



The Overlooked Hybrid: Geographic Distribution and Niche Differentiation Between *Spartina* Cytotypes (Poaceae) in Wadden Sea Salt Marshes

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Abstract

Whole genome duplications (WGDs) lead to polyploid specimens and are regarded as major drivers for speciation and diversification in plants. One prevalent problem when studying WGDs is that effects of polyploidization in ancient polyploids cannot be disentangled from the consequences of selective evolutionary forces. Cytotypic differences in distribution, phenotypic appearance and in response to surface elevation (determined by HOF-modeling) were identified in a relatively young taxa-group of a hexaploid F₁-hybrid (*Spartina* × *townsendii* H. Groves & J. Groves, Poaceae) and its dodecaploid descendent (*Spartina anglica* C.E. Hubbard, Poaceae) using vegetation assessments (1029 plots; 1 × 1 m²) from the European Wadden Sea mainland salt marshes, including elevational and mean high tidal (MHT) data. While the F₁-hybrid was mainly present in the eastern part of the Wadden Sea, its dodecaploid descendent occurred in the entire Wadden Sea area. The *Spartina* cytotypes differed in phenotypes (median of *Spartina* cover: hexaploid = 25% vs. dodecaploid = 12%) and in elevational niche-optimum (hexaploid = −49.5 cm MHT vs. dodecaploid = 8.0 cm MHT). High ploidy levels correlated with establishment success in *Spartina* along geographic gradients but did not seem to increase the capacity to cope with abiotic severity downwards the elevational gradient in salt marshes.

Keywords Allopolyploidy · *Sporobolus* · Whole genome duplication (WGD) · Niche differentiation · Elevational gradient · HOF modeling

Introduction

Whole genome duplication (WGD; or polyploidization) is a key mechanism in plant evolution (Soltis et al. 2014; Soltis and Soltis 2016; Čertner et al. 2017) with profound consequences for plant ecology (e.g., Sonnleitner et al. 2015; Barker et al. 2016a, b, Segraves

and Anneberg 2016). WGD can alter plant physiology, development, and growth (cf. Wendel 2000; Leitch and Leitch 2008; Birchler 2012; Laport et al. 2016). Therefore, it may increase the capacity of polyploids to establish in recently deglaciated areas (cf. Ehrendorfer 1980; Theodoridis et al. 2013; Novikova et al. 2018) and at high latitudes (Brochmann et al. 2004; Rice et al. 2019). Moreover, these WGD-related alterations may explain differences between polyploids and their progenitors in the range along climate-related gradients, such as temperature, precipitation conditions, or altitude above sea-level (e.g., Theodoridis et al. 2013; Marchant et al. 2016; Wefferling et al. 2017). WGD may also increase the capacity of polyploids to live under increased abiotic severity, such as anoxia, salinity, or pollution (cf. Maherali et al. 2009; Godfree et al. 2017; Cavé-Radet et al. 2019).

Naturally formed polyploids live in sympatry with their progenitors and have immediately to overcome reproductive disadvantages, such as minority cytotype exclusion (Levin 1975) or genomic changes generated by homoeologous

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recombination (Gaeta and Pires 2010). Polyploidization can aid to overcome hybrid infertility (Birchler 2012; Charron et al. 2019; Meeus et al. 2020) and hybridization barriers by enabling gene flow between reproductively isolated parental taxa (Lafon-Placette et al. 2017; Marburger et al. 2019). However, being inherently different from their progenitors in the capacity to cope with environmental factors may help neopolyploids to escape from the sympatric niche.

For ancient polyploids, the effects of former WGD cannot be distinguished from effects of subsequent evolution (Soltis et al. 2016). Therefore, studying neopolyploids opens the possibility to disentangle the effects of selective evolution from WGD on niche differentiation. For example, Maherali et al. (2009) concluded by comparing extant di- and tetraploid with experimentally synthesized neotetraploid *Chamerion angustifolium* that tetraploids developed the enhanced ability to survive water stress after polyploidization. In addition, Ramsey (2011) compared tetra-, hexa-, and neohexaploid *Achillea borealis* and concluded that the hexaploid *A. borealis* had achieved the ability to adapt to a novel environment particularly through polyploidization. In our study, we aim to investigate the effects of WGD in the genus of *Spartina*, a well-established model system for studying recent (<200 years) hybridization and WGD (e.g., Ferreira de Carvalho et al. 2017; Chelaifa et al. 2010; Ainouche et al. 2012), by focusing on the establishment success along geographic and abiotic gradients.

Spartina anglica C.E. Hubbard (dodecaploid cytotype) evolved by WGD from the F₁-hybrid *Spartina × townsendii* H. Groves & J. Groves (hexaploid cytotype; Marchant 1968; Baumel et al. 2003; Ainouche et al. 2003) in the second half of the nineteenth century in Britain (Marchant 1967). *Spartina × townsendii* in turn emerged from hybridization of *Spartina alterniflora* Loiseleur and *Spartina maritima* (Curtis) Fernald. All these taxa belong to a monophyletic lineage of *Spartina*, recently included in the genus *Sporobolus* (Peterson et al. 2014). *Spartina* has been the subject of various research disciplines, e.g., in ecology, biogeography, and molecular biology (reviewed in Bortolus et al. 2019). However, only a few studies have been dealing with direct comparisons of *Spartina* cytotypes (e.g., Hubbard 1969; Raybould 2005; Proença et al. 2019), and so far, detailed studies with respect to geographic distributions and ecological niches of the cytotypes are lacking.

The cytotypes *Spartina × townsendii* and *Spartina anglica* differ in their reproductive and associated dispersal capacities. While the hexaploid cytotype is mostly capable of vegetative spreading, the dodecaploid cytotype regained fertility with WGD and spreads vegetatively as well as by seeds (cf. Marchant 1968; Hubbard 1970; Marks and Truscott 1985). Recent publications reported that the hexa-

and dodecaploid cytotypes co-occur (Drok 1983; Partridge 1987; Vinther et al. 2001; Michaelis 2008; Saarela 2012; Huska et al. 2016; Wong et al. 2018). However, a systematic understanding of the distribution of *Spartina × townsendii* and *Spartina anglica* in salt marshes is missing (cf. Raybould 2005).

The globally most important habitat of *Spartina* cytotypes are salt marshes. These ecosystems develop along sheltered coastlines under tidal inundations. With increasing duration and frequency of flooding along the decreasing elevation in salt marshes, severity of anoxic conditions increases (Colmer and Flowers 2008; Bakker et al. 2020; Mueller et al. 2020). Another abiotic stressor of plant growth in salt marshes is increased salinity. Usually, salinity in salt marshes reflects salinity of the neighboring water body (e.g., de Leeuw et al. 1991). It is, however, also affected by single precipitation events, extraordinary heat waves (cf. Strain et al. 2017; Wong et al. 2018), and regular annual summer droughts (cf. Schröder et al. 2002). Along the elevational salt marsh gradient, vegetation often shows distinct zones resulting from the interplay of plant adaptations to abiotic stress (mainly anoxia and salinity; Suchrow et al. 2015) and competitive interactions among plants (Adam 1993; Suchrow and Jensen 2010; Engels et al. 2011). Thus, ecological advantages of WGD could be reflected by an increased capacity of the dodecaploid *Spartina* cytotype to deal with increased abiotic severity (e.g., by effective root oxygenation; cf. Koop-Jakobsen and Wenzhöfer 2015), resulting in niche shifts (cf. Levin 2003) towards lower elevated habitats with increased flooding frequencies.

Niche differences between cytotypes have already been demonstrated in salt marshes for the genus *Salicornia* (Chenopodiaceae). Here, diploid (*Salicornia europaea*) and tetraploid (*Salicornia stricta*, *Salicornia procumbens*) cytotypes (König 1939) co-occur with genetically little differentiated lineages (Kadereit et al. 2007). These *Salicornia* cytotypes show considerable phenotypic plasticity, which may be a suitable mechanism of pioneer species to cope with high dynamics of abiotic conditions in salt marshes (Kadereit et al. 2007). Furthermore, *Salicornia* cytotypes have clear preferences to grow in specific salt marsh habitats (König 1960): The diploid *Salicornia* cytotype mainly occurs in low marshes and thus on higher elevations compared to the tetraploid *Salicornia* cytotype, which mainly occurs further down in the pioneer zone (König 1960; Teege et al. 2011; Witte et al. 2018). In *Spartina*, the dodecaploid cytotype has also been shown in reciprocal transplant experiments to exhibit high phenotypic plasticity, i.e., distinct morphologies related to the growth conditions (Thompson et al. 1991a, b). During our preliminary studies, the hexaploid cytotype showed comparatively higher stem

density. However, detailed knowledge on morphology and ecological niches of *Spartina* cytotypes is still lacking.

Approximately 90 years ago, *Spartina* fragments were planted in the European Wadden Sea in land reclamation experiments (especially for sediment trapping and marsh surface stabilization; Thijsse 1924; König 1948; Esselink 1998; Nehring and Hesse 2008). Almost all planted fragments originated from Poole Harbour, approximately 30 km southwest of Southampton (UK), where both *Spartina* cytotypes co-occurred (Ranwell 1967; Raybould 2005). Most likely, fragments of both the hexaploid and dodecaploid cytotype were introduced to the Wadden Sea area. Since the middle of the twentieth century, *Spartina* has widely increased in abundance in salt marshes of the Wadden Sea (Esselink et al. 2017). However, most of the studies on salt marsh vegetation of the Wadden Sea did not distinguish between the *Spartina* cytotypes. In addition, the name of *Spartina anglica* is sometimes synonymously used for both *Spartina anglica* and the F₁-hybrid *Spartina* × *townsendii* (e.g., Nehring and Adersen 2006). Therefore, ecological differences between *Spartina* cytotypes may have been widely ignored and the F₁-hybrid overlooked. The

objectives of this study are to analyze the geographic distribution of both *Spartina* cytotypes in the Wadden Sea area, and to compare their ecological niches along the elevational salt marsh gradient. We tested the following hypotheses:

- 1) Hexa- and dodecaploid *Spartina* cytotypes occur along the Wadden Sea coast with similar frequencies. To test this, we scanned for *Spartina* cytotypes along a European Wadden Sea transect from Den Helder (The Netherlands) through Lower Saxony and Schleswig-Holstein (Germany) to Skallingen (Denmark). We determined the cytotypes' frequencies for six regions in our focus area, i.e., the mainland salt marshes in Schleswig-Holstein.
- 2) The hexa- and dodecaploid *Spartina* cytotypes show distinguishable phenotypes. To verify this hypothesis, we determined the cover as proxy for stem density of *Spartina* phenotypes in the focus area.
- 3) Due to increased stress tolerance as a consequence of WGD, the ecological niche of the dodecaploid cytotype includes the most stressful habitats within the frequently flooded pioneer zone of the salt marsh. This

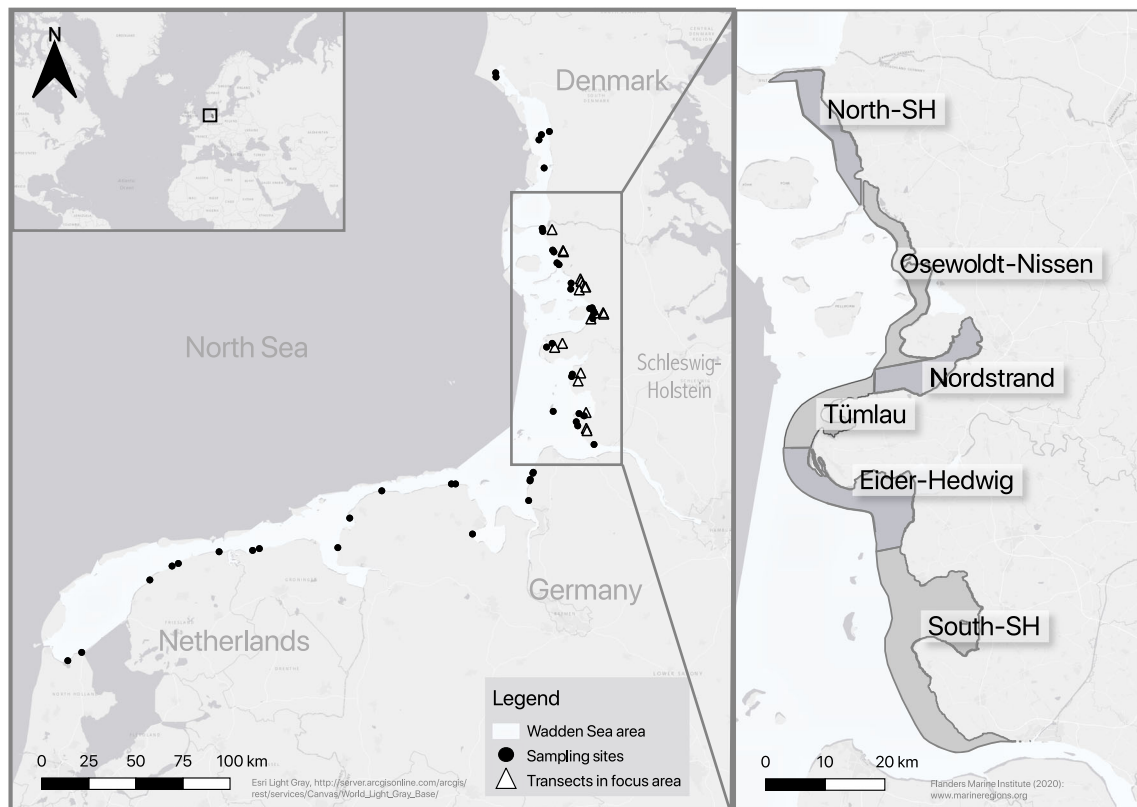


Fig. 1 *Spartina* sampling sites (black dots) in mainland salt marshes along the European Wadden Sea coast (left side frame) and transects (white triangles) in six regions of the focus area (right side frame) in Schleswig-Holstein (SH), Germany

hypothesis was tested by comparing the response of both *Spartina* cytotypes to elevation.

Materials and Methods

Study Area

For an initial scan of the geographical distribution of *Spartina* cytotypes, 96 plots covered by *Spartina* were investigated in salt marshes of the European Wadden Sea (Fig. 1). From Den Helder in the Netherlands to Skallingen, Denmark, plant material was collected in 2017/18 from *Spartina* clones at sites approximately 50 km in distance to each other. From 2017 to 2019, *Spartina* was additionally sampled along 19 transects in mainland salt marshes at the North Sea coast of Schleswig-Holstein, Germany, hereafter referred to as focus area. In the focus area, the transects were arranged as described in Granse et al. (2021). Accounting for differences in tidal range, the focus area was split into six regions (Fig. 1) related to groups of equal tidal ranges and by following the regional tide-gauges classifications from Balke et al. (2016). Each of the 19 sampled transects spanned the elevational gradient from bare tidal flats to high marsh communities.

Information on *Spartina* plantings in the focus area was taken from König (1948). The northernmost *Spartina* planting site and the northernmost *Spartina* occurrence in 1947 was near Dagebüll in the Osewoldt-Nissen region (König 1948). We used the geographic distance between the northernmost planting site and today's northernmost occurrence of *Spartina* to estimate dispersal distances of *Spartina* cytotypes.

Cytotypes

Two major cytotypes of *Spartina* taxa can be found in the salt marshes of the study area (cf. Hubbard and Sampson 1992), one being hexa- and one being dodecaploid. The hexaploid cytotype includes the F₁-hybrid *Spartina* × *townsendii* ($2n = 62$, Marchant 1968), as well as its parental taxa *Spartina alterniflora* ($2n = 62$, Marchant 1968) and *Spartina maritima* ($2n = 60$, Marchant 1968). The dodecaploid cytotype is represented by *Spartina anglica* ($2n = 120, 122, \text{ or } 124$, Marchant 1968). The hexa- and dodecaploid cytotypes were distinguished by means of nuclear DNA content (cf. Baumel et al. 2003; Doležel et al. 2007) using flow cytometry and a DAPI-staining protocol (cf. Galbraith et al. 1983). Fresh young leaves from a *Spartina* clone and fresh leaves of *Pisum sativum* (standard) were co-chopped (Hanson et al. 2005) with a new razor in 0.5 ml staining buffer (CyStain UV Ploidy DAPI staining solution, Partec, Germany) for 30 s. After addition of 0.5 ml

staining buffer and 30 s of incubation, the solution was filtered with a 30 μm mesh and analyzed in a flow-cytometer (Partec GmbH, Münster, Germany). The resulting fluorescence peaks were accepted when peak height exceeded a nuclei count of 50 with a coefficient of variation (CV) smaller than 8% (cf. Suda and Trávníček 2006; Doležel and Bartoš 2005).

Hexaploid cytotype taxa were distinguished according to morphological differences (e.g., Saarela 2012). In cases of hexaploid clones with ambiguous morphology, taxon affiliation (*Spartina* × *townsendii*, *Spartina alterniflora*) was determined for flowering plants in the greenhouse by means of pollen viability analysis using microscopy (Marchant 1968; Partridge 1987). Pollen viability was assessed by differential staining of aborted and non-aborted pollen grains (Peterson et al. 2010). Pollen abortion is often indicative of failures in chromosome segregation during meiosis. Indeed, chromosome spreads of male meiocytes revealed multivalent and missegregated chromosomes as often observed in polyploid species (Marchant 1968; Ramsey and Schemske 2002).

Spartina Phenotypic Variation and *Spartina* Cytotype Sampling

To analyze intercytotypic differences in phenotypes, *Spartina* cover was recorded on 1029 plots of 1 × 1 m² in the focus area. The positions of the plots were the same as the plots described in Granse et al. (2021) which are based upon 362 resampled plots from a 30-year-old initial vegetation study (Suchrow and Jensen 2010) and 667 additional plots located in newly developed salt marsh areas. The plots were arranged in clusters at 50–400 m intervals along each transect (see Online Resource, Fig. 5). Within a cluster and to ensure methodological continuity with Suchrow and Jensen (2010), the plot positions were selected by considering the spectrum of visually distinguishable vegetation units. Therefore, plots were placed side-by-side accounting for small-scale changes in vegetation or positioned at some distance where vegetation changed on a larger scale, e.g., at isolated *Spartina* clones surrounded by the mudflat.

Spartina cover was visually estimated as a percentage value at the herb layer (Mueller-Dombois and Ellenberg 1974, “basal” cover) of plants which were rooting on the plot (“rooted” cover; Dengler 2008). Due to the upright protruding stem morphology of *Spartina* plants, according to our preliminary studies, “rooted” and “basal” assessed vegetation cover directly translates into stem density reflecting the *Spartina* phenotype.

In order to assign a *Spartina* cytotype to a plot, a fragment from a *Spartina* plant of the plot's dominant *Spartina* phenotype was cut and cultivated in the greenhouse at Universität Hamburg until cytotype determination. Usually,

one phenotype was observed per plot which extended in some cases largely over the sampling area. Therefore, if the dominant *Spartina* phenotype extended over neighboring plots, one *Spartina* fragment was considered to be representative for plots in the vicinity of maximal 5 m around the sampling-position. Neighboring but differing *Spartina* phenotypes were visually distinguished from each other by means of spatially varying appearance, e.g., stem density, state of flowering, leaf color, leaf angle (Marchant 1967; Wong et al. 2018), and degree of claviceps infection (see Boestfleisch et al. 2015; Raybould 2005). For *Spartina* cytotype determination, these criteria allowed to pool plots by taking just one sample that represented two or more plots and hence reducing the sampling amount: pooling of two plots (70 cases), three plots (34 cases), four plots (14 cases), and five or more plots (2 cases). Overall, 417 sampled *Spartina* fragments were assigned to 607 plots (hexaploid: 88 to 108; dodecaploid: 329 to 499). The frequency of *Spartina* cytotypes is reported as the proportion of plots with the respective cytotype of all regarded plots within a region.

Elevation

As a basis for analyzing the ecological niche of both *Spartina* cytotypes along the elevational salt marsh gradient, elevation of all 1122 plots (including 93 uncovered plots) in the focus area was determined by means of a Laser Leveling device (LL500 combined with HL700 receiver by Trimble, CA, USA) and by averaging five elevation measurements per plot as described in Granse et al. (2021). The elevation of plots was calculated in relation to nearby benchmarks of the vertical control survey-net of the German height reference system or to permanently installed sedimentation erosion bars. Measured values were related to the German height reference system (absolute elevation value; cm NN). In line with Suchrow and Jensen (2010), a mean high tide value (cm MHT) was calculated for each transect by interpolation between two adjacent tide gauges from the previous “water year”. Via this MHT value, for each plot along a transect its position in relation to MHT was calculated.

Niche Differentiation

Ecological niche analysis was conducted by means of HOF-modeling (Huisman et al. 1993) with elevation as a proxy for flooding frequency and flooding duration, which represents increasing abiotic severeness with decreasing elevation (Adam 1993; Suchrow and Jensen 2010). The response (presence on plots) of *Spartina* cytotypes to elevation was fitted to one out of seven HOF-model types (Jansen and Oksanen 2013) by using the eHOF-package

in R (Oksanen and Minchin 2002). The best-fitted model was selected by means of the AICc estimator after calling the HOF-function with standard parameter against the binomial error distribution family and with a bootstrap of 100 (for HOF-model parameters see Online Resource, Tables 1–3). The HOF-modeling reports a raw mean (mean of the observed variable), a niche-optimum (value along the gradient with highest predicted occurrence) and an expectancy (calculated as a mean of 10,000 values along the gradient weighted by their predicted occurrence; for details see Jansen and Oksanen 2013). Converging values of raw mean, optimum and expectancy indicate a high goodness of fit for the resulting model. In addition, the observed frequency of occurrence of *Spartina* cytotypes was transformed into a binary presence/absence-status (presence: cover > 0; absence: cover = 0). The binary status was grouped over binning classes of 10 cm MHT of elevation and allowed a visual comparison of observed vs. predicted data.

Statistics and Software

Frequencies of *Spartina* cytotypes in the entire focus area were compared by means of Fisher’s exact test for count data. To test for differences between *Spartina* cytotypes in elevation and *Spartina* cover, non-parametric Mann-Whitney *U*-tests were used because the data was not normally distributed. Statistic evaluation was conducted by calling routines from R-packages of version 3.6.1 (R Development Core Team 2011). Analysis of dispersal distances between the northernmost planting site and the current northernmost occurrence in a specific transect was conducted using QGIS 3 (Madeira) with HCMGIS-plugin (including Esri World Light Grey Basemap) and Marine Regions shape file (Flanders Marine Institute 2020).

Results

Geographic Distribution

The dodecaploid cytotype (*Spartina anglica*) was present along the entire European Wadden Sea coast (Fig. 2), whereas the hexaploid cytotype (*Spartina* × *townsendii*) only occurred in the northeast, from Wangerland in Lower Saxony (Germany) to Skallingen (Denmark). In each of the regions in the focus area, the frequency of the dodecaploid cytotype was higher than that of the hexaploid, and the frequency of the hexaploid cytotype varied considerably between the regions (Fig. 2; Online Resource, Table 4). The highest frequency of the hexaploid (24.4%; $n = 127$) was found north of the peninsula of Eiderstedt. Both the hexaploid- and the dodecaploid cytotype were present

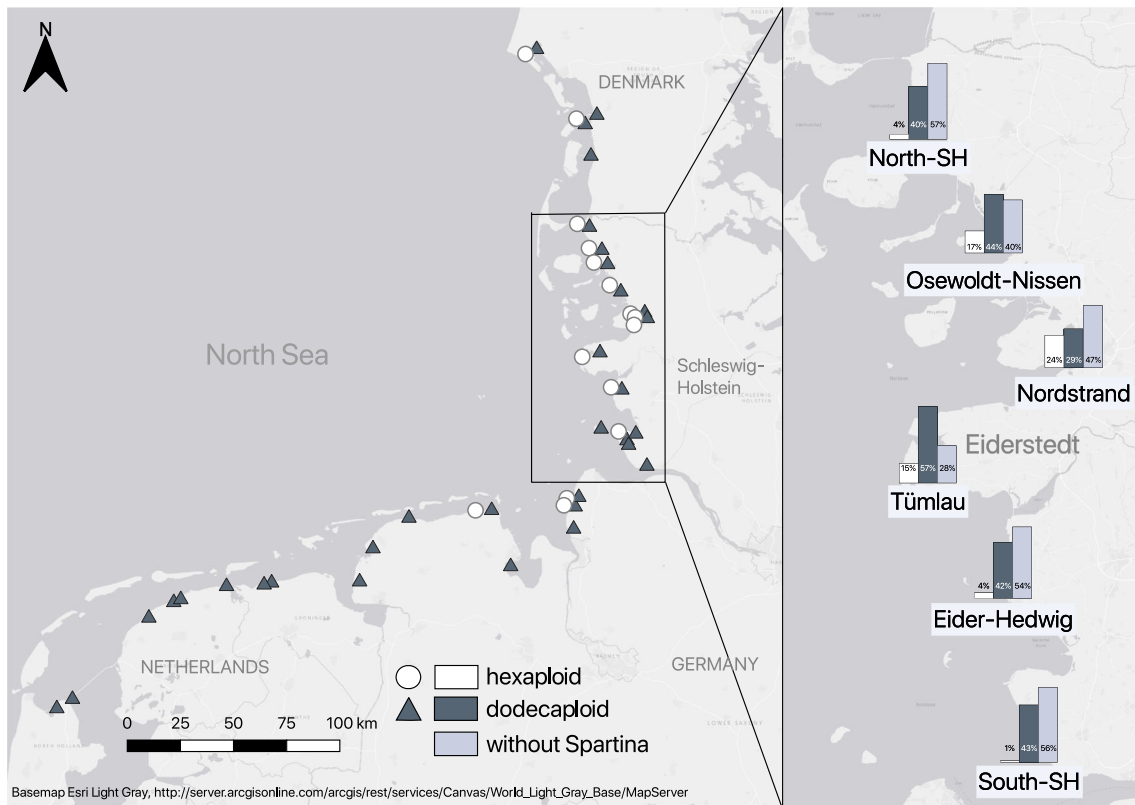


Fig. 2 Distribution of *Spartina* cytotypes (hexa- and dodecaploid) at sampling sites in mainland salt marshes in the European Wadden Sea (left side frame) and in the focus area (right side frame) along the North Sea coast of Schleswig-Holstein (SH), Germany. The bar-charts show

the frequency of the hexa- and dodecaploid *Spartina* cytotype as well as plots without *Spartina*, separately for the six regions of the focus area ($n = 883$; see also Online Resource, Table 4)

in the North region, approximately 20 km north of the northernmost planting site.

A hexaploid *Spartina alterniflora* clone was found near the island of Mandø, Denmark, while *Spartina maritima* was not observed in the study area. We did not observe nonaploids or other forms of intermediate backcrossing between the hexa- and dodecaploid *Spartina* cytotypes. *Spartina* \times *townsendii* plants did not show any viable pollen, while the pollen of *Spartina anglica* appeared to be mostly intact (see Online Resource, Fig. 6).

Cytotype Frequency, Elevation and *Spartina* Cover

In the focus area, the dodecaploid cytotype was more frequent on vegetated plots than the hexaploid cytotype (Fig. 3a). In comparison with the dodecaploid cytotype, the hexaploid cytotype colonized plots at significantly lower elevations (Fig. 3b). At the lowest elevations near -86.0 cm MHT, the hexaploid cytotype occurred with both higher plot cover and frequency compared to the only occasionally occurring dodecaploid cytotype (see outliers in Fig. 3b). The *Spartina* cover was generally higher on plots with the

hexaploid cytotype (median: 25%; Fig. 3c) than on plots with the dodecaploid cytotype (median: 12%).

Niche Differentiation

The HOF-model type V was the best fitted model type for the elevational response of the dodecaploid, i.e., a unimodal curve with an optimum at 8.0 cm MHT and a probability of occurrence of the dodecaploid about 83.8% at this elevation (Fig. 4). The niche-optimum and expectancy had approximately the same value and differed from the raw mean only slightly by 7.1 cm.

The response of the hexaploid cytotype to elevation was best described by model type IV. The model predicted a niche-optimum at -49.5 cm MHT with a probability of occurrence of 22.6%. In comparison with the dodecaploid cytotype, niche-optimum and expectancy of the hexaploid cytotype were equal with a higher difference to raw mean. Nonetheless, for both cytotypes a good agreement on the model prediction was indicated by a relatively high similarity between predicted and observed data (see also detailed HOF-model diagrams in Online Resource, Fig. 7 and

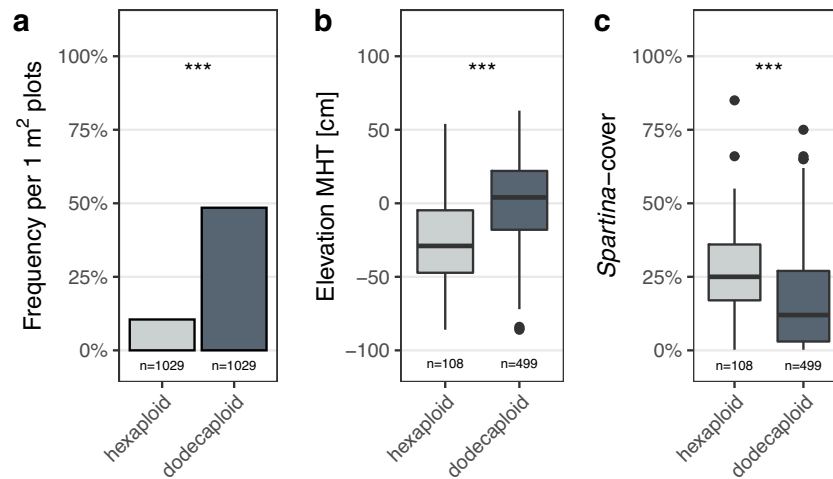


Fig. 3 **a** Frequency of *Spartina* cytotypes (hexa- and dodecaploid) on plots along transects of the focus area (***: Fisher's exact test for count data; $P < 0.001$; n : plots). **b** Occurrence of *Spartina* cytotypes on plots in the focus area in relation to elevation MHT (***: Mann-Whitney U -test, $U = 52.6$, $P < 0.001$, $df = 1$). **c** Cover of

Spartina cytotypes on plots in the focus area (***: Mann-Whitney U -test, $U = 33.5$, $P < 0.001$, $df = 1$). 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)

predicted HOF-model responses in Online Resource, Table 3).

Discussion

Detailed studies with respect to the geographic distribution of *Spartina* cytotypes in the European Wadden Sea have been lacking so far. With this study, we show that two different *Spartina* cytotypes occur in the mainland salt marshes along the Wadden Sea coast, the hexaploid F_1 -hybrid *Spartina* \times *townsendii* as well as the maternal *Spartina alterniflora*, and the hybrid's dodecaploid descendent *Spartina anglica*. However, we reject our first hypothesis of expecting evenly distributed cytotypes because the hexaploid cytotypes mainly occurred in eastern parts of the study area with varying frequencies, while the dodecaploid cytotypes were regularly present along the entire Wadden Sea coast. The presence of hexaploid *Spartina alterniflora* near the island of Mandø, Denmark, confirms two earlier records reporting its occurrence in Denmark (Møller et al. 2018). The Danish region is therefore a suitable study area for further investigations of backcrosses between *Spartina anglica* and *Spartina alterniflora* (cf. Renny-Byfield et al. 2010; Huska et al. 2016). Crosses between *Spartina* \times *townsendii* and *Spartina anglica* would be highly unlikely because of the strict infertility of *Spartina* \times *townsendii*. The meiotic defects reflected by the pollen inviability of *Spartina* \times *townsendii* indicate that selective evolution can be widely excluded as an explanation for the distribution pattern of the hexaploid F_1 -hybrid.

In the southwestern Wadden Sea, the hexaploid *Spartina* cytotypes were reported to be a rare species with two records on island salt marshes in the Netherlands in the 1950s (Mennema et al. 2013). We cannot rule out that we overlooked sporadic occurrences of the hexaploid *Spartina* cytotypes in the southwestern Wadden Sea area due to our sampling method with 50 km distance between sampling positions. Nevertheless, the main distribution area of the hexaploid cytotypes was restricted to the eastern parts of the Wadden Sea. This might be explained by differences in climate and geomorphology. The north-south trending Wadden Sea developed differently from the east-west trending Wadden Sea (Wiersma et al. 2009). While the latter Wadden Sea area was reported to be stable, the

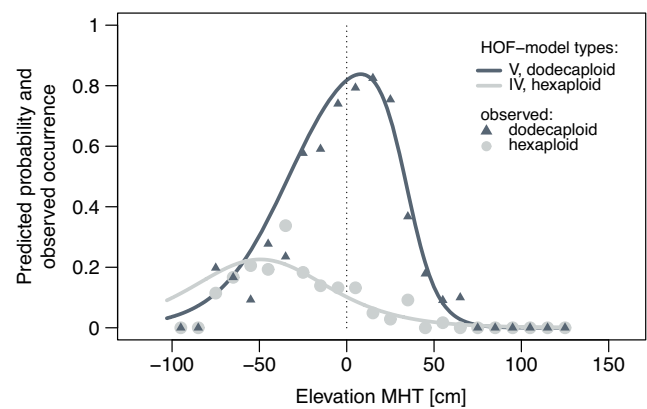


Fig. 4 HOF-modeled presence/absence response curves and observed frequencies of hexa- and dodecaploid *Spartina* cytotypes along the elevational gradient ($n = 1094$ plots)

northeastern part is undergoing land loss or subsidence. Furthermore, the northeastern part has colder winters (Oost et al. 2017; Philippart et al. 2017). Whether the hexaploid cytotype benefits from high geomorphodynamics in the eastern part and/or the dodecaploid cytotype is favored by milder climate in the southwestern part of the Wadden Sea needs to be tested in additional studies.

The hexaploid cytotype occurred with the highest frequency in the region north to the peninsula of Eiderstedt and in relative vicinity to former planting sites (Bay of Nordstrand, e.g., Sophien-Sommer-Koog or Dockkoog, König 1948). Presumably, these plants were donors of hexaploid clones which could establish in areas without *Spartina* plantings (cf. König 1948). Although the frequency of the hexaploid cytotype decreased with increasing geographic distance to the donor plantings, it spread vegetatively over dispersal distances comparable to the dispersal distances of the dodecaploid cytotype. This underpins the important role of vegetative spreading of polyploids (Herben et al. 2017). Besides vegetative spread, both the capacity for seed production (Marchant 1967; Hubbard 1970; Gray et al. 1990) and long-lasting floating of seeds in sea water (Marks and Truscott 1985; Huiskes et al. 1995; Koutstaal et al. 1987) may have increased the establishment success of the dodecaploid cytotype compared to the hexaploid (cf. Loebl et al. 2006; te Beest et al. 2012). In line with Glennon et al. (2014), who showed that dispersal capabilities can explain polyploid persistence in the long term, differences in spreading efficiency may explain why the hexa- and dodecaploid *Spartina* cytotypes differed widely in frequency along the geographic range of the study area.

Hexa- and dodecaploid *Spartina* cytotypes occurred with distinguishable phenotypes, which was reflected by different *Spartina* cover. This supports our second hypothesis. Stem density is an important factor controlling the capacity to catch suspended sediment and stabilize the marsh surface against sediment re-suspension by reducing the turbulent kinetic energy of water currents (Mudd et al. 2010; Tinoco and Coco 2018). Therefore, differences in *Spartina* cover may imply that the hexa- and dodecaploid cytotypes differ in their role in ecosystem functioning (van Hulzen et al. 2007; Bouma et al. 2009). Further investigations of *Spartina* cytotypes with respect to their contribution to ecosystem functioning are therefore strongly recommended.

The hexa- and dodecaploid cytotypes differed only slightly in their range of occurrence along the elevational gradient, although the estimated optimum of the hexaploid cytotype was approximately 50 cm lower than that of the dodecaploid. This did not support our third hypothesis. WGD in *Spartina* did not increase the capacity to colonize stressful habitats at the lower end of the elevational gradient. In tidal areas, decreases in elevation, even in the centimeter

range, translate directly into increases in both frequency and duration of flooding, and thus in abiotic stress (Maricle and Lee 2007; Engels et al. 2011; Davy et al. 2011) as well as increased biomechanical stress induced by winter-ice scrub and wave dynamics (Widdows et al. 2008). Regarding assumed abiotic and biophysical stressors, our data reflect that WGD in *Spartina* did not necessarily increase fitness nor change the niche breadths (cf. Visser and Molofsky 2015; Casazza et al. 2016; McIntyre and Strauss 2017). The hexaploid F₁-hybrid already showed the capacity to cope with these stressors proxied by elevation.

In contrast to *Salicornia*, the occurrence of *Spartina* cytotypes along the elevational gradient was not clearly constricted to marsh zones. In *Salicornia*, the cytotype with the larger genome (tetraploid) prefers habitats at low elevations, whereas it is replaced by the diploid *Salicornia* cytotype at higher and less stressful elevations (König 1960; Piirainen 2015; Witte et al. 2018). In *Spartina*, the cytotype with the larger genome (dodecaploid) was more frequent on high elevations than the hexaploid cytotype. This shows that WGD seems not to be a universal mechanism to increase the capacity for coping with abiotic severity.

Other factors than the above-mentioned may have been the reason for the differences in marsh zone preferences between *Spartina* and *Salicornia* cytotypes. While *Spartina* is perennial, in the annual *Salicornia*, seed germination and success of seedling establishment may select for the habitat which is specific for the respective cytotype (Witte et al. 2018). Furthermore, diversification in *Salicornia* is based on at least two independent WGD events (Kadereit et al. 2007). Therefore, habitat preferences in *Salicornia* cytotypes might be related to specific genotypes (Teege et al. 2011) because genetic variability can increase the ecological amplitude (e.g., Meimberg et al. 2009). Opposed to this, WGD in *Spartina* is assumed to be a unique event (Baumel et al. 2001; Ainouche et al. 2012) followed by a relatively short evolutionary history. A short evolutionary history after WGD did not allow for accumulation of genetic differences between *Spartina* cytotypes (Ramsey 2011; Soltis et al. 2016). Thus, differences in habitat preferences in *Spartina*, as indicated by differences in niche-optimum between *Spartina* cytotypes, are likely based on adaptive responses and competitive interaction between the cytotypes, and not on genetic diversification.

The hexaploid *Spartina* cytotype showed its optimum occurrence lower along the elevation gradient, presumably due to competitive exclusion by the dodecaploid cytotype (cf. Gray et al. 1990; Glennon et al. 2014; Casazza et al. 2016). Once established, the dodecaploid *Spartina* cytotype can show biotic resistance to the colonization of its patches by other closely related cytotypes (Proença et al. 2019). The first colonizing *Spartina* cytotype obviously gains advantage in long-term establishment. This is well

reflected by the observation that the hexaploid cytotype is still dominant in salt marsh areas near the hybridization site in Britain (Renny-Byfield et al. 2010; Huska et al. 2016). Elsewhere, the hexaploid F₁-hybrid may have been overlooked due to low establishment success. However, it may have a similar competitive capacity to its dodecaploid descendent. Therefore, competitive interactions between *Spartina* cytotypes require further experimental testing.

Conclusions

The hexaploid F₁-hybrid *Spartina* × *townsendii* and its dodecaploid descendent *Spartina anglica* occur with vital stands in European Wadden Sea mainland salt marshes. While the dodecaploid cytotype was present along the entire coast, the presence of the hexaploid cytotype was mostly confined to the northeastern parts of the Wadden Sea with regionally varying frequency. We infer that the hexaploid cytotype mainly established in vacant niches at the lower end of the elevational gradient where abiotic stress was presumably more severe but intercytotypic competition decreased. By contrast, in the dodecaploid *Spartina* cytotype, WGD increased the capacity for more efficient establishment along the geographic gradient but did not increase the capacity for establishment in stressful habitats or highly dynamic environments. Further studies are required to quantify differences between *Spartina* cytotypes in plant traits, performance, and their diverging role in ecosystem functioning of salt marshes.

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Declarations

Conflict of Interest The authors declare no competing interests.

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