continuous	0	149.6	32.4

Table 3: Mean (SD) values for vegetation characteristics in the saltmarsh blocks (surface area = 0.12 m²) following 5 months of growth with different nutrient and CO₂ concentrations. AGB = above ground biomass, BGB = below ground biomass, SLA = specific leaf area. * Predictors included in the BRT model. Different letters denote significant differences among treatments (p<0.05), N = 9 for each measurement.

Parameter	Ambient CO ₂		Elevated CO ₂	
	Low Nutrient	High Nutrient	Low Nutrient	High Nutrient
Total AGB (g)	68.5 (37.3) ^a	131.3 (21.8) ^b	59.4 (20.7) ^a	119.1 (24.7) ^b
Total BGB (g) *	129.2 (71.6) ^a	151.1 (34.8) ^a	132.6 (60.9) ^a	165.1 (96.0) ^a
<i>A. portulacoides</i> AGB (g) *	42.7 (47.2) ^a	47.3 (37.4) ^a	22.8 (15.4) ^a	66.5 (35.3) ^a
<i>P. maritima</i> AGB(g) *	11.6 (13.2) ^a	7.6 (8.9) ^a	14.1 (27.5) ^a	12.5 (9.8) ^a
<i>S. maritima</i> AGB (g) *	9.1 (6.5) ^a	72.7 (50.3) ^b	14.7 (9.1) ^a	33.3 (24.9) ^c
<i>L. binervosum</i> AGB (g)	0.4 (1.3) ^a	0.6 (1.6) ^a	0.009 (0.03) ^a	0.5 (1.6) ^a
<i>A. tripolium</i> AGB (g)	4.6 (9.8) ^a	3.0 (6.9) ^a	7.6 (14.8) ^a	6.2 (13.7) ^a
<i>C. anglica</i> AGB (g)	0.1 (0.07) ^a	0.04 (0.5) ^a	0.09 (0.2) ^a	0.07 (0.14) ^a
<i>A. portulacoides</i> SLA (cm ² g ⁻¹)	97.6 (28.3) ^a	97.5 (13.6) ^a	98.1 (23.2) ^a	98.3 (16.6) ^a
Root:Shoot Ratio	2.3 (1.5) ^a	1.2 (0.3) ^b	2.6 (1.9) ^a	1.4 (0.7) ^b
Root C:N	29.4 (4.1) ^a	27.9 (2.5) ^a	27.5 (3.2) ^a	27.1 (3.1) ^a
Root N:P	4.1 (1.8) ^a	3.6 (1.6) ^a	4.7 (2.8) ^a	4.5 (1.5) ^a
Root N (%) *	1.2 (0.2) ^a	1.2 (0.3) ^a	1.3 (0.3) ^a	1.4 (0.3) ^a
Non-vegetated area (% cover) *	20.6 (7.4) ^a	11.4 (6.7) ^b	20.7 (10) ^a	8.5 (4.4) ^b

Figure Legends:

Figure 1: A schematic of the open top chambers (a) side view and (b) top view showing the shape and dimensions of the chambers and location of ventilation pipe, saltmarsh blocks, CO₂ controller and data loggers (white point bullet). (c) Schematic of the custom Surface Elevation Table (SET), shown attached to the slots on the saltmarsh block crate and with measurement pins in positions 5 and 7 (out of 9 possible positions).

Figure 2: Mean (\pm SE) surface elevation change over time relative to the June baseline measurement. N = 9 saltmarsh blocks for each point. Square symbols are ambient CO₂ (400 ppm), round symbols are elevated CO₂ (800 ppm), filled symbols are high nutrient and open symbols low nutrient treatment.

Figure 3: Boosted regression tree analysis partial dependence plots, visualising the relationship between each predictor and surface elevation change after accounting for the average effect of all other predictors in the model. The relative influence (%) of each predictor on surface elevation change is included in each panel (top right). Values above the dotted line indicate a positive effect on surface accretion, and values below the dotted line denote a negative effect. The relative influence of the nutrient treatment was <1%.

Figure 4: Average (\pm SE) well colour development over time of the nine soil samples from each treatment. Square symbols are ambient CO₂ (400 ppm), Round symbols are elevated CO₂ (800 ppm), filled symbols are high nutrient treatments while open symbols are low nutrient. The kinetic function fitted to the data (solid line, elevated CO₂, broken line, ambient CO₂ concentration) is the Weibull distribution function ($R^2 = 0.88, 0.82, 0.74$ and 0.86 and rate coefficient $k = 0.0158, 0.0155, 0.014$ and 0.014 for 400 ppm/Low

Nutrient, 400 ppm/High Nutrient, 800 ppm/Low Nutrient and 800 ppm/High Nutrient respectively).

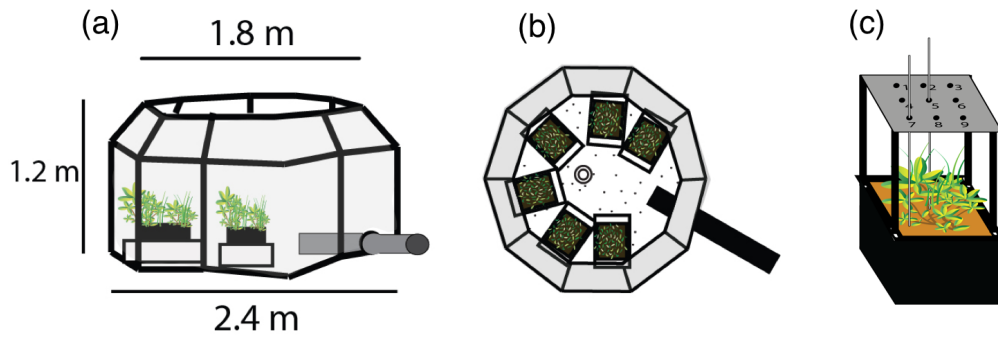


Figure 1

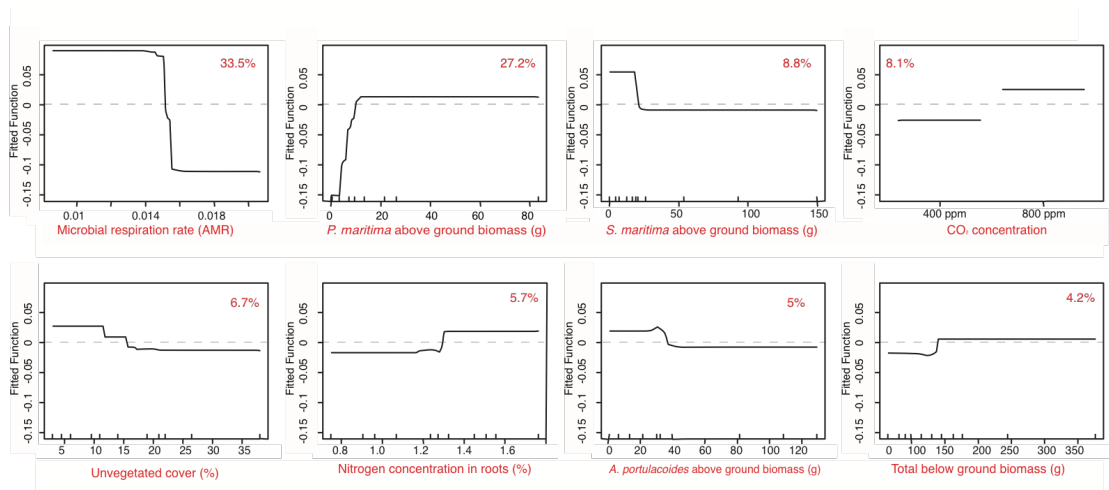


Figure 2

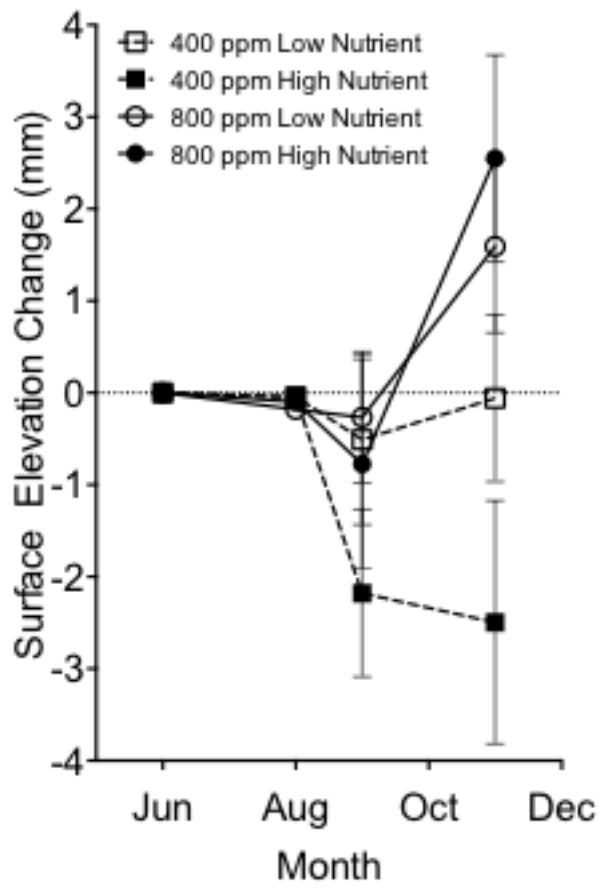


Figure 3

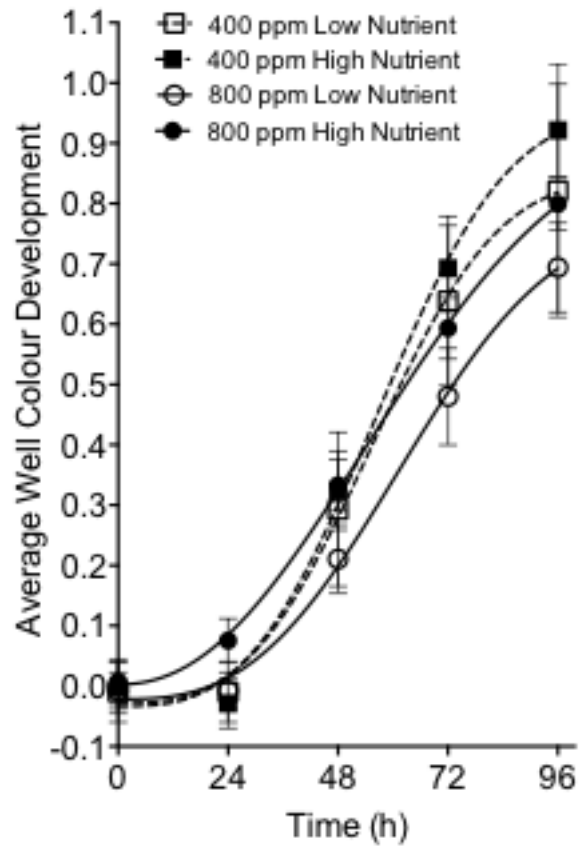


Figure 4

Supplementary Figure 1: An example of diurnal variations in CO₂ concentrations (black solid line) and temperature (red dotted line) in an open top chamber on the 21/7/2015.

Supplementary Figure 2: Surface elevation change (mm) over the five-month measurement period as a function of standing root biomass (g) for blocks receiving either ambient (open circles) or elevated (closed circles) CO₂ concentrations. The fitted line is of the form $Y=0.008X-1.19$ ($R^2 = 0.04$). The slope of the regression is not significantly different to 0 ($p = 0.2$).

Supplementary Figure 3: (a) Leaf water use efficiency measured between 10:00-13:00 for *Atriplex portucaloides* using a Licor-6400 gas exchange photosynthesis machine following five months of growth in the mesocosms. WUE_i was calculated as C assimilation rate (A) divided by stomatal conductance (Gs). (b) Canopy transpiration rate for that period was calculated from stomatal conductance and total *A. portucaloides* leaf area. Each bar represents the mean for each block. Each block was represented by three leaf measurements. Filled bars are the mean for blocks from the elevated CO₂ treatment and open bars the mean for plants grown under ambient CO₂ concentrations.

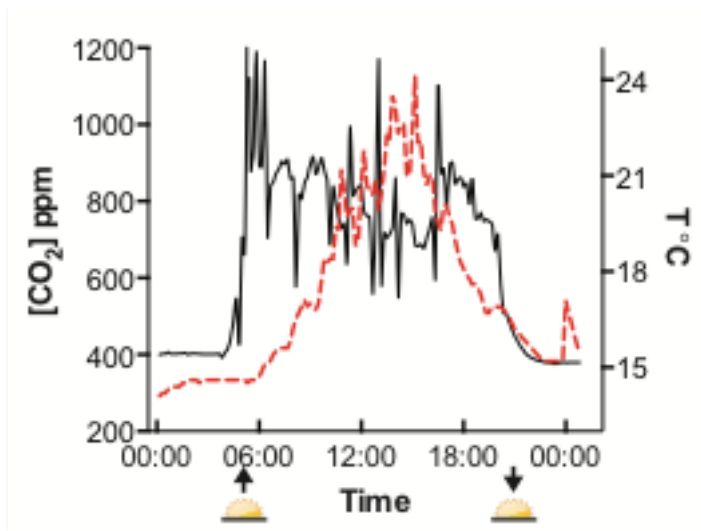


Figure S1

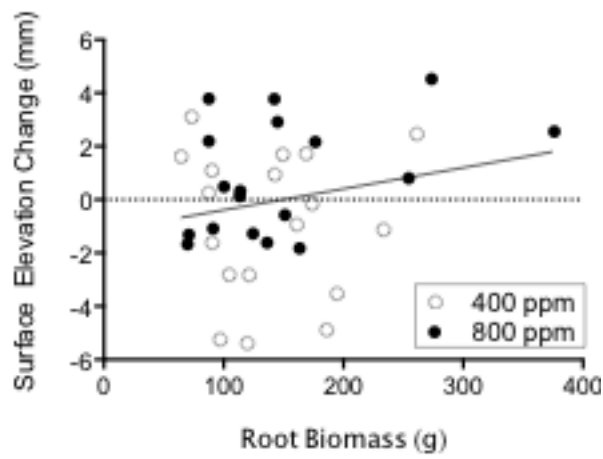


Figure S2

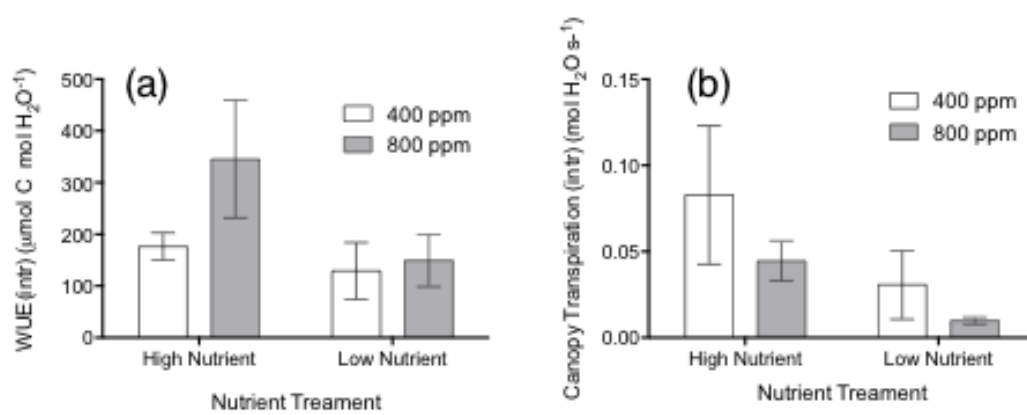


Figure S3