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Seedling stability in waterlogged sediments: an experiment with saltmarsh plants

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ABSTRACT

Saltmarsh seedlings are exposed to extreme soil conditions in combination with mechanical disturbance by waves and tides, especially at the seaward fringe. We tested whether soil waterlogging affects resistance of seedlings against physical disturbance, thereby potentially influencing the distribution of saltmarsh species. A greenhouse experiment was conducted to investigate effects of waterlogging on plant traits, in particular root growth, and tolerance of seedlings against sediment erosion. Three species, each dominating different elevations in NW European salt marshes (*Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica*), were selected for the experiments. Individual seedlings were grown under different waterlogging treatments and finally subjected to an erosion treatment. The depth of erosion at which the seedlings toppled (E_{crit}) was determined and related to above- and below-ground morphological traits of the seedlings. Resistance against erosion decreased in all three species from drained to completely waterlogged soil conditions, with the strongest negative impact of waterlogging on the upper marsh species *E. atherica*. Root length and biomass, shoot biomass and the root:shoot biomass ratio were the most important traits positively affecting E_{crit}. The experiment demonstrates that rapid root growth is essential for the stability of seedlings, which is presumably of great importance for their successful establishment on tidal flats where sediment erosion may be a limiting factor. Root growth, in turn, is affected by a species-specific response to waterlogging. Our study suggests that this species-specific effect of waterlogging on seedling stability contributes to species sorting along the inundation gradient of coastal ecosystems.

KEYWORDS: Coastal ecosystems, Erosion, Root growth, Species distribution, Tidal inundation, Vegetation establishment

INTRODUCTION

The establishment of seedlings is a crucial phase in plant ontogeny (Grubb 1977). Salt marshes are dynamic ecosystems with phases of lateral expansion, when new vegetation establishes on tidal flats, and phases of retreat due to lateral erosion or drowning (Balke et al. 2014, Bouma et al. 2016). Saltmarsh seedlings generally establish above Mean High Water of Neap Tides (MHWN, Balke et al. 2016) and are exposed to extreme abiotic conditions, particularly during immersion. Vascular saltmarsh plants require a high degree of adaptation to their physically and physiologically stressful habitat (Bertness & Ellison 1987, van Diggelen 1991, Noe & Zedler 2000). Regular inundation by seawater leads to high salinity of saltmarsh soils and to waterlogged soil conditions accompanied by soil anoxia, increased concentrations of toxic compounds and decreased availability of nutrients (Armstrong et al. 1985, Pennings & Callaway 1992). High concentrations of soluble sulfide in waterlogged soils are both directly toxic to plants and reduce availability of essential elements such as Fe, Mn, Cu and Zn (Havill et al. 1985, Lamers et al. 2013). Apart from waterlogged soil conditions, seedling establishment in salt marshes is strongly impacted by physical disturbance by waves and tidal currents. Resuspension of sediment from the tidal flat can lead to short-term erosion of several centimeters (Hu et al. 2015, Hu et al. 2017) and hence to toppling or excavation of seedlings.

With increasing distance from the sea (i.e. increasing elevation and less frequent inundation) there is a gradual change in abiotic conditions leading to a zonation of saltmarsh vegetation with distinct species compositions (Fig.1; Armstrong et al. 1985, Bockelmann et al. 2002). Salinity and flooding are the main abiotic factors controlling the establishment and species distribution in saltmarsh plant communities (Cooper 1982, Armstrong et al. 1985, Rozema et al. 1985, Ungar 1998). The local determinants of plant zonation in salt marshes may also include herbivory and facilitation (Ungar 1998, Noe & Zedler 2001, Ewanchuk & Bertness 2004,

63 Pennings et al. 2005, Davy et al. 2011, He et al. 2015). In general, the seaward edge of the salt

64 marsh is only inhabited by a few species, which are able to tolerate stressful abiotic conditions,

65 whereas at higher elevations more competitive and less stress-tolerant species prevail (Levine et

66 al. 1998, Rand 2000, Pennings & Moore 2001, Crain et al. 2004, Farina et al. 2009).

67   Waterlogged soil conditions are common, especially in the lower salt marsh zones, and

68 may directly affect saltmarsh vegetation through reduced germination of seeds (Clarke & Hannon

69 1970), the inhibition of root emergence at the seedling stage (Wijte & Gallagher 1996), or

70 through growth inhibition in general (Cooper 1982). These effects vary between species from

71 different saltmarsh zones, which leads to the characteristic vegetation pattern (Clarke & Hannon

72 1970). However, it has not been assessed how the tolerance against erosion of different saltmarsh

73 species is affected by waterlogging, and how this influences the observed zonation. In general,

74 seedlings are less tolerant to stressful environmental conditions than adult plants (Ungar 1978),

75 while their establishment is crucial for vegetation formation. The first step of successful

76 establishment of a seedling on the tidal flat is the rapid anchoring during a disturbance-free

77 period, the so-called Window of Opportunity (Balke et al. 2014). After anchoring, seedling

78 survival depends on resistance to dislodgement by hydrodynamic forces as well as on

79 physiological abilities to cope with abiotic stress in tidally inundated soils (Balke et al. 2011,

80 Davy et al. 2011, Friess et al. 2012).

81   Waterlogged soils in combination with physical disturbance affect a number of

82 ecosystems besides salt marshes. In riparian floodplains, seedling survival is strongly dependent

83 on the hydrological regime, sediment erosion and deposition as well as the ability to root quickly

84 (Segelquist et al. 1993, Mahoney & Rood 1998, Corenblit et al. 2007). Seagrass beds have been

85 found to die off during events of extreme soil anoxia (Moore et al. 1993). However, populations

86 of *Zostera marina* are able to recolonize quickly after such anoxic crises despite continuous

87   sediment resuspension and strong hydrodynamic forces. This is due to rapid vegetative expansion

88   after initial seedling recolonization (Plus et al. 2003). Waterlogging and associated anoxic soil

89   reduce root growth and rooting depth across different wetland ecosystems (Visser et al. 1996,

90   Bouma et al. 2001). This reduced development of plant roots should in turn make plants more

91   susceptible to physical disturbance and thus play an essential role for the distribution of vascular

92   plants along inundation and disturbance gradients. The interactive effects of seedling trait

93   plasticity due to waterlogging and physical disturbance leading to plant toppling are currently

94   poorly understood, despite their potential relevance across biogeomorphic ecosystems (Corenblit

95   et al. 2015).

96   Our study addresses the effect of waterlogged soil conditions on the stability of newly

97   establishing seedlings in physically disturbed ecosystems such as salt marshes. We conducted a

98   greenhouse experiment using seedlings of three species dominating the three saltmarsh zones in

99   NW European salt marshes: the annual pioneer species *Salicornia europaea* (Chenopodiaceae),

100   which dominates the lowest margin of the salt marsh (i.e. the 'pioneer zone', Fig. 1), the dwarf

101   shrub *Atriplex portulacoides* (Chenopodiaceae) from the lower salt marsh, and *Elytrigia atherica*

102   (Poaceae), which occupies well-aerated soils in the upper salt marsh. The pioneer zone just above

103   MHWN is inundated during almost every high tide throughout the year (Balke et al. 2017) and

104   species are subjected to permanently waterlogged and reduced soil conditions. The lower salt

105   marsh lies just above the Mean High Tide (MHT) level and is inundated only during high water

106   of spring tides, and the upper salt marsh is only inundated during very high spring tides and storm

107   events. The lower and upper saltmarsh soils are generally well-drained and aerated during most

108   of the summer (Armstrong et al. 1985, Veeneklaas et al. 2013).

109   Considering the lack of data on early root growth in the context of intertidal wetland

110   succession (Friess et al. 2012), our study focuses on below-ground growth of seedlings in relation

111   to shoot growth under the given experimental conditions. We hypothesize that: (i) Root growth

112   plays an important role for the ability of seedlings to resist physical disturbances. (ii)

113   Waterlogged soil conditions negatively affect root growth of developing saltmarsh seedlings,

114   leading to reduced resistance against physical disturbance. (iii) Seedlings of pioneer zone species

115   cope more successfully with waterlogged soil conditions and are more resistant to physical

116   disturbances (i.e. erosion) under these conditions than lower and upper saltmarsh species. (iv)

117   Environmental stress (i.e. waterlogged soil) affects root morphology and leads to an increase in

118   specific root length and a decrease in root tissue density, thus increasing the efficiency of soil

119   exploitation at lower construction costs (Eissenstat et al. 2000).

120   Understanding the combined effects of soil waterlogging and disturbance on species

121   distribution across the elevational gradient of the saltmarsh environment is an important step

122   towards a better understanding of marsh zonation and improving the design of conservation and

123   restoration measures. This is especially important in light of accelerated sea level rise and

124   changing wave climates. Furthermore, linking soil anoxia and seedling stability to key plant traits

125   allows drawing conclusions that are also relevant for vegetation establishment in other frequently

126   flooded and physically disturbed ecosystems (e.g. mangroves, riparian forests or seagrass beds).

127

128   **MATERIALS AND METHODS**

129   Three experimental tanks (1 m (L) x 1 m (W) x 0.5 m (H)) were set up in a greenhouse at

130   the ICBM Terramare Wilhelmshaven (University of Oldenburg, Germany). A fourth tank that

131   served as water reservoir was placed beneath the three experimental tanks. Tidal inundation was

132   simulated by pumping water from the reservoir to the experimental tanks (Eheim universal pump

133   1048, 600 l/h; EHEIM GmbH & Co. KG, Deizisau, Germany). Seawater was mixed with

134   freshwater to obtain a salinity of 6.5, which corresponded to the salinity of the natural sediment

135 collected from Jade Bay, Germany (53°29'9''N; 8°10'50''E). A timer on the pumps was used to

136 fill the experimental tanks automatically, while switching off the pumps resulted in drainage of

137 the upper tank through the pump back into the reservoir. An overflow return pipe inside the

138 experimental tanks maintained the water depth at approximately 80 mm above the top of the plant

139 pots. Each experimental tank was flooded twice daily for 1.5 h, once during daytime and once at

140 night. Salinity in the mesocosms was measured every 2-3 days and maintained at 6.5 by the

141 addition of fresh water to compensate for evaporation.

142 Seeds of *Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica* were

143 collected in the salt marsh at the south side of the East Frisian Island Spiekeroog (Germany,

144 53°45'44''N; 7°43'23''E) in autumn 2014, air dried and stored dry at 7 °C until the start of the

145 experiment in early summer 2015.

146 Experimental pots were made from PVC pipes of 12 cm diameter and 15 cm length. The

147 pots were prepared in order to obtain three different levels of waterlogging within the pots: (a)

148 drained, (b) partly-waterlogged and (c) waterlogged. Treatments were chosen to simulate

149 permanently waterlogged soils on the tidal flats (i.e. initial location of pioneer establishment) and

150 better drained soils in the lower and upper saltmarsh zones. For the drained treatment, slits were

151 cut into the sides of the pots and pots were lined with a water permeable fleece to allow complete

152 drainage. For the partly-waterlogged treatment, holes with a diameter of 3 mm were drilled into

153 the upper three centimeters of the pots. The lower part of the pots, which was not perforated, was

154 lined with a plastic bag. In addition, fleece was inserted into the pots to avoid sediment loss

155 through the holes. For the waterlogged treatment, pots were entirely lined with plastic bags.

156 Sediment was collected from the tidal flats of the Jade Bay. The grain size distribution of the

157 sediment was: Sand ($> 63\,\mu m$): 95.9 %; Silt ($< 63\,\mu m$): 4.1 %; Clay ($< 2\,\mu m$): 0 %. After

158 collection, the sediment was frozen at -18 °C for three days in order to remove any live

159   zoobenthos. Afterwards, the sediment was sieved (mesh size: 5 mm) and filled into the

160   experimental pots. The pots were placed into the experimental tanks. Seven days after initiation

161   of the tidal regime different redox-potentials established according to the treatments (Table 1)

162   and seedlings were transferred to the experimental pots (see below). Redox-potential was

163   measured as an index for soil aeration and we expected waterlogged treatments to be associated

164   with low redox-potentials (Davy et al. 2011). Each experimental tank included one reference pot

165   to measure redox-potential. This was done every 2-3 days throughout the experiment at three

166   different sediment depths (2.5 cm, 5 cm and 10 cm) at varying locations in each reference pot by

167   means of a metal combination electrode with an Ag/AgCl reference system (3 M KCl) and a

168   platinum sensor (Pt 61, SI Analytics GmbH, Mainz, Germany). Measured values were corrected

169   by adding the potential of the reference electrode (210 mV) with respect to the standard hydrogen

170   electrode. In addition, the redox-potential was measured in the three saltmarsh zones and on the

171   tidal flat with beginning seedling colonization at Spiekeroog Island (Table 1).

172   Seeds were sown in the same sediment outside of the mesocosms and seedlings were

173   transferred 3-4 days after germination to the experimental pots. Each pot was planted with one

174   seedling with visible cotyledons and a size of a few millimeters (Fig. 2a). Seedlings were

175   assigned to pots using a random number list whereby species and treatments were distributed

176   evenly among the three experimental tanks. Per species and treatment, 18 (*E. atherica* and *S.*

177   *europaea*) or 12 (*A. portulacoides*) replicate pots were used. The seedlings were grown in the

178   experimental pots inside the mesocosms for a period of 47 to 55 days and monitored throughout

179   the experiment for survival and height three times per week. On the last day, all surviving

180   seedlings were subjected to an erosion treatment. Following previous studies (see Han et al. 2012

181   for seagrass; Balke et al. 2013 for mangroves; Cao et al. 2017 for *Spartina* spp.), erosion was

182   mimicked by placing 3 mm thick discs from the bottom into the experimental pots and pushing

183   the sediment above the edge of the pot. Protruding sediment was carefully removed by water

184   spray without breaking seedlings or roots. Additional discs were inserted until the seedlings

185   toppled under their own weight (Fig. 2b). This was defined as the critical erosion depth (E_{crit}).

186   Toppled seedlings were removed from the sediment, washed and maximal root length (length of

187   the longest root) and shoot height were determined. Furthermore, fresh roots and shoots were

188   separated from each other and roots were scanned under a flatbed scanner to determine total root

189   length, root surface area, root volume and root diameter (software WinRhizo; Regent

190   Instruments, Quebec, Canada). After scanning, roots and shoots were oven dried at 70°C for 72 h

191   and weighed to determine dry mass. Specific root length (SRL, root length/root dry weight),

192   specific root area (SRA, root surface area/root dry weight) and root tissue density (RTD, root dry

193   weight/root volume) were calculated from these measurements.

194   In addition, *Salicornia* sp. seedlings from a natural tidal flat close to a salt marsh near

195   Westerhever (Schleswig-Holstein, Germany, 54°37'50''N; 8°63'52''E) were subjected to the

196   same erosion treatment by entering one of the experimental pots into the sediment around a

197   seedling, digging out the pot containing the seedling and surrounding sediment, and performing

198   the critical erosion test as described above. Seedlings were brought to the laboratory, washed,

199   maximal root length and shoot height were determined and roots were scanned, dried and

200   weighed for the determination of root morphological traits as described above. Seedlings were

201   chosen with a similar shoot height as the seedlings grown in the mesocosm experiment. Due to

202   difficult differentiation between taxa at the seedling stage and the challenging taxonomy of

203   *Salicornia* in general (Kadereit et al. 2012), we here refer to the genus *Salicornia*.

204

205   *Statistical analyses*

206   Statistical analyses were conducted using R 3.3.2 software (R Development Core Team,

207   2016). A growth curve for each species was fitted to a three parameter-logistic growth model

208   according to Paine et al. (2012) using the package 'nlme' (equation 1):

209 $$H\ (t) = \frac{H_0 \cdot K}{H_0 + (K - H_0) \cdot e^{-r \cdot t}}$$ **Equation 1**

210   with H: seedling height at time t, H_0: seedling height at start of experiment (when transferred to

211   experimental pots), K: seedling height at harvest, and r: relative growth rate. H_0, K and r were

212   treated as random effects on the individual level. To test for differences between treatments the

213   restricted maximum likelihood method was used.

214   To account for species differences in initial seedling size and to compare shoot and root

215   growth between species, absolute growth rates were calculated as Δseedling height/Δt or

216   Δroot length/Δt as the increase in seedling height or root length over the exposure period of the

217   experiment (Δt) (Paine et al. 2012). Absolute growth rates are appropriate to capture age- and

218   size-dependent growth (i.e. initial seedling growth in our study) (Paine et al. 2012). Growth rates

219   and seedling morphology data were log-transformed to achieve normality of residuals and

220   homoscedasticity according to Shapiro-Wilks test (Shapiro.test) and Levenes test (leveneTest,

221   package 'car'), respectively. Two-way factorial ANOVAs were conducted to compare the main

222   effects of species and treatments and the interaction between species and treatments on the

223   different morphological traits and growth rates. Tukey HSD tests allowed multiple comparisons

224   between species and treatments (Anova and HSD.test, packages 'car' and 'agricolae',

225   respectively). In cases of significant interaction effects, one-way ANOVAs with subsequent

226   Tukey HSD tests were conducted to investigate significant differences between levels within the

227   variables (species, treatment) separately. Where normality of residuals could not be achieved (for

228   values of E_{crit}), a Kruskal-Wallis test (kruskalmc, package 'pgirmess') was used for multiple

229   comparisons of E_{crit} between treatments and species. Statistical significance was based on a 0.05

230   probability level. A principal components analysis (PCA) was used to assess how parameters of

231   seedling size and stability interrelate between species and treatments using the software

232   CANOCO, version 5.02 (Biometris, the Netherlands).

233

234   **RESULTS**

235   *Growth of seedlings depending on waterlogging treatment*

236   Shoot growth rates differed between the three species in all treatments with highest shoot

237   growth rates for *Elytrigia atherica* and lowest shoot growth rates for *Atriplex portulacoides* (Fig.

238   3, Fig. 4a, $p < 0.001$). This resulted in substantial differences in seedling size at the end of the

239   experiment. Seedlings of *E. atherica* (252 mm shoot height in the drained treatment) were 4 times

240   and 8 times taller than those of *Salicornia europaea* (75 mm) and *A. portulacoides* (34 mm),

241   respectively (Table 2, see also Table S1 for measurements of seedling height and Table S2 for

242   results of two-way factorial ANOVAs). Absolute root growth rates in the drained treatment

243   differed between the three species ($p < 0.001$, Fig. 4a). Root growth rates of *E. atherica* were

244   significantly higher than those of *S. europaea* and *A. portulacoides*. Under waterlogged

245   conditions there were no significant inter-specific differences.

246   Seedling size at the end of the exposure period was significantly affected by waterlogging

247   treatments within species for *S. europaea* and *E. atherica*. Performance of *S. europaea* seedlings

248   was slightly better under partly-waterlogged and fully waterlogged conditions compared to the

249   drained treatment. However, only the partly-waterlogged treatment led to a significant increase in

250   shoot height (21.5 %) compared to the drained treatment ($p < 0.05$). *E. atherica* was affected

251   negatively in its growth by waterlogging. Shoot height of seedlings was lower by 37 %

252   ($p < 0.001$) in the waterlogged treatment compared to the drained treatment (Fig. 3 and Table 2).

253   Absolute root growth rates of *A. portulacoides* and *E. atherica* were reduced by waterlogging

254   treatments (Fig. 4b). Absolute root growth rate of *A. portulacoides* seedlings was reduced by

255   36 % (p < 0.05) when waterlogged. This effect was also evident for *E. atherica* (70 % reduction

256   of absolute root growth rate, p < 0.001). Root and shoot biomass showed similar patterns as shoot

257   height and root length (Table S1).

258

259   *Effects of waterlogging on seedling morphology*

260   In the three species, root:shoot length ratios tended to decrease from the drained to the

261   waterlogged treatment, although this trend was only significant for *S. europaea* (33 % decrease)

262   and *E. atherica* (40 % decrease, p < 0.05, Fig. 4c). Root:shoot length ratios differed between all

263   three species in all treatments (p < 0.001) and were highest in *A. portulacoides* seedlings and

264   lowest in *E. atherica*. The root morphological traits SRL, SRA, RTD and root diameter were not

265   affected by the treatments (Fig. 4d-f, Table S1). *S. europaea* seedlings showed higher SRL and

266   SRA and lower RTD under drained and partly-waterlogged conditions compared to the other

267   species (p < 0.001).

268

269   *Effects of waterlogging on seedling stability*

270   A significant decrease of E_{crit} from the drained to the waterlogged treatment was only

271   found in *E. atherica* (80 % decrease, Kruskall-Wallis, p < 0.05, Fig. 5). Furthermore, *E. atherica*

272   seedlings from the drained and partly-waterlogged treatments showed a significantly higher E_{crit}

273   compared to *S. europaea* and *A. portulacoides* within treatments. Under waterlogged conditions,

274   critical erosion depth of *E. atherica* was similar to that of *S. europaea* and *A. portulacoides*.

275

276   *Comparison with Salicornia seedlings from the tidal flat*

277   *Salicornia* sp. seedlings naturally established in the field showed significant differences

278   compared to experimental plants. Although similar in shoot height (Table S1), they had higher

279   root biomass, shoot biomass, root length and ratios of root:shoot biomass and length (one-way

280   ANOVA with Tukey HSD tests, $p < 0.001$ respectively, Table S1). SRL and SRA were lower

281   ($p < 0.001$), whereas RTD ($p < 0.05$) and root diameter ($p < 0.001$) were higher compared to

282   seedlings from the greenhouse. Critical erosion depth of naturally recruited seedlings was more

283   than 5-fold higher compared to those grown in the experimental mesocosms (Fig. 5). Redox-

284   potentials measured at the tidal flat, where seedlings were collected, were intermediate between

285   the values of partly-waterlogged and waterlogged treatments in the experiment at shallow depth

286   (+87 mV in upper 2.5 cm), but more negative compared to the experimental pots in deeper

287   sediment (approx. -200 mV at 10 cm) (Table 1). Redox-potential in the vegetated saltmarsh zones

288   was positive in the pioneer zone (approx. +200 mV) and increased to highly oxidized conditions

289   in the upper salt marsh (approx. +400 mV).

290

291   *Linking seedling morphology to stability of seedlings against erosion*

292   In the Principal Components Analysis (PCA, Table S3, Fig. 6), critical erosion depth was

293   strongly positively associated with the first axis (eigenvalue 0.63) together with root length and

294   biomass as well as shoot biomass and the ratio in root:shoot biomass. Furthermore, shoot height

295   was strongly negatively associated with the second axis (eigenvalue 0.33), while the ratio in root

296   length: shoot height was positively associated with this axis. The PCA plot in Fig. 6 indicates that

297   *S. europaea* and *A. portulacoides* seedlings resembled each other in terms of seedling size and

298   stability in all three treatments, while the drained and the partly-waterlogged treatment formed a

299   cluster separated from the waterlogged treatment in the case of *E. atherica*. *Salicornia* sp.

300 seedlings grown under natural field conditions did not group with any of the treatments of *S.*

301 *europaea* in the greenhouse or with the other two species.

302

303 **DISCUSSION**

304   Seedling establishment is a critical phase in plant ontogeny, especially in frequently

305 disturbed ecosystems such as salt marshes, mangroves and riparian forests. Short-term sediment

306 erosion during inundation can excavate and dislodge seedlings; rapid root anchorage is thus

307 crucial for seedling survival in these environments. Understanding bottlenecks for vegetation

308 establishment is particularly important when attempting restoration of tidal wetlands, which are

309 increasingly acknowledged for their ecosystem services. Our study demonstrates that

310 waterlogged soil conditions may inhibit root growth of saltmarsh seedlings, leading to decreased

311 resistance of seedlings against physical disturbance. The strongest negative effect of

312 waterlogging was found for the upper saltmarsh species *Elytrigia atherica*. While seedlings from

313 *E. atherica* grew fastest throughout the experiment under drained conditions, they were most

314 susceptible to waterlogging (Figs 3 to 5). This result supports previous findings that *Elytrigia*

315 *atherica* is a highly competitive species, but very sensitive to waterlogging (Armstrong et al.

316 1985, Schröder et al. 2002, Veeneklaas et al. 2013). Along the NW European North Sea coast, *E.*

317 *atherica* spreads rapidly in many sites frequently forming monospecific stands at the rarely

318 inundated upper salt marsh (Bockelmann & Neuhaus 1999, Stock et al. 2005). Rhizomes of *E.*

319 *atherica* can spread rapidly and locally outcompete other species, but successful seedling

320 establishment is still necessary over larger distances (Veeneklaas 2013). Our study indicates that

321 successful establishment of *E. atherica* seedlings on tidal flats may be limited by a strong

322 inhibition of root growth and the resulting decreased stability of seedlings during erosion events.

323 In the upper salt marsh however, *E. atherica* is able to outcompete *Salicornia* sp. and *Atriplex*

324 *portulacoides* due to its rapid root and shoot growth under drained conditions.

325 Bockelmann & Neuhaus (1999) investigated competition between *E. atherica* and *A.*

326 *portulacoides* and concluded that *E. atherica* is excluded from the lower salt marsh due to

327 competition with *A. portulacoides* rather than by abiotic factors. Our study suggests that *E.*

328 *atherica* may also be disadvantaged at frequently flooded sites in the absence of competition due

329 to a higher sensitivity to waterlogging at the seedling stage. This may be especially important

330 where newly available habitats are colonized by saltmarsh plants (Balke et al. 2017).

331 In contrast to the strong negative impact of waterlogging on *E. atherica*, *S. europaea* and

332 *A. portulacoides* were hardly affected in their growth by the waterlogging treatments. Shoot

333 height of *Salicornia* was even higher under partly-waterlogged conditions compared to the

334 drained treatment (Fig. 3, Table 2), indicating the good adaptation of this species to waterlogged

335 conditions on tidal flats. Although root growth of *A. portulacoides* was reduced under

336 waterlogged conditions, there was no difference between seedling stability of *S. europaea* and *A.*

337 *portulacoides*. Thus, further abiotic and biotic components and their interactions need to be

338 considered when explaining niche separation across the saltmarsh gradient, such as salinity

339 tolerance (Cooper 1982, Rozema et al. 1983, Armstrong et al. 1985, Rozema et al. 1985,

340 Redondo-Gomez et al. 2007, Katschnig et al. 2013), interspecific competition (Huckle et al.

341 2000, Balke et al. 2017), or herbivory (He et al. 2015).

342 Frequent inundation and accompanying strongly reduced soil conditions as simulated in

343 our experiment are especially common on bare tidal flats suitable for new colonization, but also

344 in the lowest elevations of the salt marsh. Anoxia persists in this zone throughout the growing

345 season even in the upper centimeters of the sediment (Table 1, Armstrong et al. 1985). All

346 treatments of our experiment had lower redox-potentials compared to field measurements in the

347 salt marsh (including the pioneer zone), whereas sediment of the tidal flat was overall more

348 reduced than the partly-waterlogged and drained treatments. In Davy et al.'s (2011) study on the

349 relationship of species distributions and redox-potential, *Salicornia europaea* was found to

350 tolerate redox-potentials of < -100 mV, *A. portulacoides* was absent in plots below a threshold of

351 100 mV and *E. atherica* was absent below 200 mV. Comparing these thresholds to the values

352 measured in our experimental treatments shows that seedlings were subjected to extremely

353 reduced conditions below the limits in their natural habitats (Table 1). However, seedlings of all

354 three species were able to survive these extreme conditions still showing treatment-dependent

355 effects. This suggests an effect of anoxia on seedling development that may also depend on site

356 (e.g. sediment type, salinity, wave exposure) and life stage (e.g. isolated seedling, adult plant in

357 competition with other species). Relatively small differences in redox-potential between

358 treatments in deeper sediment layers, despite the differences in water level of the sediment,

359 indicate that a less negative redox-potential in the upper sediment layers is already sufficient for

360 the seedlings to establish roots which are strong enough to withstand erosion.

361   Unexpectedly, there were no effects on root morphology caused by the waterlogging

362 treatments within species. This indicates that these herbaceous and grass species do not adjust

363 their root morphology under changing environmental conditions as found for example for tree

364 species (Eissenstat et al. 2000, Ostonen et al. 2007, Vanguelova et al. 2007). *S. europaea* had

365 significantly higher SRL and SRA and lower RTD compared to *E. atherica* and *A. portulacoides*

366 in the drained and the partly-waterlogged treatments. This is consistent with findings that roots

367 with shorter lifespan have lower RTD (Ryser 1996) and higher SRL and therefore relatively

368 small investments in structural carbon (Eissenstat et al. 2000). This is for example typical for *S.*

369 *europaea* as an annual plant. Moreover, the tap root system of *S. europaea* and *A. portulacoides*

370 may have advantages for plant stability compared to the fibrous root system of *E. atherica*, as

371   common for monocotyledons. The fibrous root system may also explain the strong competitive

372   abilities of *E. atherica* since it provides better opportunities for resource exploitation. However,

373   from the roots at the seedling stage (i.e. time of harvest in our experiment) differences in root

374   structure could not be observed between species (recognized in the WinRhizo images, not

375   shown). We therefore conclude that these differences in root structure do not yet play a role at the

376   early seedling phase and may only become important during later development stages.

377   We found substantial differences between naturally recruited seedlings and those grown

378   in the greenhouse experiment. Although similar shoot heights were chosen, seedlings from the

379   tidal flat showed significantly higher stability, which may be related to a higher root length (Figs

380   5 & 6, Tables S1 & S3), and possibly also to the already well-developed tap root (WinRhizo

381   images) which the experimental seedlings were still lacking. Field material was harvested in late

382   June and hence approximately 2-3 months after germination in March to April (i.e. they were

383   approximately of same age as the experimental seedlings). Differences between field and

384   greenhouse-grown plants have been observed in various ecosystems e.g. for germination rates

385   (Elberse & Breman 1990), photosynthetic induction (Zotz & Mikona 2003) or salt tolerance in

386   *Salicornia* (Riehl & Ungar 1982). This asks for caution when interpreting data from laboratory

387   studies. In our study, differences between field and experimental seedlings indicate that

388   permanently acting mechanical stress from wind and waves, which was not simulated in the

389   greenhouse, may lead to important plastic morphological responses (i.e. thigmomorphogenesis;

390   Jaffe 1973, Chehab et al. 2009). Increased root allocation of field grown seedlings by

391   thigmomorphogenesis increases their resistance to mechanical perturbation ('tolerance strategy',

392   Puijalon et al. 2011) and has been observed by other authors in aquatic (Puijalon & Bornette

393   2006) and terrestrial (Crook & Ennos 1996, Goodman & Ennos 1996) plants as a response to

394   mechanical stimulation. In addition, lower light levels in the greenhouse may have affected

395 growth rates and seedling morphology in relation to surveyed seedlings in the field. Pennings et

396 al. (2005) conducted field and greenhouse experiments with *Juncus roemerianus* and made

397 similar observations: biomass was much higher in individuals grown in the field than in those

398 grown in the greenhouse, but the response of seedlings to various flooding and salinity treatments

399 was highly correlated between field and glasshouse. Thus, we conclude that the results of our

400 mesocosm experiment are of ecological relevance, especially when comparing the three species

401 grown under same, controlled conditions in the greenhouse among each other. However, this

402 study highlights that the effects of thigmomorphogenesis for seedling stability may also play a

403 role in seedling establishment on tidal flats and requires further experimental investigation.

404   The close relationship between the critical erosion depth of seedlings grown in the

405 experimental mesocosms and seedling traits such as root and shoot biomass and length (Fig. 6,

406 Table S3) may also be relevant to other plant species in biogeomorphic ecosystems (i.e.

407 mangroves, riparian vegetation or seagrass beds). Rapid root growth of seedlings in their first

408 weeks of development is crucial for their tolerance against physical disturbance in these habitats.

409 It is known that several intertidal wetland pioneer species (i.e. *Salicornia* spp., *Spartina* spp. and

410 *Avicennia* spp.) show rapid root emergence and development (Friess et al. 2012). With rapid root

411 growth, saltmarsh and mangrove pioneers are able to utilize disturbance free Windows of

412 Opportunity to gain tolerance against subsequent disturbance by inundation, wave action and

413 short-term sediment erosion (Balke et al. 2011, Balke et al. 2014, Cao et al. 2017). The present

414 study showed that seedling stability within the first weeks after emergence can be severely

415 limited by soil waterlogging through reduced root growth.

416

417 **CONCLUSIONS**

418   Our study showed that waterlogged and anoxic soil conditions can eliminate species-

419   specific differences in root growth and tolerance of seedlings against erosion that otherwise exist

420   in drained conditions. Niche separation in salt marshes may thus not only be attributed to

421   tolerance of salt and inundation stress or competitive strength, since tolerance against physical

422   disturbance at the seedling stage may be strongly influenced by soil waterlogging. This

423   interaction could be demonstrated for the upper saltmarsh species *Elytrigia atherica* in our study

424   and may be one determinant for the distribution of this species across the elevational saltmarsh

425   gradient. Further studies are suggested across frequently disturbed and inundated ecosystems

426   (mangroves, riparian forests, seagrass beds) to investigate the effects of soil anoxia on plant traits

427   and stability, and the spatial relationship between exposure to disturbance and soil anoxia of

428   suitable habitats for colonization. This is especially important to improve restoration success in

429   coastal wetland ecosystems.

430

438

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609

610 **Table 1:** Sediment redox-potential (means ± se) measured at different sediment depths for the three

611 treatments of the mesocosm experiment and in the three saltmarsh zones and a tidal mudflat at Spiekeroog

612 Island (Germany). Measurements at the field site were taken during the growing period (August).

613 Measured values were corrected by adding the potential of the reference electrode (210 mV) with respect

614 to the standard hydrogen electrode.

| sediment depth	redox-potential (mV)						
	experimental pots			field reference			
	drained	partly-waterlogged	waterlogged	upper salt marsh	lower salt marsh	pioneer zone	mudflat with beginning colonization
2.5 cm	+126.5	+107.5	+6.2	+412.7	+345.6	+236.0	+87.0
	± 9.1	± 7.9	± 5.32	± 10.8	± 10.2	± 33.2	± 107.0
5 cm	-2.5	+4.1	-18.2	+409.0	+355.7	+289.2 ±	-26.6
	± 5.2	± 8.0	± 3.4	± 7.3	± 30.0	36.5	± 92.2
10 cm	-54.2	-39.9	-40.4	+424.0	+371.8	+254.9	-196.9
	± 2.7	± 3.1	± 2.3	± 11.5	± 25.0	± 55.0	± 19.0

615 **Table 2:** Parameters of a three-parameter logistic model for the growth of *Salicornia europaea*, *Atriplex*

616 *portulacoides* and *Elytrigia atherica* seedlings exposed to three waterlogging treatments. H_0: height at

617 beginning of the experiment (mm), K: shoot height at harvest (mm); r: relative growth rate (mm mm^{-1}

618 day^{-1}). Values for partly-waterlogged and waterlogged treatments are given as deviation from the drained

619 treatment with p values indicating a significant deviation (restricted maximum likelihood test).

|	$H_0 \pm SE$	p	$K \pm SE$	p	$r \pm SE$	p	Residuals
S. europaea							
drained	6.2 ± 0.5	-	75.4 ± 3.4	-	0.0868 ± 0.0030	-	2.095
partly-waterlogged	0.3 ± 0.7	n.s.	9.7 ± 4.9	*	0.0003 ± 0.0041	n.s.	2.095
waterlogged	-0.6 ± 0.7	n.s.	7.3 ± 4.8	n.s.	0.0062 ± 0.0041	n.s.	2.095
A. portulacoides							
drained	8.7 ± 1.0	-	34.0 ± 3.0	-	0.0797 ± 0.0060	-	1.855
partly-waterlogged	-0.3 ± 1.3	n.s.	4.4 ± 4.1	n.s.	-0.0014 ± 0.0079	n.s.	1.855
waterlogged	-1.4 ± 1.3	n.s.	2.3 ± 4.2	n.s.	-0.0002 ± 0.0080	n.s.	1.855
E. atherica							
drained	32.8 ± 1.9	-	251.5 ± 10.3	-	0.1031 ± 0.0090	-	10.966
partly-waterlogged	-0.9 ± 2.6	n.s.	-8.4 ± 14.4	n.s.	0.0100 ± 0.0122	n.s.	10.966
waterlogged	-4.5 ± 2.8	n.s.	-92.5 ± 15.1	***	0.0127 ± 0.0132	n.s.	10.966

620 $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***, n.s.: not significant
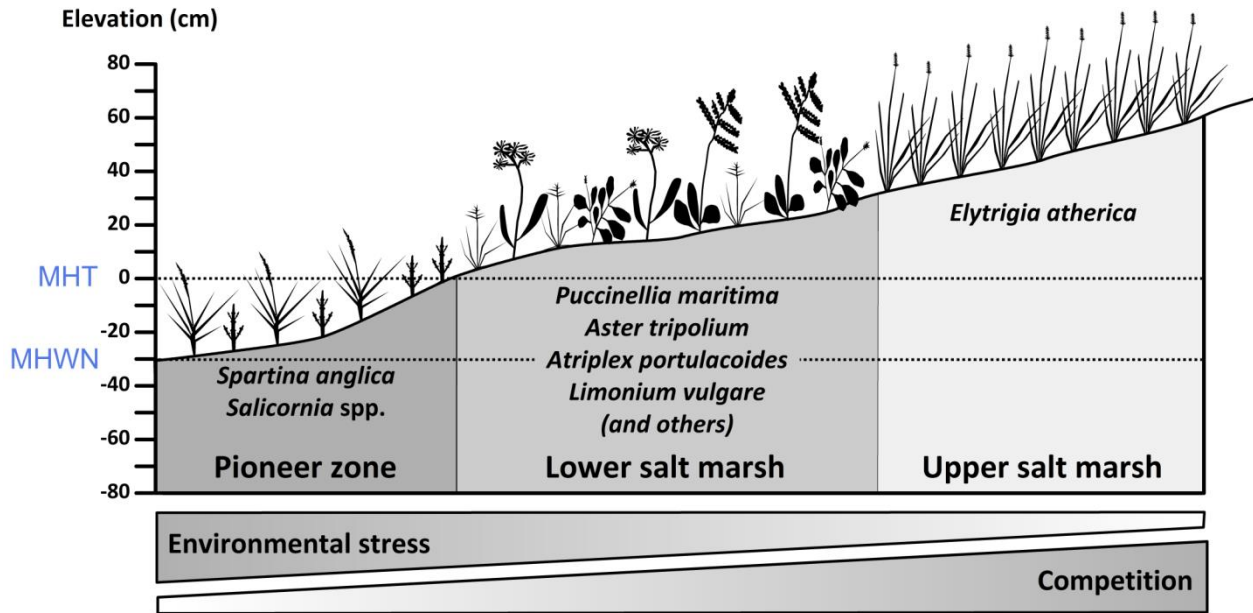
Figure 1: The three zones of a NW European salt marsh with their elevations relative to the Mean High Tide (MHT) level and characteristic species. Mean High Water of Neap tides (MHWN) marks the transition from the bare tidal flat to the pioneer zone. Figure by Dietrich Hertel and R. Redelstein.
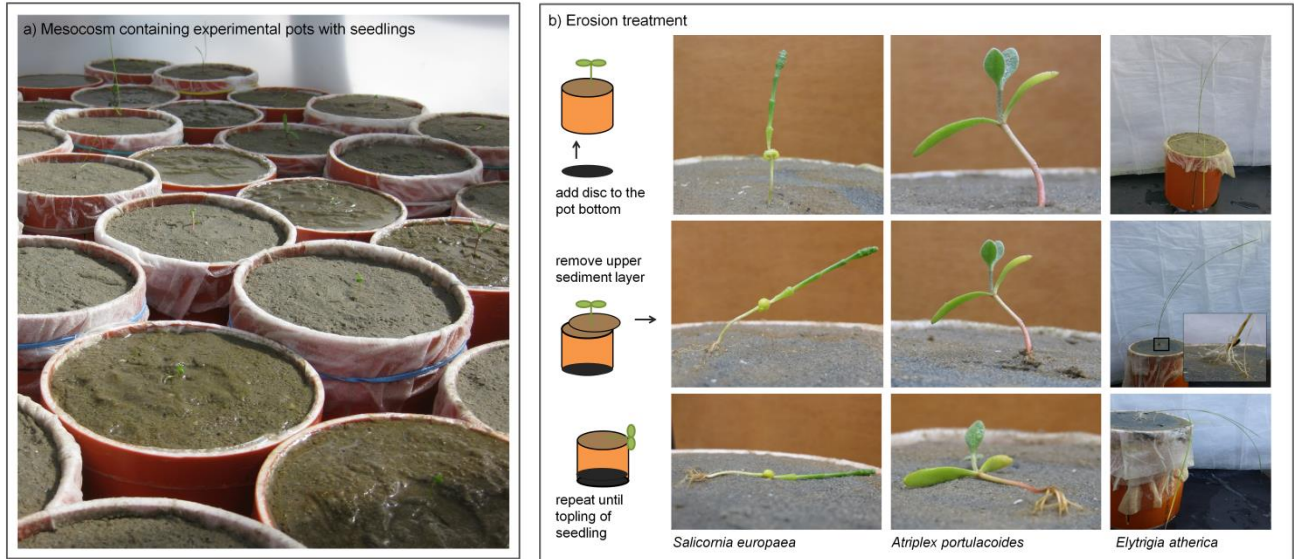
625 **Figure 2:** Photograph of the experimental pots inside of the mesocosms planted with seedlings (a) and

626 design and procedure of the critical erosion test (b). Photographs: R. Redelstein.
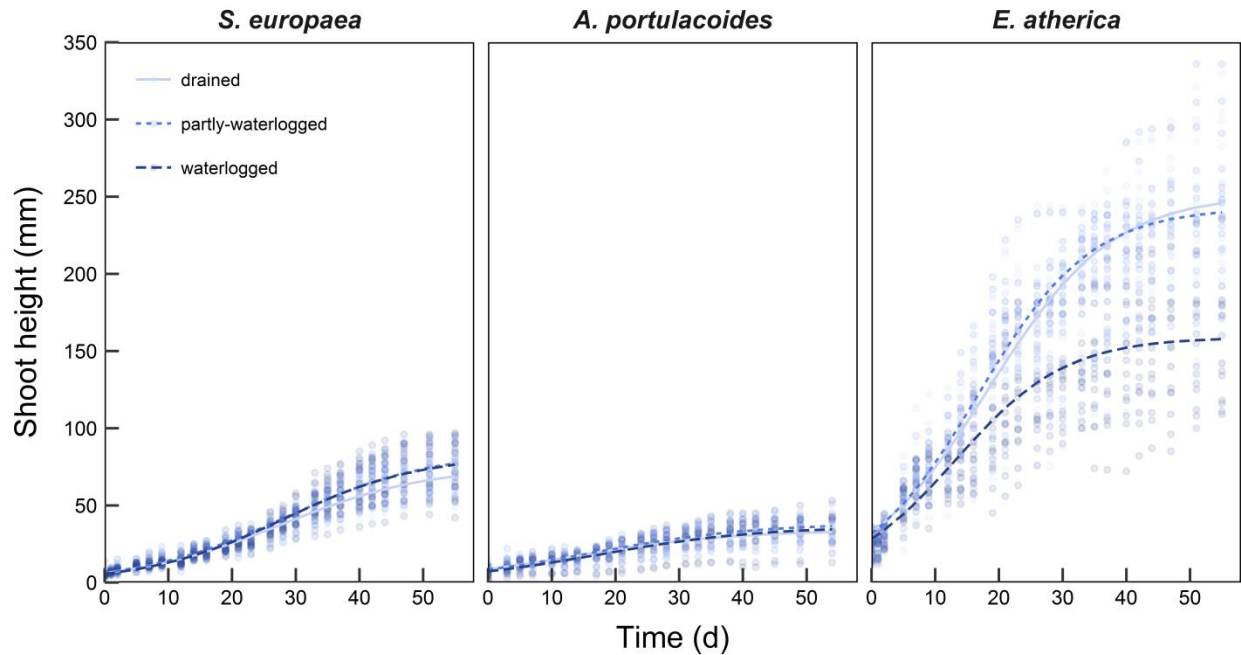
Figure 3: Growth of *Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica* seedlings during the experiment depending on waterlogging treatments. Dots represent measurements of individual seedlings; lines represent predictions of a three-parameter logistic model for the different treatments. Note overlaying treatment lines for *S. europaea* and *A. portulacoides*.

632


633
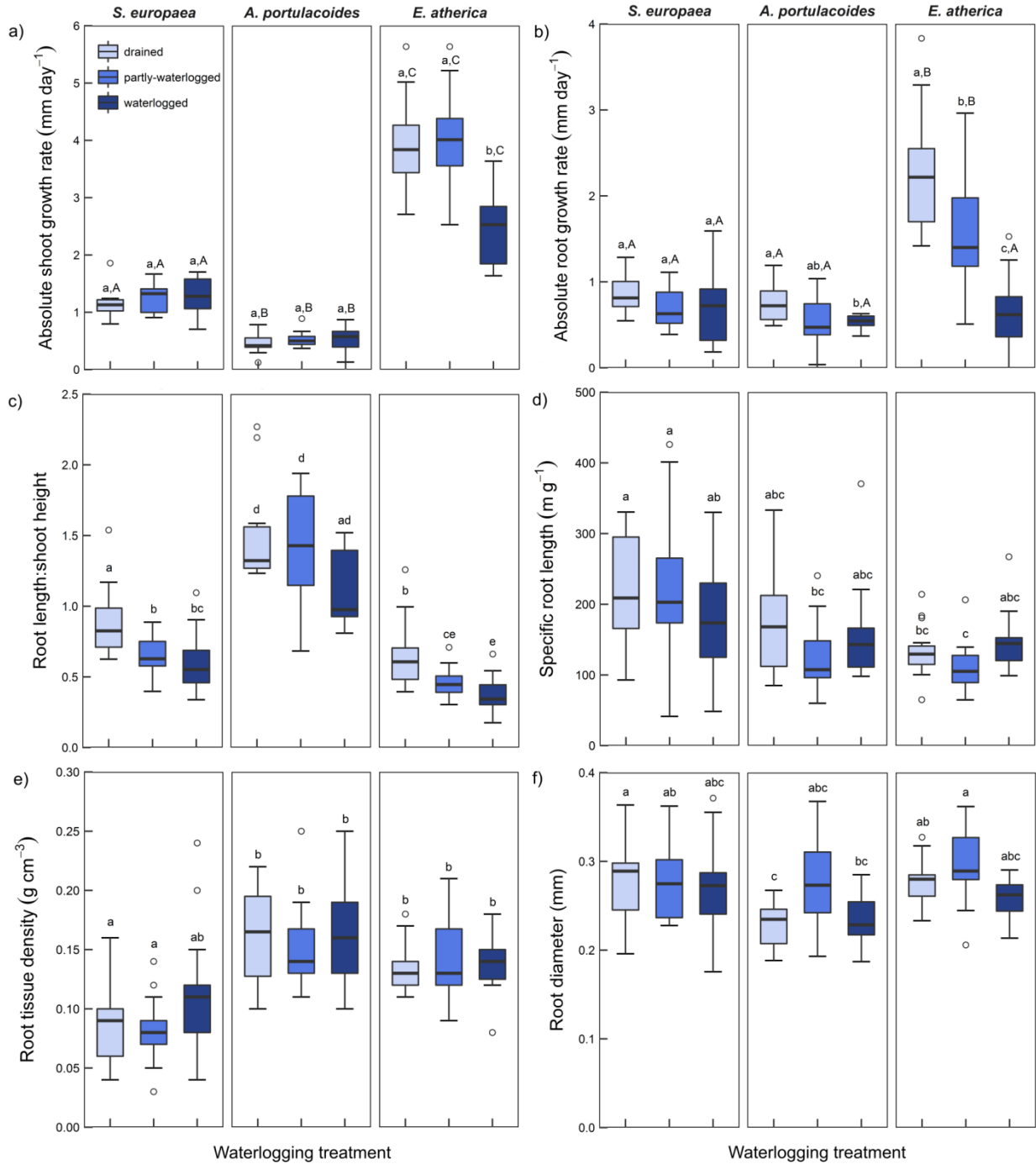
Figure 4 a-f): Absolute root and shoot growth rates, and measures of root morphology of *Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica* seedlings depending on waterlogging treatments (drained, partly-waterlogged, waterlogged). Horizontal lines indicate median values, boxes the interquartile range and error bars minimum and maximum values. Open circles represent outliers.

638   Different lower case letters indicate statistical differences between treatments within species, upper case

639   letters mark significant differences between species within treatments according to one-way ANOVA with

640   Tukey HSD tests ($p < 0.05$) when the interaction effect was significant. Else different lower case letters

641   indicate significant differences comparing species and treatments by two-way factorial ANOVA with

642   Tukey HSD tests ($p < 0.05$).
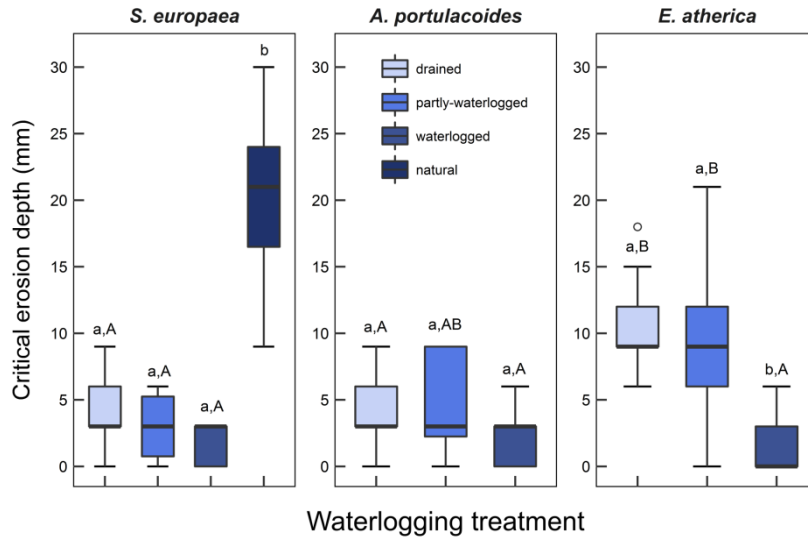
Figure 5: Critical erosion depth of *Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica* seedlings depending on sediment conditions in the greenhouse experiment and of *Salicornia sp.* seedlings grown under natural field conditions. Lower case letters mark statistically significant differences between treatments within species, upper case letters mark statistically significant differences between species within treatments (Kruskal-Wallis multiple comparisons with $p < 0.05$).
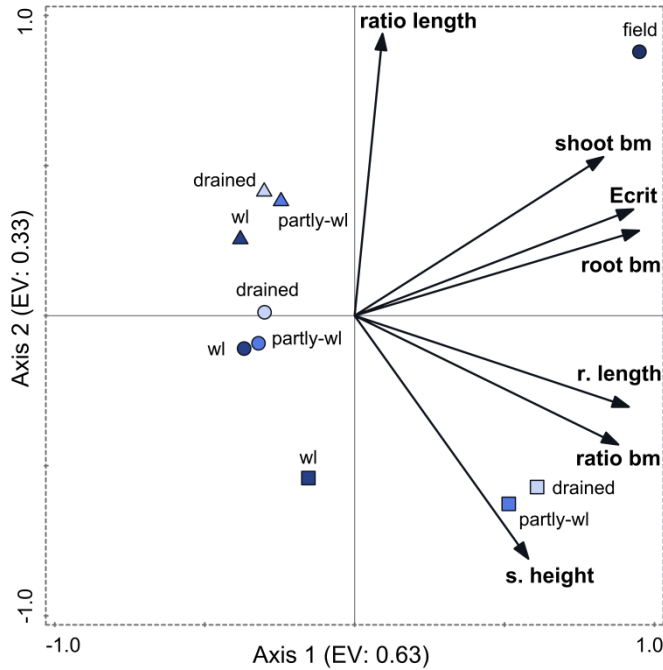
Figure 6: Results of a Principal Components Analysis regarding different measures of seedling size (root length (r. length), shoot height (s. height), root biomass (root bm), shoot biomass (shoot bm), root:shoot ratios in length (ratio length) and biomass (ratio bm)) and their critical erosion depth (Ecrit). Species: triangle: *Atriplex portulacoides*, circle: *Salicornia* spp., square: *Elytrigia atherica*. Each species was subjected to three treatments: drained, partly-waterlogged (partly-wl) and completely waterlogged (wl). Shown are the inter-relationships along the first two axes and their eigenvalues (EV). Vector length and angle are proportional to the direction and degree of their correlation with the plot ordination scores. Table S3 gives detailed results of the PCA.