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Abstract Root-aerenchyma in wetland plants facilitate transport of oxygen from aboveground sources (atmosphere and photosynthesis) to belowground roots and rhizomes, where oxygen can leak out and oxygenate the otherwise anoxic soils. In salt marshes, the soil oxygenation capacity varies among different *Spartina*-taxa, but little is known about structural pattern and connectivity of root-aerenchyma that facilitates this gas transport. Both environmental conditions and ploidy level play a role for the root-system morphology. Root-system morphology of polyploid *Spartina*-taxa was studied, quantifying root-tissue volume and root-aerenchyma volume of hexaploid *Spartina alterniflora*, *Spartina maritima*, and *Spartina* × *townsendii* as well as dodecaploid *Spartina anglica* from different habitats. Computed tomography (CT)-scan image analysis was applied to quantify the volume of roots and aerenchyma, and to determine the root-system structure (ratio of aerenchyma to root-tissue volumes) and aerenchyma connectivity. On average, *Spartina*-roots accounted for 12% (v/v) and root-aerenchyma accounted for 1% (v/v) of the soil volume in the pioneer marsh. About 90% (v/v) of all roots were associated with aerenchyma. Root-system structures of

S. × *townsendii* and *S. anglica* differed and showed clear responses to habitat conditions, such as flooding regime and redox potential. The development of large well-connected aerenchyma fragments were specifically shown in *S. anglica* and to a minor extend in *S. maritima*. Aerenchyma in *S. alterniflora* and *S.* × *townsendii* consisted only of smaller fragments. *Spartina*-dominated tidal pioneer marsh soils show high connectivity with the atmosphere via root-aerenchyma. The high ploidy level in *S. anglica* comes along with high connectivity in root-aerenchyma.

Keywords: marker-controlled watershed segmentation · skeleton analysis · tidal salt marsh ecosystem · *Sporobolus* · polyploidization · whole genome duplication

1 Introduction

Spartina-populations cover substantial areas in tidal wetlands around the globe (e.g., An et al., 2007; Esselink et al., 2009; Strong and Ayres, 2013; Bortolus et al., 2015). *Spartina*-plants are known for their capacity to engineer coastal habitats (Hulzen et al., 2007; Balke et al., 2012), catching and fixing tidal sediments (e.g., König, 1948; Ranwell, 1967), oxygenating the soil via plant-mediated oxygen transport (Teal and Kanwisher, 1966; Maricle and Lee, 2007; Koop-Jakobsen et al., 2017), and thereby facilitating nitrogen retention (Hamersley and Howes, 2005; Koop-Jakobsen and Giblin, 2010; De Lange and Paulissen, 2016). The belowground biomass structure and oxygen transport capacity of perennial *Spartina* grasses play a key role for these ecosystem functions in salt marshes and for connecting tidal soils with the atmosphere.

Spartina thrives in low-laying salt marshes (pioneer zone) and withstand waterlogged anoxic and sulfidic soil conditions as well as daily flooding by sea water (Gray et al., 1991). In this stressful environment, belowground oxygen transport plays a key-role providing

oxygen for root respiration. Furthermore, roots can leak oxygen to the rhizosphere, mainly near the root-tips (Armstrong, 1972; Visser et al., 2000; Koop-Jakobsen and Wenzhöfer, 2015), where oxygen improves nutrient uptake (Bradley and Morris, 1990; Lai et al., 2012) and acts as an oxidant that decreases the impact of toxic, reduced inorganic compounds, especially H_2S, by oxidizing them (Lee et al., 1999; Pezeshki, 2001; Lee, 2003).

To facilitate oxygen transport to root-cells in waterlogged soils, many wetland plants exploit air-filled spaces inside roots, commonly termed aerenchyma (Justin and Armstrong, 1987; Jackson and Armstrong, 1999; Evans, 2004). The translocated oxygen originates directly from the atmosphere and from photosynthesis (Koop-Jakobsen and Wenzhöfer, 2015; Koop-Jakobsen et al., 2018), and can be passed through the stem via channels of low gas-flow resistance into the root-aerenchyma, by pressurized continuous gas-flow driven by venturi- and humidity-induced convection (Armstrong et al., 1992; Brix et al., 1992; Armstrong and Armstrong, 2009).

Root-aerenchyma formation can alter the biomechanical characteristics of roots (Justin and Armstrong, 1987). Justin and Armstrong (1987) demonstrated that wetland species show predominantly cubic cell packing in the cortex of roots as a prerequisite for effective lysigenous aerenchyma formation by apoptotic cell death under waterlogged conditions. Opposed to cubic packing, hexagonal packing of cells in the root cortex provides a higher resistance against biomechanical stress (Justin and Armstrong, 1987). As a response to mechanical stress imposed by the conditions in salt marsh habitats, a significant proportion of hexagonal packing was observed in *Spartina anglica* (Justin and Armstrong, 1987). At the same time, *Spartina*-taxa exhibit a high capacity to form aerenchyma in response to waterlogged conditions (Maricle and Lee, 2007). This leads to the assumption of a trade-off between the suitable root-oxygenation by forming aerenchyma and the maintenance of biomechanical integrity of roots by avoiding aerenchyma.

The biomechanical integrity of roots (high tensile strength) is regarded as a prerequisite for anchoring in unstable soils of salt marsh and periglacial environments (Van Eerdt, 1985; Hudek et al., 2017a). In salt marshes, plants have to cope with varying habitat conditions of both a high demand of roots for oxygen imposed by waterlogged conditions and tides (e.g., Koop-Jakobsen and Gutbrod, 2019; Mueller et al., 2020) as well as physicomechanical stress imposed by hydrodynamic forces (tidal currents and waves; e.g., French and Stoddart, 1992; Widdows et al., 2008; Callaghan et al., 2010; Edmaier et al., 2011; Belliard et al., 2019). Therefore, the root-system structure, i.e., the spatial distribution of root-tissue and root-aerenchyma in the three-dimensional (3D) root-system, is an important factor for the establishment and survival of *Spartina* plants in salt marsh habitats.

Different phenotypes driven by variation of soil chemistry are well-known for the aboveground biomass (Valiela et al., 1978; Mendelssohn et al., 1981; Mendelssohn and McKee, 1988) and the belowground biomass (Thompson et al., 1991; Redelstein et al., 2018) in *Spartina*. Four polyploid *Spartina*-taxa are common on European saltmarshes (Marchant, 1967, 1968): The native hexaploid *Spartina maritima* (Curtis) Fernald (2n = 6x = 60), the introduced (native American) hexaploid *Spartina alterniflora* Loiseleur (2n = 6x = 62), their homoploid F_1-hybrid *Spartina* × *townsendii* H. Groves & J. Groves (2n = 6x = 62), and their derived allododecaploid *Spartina anglica* C.E. Hubbard (2n = 12x = 120 — 124), which has rapidly expanded in range since its formation during the 19th century (Ainouche et al., 2009). The hybrids *S.* × *townsendii* and *S. anglica* inhabit a wide variety of habitats and marsh zones (e.g., Gray et al., 1991; Hacker et al., 2001; Granse et al., 2020) in- and outside the parental range (e.g., Maricle et al., 2006; Wong et al., 2018; Proença et al., 2019, Granse et al., accepted). *S. anglica* and parental *S. alterniflora* have gained attention as invasive species which spread in coastal habitats around the globe (e.g., Ranwell, 1967; An et al., 2007; Strong and Ayres, 2013; Bortolus et al., 2015; Shang et al., 2019). The high affinity of both

S. anglica and *S. alterniflora* for belowground relocated oxygen is considered to be beneficial in hypoxic soils and may increase their invasive success (Maricle et al., 2006; Maricle and Lee, 2007).

Polyploidy has been shown as an important mechanism shaping *Spartina*-genome evolution (Ainouche et al., 2012) as well as phenotypic evolution, including stress tolerance and plasticity in these species (Cavé-Radet et al., 2018). Another immediate consequence of polyploidization is described as the so-called "gigas effect", indicating marked increases in cell size that can result in general in larger structures, like e.g., larger flowers, pollen grains, and seeds (Müntzing, 1936; Stebbins, 1971; Ramsey and Schemske, 2002; Meeus et al., 2020). Studies have also demonstrated that polyploidization can cause allometric effects due to larger cell and tissue volumes (Finigan et al., 2012; Doyle and Coate, 2019; Roddy et al., 2019; Fox et al., 2020), which has been shown to alter the vascular transport network resulting in higher hydraulic conductivity of the xylem (Maherali et al., 2009). Therefore, *Spartina*-taxa with different ploidy levels (hexa- and dodecaploid) may show a marked variation in root-system structure and aerenchyma.

Oxygen transport from the atmosphere to the root tips requires that aerenchyma provide an unbroken airspace-compartment from the stems to the roots (Teal and Kanwisher, 1966). By comparing aerenchyma development responses to flooding (Maricle and Lee, 2002) and gas-flow capacities (Lee, 2003), dodecaploid *S. anglica* was shown to transport oxygen more efficiently to root cells than hexaploid *Spartina alterniflora*, which may be based on ploidy level effects.

Medicinal computed tomography image analysis facilitates studying the 3D root morphology of vegetation in undisturbed tidal marsh soils (Davey et al., 2011; Blum and Davey, 2013; Hanson et al., 2016; Wigand et al., 2016). CT-scanning enables the distinction

of air-spaces, organic structures and mineral particulates by means of a standardized X-ray response (Hounsfield units HU; Hounsfield, 1979), which allows the 3D root-system structures (root-tissue and root-aerenchyma) to be reconstructed in-silico using segmentation and skeleton analysis methods (Gao et al., 2019; Chirol et al., 2021).

In this study, CT-scanning was applied to investigate the root-systems of four *Spartina*-taxa (Fig. 1), which represent a particularly suitable model system to explore the consequences of recent hybridization and polyploidy (Ainouche et al., 2012). The study aims to elucidate the difference among taxa naturally occurring along the Atlantic coastline of Northern Europe: the F_1-hybrid *S.* × *townsendii* and the neododecaploid *S. anglica* in the following termed *Spartina*-hybrids, as well as the maternal parent *S. alterniflora* and paternal parent *Spartina maritima*, in the following termed (hexaploid) *Spartina*-parents or parental taxa. *Spartina*-hybrids grow in close vicinity to each other at sites in the eastern part of the European Wadden Sea (Granse et al., accepted), while parental taxa can be found at the Atlantic coast in France (Fig. 2A). The differences in root-system structures can be identified by the proportion of roots associated with aerenchyma and the ratio of aerenchyma to root-tissue. Thereby, roots with discontinuous aerenchyma will have structural functions, such as maintaining the biomechanical integrity of roots, but show resistance to gas-flow. Therefore, in addition, aerenchyma connectivity is estimated from continuous aerenchyma as a proxy for the capacity of unimpeded gas-exchange between the atmosphere and root-cells.

In order to elucidate the impact of habitat conditions and polyploidization, we hypothesize that

- *Spartina* shows distinct root-system structures in response to habitat conditions differing in flooding regime, soil characteristics, and tidal hydrodynamics, and

- *Spartina*-taxa of different ploidy levels (hexa- and dodecaploid) show distinct root-system structures when growing in similar habitat conditions, and
- the allododecaploid *S. anglica* shows a higher aerenchyma connectivity than the hexaploid F_1-hybrid and its parental *Spartina*-taxa.

2 Methods

2.1 Study design

Figure1.pdf; See also affiliated PDF-file version!

Fig. 1: Illustration of kinship relations between *Spartina*-taxa with respect to ploidy levels (hexaploid, dodecaploid), F_1-hybrid formation and whole genome duplication (polyploidization), adapted from Ainouche et al. (2012).

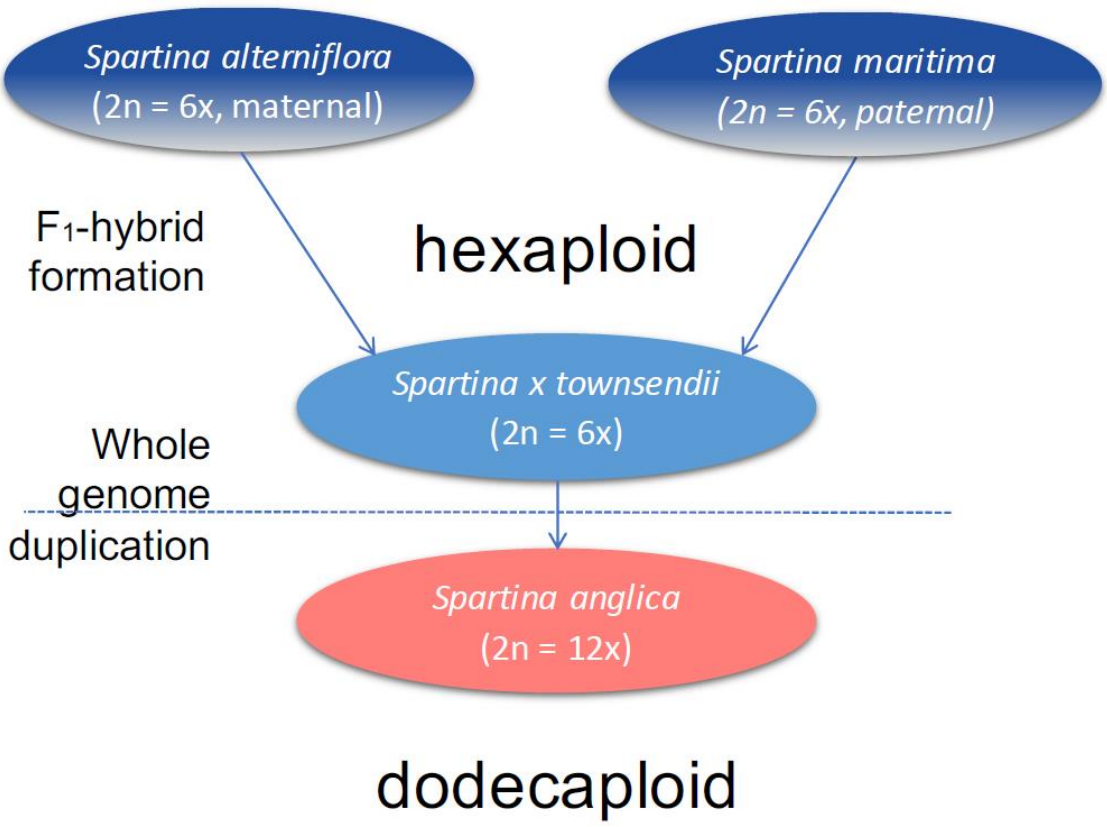
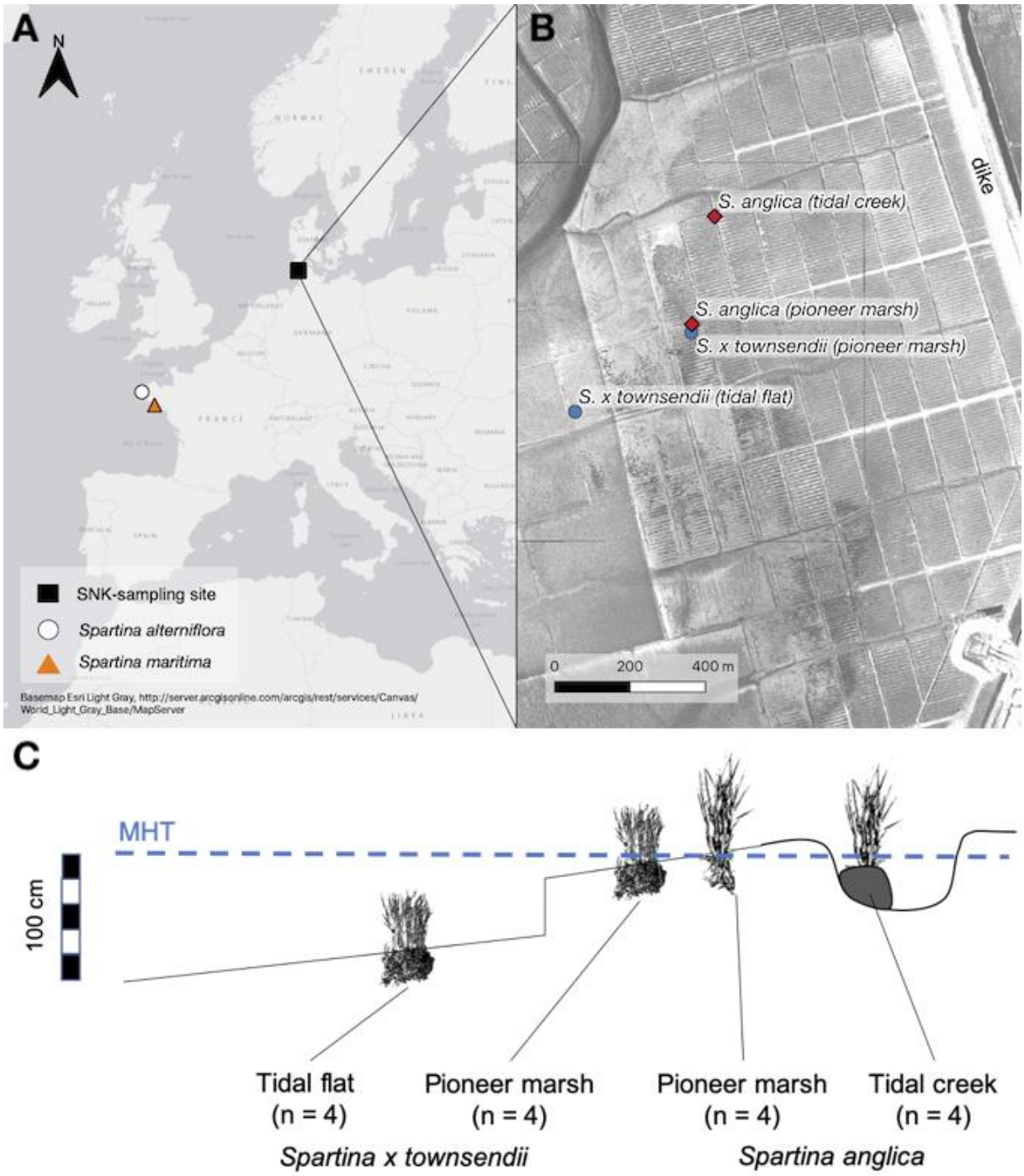


Figure2.png; See also affiliated PDF-file version!

Fig. 2: A) Sampling sites of *Spartina* soil cores at the Atlantic coast in Brittany, France (*S. alterniflora*, *S. maritima*), and in the European Wadden Sea (*S.* × *townsendii*, *S. anglica*) at Sönke-Nissen-Koog (SNK), Schleswig-Holstein, Germany. B) Positions of sampled *Spartina* at SNK in different habitats. C) Scheme of sampling positions of *S.* × *townsendii* (habitats: tidal flat and pioneer marsh) and *S. anglica* (habitats: pioneer marsh and tidal creek) at the SNK study site with respect to the elevation of sampling positions to mean high tide (MHT; see also environmental parameters in Table 1).



The parental *Spartina*-taxa of the hybrids were sampled at the Atlantic coast in Brittany, France (*S. maritima*: Plouharnel, 47◦ 35’N 3◦ 07’W; *S. alterniflora*: Faou estuary, 48◦ 17’46"N 4◦ 11’00"W; Fig. 2A).

In order to investigate the impact of environmental conditions on the development of the belowground biomass, hexaploid *S.* × *townsendii* and dodecaploid *S. anglica* were collected at Sönke-Nissen-Koog, Schleswig-Holstein, Germany (SNK; 54◦ 36'N 8◦ 53'E; Fig. 2B), considering differences in elevation, bulk density, soil redox potential, and microhabitat (tidal flat, pioneer marsh, tidal creek; see Fig. 2C, Table 1). Flooding and exposure to hydrodynamic forces are more frequent and inundations last longer at lower elevations. The *Spartina*-clone at the tidal flat position showed the lowest elevation and the flooding duration was longer compared to the other clones. The *Spartina*-clone in the tidal creek have been growing on a hummock, which was exposed to tidal currents.

The ploidy levels of *Spartina*-taxa were determined according to Granse et al. (accepted) by means of flow-cytometer analysis (Partec GmbH, Münster, Germany) using a DAPI staining protocol and a standard (*Pisum sativum*). The combination of ploidy level and habitat resulted in four sampling positions, in the following denoted as *Spartina*-clones termed *Spartina* × *townsendii* (tidal flat), *Spartina* × *townsendii* (pioneer marsh), *Spartina anglica* (pioneer marsh), and *Spartina anglica* (tidal creek). These sampling positions allowed to test the root-system responses of the hybrids to different flooding regimes with four replicates ($n = 4$) at each position. In particular, this study design allowed for comparisons among individual *Spartina*-taxa growing in different habitats, and among different *Spartina*-taxa growing in identical habitats.

2.2 Soil Characteristics and stem density

At the Wadden Sea site, soil parameters (elevation, redox potential) were measured in the habitats with *S.* × *townsendii* and *S. anglica* (see Fig. 2C) in August 2017 before sampling soil cores for CT-scanning.

Elevation mean high tide (MHT) was referenced against the German Ordnance Datum and regional mean high tide gauge as described in Granse et al. (2020).

Soil bulk density was determined in the topmost layer (0 — 5 cm) using a volumetric ring (100 cm^3). Litter layers were removed prior to sampling. Soil dry weight was determined after air drying the volumetric cores at 105 $^{\circ}C$ for 48 h.

The redox potential was measured before and after a tidal inundation at high tide. Redox values were examined at 5 cm soil depth (n = 3) using a platinum-tipped electrode and an Ag/AgCl reference electrode after Mansfeldt (2003).

The reducing depth was determined by visual identification as the depth where iron sulphide precipitation is clearly visible, as an easily distinguishable black layer. In the presence of sulphur, iron is reduced forming black colored Pyrite, which is widely independent of tidal and seasonal fluctuations and therefore a useful proxy for identification of permanently anaerobic soil horizons.

Table 1: Soil characteristics and stem densities of *S.* × *townsendii* and *S. anglica* (n = 1). Table1.docx; For table details also see affiliated PDF-file version!

2.3 Soil core sampling for CT-scanning analysis

The soil cores of *Spartina*-hybrids were sampled in March 2018 at the SNK field site in the Wadden Sea, Schleswig-Holstein, Germany (Fig. 2). The soil cores of the parental taxa of the *Spartina*-hybrids were collected in June 2018 at the Atlantic coast in Brittany, France. At each of the sampling positions, four *Spartina* soil cores were sampled (n = 4) and the GPS

coordinates recorded. All sampled *Spartina*-habitats represent individual *Spartina*-clones, which were monospecific and clearly demarcated against other *Spartina*-clones.

All soil cores were sampled using a metal-corer with a diameter of 25 cm and 30 cm in height. After sampling, the soil cores were potted in plastic pots (d = 29 cm, h = 23 cm; material: polypropylene). Gaps were filled with autoclaved sand. Until CT-scanning in September 2018, the samples were kept in a tidal outdoor-basin at Universität Hamburg to acclimate the plants by simulating two inundations per day with artificial sea water (20 psu). A salinity level approximately 66% the full-strength of seawater was shown to prevent root-hair growth (Bouma et al., 2000). Before CT-scanning, the pots were placed into cylindrical polypropylene transport-container (density 0.9 g cm^{-3}; wall thickness of pot and transport container < 1 mm). The low wall thickness, the low density and the light elemental composition (mainly carbon and hydrogen) of the pots and transport containers secured a minimal x-ray attenuation. The preparation of the pots for their transport were conducted 24 hours before CT-scanning. Therefore, the pots were in drained state during CT-scanning.

2.4 Computed tomography and CT-scan image analysis

Computed tomography scanning and CT-scan image analysis are described in detail in the Supplementary Material (CT-scan image analysis methods) and are only briefly summarized here.

2.4.1 Computed tomography

All *Spartina*-cores were scanned by a Toshiba Aquilion 64 computer tomograph at the hospital Klinikum Bremen-Mitte, Bremen, Germany, with an X-ray source voltage of 120 kV and a current of 600 mA. The resulting CT-image stacks contain grey-scale images of X-ray attenuation in standardized Hounsfield Units (HU; air: -1000 HU, distilled water: 0 HU; Hounsfield, 1979). Medicinal CT-scanners are regularly calibrated with a standardized

procedure using phantoms containing various materials with different densities. Using HU provides principal compatibility of data from different medical-CT devices (Cnudde and Boone, 2013). The resolution of medicinal CT-scanning is limited to approximately 0.4 mm (reconstruction unit), meaning that roots with a diameter of 1 mm are represented by 3 voxel.

2.4.2 CT-scan image analysis

The CT-scans of the cores were cropped to cylindrical shape (d = 18 cm, h = 25 cm) representing the top 20 cm of the soil and 5 cm of the aboveground biomass.

To differentiate between roots (including aerenchyma), sediment, and air-filled pore space we followed a specific segmentation strategy. First, roots including the aerenchyma and sediment were segmented using a marker-controlled watershed algorithm. This algorithm does not require calibration of HU as necessary for threshold-based segmentation methods because X-ray attenuation is influenced by the density and the composition of the material. In contrast to a threshold-based segmentation method, used for example by Davey et al. (2011), the marker-controlled watershed algorithm allows to compensate X-ray attenuation differences within and between samples as markers are set in areas that can be designated without difficulty to one or another material. The algorithm searches the boundary between the materials by expanding the areas of the markers to the region of maximal change in X-ray attenuation. Second, the values within the segmented areas were averaged with a moving window of 15 × 15 voxels. As air filled pores and bioturbation traces are exclusively filled by air, they exhibited clearly lower values than roots with or without aerenchyma. To separate the latter, we used a threshold segmentation with a value of -250 HU. Third, within the remaining root material, we separated root-tissue and root-aerenchyma by threshold segmentation with a threshold of -500 HU. The separation of aerenchyma from root-tissue is not affected by material-density or material-composition and could be separated with a

threshold segmentation without calibration because the materials between the samples are always the same, root-tissue versus air. Furthermore, we checked that the aerenchyma is always connected to a root-tissue.

The root-system structure was identified by means of skeleton analysis (automated detection of the central root axes). Afterwards the root-system characteristics (root-tissue and root-aerenchyma volumes) were quantified by means of a voxel-based reconstruction of the root-system from the root-skeleton. The root-tissue and root-aerenchyma volumes are reported as mean per soil depth profile. The percentage of "roots with aerenchyma" were calculated by dividing the volume of roots which contain aerenchyma by the total root volume (root-tissue + root-aerenchyma).

2.4.3 X-ray density

As approximation for the material densities inside the soil core body (excluding: roots, aerenchyma, air-spaces) the mean X-ray attenuation in HU per soil depth profile were calculated. A two-category density classification (sediment fraction) was used according to Davey et al. (2011), separating X-ray densities into particulates (< 750 HU; clay, silt, precipitates, and peat) and sand (≥ 750 HU).

2.4.4 Aerenchyma connectivity

The aim of the aerenchyma connectivity analysis was to identify pathways of low resistance that facilitate gas-flow from the top soil into deep soils. Unimpeded transport of gaseous molecules over longer distances is necessary for belowground gas transport and requires aerenchyma, which are well connected from the surface to the roots. If the air-filled aerenchyma compartments are fragmented, unimpeded gas flow is not possible. Furthermore, it is a requirement that the aerenchyma has a considerable length and width. Short and thick rhizomes may have a considerable volume, but do not facilitate long-distance transport.

In order to investigate the morphological differences among the *Spartina*-clones controlling their gas transport capacity, we conducted an analysis of aerenchyma fragment volumes, as a proxy for aerenchyma connectivity. The analysis was based on the root-skeleton reconstruction, and specifically targeted rhizomes facilitating long-distance transport, which had a diameter ≥ 1.4 mm and a length ≥ 70 mm. *Spartina*-clones with the largest aerenchyma fragment volumes were considered to have highest aerenchyma connectivity. Each individual aerenchyma fragment was assigned to a unique color in the reconstruction images. This allows for visual distinction of aerenchyma consisting of fewer large fragments, which are all connected, and aerenchyma consisting of many smaller fragments, which are not connected. The term "extraordinarily extended" is in the following used to target aerenchyma fragments with a volume orders of magnitude larger than the median volume (identified as outlier outside the 1.5 of the interquartile range). Aerenchyma fragments which expanded over more than one rhizome will be termed "connected aerenchyma network".

2.5 Software and statistics

Geographic maps were created using QGIS 3 (Madeira) with a HCMGIS-plugin (including Esri World Light Grey Basemap). The CT-scan images were processed with the ZIB edition of the Amira software (version 2019.35, Stalling et al., 2005, http://amira.zib.de). All statistics were calculated using R (version 3.6.1, Team, 2011). The volumes of root-tissue and aerenchyma, as well as ratios between them were analyzed by means of a two-way ANOVA (response ~ habitat * soil-depth) followed by Tukey HSD post-hoc tests, comparing *Spartina*-hybrids from different habitats (tidal flat, pioneer marsh, tidal creek) at two soil depth intervals, i.e., top soil (1 — 10 cm) and deep soil (10 — 20 cm). Normality and homogeneity were confirmed by means of Shapiro-Wilk Normality and Levene's test. Differences in aerenchyma fragment volume were tested by means of a Kruskal-Wallis test followed by Mann-Whitney *U* tests and Bonferroni-Holm adjustment. The linear regression analysis was

conducted using the diagram generator of the R-package *ggplot2* by invoking function *geom_smooth*(method = 'lm', formula='y ~ x'). Ellipses for highlighting point-clouds were generated by function *stat_ellipse*(). The correlation coefficients were calculated using function *cor.test*(method = 'spearman').

3 Results

3.1 Root and aerenchyma Volumes

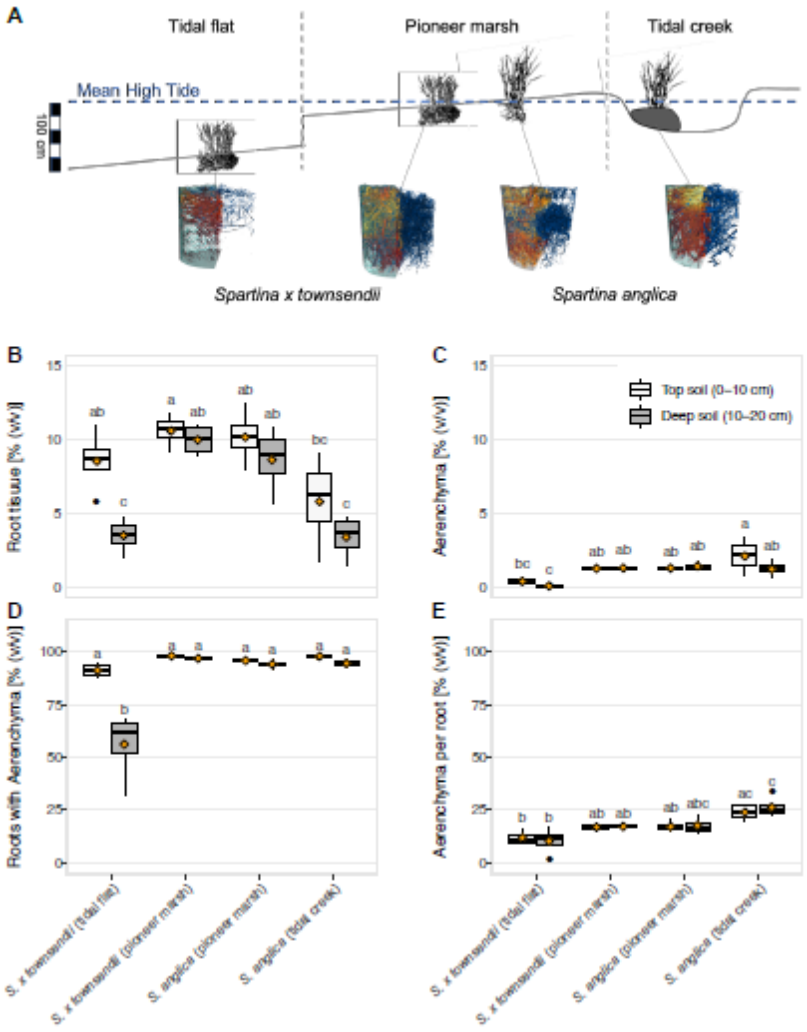
The root-system structure of *S.* × *townsendii* and *S. anglica* differed widely in different habitats (Fig. 3A). The root-tissue volume of *S.* × *townsendii* and *S. anglica* accounted for approximately 10% (v/v) of the top soil volume (overall median: 9.1% (v/v), interquartile range: 7.8 — 10.6% (v/v); Fig. 3B). The root-aerenchyma volume in the top soil ranged from 0.4% (v/v; median; Fig. 3C) in *S.* × *townsendii* from the tidal flat to 2.2% (v/v; median) in *S. anglica* from the tidal creek. Deep rooting (> 10 cm) was common in *S.* × *townsendii* and *S. anglica* in the pioneer zone, where the belowground root-tissue and root-aerenchyma volumes were very similar in the top and deep soil (deep soil, root-tissue median: 10.1 and 9.1% (v/v), respectively). In contrast, deep root-tissue volume was limited in *S.* × *townsendii* from the tidal flat and *S. anglica* from the tidal creek (deep soil median: 3.6 and 3.7% (v/v)).

In the top soil, *S.* × *townsendii* from the tidal flat had a slightly lower proportion of roots with aerenchyma (91% (v/v), median) than *Spartina* × *townsendii* (pioneer marsh), *Spartina anglica* (pioneer marsh), and *Spartina anglica* (tidal creek), where the proportion of roots with associated aerenchyma was more than 96% (v/v) (Fig. 3D). This difference was significant in the deep soil ($P < 0.05$) where *Spartina* × *townsendii* (tidal flat) had an even lower proportion of roots with associated aerenchyma (62% (v/v), median), whereas the

Spartina × *townsendii* (pioneer marsh), *Spartina anglica* (pioneer marsh), and *Spartina anglica* (tidal creek) remained at the same level compared to the top soil.

Figure3.pdf; See also affiliated PDF-file version!

Fig. 3: Root-system structure of *S.* × *townsendii* (tidal flat, pioneer marsh) and *S. anglica* (pioneer marsh, tidal creek). Illustration: A) Elevational gradient profile of *Spartina* habitats (tidal flat, pioneer marsh, tidal creek) in relation to mean high tide and examples for root-system reconstructions (red—yellow: roots; blue: aerenchyma). B — E: Diagrams of the root-tissue and root-aerenchyma volumes as well the relations between them in the top soil and deep soil. The letter-codes (a, b, c, d) are based upon ANOVA analyses followed by Tukey HSD post-hoc tests (df = 3, n: 4 soil cores) and indicate differences in B) root-tissue volume (F = 16.4, P < 0.05), C) root-aerenchyma volume (F = 14.7, P < 0.05), D) the proportion of root-tissue volume associated with aerenchyma (F = 28.1, P < 0.05), and E) the proportion of aerenchyma volume per root-volume (F = 18.4, P < 0.05). In the boxplots, the median is displayed as black horizontal line, the mean as orange diamond, and outliers as black dots outside the 1.5 of the interquartile range (box and whiskers).



The root-system structure of *Spartina anglica* (tidal creek) was markedly different than *Spartina* from other habitats. In the tidal creek, *S. anglica* had the highest proportion of aerenchyma accounting for 27% (v/v) of the root volume (top soil; Fig. 3E). This was significantly different from *S.* × *townsendii* ($P < 0.05$) and slightly higher than in *Spartina* from pioneer marsh habitats (top soil; overall median: 16% (v/v), interquartile range: 15 — 20).

Examples for root-system reconstructions of *Spartina*-taxa as well as root-tissue and root-aerenchyma volumes in relation to the considered soil depth are given in the Supplementary Material, Fig. S5A, C, D. Aerenchyma per root-volume was negatively correlated with X-ray

density (r = -0.56, $P < 0.001$; Supplementary Material, Fig. S6). *S.* × *townsendii* from the tidal flat showed a low proportion of aerenchyma per root-volume while mainly rooting in soil with comparatively higher X-ray density (sand fraction). Other *Spartina* (pioneer marsh, tidal creek) have been growing in soils with comparatively lower X-ray density (particulates fraction) and showed higher aerenchyma per root-volumes than *S.* × *townsendii* from the tidal flat.

For hexaploid *S.* × *townsendii* in the top soil, the root-tissue volume, root-aerenchyma volume, proportion of roots with aerenchyma, and aerenchyma per root-volume were only slightly lower in the tidal flat than in the pioneer marsh. In contrast, in the deep soil, the root-tissue and aerenchyma volume of *S.* × *townsendii* stayed stable in the pioneer marsh, but the root-tissue volume decreased below 5% (v/v) and aerenchyma volume dropped close to 0% (v/v) in the tidal flat. This was also reflected in the about 35% difference of the proportion of roots with aerenchyma in the deep soil between *S.* × *townsendii* from the tidal flat and the pioneer marsh.

For dodecaploid *S. anglica*, the root-tissue volume in the pioneer marsh accounted for 10% (v/v) of the soil volume and was larger than in the tidal creek (6% (v/v)). This was only significant in the deep soil ($P < 0.05$), where the root-tissue volume of *S. anglica* in the tidal creek decreased below 5% (v/v). Root-aerenchyma volumes and the percentage of roots with aerenchyma differed only slightly. Furthermore, *S. anglica* from the pioneer marsh showed a lower (not significant, $P \geq 0.05$) proportion of aerenchyma in roots, compared to plants from the tidal creek.

Hexaploid *Spartina* × *townsendii* (pioneer marsh) and dodecaploid *Spartina anglica* (pioneer marsh) differed only slightly (not significant, $P \geq 0.05$) in root-tissue volume, aerenchyma volume, percentage of roots with aerenchyma, and proportion of aerenchyma in

roots. However, as described above, the differences in some of these parameters were higher between *Spartina* of the same ploidy level, i.e., hexaploid *Spartina* × *townsendii* (tidal flat) vs. *Spartina* × *townsendii* (pioneer marsh), and dodecaploid *Spartina anglica* (pioneer marsh) vs. *Spartina anglica* (tidal creek).

3.2 Aerenchyma connectivity

The root-aerenchyma fragment volumes differed significantly between *Spartina* ploidy levels ($P < 0.001$; Fig. 4B) and *Spartina*-clones ($P < 0.05$; Fig. 4C). However, the majority of root-aerenchyma fragments showed relatively small volumes below 1 cm^3 ranging from 0.021 to 0.083 cm^3 (median) regarding all *Spartina*-clones. Opposed to this, some aerenchyma fragments in the roots of *S. anglica* were extraordinarily extended (see outlier in Fig. 4C and Table 2) with a maximum fragment volume of 53.0 cm^3 in the rhizome network of *S. anglica* in the tidal creek.

S. × *townsendii* in the tidal flat and in the pioneer marsh did not form extensively connected aerenchyma volumes. Opposed to this, the aerenchyma was highly connected in *S. anglica* in the tidal creek, where tube-like aerenchyma structures resulted in the largest root-aerenchyma fragment volumes and presumably a high connectivity into deeper soil layers (Fig. 4A). In *S. anglica* from the pioneer marsh, some aerenchyma fragment volumes were extraordinarily extended, showing a connected aerenchyma network. *S. maritima* also showed a connected aerenchyma network comparable to *S. anglica* from the pioneer marsh. However, these aerenchyma extents in *S. maritima* were approximately half in volume compared to *S. anglica* and mostly located in the upper half of the soil core (Fig. 4A; see also root system reconstruction in Supplementary Material, Fig. S7 — S12). *S. alterniflora* showed relatively small aerenchyma fragment-volumes and the maximum fragment-volume were approximately only a quarter of the largest fragment of *S. maritima*.

Figure4.pdf; See also affiliated PDF-file version!

Fig. 4: Aerenchyma connectivity analysis of hexaploid *S. alterniflora*, *S. maritima*, *S.* × *townsendii* (tidal flat), and *S.* × *townsendii* (pioneer marsh) as well as dodecaploid *S. anglica* (pioneer marsh) and *S. anglica* (tidal creek). Illustrations: A) Reconstruction of root-aerenchyma fragments inside rhizomes (colors: separated root-aerenchyma fragments; white arrows: aerenchyma with extensive connectivity). Diagrams: B) Root-aerenchyma fragment volumes of *Spartina* of different ploidy levels (hexaploid, dodecaploid; y-axis restricted to ≤ 1 cm^3; ***: Mann-Whitney-U test, $U = 14.6$, $P < 0.001$, $df = 1$). C) Distribution of root-aerenchyma fragment volumes inside rhizomes of *Spartina*-clones (left diagram: zoomed view ≤ 1 cm^3; right diagram: full view). The letter-codes (a, b, c, d) indicate differences between *Spartina*-clones (Kruskal-Wallis test followed by Mann-Whitney *U* tests and Bonferroni-Holm adjustment, $H = 150.0$, $P < 0.05$, $df = 5$). In the boxplots, the median is displayed as horizontal line and outliers as dots outside the 1.5 of the interquartile range (box and whiskers); *n*: root-aerenchyma fragments; all aerenchyma fragment volumes limited to ≥ 10 mm^3.

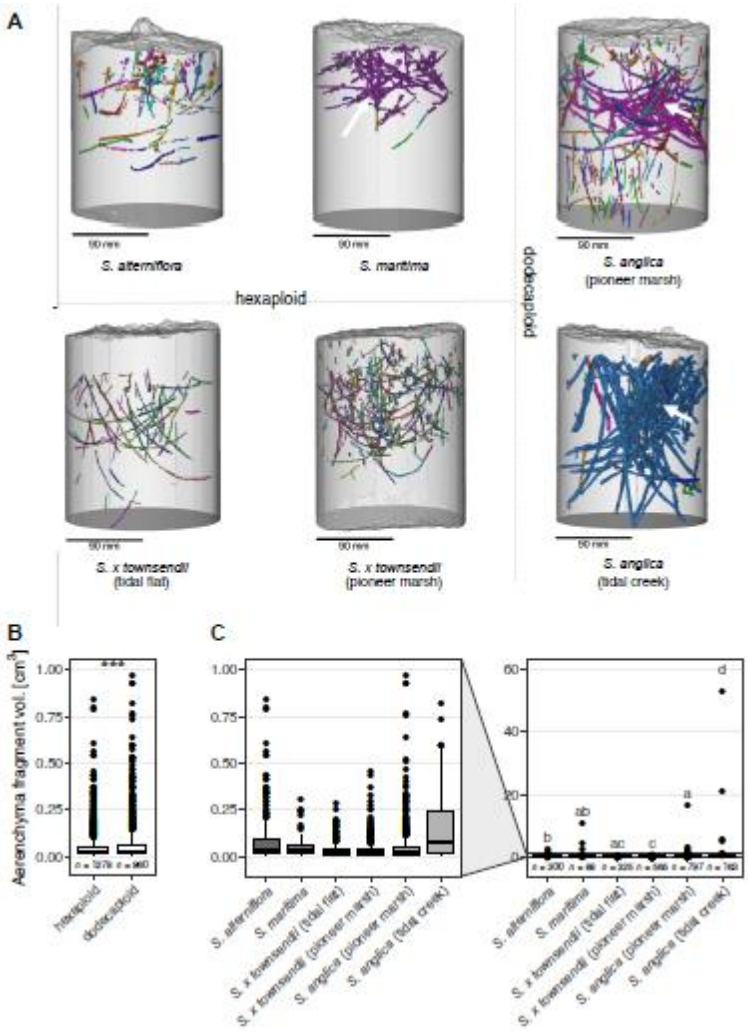


Table 2: Root-aerenchyma connectivity between ploidy levels (hexaploid and dodecaploid *Spartina*-clones) and of individual *Spartina*-clones considering soil depths deeper than 5 cm and regarding larger rhizomes with a minimum diameter of 1.4 mm and 70 mm in length. Inside rhizomes, the aerenchyma fragments with a minimum volume (≥ 1 cm^3) indicate root-aerenchyma connectivity, particularly outliers with volumes above the 1.5 of the interquartile range. The letter-codes (A, B) indicate differences in aerenchyma fragment volumes (median) between ploidy levels (Mann-Whitney-U test, $U = 14.6$, $P < 0.001$, $df = 1$). The letter-codes (a, b, c,

d) indicate differences in aerenchyma fragment volumes (median) between individual *Spartina* clones (Kruskal-Wallis test followed by Mann-Whitney *U* tests and Bonferroni-Holm adjustment, $H = 150.0$, $P < 0.05$, $df = 5$).

Table2.docx; For table details see also affiliated PDF-file version!

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4 Discussion

4.1 Habitat control of *Spartina* root-system structure

The root-system structures of *Spartina*-clones differed widely and showed clear responses to the conditions of their respective habitat. The presented results exhibit clear differences in deep soil root-tissue and root-aerenchyma volumes as well as the percentage of roots associated with aerenchyma between *S.* × *townsendii* from the tidal flat and the pioneer marsh. In deep soil, *S. anglica* from the tidal creek showed a higher proportion of aerenchyma than *Spartina* from the pioneer marsh. This supports for our first hypothesis that *Spartina* shows distinct root-system structures in response to habitat conditions differing in flooding regime, soil characteristics, and tidal hydrodynamics.

The belowground biomass structure of *S. anglica* in the tidal creek was different from *Spartina*-clones in other habitats. Compared to *Spartina*-clones from the pioneer marsh, *S. anglica* from the tidal creek showed comparable aerenchyma volumes, but the root-tissue volumes were smaller resulting in a higher proportion aerenchyma per root (Fig. 3B — D).

Most striking, the aerenchyma volume of *S.* × *townsendii* from the tidal flat was smallest in all soil depths. Even though it was the *Spartina*-clone on lowest elevation with the strongest flooding regimes. Specimens from this habitat should show the highest demand for root oxygenation under these waterlogged conditions, and therefore expected to form

extensive aerenchyma (Evans, 2004; Purcell et al., 2019). This was however, not the case. These observations show that the flooding conditions alone cannot predict the structure of the belowground biomass among different *Spartina* hybrids.

Redox potentials are known to play a key role in aerenchyma formation, showing extended aerenchyma formation under low redox conditions (Evans, 2004). In our study, aerenchyma responses were contrary to these expectations. *S. anglica* showed the highest aerenchyma formation in the tidal creek, which had the highest redox potential, and *S.* × *townsendii* showed lower aerenchyma development in the tidal flat than in the pioneer marsh, although the redox potentials were similar. Consequently, factors other than redox potential were important for shaping root-system structures in these marshes. It is noteworthy, that the redox potential in these marshes are higher than other more permanently water-logged marshes, and that the redox potential is highly dependent on flooding events (Table 1). The root-system development in *S.* × *townsendii* from the tidal flat may also have been affected by increased material density relative to other *Spartina* (pioneer marsh, tidal creek; Supplementary Material, Fig. S6). Opposed to *S.* × *townsendii* from the tidal flat, *S. anglica* from the tidal creek showed the highest aerenchyma response under comparatively high redox potentials. Consequently, factors other than redox potential have additionally been important in shaping root-system structures, such as nutrient supply by sea water.

Other factors such as biomechanical stress imposed by tidal hydrodynamic forces can also play a key role for the structural development of the biomass (Justin and Armstrong, 1987). Assuming that the biomechanical stress decreases with distance from the sea (tidal flat > pioneer marsh > tidal creek; cf. Möller and Spencer, 2002), aerenchyma formation was negatively correlated to biomechanical stress in our study. This is in line with Justin and Armstrong (1987), who showed a decreased predisposition for aerenchyma formation in *S. anglica* under biomechanical stress.

4.2 Ploidy level versus habitat influence on *Spartina* root-system structure

In the pioneer zone, monospecific stands of hexaploid *S.* × *townsendii* and dodecaploid *S. anglica* are located within a few meters of each other. This allows for a comparison of different hybrids with different ploidy-level under almost identical natural habitat conditions. None of the tested parameters, i.e., root-tissue volume, aerenchyma volume, proportion of roots with aerenchyma, and aerenchyma per root-volume, exhibited distinct differences between the two *Spartina*-taxa from the pioneer marsh (Fig. 3B — E). Therefore, we reject the 2nd hypothesis that *Spartina*-taxa of different ploidy levels (hexa- and dodecaploid) show distinct root-system structures when growing in similar habitat conditions. Quite the opposite was the case, the root-system structures differed between *Spartina*-habitats rather than between *Spartina*-ploidy levels.

The only difference found between the hexaploid *S.* × *townsendii* and the dodecaploid *S. anglica* (Table 1) was in regard to stem-density. However, since none of the belowground biomass traits differed (Fig. 3B), our results indicate that root-biomass accumulation was driven by the condition of the habitat (cf. Mendelssohn and McKee, 1988; Koevoets et al., 2016; Mesa-Marín et al., 2018), rather than by polyploidization related effects, such as increased gene dosage (i.e., a doubling of the number of copies of a particular gene due to genome duplication and possibly accompanied by increases in the amount of gene products) or organ size (cf. Birchler et al., 2010; Doyle and Coate, 2019).

4.3 Ploidy level controls aerenchyma connectivity

The dodecaploid *S. anglica*-clones showed the largest root-aerenchyma fragment volumes compared to the hexaploid *Spartina*-clones. The highest aerenchyma connectivity was observed at *S. anglica* from the tidal creek bridging top soil and deep soil layers by highly aerenchymatous tube-like roots and rhizomes (Fig. 4A). Also in the pioneer marsh did

dodecaploid *S. anglica* form a substantial aerenchyma network consisting of large fragments which was approximately five times larger than the largest aerenchyma network of the hexaploid samples (*S. maritima*). In the hexaploid parental *S. alterniflora* and hexaploid F_1-hybrid *S.* × *townsendii*, extraordinarily large aerenchyma fragments were missing. The observation of the largest aerenchyma fragment volumes present in *S. anglica* was support for our 3rd hypothesis that the dodecaploid *S. anglica* shows a higher aerenchyma connectivity than the hexaploid F_1-hybrid and its parental *Spartina*-taxa. Interestingly, the hexaploid F_1-hybrid *S.* × *townsendii* exhibited lower aerenchyma connectivity than its genome duplicated descendent *S. anglica,* which suggests that following this recent whole genome duplication, polyploidization per se, rather than hybridization affects this trait.

Aerenchyma fragment volumes differed generally between ploidy levels (Fig. 4B), which however, is rather difficult to consider in the assessment of aerenchyma connectivity because the majority of aerenchyma fragment volumes were relatively small (Table 2; overall median: 0.03 cm^3). Our visual analysis of the reconstructed aerenchyma fragments revealed that the fragments were highly variable in length and diameter. The reconstructed aerenchyma fragments were often departing from the notion of tube-like aerenchyma formation that bridges root-tips with plant parts in the top soil. Rhizomes and roots with extended aerenchyma fragment volumes, i.e., orders of magnitude larger than the median, can be considered to be highly effective in aerenchyma connectivity, substantially lowering the resistance to continuous gas-flow (cf. Armstrong, 1980; Colmer, 2003). Maricle and Lee (2007) showed that the dodecaploid *S. anglica* has a significantly higher capacity for oxygen transport via root aerenchyma than the hexaploid *S. alterniflora*.

Previous findings by Maricle and Lee (2002) demonstrated by using light microscopy and cross-sectional area measurements that aerenchyma development in *S. alterniflora* and *S. anglica* was not different under drained but more extensive in *S. alterniflora* under flooded

condition. In our study, the aerenchyma fragment volumes (median) of *S. alterniflora* were higher than the fragment volumes of *S. anglica* in the pioneer marsh (Table 2). In agreement with Maricle and Lee (2002) who directly measured oxygen transport capacity to be higher in *S. anglica*, we infer a higher capacity for gas-flow in *S. anglica* from our results. Our volume-based analysis of root-system structures allows to identify large aerenchyma structures in plants from undisturbed soil, and it also accounts for allometric growth effects (Weiner, 2004; Sugiyama, 2005): Cell-size and cell-volume immediately increase with polyploidization (e.g., Finigan et al., 2012; Roddy et al., 2019) and polyploid cells may therefore also differ in metabolic demands (Doyle and Coate, 2019). Due to allometric relationship, the volume-to-surface ratio of comparatively larger cells in polyploids is increased and may result in increased aerenchyma fragment volumes. Regarding lysigenous aerenchyma formation in plants on high ploidy level, such as dodecaploid *S. anglica*, large apoptotic cells in the root cortex would create relatively large aerenchyma volumes on a per cell base. In consequence, aerenchyma connectivity increases with ploidy level, if effects of polyploidization on cell size lead to merging aerenchyma fragments into large aerenchyma volumes.

The aerenchyma connectivity differed between the hexaploid *S.* × *townsendii* and the dodecaploid *S. anglica* as well as between *S. anglica* and the hexaploid parents. *S.* × *townsendii* was mimicking the phenotype of *S. alterniflora*: in both taxa, the aerenchyma formation was dominated by smaller fragments. In contrast, fragment volumes of *S. maritima* and *S. anglica* were larger with largest fragment volumes in *S. anglica* (Table 2). This may demonstrate maternal (*S. alterniflora*) dominance in aerenchyma connectivity in the F_1-hybrid (*S.* × *townsendii*), shifting towards a transgressive phenotype (exceeding that of the largest parental phenotype, paternal *S. maritima*) after genome duplication (*S. anglica*). Other transgressive physiological traits were also observed in *S. anglica*, e.g., increased stress tolerance compared to the parents (Cavé-Radet et al., 2018). Effects of hybridization and

whole genome duplication on the transcriptome of *S.* × *townsendii* and *S. anglica* were reported in previous investigations in this system (Chelaifa et al., 2010; Cavé-Radet et al., 2020), however, the way genetics is involved in the aerenchyma development in newly formed hybrids and allopolyploids is still an open question.

4.4 Considerations for the ecosystem

In *Spartina* dominated pioneer marshes, the root-tissue and aerenchyma combined accounted for a marked proportion of the top soil volume of 12% (v/v) (Fig. 3B — C). Accordingly, root-systems in salt marshes can have approximately twice the volume as the root-systems in terrestrial grasslands, for which Kuka et al. (2013) reported up to 7.1% (v/v). Hence the belowground roots-system contributes to stabilization of the soil and prevention of erosion (cf. Van Eerdt, 1985; Ford et al., 2016; Hudek et al., 2017a). Furthermore, belowground biomass production contributes a substantial supply of organic carbon below the soil surface (Hudek et al., 2017b), which may support carbon sequestration in salt marshes and geomorphological resistance of salt marshes against sea level rise (Granse et al., 2020).

Our study showed that *S. anglica* had a well-developed aerenchyma-system consisting of larger fragments. This demonstrates that this dodecaploid *S. anglica*, in contrast to *S.* × *townsendii* and *S. alterniflora*, developed biomass structures that were particularly well-adapted for belowground transport of oxygen. These findings support previous studies by Maricle and Lee (2007), showing that *S. anglica* has an outstanding gas transport capacity in comparison to other common wetland species. This trait provides *S. anglica* with the ability to modify its immediate belowground environment, removing phytotoxins and improving nutrient uptake. It predisposes the dodecaploid *S. anglica* for establishing in waterlogged anoxic soils outside the range of its hexaploid progenitors as a consequence of polyploidization (cf. Thompson, 1991; te Beest et al., 2012). The outstanding gas transport

capacity of *S. anglica* may therefore be an important factor in its successful invasion of tidal wetlands around the world, from Australia to North America in a little more than a century.

5 Conclusions

Medical-CT-scanning followed by skeleton analysis was used for the 3D reconstruction of the roots-system architecture from different *Spartina* taxa and habitats. This approach enabled a quantitative measurement of the spatial distribution of roots and aerenchyma in undisturbed salt marsh soils, giving insights into aerenchyma formation and connectivity which cannot be obtained by other methods.

Soils in *Spartina*-dominated habitats are highly connected to the atmosphere via root-aerenchyma. The presence of root-aerenchyma of *Spartina* can exert strong impacts on the biogeochemistry of marsh soils. Our results stress the important role of *Spartina* as a key taxon for ecosystem functioning in salt marshes. We demonstrate that about 90% (v/v) of the roots of *Spartina* have well developed aerenchyma and consequently more than 1% (v/v) of the top soil volume in pioneer marshes consists of aerenchyma inside roots and rhizomes. This points to a high potential for plant-mediated oxygenation of anoxic soils.

The hexaploid *S.* × *townsendii* and the dodecaploid *S. anglica* showed similar aerenchyma when growing in the pioneer marsh. *S. anglica* from a tidal creek habitat showed smaller root biomass with more aerenchyma, while aerenchyma was lowest in *S.* × *townsendii* in the tidal flat. These results demonstrate that physicochemical habitat conditions control both root morphology and aerenchyma formation in the hexaploid *S.* × *townsendii* and the dodecaploid *S. anglica*. Flooding regime and soil redox conditions are likely to be main drivers of the observed habitat effects. Further studies are needed to specifically analyze the role of driving factors like biomechanical stress imposed by tidal forces in root and aerenchyma formation. Overall, environmental conditions seem to exert a stronger impact on the root-system

structure of *Spartina* than ploidy level. However, a higher connectivity of root-aerenchyma was found in the dodecaploid *S. anglica* than in the hexaploids *S.* × *townsendii*, *S. alterniflora* and *S. maritima*. This may explain why earlier studies demonstrated a markedly higher oxygen transport capacity in *S. anglica* compared to other *Spartina*-taxa with lower ploidy levels.

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7 Author contributions

Dirk Granse: Conceptualization, Methodology, Data curation, Writing (original draft preparation), Visualization, and Investigation. Jürgen Titschack: Validation, Methodology, and Writing (reviewing and editing). Kai Jensen, Ketil Koop-Jakobsen: Supervision, Writing (reviewing and editing). Malika Ainouche: Writing (reviewing and editing).

8 Declarations of interest

Declarations of interest: none

9 Research data

The research data is published at PANGAEA - Database (Data Publisher for Earth & Environmental Science, Ecology; https://doi.org/10.1594/PANGAEA.931784).

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Credit-Author-Statement

Dirk Granse: Conceptualization, Methodology, Data curation, Writing (original draft preparation), Visualization, and Investigation. Jürgen Titschack: Validation, Methodology, and Writing (reviewing and editing). Kai Jensen, Ketil Koop-Jakobsen: Supervision, Writing (reviewing and editing). Malika Ainouche: Writing (reviewing and editing).

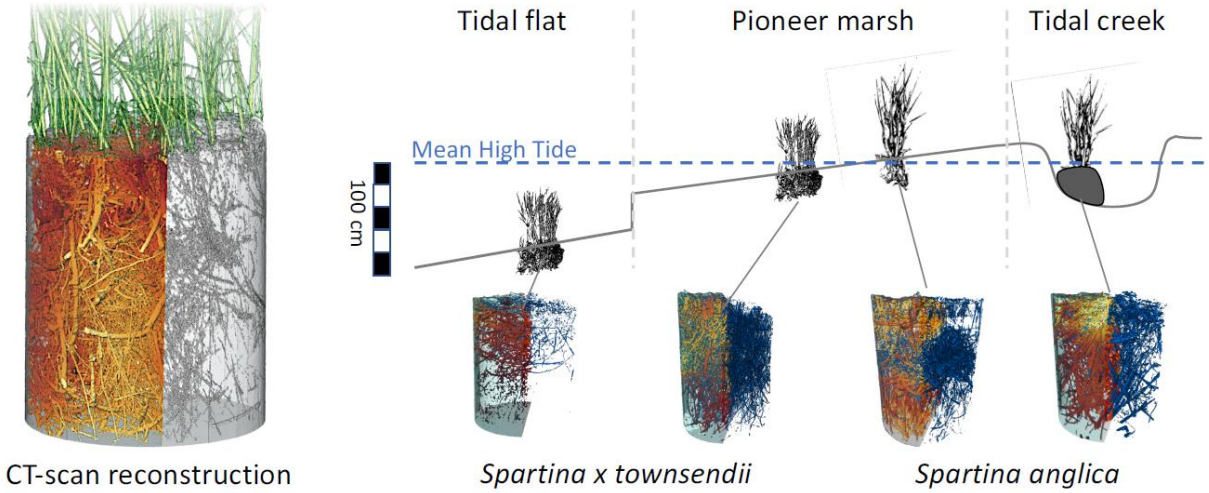
Table 1:

	S. × *townsendii*		*S. anglica*	
	tidal flat	pioneer marsh	pioneer marsh	tidal creek
Elevation MHT [cm]	-86	-6	7	-5
Soil bulk density [g · 100 cm^{-3}]	121	75	94	68
Redox after high-tide [mV]	82	-37	-28	194
Redox before high-tide [mV]	264	318	273	367
Reducing depth [cm]	0	9	0	14
Stem density [m^{-2}]	1329	2304	975	414
Old stem density [m^{-2}]	148	473	414	0

	hexaploid	dodecaploid	*S. alterniflora*	*S. maritima*	*S.* × *townsendii* (tidal flat)	*S.* × *townsendii* (pioneer marsh)	*S. anglica (pioneer marsh)*	*S. anglica* (tidal creek)
Rhizome volume [cm^3]	782	875	184	80	195	301	564	310
Aerenchyma fragment volume [cm^3]								
- total	86	182	30	22	13	21	71	111
- total (outlier)	52	153	17	20	5	8	49	90
- maximum	10.7	53.0	2.2	10.7	0.3	0.5	16.5	53.0
- median	0.02^{B}	0.03^{A}	0.04^{b}	0.03^{ab}	0.02^{ac}	0.02^{c}	0.03^{a}	0.08^{d}
- outlier (%)	60%	84%	58%	87%	38%	40%	70%	81%

Table 2:

Graphical abstract



Highlights

- 3D root-system architecture of *Spartina* visualized by CT-scanning
- Root-system quantification of *Spartina* in native soils using skeleton analysis
- *Spartina* root-system structure formation is controlled by habitat conditions
- High capacity for aerenchyma development in both hexaploid and dodecaploid *Spartina*
- Genome duplicated *Spartina anglica* shows markedly higher oxygen transport capacity