

Recolonization and facilitation in Baltic salt marsh vegetation

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Received 18 Nov. 2013, final version received 11 Dec. 2014, accepted 16 Dec. 2014

Ludewig K., Wanner A. & Jensen K. 2015: Recolonization and facilitation in Baltic salt marsh vegetation. — *Ann. Bot. Fennici* 52: 181–191.

Vegetation gaps are considered to be important for germination and establishment of species, which are weak competitors but have long-lived seeds in the soil. Vegetative growth is a colonization strategy especially important in regularly disturbed grasslands. In a salt marsh on the Baltic coast of Germany, we studied (i) the role of seedling recruitment and vegetative growth in recolonization of gaps, (ii) if gaps are necessary for seedling recruitment and (iii) whether gaps contribute to species diversity and composition of the salt marsh. We carried out a two-factorial field experiment during two years. We created 48 gaps of 0.04 m² in size in autumn 2006. We eliminated the seed bank by sterilization and prevented vegetative growth into these gaps with dense meshes. We used a full-factorial design with four treatments: (1) seed bank and vegetative growth eliminated, (2) seed bank eliminated and vegetative growth intact, (3) seed bank intact and vegetative growth eliminated, (4) both intact. Seedlings and ramets were counted in these gaps in summers 2007 and 2008. In the established vegetation we counted the dicot seedlings in 12 control plots without manipulation. Both seed bank and vegetative growth contributed to the recolonization of the gaps. Nevertheless, seedling establishment was limited due to flooding of the site for six weeks in summer 2007. Vegetative growth was more successful in recolonizing the gaps. No increase in species richness occurred due to gaps in this salt marsh. Interestingly, more dicot seedlings emerged in the undisturbed control plots than in the gaps with intact seed bank. Vegetation gaps, thus, do not appear to be necessary for establishment of dicots in Baltic salt marshes. Nevertheless, some dicot species profit from gaps. We assume that the erect structure of the vegetation dominated by the evergreen plants *Juncus gerardii*, *Triglochin maritimum* and *Plantago maritima* facilitates germination in the undisturbed vegetation.

Introduction

Vegetation gaps are spaces with reduced competition from neighboring plants (Bullock 2000). These gaps play a central role for plant spe-

cies coexistence and vegetation dynamics in many ecosystems (Grubb 1977, Thompson 2000, Fibich *et al.* 2013). In grasslands, gaps are usually created by herbivores (e.g. hoof prints from sheep or cattle) and burrowing animals (e.g.

moles). Larger disturbances, caused by drought, flooding or fire, occur in some types of grasslands, but overall most gaps in grasslands are relatively small (Bullock 2000). Plants can recolonize these gaps by different strategies: as seedlings from seeds in the soil seed bank and from the seed rain, or vegetatively from the margins of the gaps.

Germination from the soil seed bank in gaps is considered to be important for many plant species especially in regularly disturbed habitats (Thompson 2000). Seeds of several species have mechanisms to detect plant-free spaces in the vegetation, and can therefore preferentially germinate in gaps (Fenner & Thompson 2005). In grasslands, seedlings from the seed bank may (Pakeman *et al.* 1998, Kalamees & Zobel 2002) or may not significantly contribute to recolonization of gaps (Milberg 1993, Arnthórsdóttir 1994, Bullock *et al.* 1994). Species composition of seed bank and vegetation can differ (Jensen 1998, Thompson 2000) or be largely similar (Hölzel & Otte 2001), which probably depends on the ecosystem type and the successional stage.

Vegetative growth is another important strategy to recolonize gaps, especially in temperate perennial grasslands (Milberg 1993, Arnthórsdóttir 1994). Many plant species in these ecosystems possess clonal organs such as runners or rhizomes. Vegetative growth is usually more successful in recolonizing gaps, when the gaps are relatively small (Bullock *et al.* 1995, Eckstein *et al.* 2012).

A dense vegetation cover usually hampers germination and establishment of seedlings, especially when large amounts of litter are produced (Jensen & Gutekunst 2003, Fenner & Thompson 2005, Loydi *et al.* 2013). In harsh environments, however, facilitative effects by the established vegetation are possible. Facilitation in the context of germination, establishment and gap colonization processes implies that conditions within the vegetation are favorable to conditions in the gaps (Bertness & Callaway 1994). Generally, little is known about the influence of facilitation on species diversity in coastal wetland plant communities (for a review *see* Zhang & Shao 2013). For example, in Wadden Sea salt marshes, a facilitative effect of halophytes on the growth and survival of glycophytes was demon-

strated (Engels & Jensen 2010), and in New England salt marshes, *Triglochin maritimum* created elevated rings supporting high plant cover as compared with almost bare adjacent substrate (Fogel *et al.* 2004).

While gap recolonization experiments were conducted in a wide range of grassland ecosystems such as wet (Milberg 1993, Stammel & Kiehl 2004, Fibich *et al.* 2013), acidic (Bullock *et al.* 1994), mesic (Edwards & Crawley 1999a), calcareous (Kalamees & Zobel 2002) and nutrient-poor grasslands (Eckstein *et al.* 2012), studies of coastal ecosystems are scarce. To our knowledge, only two studies on (North American) salt marshes exist (Hartman 1988, Ewanchuk & Bertness 2003), but salt marshes differ in many aspects from other grasslands. Due to the harsh environmental conditions — salinity, tidal or non-tidal flooding, anoxic soil conditions — they harbor relatively few plant species with a high proportion of specialists *i.e.* halophytes (Dijkema 1990).

Salt marshes along the Baltic coast differ in many respects from salt marshes along other coasts: They are affected by irregular flooding with brackish water; they are dominated by halophyte species, but usually do not show a distinct vegetation zonation like *e.g.* the Wadden Sea salt marshes do (Suchrow & Jensen 2010). Their soil conditions also differ: While Baltic salt marshes are mostly built up by autochthonous peat formation, other European salt marshes are usually created by allochthonous sediment deposition. Furthermore, Baltic salt marshes are considered semi-natural ecosystems, because they depend on grazing (*e.g.* Jutila 2001). They have replaced brackish reeds dominated by *Phragmites australis* as a consequence of a long grazing history (Härdtle 1984) and are relevant for nature conservation, because sea birds favor their short vegetation as breeding grounds. However, there is scant knowledge about processes that maintain the characteristic species composition of Baltic salt-marsh vegetation. The role of seed banks, vegetative growth, and vegetation gaps in the regeneration of characteristic salt marsh species is not yet known. Vegetation gaps, such as hoof prints from cattle, or those created by ice scouring, wild boar, or flooding, occur frequently in these marshes.

We conducted a field experiment in a Baltic salt marsh by creating vegetation gaps and recording the gap recolonization process over a period of two years. For evaluating the importance of gaps for regeneration of Baltic salt marsh species, we further compared the number of seedlings germinating within gaps with the number of seedlings germinating in the undisturbed vegetation.

We aimed to answer the following questions:

(1) What is the role of seedling recruitment and vegetative growth in recolonization of gaps in Baltic salt marsh vegetation? (2) Are gaps necessary as regeneration niches for salt marsh species? (3) Do gaps contribute to species diversity and composition of the salt marsh, i.e. do the species number and composition of seedlings in the gaps represent the species number and composition of the established vegetation?

Material and methods

Study site

The experimental site was located near Heiligenhafen on the Baltic coast of northern Germany (54°22'48''N, 10°56'26''E), on the shore of a shallow lagoon. The site had an elevation of 0.12 ± 0.02 m a.s.l. (mean \pm SD) and temperate climatic conditions. The lagoon has a small connection to the Baltic Sea, thus flooding occurs during strong easterly winds and after strong westerly winds have ceased (due to compensating water fluctuations). These irregular water level fluctuations overlay a small tidal effect at the outer shore of approx. 10 cm amplitude at Heiligenhafen (Härdtle 1984). Usually, flooding occurs more often in winter and spring than in summer, but in 2007, a pronounced flooding of lasting six weeks and approx. 20–30 cm water depth was recorded from July to August. Salinity of the Baltic Sea at the outer shore of the study site varies between 10 and 13 psu (own data).

We chose an experimental site which was currently not grazed to avoid trampling by livestock. Grazing was stopped at this site in the 1980s (personal communication with local farmer). The site still showed the characteristic vegetation of grazed salt marshes dominated by

halophytes such as *Juncus gerardii*, *Triglochin maritimum* and *Plantago maritima* (Table 1). The soil seed bank of the site was dominated by *Juncus gerardii* and contained seeds of nearly all species of the aboveground vegetation (see Table 1). Two thirds of the species occurring at our studied salt marsh are able to spread vegetatively (see Table 1).

Experimental setup

We conducted a two-factorial field experiment and prepared 48 vegetation gaps of 20×20 cm by excavating the soil to 10 cm depth on 12 and 13 September 2006. We used a full-factorial design with four treatments: (1) seed bank and vegetative growth eliminated, (2) seed bank eliminated and vegetative growth intact, (3) seed bank intact and vegetative growth eliminated, (4) both intact. The gaps were laid out in a blocked design because we assumed existence of a moisture gradient in the soil of the site in the direction towards the lagoon. Twelve blocks with one gap of each treatment combination in the corners of 1 m^2 were created. The distance between the blocks was 1 m. Treatments were distributed randomly within the blocks. In the middle of each of the twelve blocks, germination of dicotyledonous (dicot) seedlings was recorded in the established vegetation within 20×20 cm control plots.

The excavated 10 cm surface layer of soil from each gap was taken to the laboratory and sieved to remove roots or rhizomes, which could re-sprout. To remove the seed bank, the soil was sterilized in an autoclave at the pressure of 50.7 kPa for two hours. The soil from the gaps without sterilization was divided into three horizontal layers (depths 0–2 cm, 2–5 cm and 5–10 cm) to make sure that each soil layer, containing possibly different amounts of seeds, was returned to its original depth. The soil of all gaps was kept in darkness in a refrigerator at 4 °C to prevent seeds from germinating.

On 11 November 2006, each soil sample was put back into exactly the same gap from which it was taken. Before the soil was put back in the gaps with vegetative growth eliminated, a dense fabric (Trenn-Vlies Geotex, Windhager, Thalgau) was placed on the bottom and the four sides

Table 1. Species composition of the studied Baltic salt marsh (vegetation cover sampled from the entire study site of 6×9 m in June 2007, cover estimated following Londo 1976); the numbers of seeds in the 0–10 cm soil layer at a site located 10 m from each plot (see Ludewig 2009); the species' strategies of vegetative growth (from BiolFlor database; Kühn et al. 2004); the numbers of germinated seedlings, established seedlings, and ramets per species growing in 45 artificial gaps of 0.04 m^2 size in summer 2007, the seedling mortality (%) of each species during 2007; and the numbers of dicot seedlings in the 12 control plots of 0.04 m^2 size in 2007. Monocot seedlings were not counted (n.c.) in the controls.

Plant species	Vegetation cover (%)	Seed bank (seeds m^{-2})	Vegetative growth possible via	Number of germinated seedlings	Number of established seedlings	Number of ramets	Seedling mortality (%)	Number of dicots in controls
<i>Juncus gerardii</i>	30	45330	rhizomes	68	24	447	65	n.c.
<i>Plantago maritima</i>	30	2800	pleiocorm shoots	9	2	7	78	1
<i>Triglochin maritimum</i>	30	2670	rhizomes	121	91	49	25	n.c.
<i>Aster tripolium</i>	10	5050	–	263	163	–	38	387
<i>Festuca rubra</i> agg.	4	720	runners	2	1	1	50	n.c.
<i>Glaux maritima</i>	4	2760	runners/turios	3	2	73	67	1
<i>Agrostis stolonifera</i>	2	2080	runners	3	0	8	100	n.c.
<i>Artemisia maritima</i>	2	210	root shoots	0	–	0	–	0
<i>Atriplex prostrata</i> agg.	2	890	–	28	9	–	68	16
<i>Cochlearia anglica</i>	2	640	–	5	2	–	60	0
<i>Limonium vulgare</i>	2	–	root shoots	0	–	3	–	4
<i>Elymus repens</i>	1	–	rhizomes	0	–	0	–	n.c.
<i>Puccinellia maritima</i>	1	170	runners	0	–	0	–	n.c.
<i>Spergularia salina/media</i>	1	4200	–	7	4	–	43	0
<i>Salicornia europaea</i>	–	210	–	1	0	–	100	0
Dicot seedlings*				80				142
Monocot seedlings*				51				
Total				641		588		551

* These dicot and monocot seedlings died before identification.

of each gap to serve as a barrier against roots and rhizomes. It also extended 6 cm above the soil surface to form a barrier against aboveground stolons. In winter 2006/2007, the fabric from three plots was accidentally removed, so the number of experimental gaps was reduced to 45. In winter 2007/2008, this happened once again, reducing the number of gaps to 44.

All seedlings and vegetative ramets in the 45 gaps (and the dicot seedlings in the 12 controls) were monitored during the vegetation period 2007 on a monthly basis from May (seedlings also in April) to August 2007. Each seedling was marked with a colored tooth pick (with a different color for each date) to recognize seedlings that had died and vanished, or had newly germinated. We counted all ramets as individuals, although many ramets could belong to one genetic individual. In the second year, the numbers of survived seedlings from 2007, of newly germinated seedlings, and of ramets were counted once in June 2008. Further, total vegetation cover was estimated for all gaps in June 2008.

The species abundance of the established vegetation was recorded at the entire study site of 6 m × 9 m in June 2007 (see Table 1). Species abundances were estimated as plant cover, following the scale of Londo (1976). Plant nomenclature follows Wisskirchen and Haeupler (1998).

Data analysis

The total number of seedlings in the experimental gaps was calculated as the sum of all occurring seedlings in each gap. Seedling mortality was calculated as the percentage of dead seedlings of all occurring seedlings per gap. Seedlings from wind- and water-dispersed seeds were quantified as percentages of the mean number of seedlings in the gaps without seed banks from the mean seedling number in the gaps with intact seed banks for each counting date. The mean percentage of wind- and water-dispersed seeds was averaged from the five values of the counting dates.

We analyzed the effects of the experimental factors seed bank and vegetative growth on the

number of seedlings per gap and the number of species per gap using two-way ANOVA, followed by Tukey's HSD *post hoc* tests when the ANOVA results were significant. The effect of the seed bank on the number of ramets was tested with one-way ANOVA. Development of seedlings and ramets in the gaps and dicot seedlings in control plots over time was analyzed with repeated-measures ANOVA. The block-factor was excluded from the analyses after we had checked using ANOVA that it had no significant effect on any of the response variables. Homogeneity of variances of the data was tested with Levene's test, and normal distribution visually with Q-Q plots. To meet the assumptions of ANOVA, seedling numbers from 2007 and 2008 were $\log(x + 1)$ -transformed. Where the assumptions of normality could not be met by means of transformations, we used a non-parametric Mann-Whitney *U*-test to analyze: (1) the effects of seed bank and vegetative growth on the number of seedlings separately for the four most abundant species, (2) the effects of seed bank and vegetative growth on individuals that germinated in 2007 and were counted in 2008, and (3) the differences in the number of seedlings between the control plots and the gaps with intact seed bank separately for each month.

Mean values in the text are followed by standard errors (SE). All statistical tests were conducted using STATISTICA 9 (StatSoft 2010).

Results

Germination and vegetative growth in experimental gaps

During summer 2007, altogether 641 seedlings germinated in the 45 experimental gaps. Of these seedlings, 131 died shortly after emergence and could only be identified as monocots or dicots. The remaining 510 seedlings belonged to 11 species (see Table 1) the most abundant being *Aster tripolium* (52% of identified seedlings), *Triglochin maritimum* (24%), *Juncus gerardii* (13%), and *Atriplex prostrata* (5%). In summer 2007, significantly more seedlings emerged in the experimental gaps with intact seed bank (mean ± SE = 25 ± 5) than in the gaps without

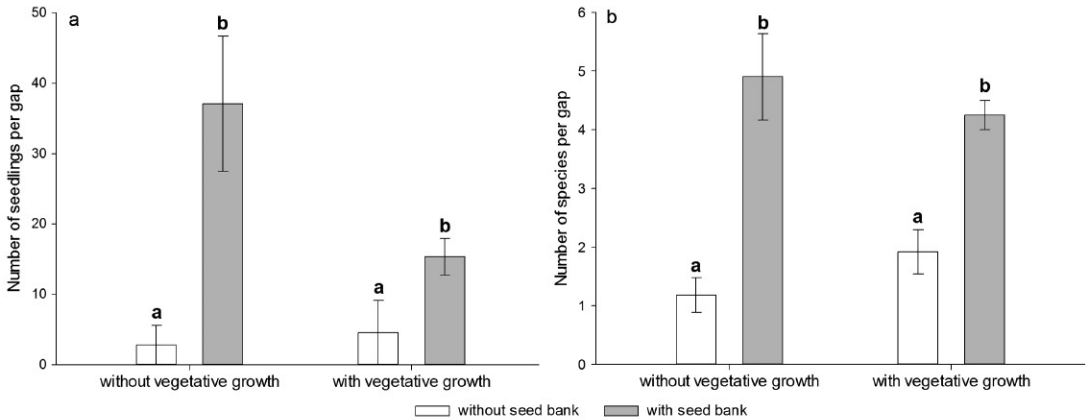


Fig. 1. Mean number of germinated (a) seedlings and (b) species per gap in the differently-treated vegetation gaps in the Baltic salt marsh in 2007 ($n = 45$, mean \pm SE). Most seedlings germinated in the gaps with intact seed bank and these gaps also contained more species than those without seed bank. 'With seed bank' refers to the gaps without soil sterilization in autumn 2006 and 'with vegetative growth' refers to the gaps without fabric used to eliminate vegetative growth. Different letters indicate significant differences (Tukey's HSD test, $p < 0.05$).

seed bank (4 ± 1 ; two-way ANOVA, factor seed bank: $F_{1,41} = 59.1$, $p < 0.001$). Most seedlings germinated in the gaps with intact seed bank but without vegetative growth (37 ± 10), and the lowest numbers of seedlings were found in the gaps with both factors eliminated (3 ± 1), indicating a significant interaction between seed bank and vegetative growth (two-way ANOVA, interaction: $F_{1,41} = 6.4$, $p = 0.016$; Fig. 1a). The factor 'vegetative growth' had no main effect on the number of seedlings in the gaps ($F_{1,41} = 0.2$, $p = 0.66$). Overall, 87% of the seedlings germinated from the seed bank, and 13% from seeds dispersed by wind or water.

Mean species number of seedlings was significantly higher in the vegetation gaps with seed bank (5 ± 0.4) than without seed bank (2 ± 0.3 ; two-way ANOVA: $F_{1,41} = 49.0$, $p < 0.001$; Fig. 1b). The four most abundant species were all significantly more abundant in the gaps with intact seed bank ($n = 22$) than in the gaps without seed bank ($n = 23$) (Mann-Whitney U -test, *Aster tripolium*: $U = 86.0$, $p < 0.001$, *Triglochin maritimum*: $U = 73.5$, $p < 0.001$, *Juncus gerardii*: $U = 74.5$, $p < 0.001$, and *Atriplex prostrata*: $U = 161.0$, $p = 0.002$). The presence or absence of vegetative growth had no effect on the number of seedlings of these four species (Mann-Whitney- U -test: all $p > 0.05$).

558 ramets belonging to seven species grew vegetatively into the 24 gaps with vegetative

growth at the end of August 2007 (Table 1). Most of the ramets belonged to *Juncus gerardii* (76% of all ramets); other ramets were those of *Glaux maritima* (12%) and *Triglochin maritimum* (8%). *Limonium vulgare* was the only species which grew vegetatively into the gaps, but was not represented by any seedling (but germinated in the controls). The number of ramets in the gaps was not affected by the presence of seed bank (one-way ANOVA: $F_{1,22} = 0.36$, $p = 0.55$).

In summer 2008, more seedlings newly germinated in the gaps without than with vegetative growth (two-way ANOVA: $F_{1,40} = 24.6$, $p < 0.001$; Fig. 2a), but their species number did not differ (two-way ANOVA: $F_{1,40} = 0.005$, $p = 0.94$). Here, the experimental removal of the seed bank two years previously had no longer an effect on seedling (two-way ANOVA: $F_{1,40} = 0.02$, $p = 0.90$) or species numbers (two-way ANOVA: $F_{1,40} = 1.7$, $p = 0.20$).

Establishment in experimental gaps

Seedlings and ramets were differently successful in establishing in the experimental gaps. The number of seedlings increased from April to June 2007, but declined from July to August 2007 (repeated-measures ANOVA, main effect of time: $F_{4,84} = 22.1$, $p < 0.001$, followed by Tukey HSD-test, see Fig. 3). Of the 641 seedlings that

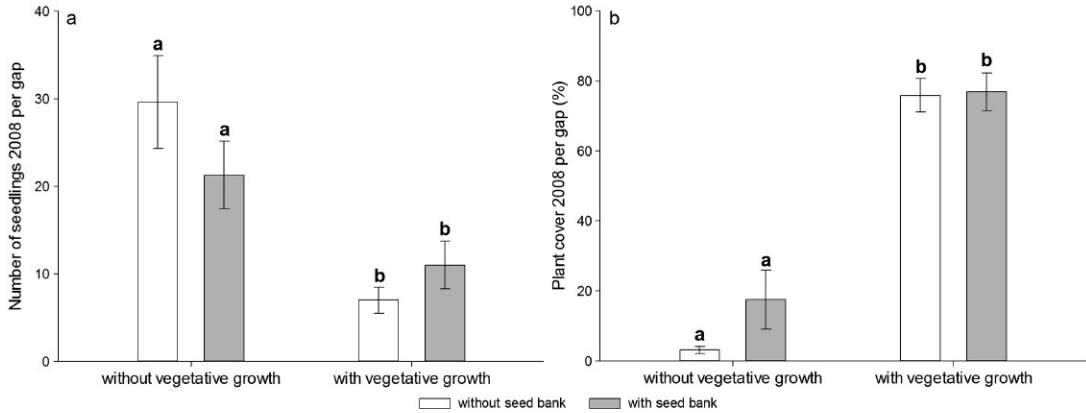


Fig. 2. (a) Mean number of seedlings newly germinated in the gaps, and (b) the corresponding vegetation cover in the differently-treated gaps in the Baltic salt marsh in the second year (June 2008, $n = 44$, mean \pm SE). 'With seed bank' refers to the gaps without soil sterilization in autumn 2006 and 'with vegetative growth' refers to the gaps without fabric used to eliminate vegetative growth. Different letters indicate significant differences (Tukey's HSD test, $p < 0.05$).

had germinated in the gaps 343 died by the end of August 2007, equating to a seedling mortality of 54% (the values for single species ranging from 25% to 100%, see Table 1). The number of ramets rose continuously in the 24 gaps with vegetative growth. In August 2007, significantly more ramets grew in the gaps than in all previous months (repeated-measures ANOVA, main effect of time: $F_{3,69} = 11.3$, $p < 0.001$, followed by Tukey's HSD test, see Fig. 3). In May 2007, the ramets made up 45% of all individuals in the vegetation gaps, and in August 2007 this percentage increased to 66%.

The number of established seedlings in August 2007 was higher in the gaps with intact seed bank than with seed bank removed (two-way ANOVA: $F_{1,41} = 17.3$, $p < 0.001$). While the factor vegetative growth had no main effect on the number of established seedlings (two-way ANOVA: $F_{1,41} = 3.3$, $p = 0.08$), it had an interactive effect with the factor seed bank (two-way ANOVA: $F_{1,41} = 4.8$, $p = 0.03$).

In June 2008, we counted 120 juveniles belonging to eight species that had germinated in 2007 and were successfully established in the gaps. The number of established juveniles was not affected by the experimental treatments anymore (Mann-Whitney U -test: seed bank: $U = 169.0$, $n = 22$ for gaps with and without seed bank, $p = 0.09$; vegetative growth: $U = 184.5$, $n = 24$ and 20 for gaps with and without vegeta-

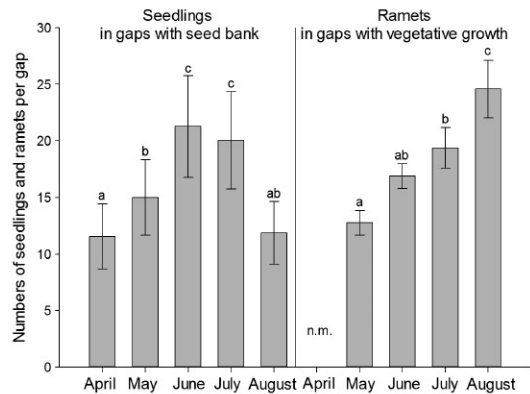


Fig. 3. Number of seedlings in the 22 gaps with intact seed bank and number of ramets in the 24 gaps with vegetative growth during the first year of recolonization 2007 (mean \pm SE; n.m. = not measured). While the numbers of seedlings declined between June and August, the numbers of ramets continuously rose until August 2007. 'With seed bank' refers to the gaps without soil sterilization in autumn 2006 and 'with vegetative growth' refers to the gaps without fabric used to eliminate vegetative growth. Different letters indicate significant differences (Tukey's HSD test, $p < 0.05$).

tive growth, respectively, $p = 0.19$). Total plant cover in the experimental gaps in June 2008 was significantly higher in the gaps with vegetative growth than in those without (Mann-Whitney U -test: $U = 5.3$, $n = 24$ and 20 for gaps with and without vegetative growth, respectively, $p < 0.001$; Fig. 2b), but was not affected by the pres-

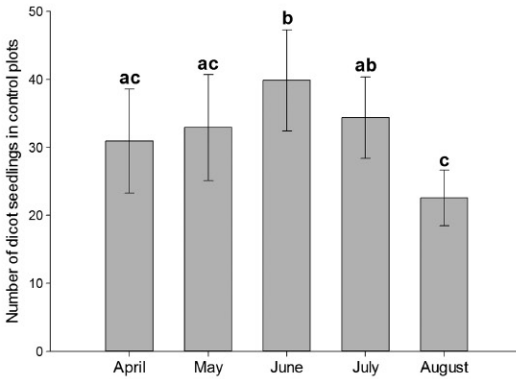


Fig. 4. Numbers of dicot seedlings in the 12 control plots in 2007 (mean \pm SE). Different letters indicate significant differences (Tukey's HSD test, $p < 0.05$). On every counting date, more dicot seedlings grew in the controls in the established vegetation than in the gaps with intact seed bank (mind the different scales when comparing with Fig. 3).

ence or absence of the seed bank (Mann-Whitney U -test: $Z = 0.59$, $n = 22$ for both groups, $p = 0.55$). While the cover of vegetative ramets reached approx. $75\% \pm 3\%$ in the gaps with vegetative growth, seedlings contributed $9\% \pm 4\%$ in the gaps with seed bank.

Dicot seedlings in controls and gaps with intact seed bank

In the control plots, we found 551 dicot seedlings belonging to five species (see Table 1), resulting in a mean number of 46 ± 9 seedlings per control plot (compared with 15 ± 3 dicot seedlings in the gaps with intact seed bank). Most abundant in the control plots was *Aster tripolium* (95.6% in August 2007). In all months (April to August 2007), significantly more dicot seedlings were found in the control plots ($n = 12$) than in the gaps with seed bank ($n = 22$) (Mann-Whitney U -test: April: $U = 48.0$, $p = 0.002$; May: $U = 54.5$, $p = 0.005$; June: $U = 43.0$, $p = 0.001$; July: $U = 47.0$, $p = 0.002$; August: $U = 37.0$, $p < 0.001$). The number of dicot seedlings in the control plots differed between months (repeated-measures ANOVA: $F_{4,44} = 9.4$, $p < 0.001$; see Fig. 4). In the control plots, 280 of the 551 germinated dicot seedlings died by the end of August 2007 (mortality of 51%). The mortality of the

dicot seedlings in the controls was thus nearly the same as the mortality of the dicot seedlings in the gaps (54%) which equaled the mortality of all seedlings in the gaps.

Comparison to the established vegetation

We documented 14 vascular plant species in the established vegetation in 2007 (Table 1). The three most abundant species of the established vegetation *Juncus gerardii* (30%), *Triglochin maritimum* (30%) and *Plantago maritima* (30%) were able to recolonize the experimental gaps by means of both strategy types. *Aster tripolium*, the species with most seedlings in the experimental gaps, contributed only 10% to the established vegetation cover. No seedlings of *Limonium vulgare*, *Artemisia maritima*, *Elymus repens* and *Puccinellia maritima* germinated in the experimental vegetation gaps, although these species grew in the established vegetation. *Salicornia europaea* was the only species that emerged in the experimental gaps without growing in the established vegetation, but was represented by only one seedling.

Discussion

Gap recolonization by seed bank and vegetative growth

Seed bank and vegetative growth both contributed to the recolonization of the experimental gaps in the Baltic salt-marsh vegetation. *Juncus gerardii* was the most successful species representing the third highest number of seedlings and the largest contribution of vegetative ramets in the gaps. Overall, vegetative growth was more successful in recolonizing the gaps than recruitment from the soil seed bank. While most germinated seedlings came from the seed bank (87%), only few seedlings germinated from wind- or water-dispersed seeds (13%). The success of germinated seedlings was reduced due to their mortality of 54%, with the mortality percentages being species-specific (see Table 1). Seedling mortality was mainly caused by flooding of the

site for six weeks in July and August 2007. Ramets were less negatively affected by the flooding; their number rose continuously during 2007. In terms of plant cover, vegetative growth was overwhelmingly more important (75% cover in the gaps with vegetative growth) than the seedlings (9% in the gaps with intact seed bank) two years after creation of the gaps. In agreement with our findings, species which spread vegetatively into the gaps seldom disappeared from artificially-created hoof prints in a calcareous fen in Germany, in which more than half of the germinated species disappeared during two years of observation (Stammel & Kiehl 2004). Accordingly, successful vegetative growth playing a role in recolonization of vegetation gaps was observed in other grasslands (Hartman 1988, Milberg 1993), especially in small gaps (Eckstein *et al.* 2012). However, seeds were important in recolonization of gaps in other studies, either from the seed rain (Bullock *et al.* 1994, Edwards & Crawley 1999b) or from seed bank (Pakeman *et al.* 1998, Kalamees & Zobel 2002, Pakeman & Small 2005, Fibich *et al.* 2013), but three of those studies did not include vegetative growth (Pakeman *et al.* 1998, Edwards & Crawley 1999b, Pakeman & Small 2005).

Competition is probably the reason for the interaction we found between seed bank and vegetative growth: In gaps with an intact seed bank, the number of seedlings was reduced by vegetative growth, while in gaps where the seed bank was removed vegetative growth had no effect on the number of seedlings. Here, seedlings were probably not affected by the occurrence of ramets because they were few in number. With a high number of seedlings in the gaps, however, the vegetative runners (in particular those lying flat on the ground) may affect the germination and establishment process by shading the soil surface. The discovered competitive interaction between vegetatively-established individuals and seedlings in the studied Baltic salt marsh is in contrast with the conclusion of Kalamees and Zobel (2002), who did not find any interaction between emerging individuals of different origin in calcareous grassland. The reason might be the different vegetative growth characteristics of the occurring species. Clonal growth is probably much slower (and thus less competitive to

seedlings) in a dry and relatively unproductive habitat than in our wet Baltic salt marsh.

Regeneration in vegetation gaps and undisturbed vegetation

One of the most striking results of our study was that more dicot seedlings emerged in the undisturbed control plots than in the vegetation gaps. Other studies found very few seedlings in undisturbed grassland vegetation, e.g. Milberg (1993) in a wet meadow in Sweden. In New England salt marshes, gaps have been shown to increase seedling numbers (Shumway & Bertness 1992). In a Wadden Sea salt marsh, a negative correlation between vegetation height and number of seedlings, and a positive correlation between bare soil and number of seedlings was reported (Bakker & de Vries 1992). We are aware of only one study reporting nearly the same number of dicot seedlings in the established vegetation as we detected (Jutila 2003). Interestingly, that study was also carried out in a Baltic salt grassland (in Finland) reporting 39 dicot seedlings on 0.04 m² (compared with 46 dicot seedlings on 0.04 m² in our study). Thus, we hypothesize that bare soil might not be a requirement for germination of characteristic halophyte species in these Baltic salt marshes. Here, the amount of light reaching the soil surface might be sufficient to induce germination, even in the established vegetation. The vegetation dominated by *Juncus gerardii* or other halophytes such as *Plantago maritima* and *Triglochin maritimum* might create light conditions favorable for germination and more balanced soil moisture conditions for supporting seedling survival. With their erect growth form and due to low litter production, these three species may facilitate germination of other plant species among their shoots. While vegetation gaps do not generally seem to be necessary for germination of dicot species in these grasslands (*see also* Jutila 2003), some dicot species, nevertheless, profit from gaps as more dicot species germinated in the gaps than in the controls (Table 1). Furthermore, we cannot conclude that *Juncus gerardii*-dominated vegetation always has the same facilitative effect on germination, as this species is also dominant in New England salt

marshes where vegetation gaps were found to increase seedling recruitment (Shumway & Bertness 1992). It is a challenge for future research to shed light on the conditions under which the role of a certain species switches from being competitive to being facilitative.

Species composition in vegetation gaps and established vegetation

Species composition of the seedlings in the vegetation gaps represented the established vegetation. No increase of species richness occurred due to vegetation gaps. This result is in line with Bullock *et al.* (1994) who likewise found no additional species in created vegetation gaps. The similarity between the composition of species in the established vegetation and seedlings from the seed bank may be a consequence of germination being possible in this system between the shoots of the dominant species. The seeds of species depending on seedling recruitment probably do not need to “wait” for adequate conditions after disturbances. Further, the species pool in this system is rather limited due to the harsh environmental conditions as compared with other grasslands with less abiotic stresses, resulting in a seed bank that is dominated by these species (Wanner 2009). Overall, gaps did not enhance biodiversity in this ecosystem but may play a role in maintaining the existing one. From the five species (or species groups) that reproduce solely via seedlings (*Aster tripolium*, *Atriplex prostrata* agg., *Cochlearia anglica*, *Spergularia salina/media* and *Salicornia europaea*; see Table 1) three germinated only in gaps (although in small numbers).

Conclusions

The most successful species in the recolonization process of gaps in the Baltic salt marsh vegetation was *Juncus gerardii*. Therefore, we conclude that soil disturbances promote *Juncus gerardii*, which is abundant in the soil seed bank and successful in vegetative growth. Vegetation dominated by *Juncus gerardii* as well as *Plantago maritima* and *Triglochin maritimum* facilitates germination

and establishment of other typical salt marsh species. At least for seedlings of some dicot species, vegetation gaps do not appear to be necessary for germination and establishment in this ecosystem. Nevertheless, vegetative growth seems to be more reliable than seedling recruitment from the soil seed bank, especially under the wet conditions in summer 2007. Overall, this study highlights the importance of considering interactions between gap recolonization processes, and facilitation as drivers for the composition and diversity of coastal marsh vegetation.

Acknowledgments

We thank the Stiftung Naturschutz Schleswig-Holstein for allowing us to work on their property and the nature conservation authorities of Schleswig-Holstein for their cooperation. We thank Claudia Mählmann and Harry Stöckmann for technical assistance and Barbara and Heiko Iven, and Jochen Wedling for kind support. We thank the working group Applied Plant Ecology in Hamburg and Tobias W. Donath as well as two anonymous referees for valuable comments on the manuscript. We thank Ian J. Bennett for revising the language.

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