

Article

Mechanisms of Seed-To-Seed Interactions between Dominant Species in the Yangtze River Estuary under Saline Condition

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Abstract: Plant community assembly is the central issue in community ecology. As plant traits differ in different life history stages, the form, intensity and mechanism of interspecific interactions may change with the ontogenetic process of plants. However, our understanding of interspecific interaction mechanisms during germination is still limited. Here, we conducted a laboratory germination experiment using five dominant species in Chongming Dongtan (*Spartina alterniflora*, *Scirpus mariqueter*, *Phragmites australis*, *Suaeda glauca* and *Tripolium vulgare*) to assess their germination performance in control (monoculture), allelopathy and mixture treatments. The results indicated that seeds could affect germination performance of neighbors through both allelopathy and salinity modification. Salinity of the solution in Petri dishes after seed germination decreased significantly in most species combinations in competition treatment, and was negatively correlated with the number of total germinated seeds. Seed leachate of invasive *Spartina alterniflora* significantly accelerated the germination of two native halophytes *Suaeda glauca* and *Tripolium vulgare*, but not *Scirpus mariqueter* and *Phragmites australis*. The salt absorption by *Spartina alterniflora* seeds had inconsistent effects compared with that of its seed leachate. On the other hand, seed leachate of native *Scirpus mariqueter* and *Phragmites australis* significantly slowed down the germination of invasive *Spartina alterniflora*. The effect of salinity modification of *Scirpus mariqueter* on *Spartina alterniflora* was positive, whereas that of other species was neutral. Considering seed-to-seed interactions is an important perspective to understand the underlying mechanisms of community dynamics, species diversity maintenance and invasion of alien species, and can improve the effectiveness in the management of invaded coastal wetlands.

Keywords: allelopathy; interspecific interactions; salinity modification; seed germination



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1. Introduction

The spatial distribution pattern of different plants and the underlying mechanism of species coexistence (i.e., plant community assembly mechanisms) have been central issues in community ecology for decades [1,2]. Interspecific interactions are thought of as the driving force of plant community assembly, especially in the later successional stages [3,4]. Positive interactions often occur in stressful environment, and plants can facilitate the survival, growth and reproduction of their neighbors via habitat modification [5]. In relatively benign environment, competition is more common, which can negatively affect the performance of adjacent plant species through resource contention, allelopathy and other mechanisms [6].

Previous studies on interspecific interactions mainly focused on established seedlings and ramets [7–9]. However, as plant traits differ in different life history stages, the form, intensity and mechanism of interspecific interactions may change with the ontogenetic

process of plants [10–12]. Researchers have recognized the importance of regeneration on community assembly and investigated some adult-to-seed and seed-to-seed interactions in recent years [13–15], but our understanding of interspecific interaction mechanisms during early life history stage of plants (i.e., germination) is still limited.

Seed germination is vital for plant life cycle. Difference in germination percentage and germination timing under various conditions has a significant impact on recruitment and potential competitive ability of seedlings [16,17], which then determines population distribution and community structure [18]. A great number of studies have demonstrated the effects of environmental factors (e.g., temperature, light, soil moisture and salinity) on seed germination [19–22], but few considered the biotic interactions among seeds. In field sites, seeds of different species often appear in the same place due to the dispersal by wind, tide or animals [23,24], which makes the germination process affected by neighboring conspecific or heterospecific seeds.

Resource competition and direct interference such as allelopathy are well-known underlying mechanisms of interspecific interactions [25,26]. Due to the small size and relatively low resource requirement of seeds, allelopathy has been considered the driving force mediating seed-to-seed interactions in grasslands and croplands [27–30], and the interaction intensity usually change with the concentration of allelochemicals [31]. On the other hand, many ecosystem engineers have indirect effects on adjacent species through habitat modification [32], which may also work during germination. To our knowledge, no study has directly examined the potential effects of microenvironment modification (e.g., salinity absorption) by seeds on germination process.

Chongming Dongtan wetland of international importance is located in the Yangtze River estuary, and plays a crucial part in water purification, biodiversity maintenance and flood control [33]. *Spartina alterniflora* originated in the Atlantic coast of North America, and was introduced to China in 1979 for siltation promotion, beach and levee protection. This invasive species has caused great negative ecosystem impacts through competition with native species and habitat modification these years [34]. *Spartina alterniflora* produces a large number of seeds [35], which disperse in a wide area in coastal salt marshes and often mix with other native species [36]. Although a lot of studies have investigated the competition between invasive *Spartina alterniflora* and dominant native species in Chongming Dongtan, such as *Scirpus mariqueter* and *Phragmites australis* [37–39], few took into account their interspecific interactions during germination (however, see [13]). As a result, we lack enough understanding of the mechanisms of seed-to-seed interactions.

This study tried to assess the interspecific interactions during germination and the underlying mechanisms using five dominant species in Chongming Dongtan (*Spartina alterniflora*, *Scirpus mariqueter*, *Phragmites australis*, *Suaeda glauca* and *Tripolium vulgare*). Specifically, the following two questions are addressed: (1) Do these plants germinate differently in monoculture, in seed leachate of competitors and in mixture with competitor seeds? (2) Does salinity modification by germinating seeds have any impact on the germination process? We predicted that *Spartina alterniflora* seeds may significantly influence the germination of native species through allelopathy and microenvironment modification (i.e., regulation of salinity) as well. The results of this study contribute to our understanding of the regeneration and community assembly mechanisms in salt marshes and provide a basis for wetland ecosystem management and restoration.

2. Materials and Methods

2.1. Study Site

Chongming Dongtan is located at the east end of Chongming Island (121°50′~122°05′ E, 31°25′~31°38′ N). It covers about 320 km² and has a subtropical monsoon climate. Dongtan has an annual average rainfall of 1145 mm and annual average temperature of 15.7 °C. The highest temperature is in July with a long-term average temperature of 27.3 °C, and the lowest temperature is in January with a long-term average temperature of 4.2 °C [40]. The

salinity of surface soil in Chongming Dongtan usually varies from 2‰ to 15‰, and can exceed 20‰ during salt water intrusion [41].

Major native plant communities in Chongming Dongtan are sedge meadows dominated by *Scirpus mariqueter* (Sm) in middle to low marshes and grass marshes dominated by *Phragmites australis* (Pa) at higher elevations. *Scirpus mariqueter* is a perennial rhizomatous species mainly distributed in the Yangtze River estuary and the Hangzhou Bay. It can reproduce both via seeds and via corms and rhizomes. As a pioneer species, it can colonize stressful habitats where other plants cannot survive [36]. *Phragmites australis* (Pa) is a perennial species that commonly distributes in inland or coastal wetlands [42]. It mainly relies on vegetative reproduction through rhizomes in mature populations, whereas seedlings play important roles in colonization of bare patches. In high marsh, *Suaeda glauca* (Sg) and *Tripolium vulgare* (Tv) often occurs in hypersaline bare patches. *Suaeda glauca* is an annual halophyte which often forms large scale communities around saline-alkaline lakes. It has high salt tolerance and can also grow in intertidal zones frequently affected by tides [43]. *Tripolium vulgare* is also an annual forb which often grows in alkaline lake wetlands with soil pH ranges from 8.10 to 9.15. It can invade *Phragmites australis* community under saline and dry conditions [44]. After the introduction of *Spartina alterniflora* (Sa), this invasive species thrived in Chongming Dongtan from middle to high marsh and formed *Scirpus mariqueter*-*Spartina alterniflora* and *Spartina alterniflora*-*Phragmites australis* mixtures [13].

2.2. Experimental Design

The seeds of *Spartina alterniflora* (Sa), *Scirpus mariqueter* (Sm), *Phragmites australis* (Pa), *Suaeda glauca* (Sg) and *Tripolium vulgare* (Tv) were collected in the pure stands of each species in Chongming Dongtan in early October, 2017. The collected seeds were stored in a refrigerator at 4 °C. *Spartina alterniflora* and *Scirpus mariqueter* seeds were immersed in fresh water and the others were kept in dry condition to maintain seed vigor [13]. The germination experiment began on 13 March 2018. All the seeds were washed with distilled water for 3~5 min three times and then placed in a Petri dish (9 cm in diameter) with two pieces of filter paper on the bottom. The Petri dishes were placed in a light incubator (PGX-600B) for germination, with the setting of 30 °C and 100% light intensity (12,000 lux) in the daytime (from 08:00 to 20:00) and 18 °C and 0% light intensity in the night (from 20:00 to 08:00).

For preparation of seed leachate, 50 g of *Spartina alterniflora*, *Scirpus mariqueter*, *Phragmites australis*, *Suaeda glauca* and *Tripolium vulgare* seeds were placed in a 500 mL conical flask, respectively. A total of 400 mL of distilled water was added into each flask. The flasks were sealed and vibrated in a shaker at room temperature for 48 h to extract the maximum concentration of allelochemicals from seeds [45]. After that, NaCl was added into the flasks to reach the salinity of 1‰, which is close to the condition of their natural habitats in Chongming Dongtan.

To highlight the effects of invasive plant on native species during germination, this study focused on the interactions between the seeds of invasive species and native species rather than those between different native species. Hence, there were four species combinations: Sa + Sm, Sa + Pa, Sa + Sg and Sa + Tv. We set three different treatments to all species combinations: control (target species seeds in monoculture), allelopathy (target species seeds + competitor seeds leachate) and competition (target species seeds + competitor seeds in mixture). In the control treatment, 20 seeds of a single species were evenly placed in a Petri dish and 6 mL of 1‰ NaCl solution was added. In the allelopathy treatment, 20 seeds of each species were evenly placed in a Petri dish with 6 mL seed leachate of its competitor seeds. *Spartina alterniflora* seeds were treated by leachate of *Scirpus mariqueter*, *Phragmites australis*, *Suaeda glauca* and *Tripolium vulgare*, respectively. Similarly, four native species seeds were treated by *Spartina alterniflora* leachate, respectively. In the competition treatment (Sa + Sm, Sa + Pa, Sa + Sg and Sa + Tv), 20 seeds of each competing species were placed in mixture in each Petri dish and 6 mL of 1‰ NaCl solution was added. Our experiment followed an additive design to focus on interspecific interactions rather than

intraspecific interactions among these species. The two density levels (20 seeds per dish or 3144 seeds m^{-2} , 40 seeds per dish or 6288 seeds m^{-2}) were set according to the soil seed bank density in Chongming Dongtan (250~8500 seeds m^{-2} for *Scirpus mariqueter* and 500~6900 seeds m^{-2} for *Spartina alterniflora*) [36]. There were 17 treatments in all (5 control + 8 allelopathy + 4 competition) and each treatment was replicated four times, making a total of 68 dishes.

Distilled water was added into each Petri dish every day to maintain a shallow layer of water. The number of germinated seeds (where root tips had protruded from the seed coat) of each species was counted and recorded every day, and then, all the Petri dishes were randomly rotated to change its position in the incubator until no seeds germinated within a week. The germination experiment lasted for about a month (13 March to 16 April). After germination, the solution in each Petri dish was diluted to 30 mL, and the salinity was determined by a portable salinometer (SANXIN 5052).

2.3. Data Analysis

Time lag was calculated as the time between the beginning of the experiment and the first germination of each species. Germination period was the time between the first germination and the last germination of each species. Germination percentage was calculated as the proportion of total germinated seeds of each species. Germination index (GI) was calculated as follows [46]:

$$GI = \sum Gi / Di$$

Mean time to germination (MTG) was calculated as follows [47]:

$$MTG = \sum (Gi \times Di) / \sum Gi,$$

where G_i is the number of germinating seeds on the i th day and D_i is the number of days after the beginning of the germination experiment.

One-way ANOVA (post hoc Tukey's HSD test) was used to examine the differences of germination traits (time lag, germination period and germination index) of each species in the control treatment. For each competing species in each species combination, one-way ANOVA (post hoc Tukey's HSD test) was used to examine the effects of different treatments on germination percentage, MTG and the final salinity of solution in Petri dishes after germination. The relationships between final salinity and the number of total germinated seeds were analyzed using linear regression for each species combination. The original germination data were log transformed if necessary to meet the assumption of homogeneity of variance. The significance level was set to 0.05 ($p < 0.05$). All the statistical analyses were carried out by STATISTICA 13.5 (TIBCO software).

3. Results

3.1. Germination Traits of Dominant Species

Tripolium vulgare had the highest time lag among the species studied, followed by *Scirpus mariqueter*. *Spartina alterniflora* and *Suaeda glauca* had a significantly lower time lag than *Tripolium vulgare* and *Scirpus mariqueter*, while *Phragmites australis* fell in between (Figure 1a). *Tripolium vulgare* had a significantly higher germination period than *Phragmites australis*, while *Spartina alterniflora*, *Suaeda glauca* and *Scirpus mariqueter* had an intermediate germination period (Figure 1b). The germination index of *Suaeda glauca* and *Spartina alterniflora* was significantly higher than that of *Phragmites australis*, *Scirpus mariqueter* and *Tripolium vulgare* (Figure 1c).

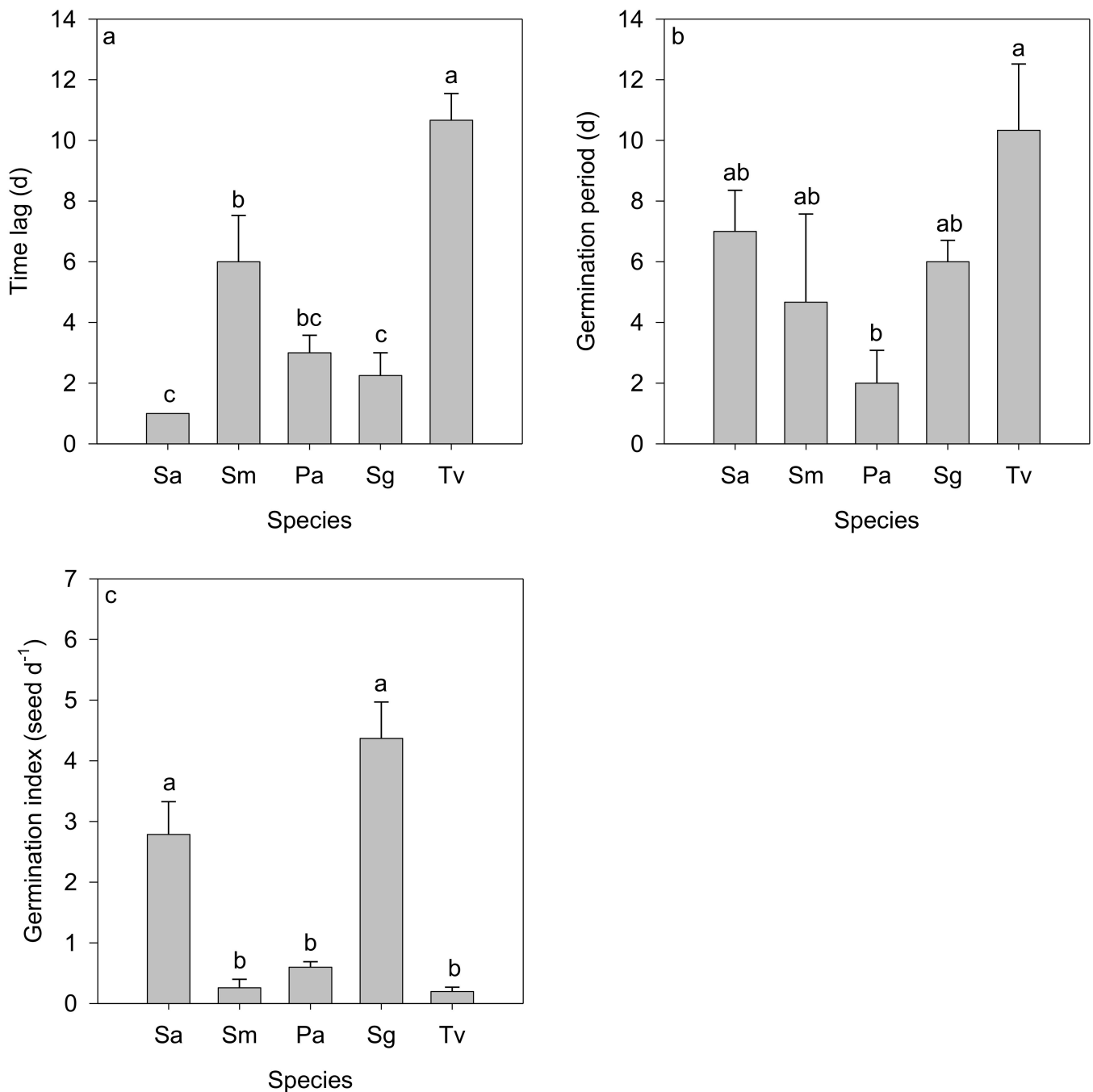


Figure 1. Germination traits of invasive *Spartina alterniflora* (Sa) and four native species (*Scirpus mariqueter*, Sm, *Phragmites australis*, Pa, *Suaeda glauca*, Sg, and *Tripolium vulgare*, Tv) in control treatment (target species in monoculture). (a) Time lag before first germination, (b) Germination period from the first germination to the last germination, (c) Germination index. Different lower cases denote significant differences among different species. Error bars are standard errors.

3.2. Effects of Interspecific Interaction on Germination

In species combination of Sa + Sm, the germination percentage of both species was significantly promoted in competition treatment than in control and allelopathy treatments (Table 1, Figure 2a). The germination percentage of *Phragmites australis* seeds was also significantly affected by interspecific interaction (Table 1). The allelopathy treatment inhibited the germination of *Phragmites australis* seeds, resulting in a significantly lower germination percentage than in the competition treatment, which had a promotion effect

(Figure 2b). Interspecific interactions between *Spartina alterniflora* and native halophytes *Suaeda glauca* and *Tripolium vulgare* did not significantly affect their germination percentage (Table 1, Figure 2c,d).

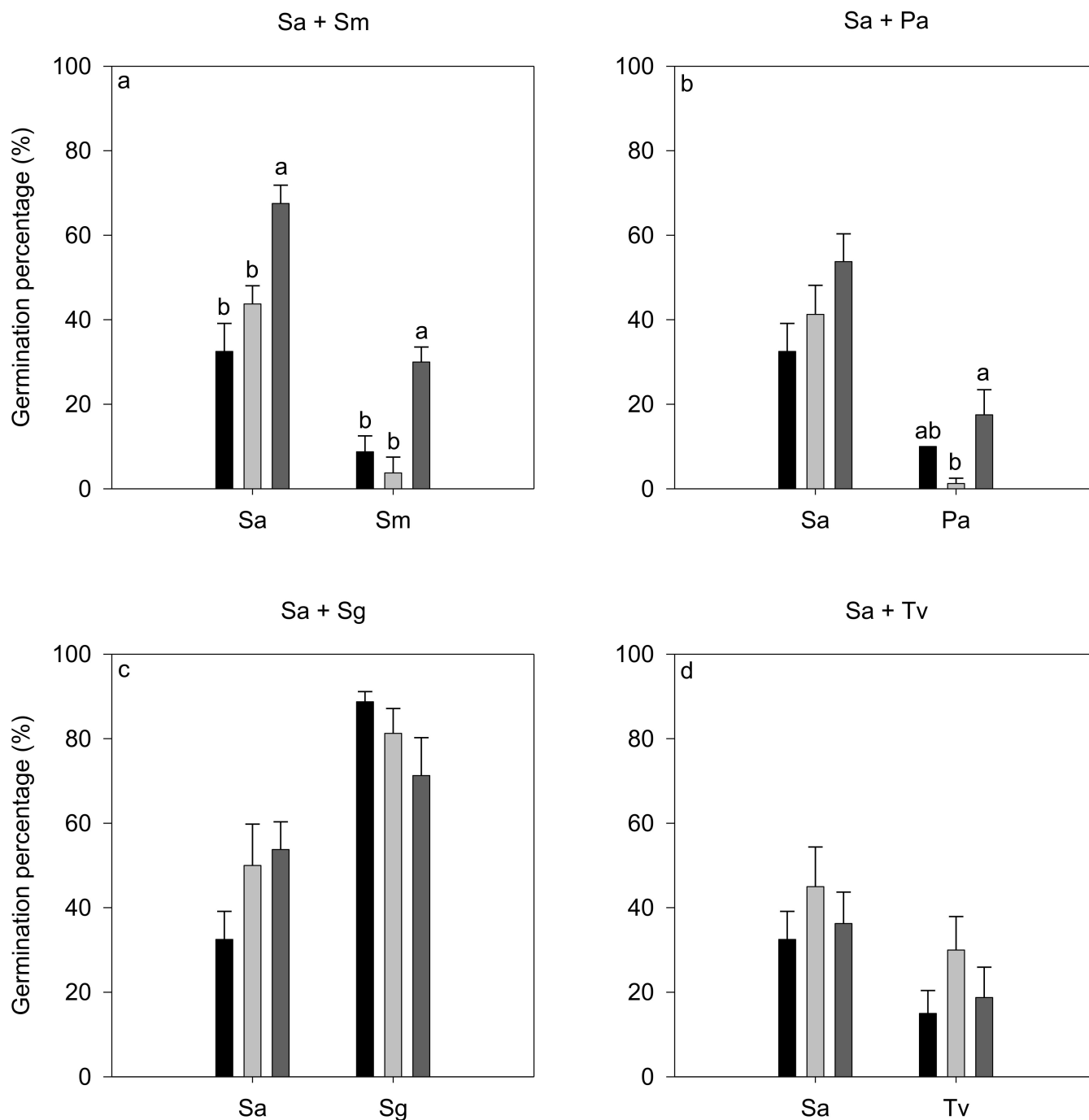


Figure 2. Seed germination percentage of invasive *Spartina alterniflora* (Sa) and four native species (*Scirpus mariqueter*, Sm, *Phragmites australis*, Pa, *Suaeda glauca*, Sg, and *Tripolium vulgare*, Tv) in different interspecific interaction treatments (control: target species in monoculture, allelopathy: target species seeds + competitor seeds leachate, competition: target species seeds + competitor seeds in mixture). (a) Species combination of Sa + Sm, (b) Species combination of Sa + Pa, (c) Species combination of Sa + Sg, (d) Species combination of Sa + Tv. Different lower cases denote significant differences among different interspecific interaction treatments of the same species. Error bars are standard errors.

The germination speed of most species (indicated by mean time to germination) was significantly affected by interspecific interaction treatment except for *Phragmites australis* seeds (Table 2). The germination of *Spartina alterniflora* seeds was the fastest (with the lowest mean time to germination) in control treatment and was significantly slowed down in allelopathy treatment with *Scirpus mariqueter* and *Phragmites australis* leachate (Figure 3a,b) and in competition treatment with *Suaeda glauca* and *Tripolium vulgare* seeds (Figure 3c,d). Competition treatment with *Spartina alterniflora* seeds significantly slowed down the germination of *Scirpus mariqueter* (Figure 3a), whereas allelopathy treatment with *Spartina alterniflora* leachate significantly promoted the germination speed of *Suaeda glauca* and *Tripolium vulgare* (Figure 3c,d).

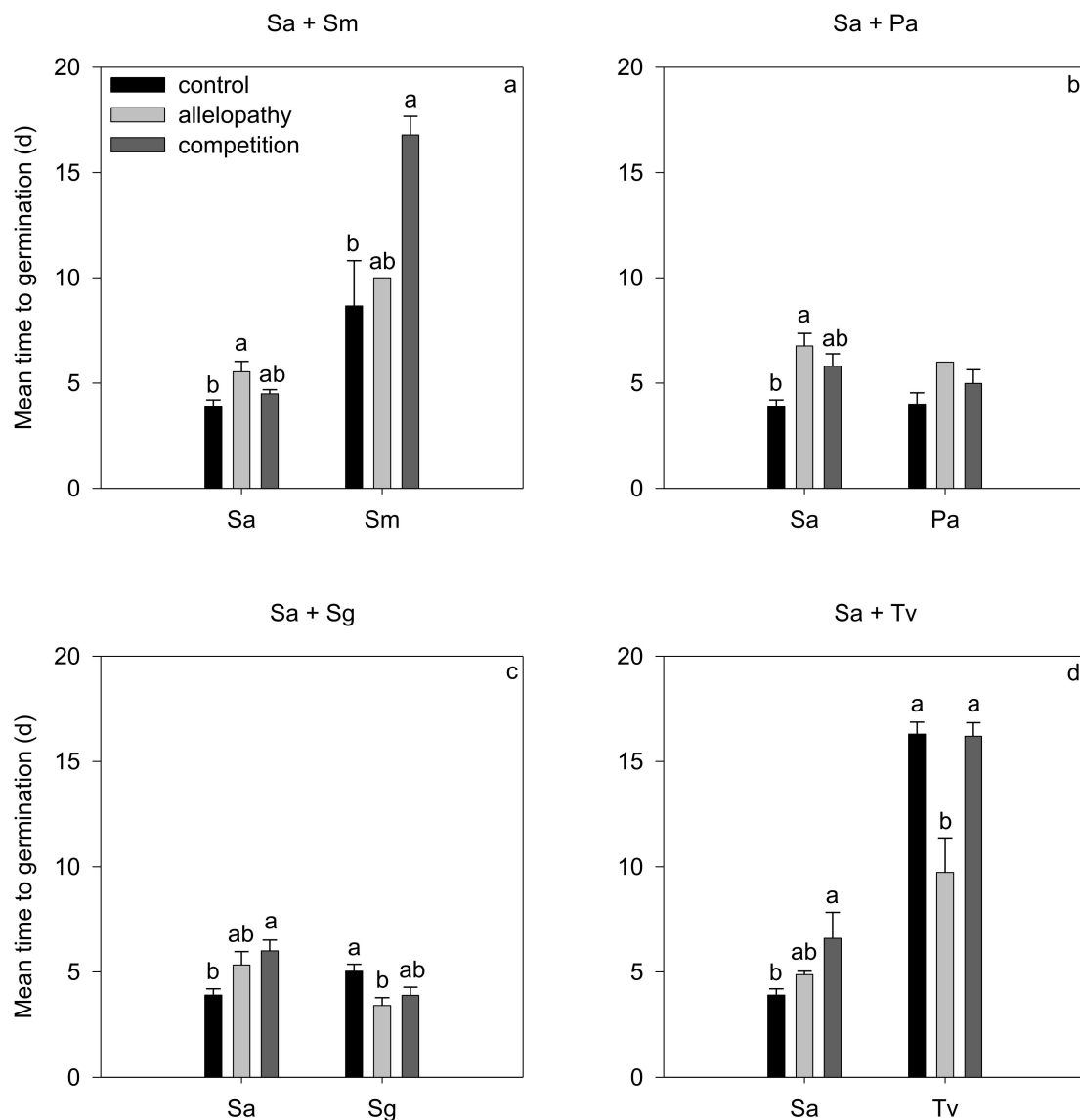


Figure 3. Mean time to seed germination of invasive *Spartina alterniflora* (Sa) and four native species (*Scirpus mariqueter*, Sm, *Phragmites australis*, Pa, *Suaeda glauca*, Sg, and *Tripolium vulgare*, Tv) in different interspecific interaction treatments (control: target species in monoculture, allelopathy: target species seeds + competitor seeds leachate, competition: target species seeds + competitor seeds in mixture). (a) Species combination of Sa + Sm, (b) Species combination of Sa + Pa, (c) Species combination of Sa + Sg, (d) Species combination of Sa + Tv. Different lower cases denote significant differences among different interspecific interaction treatments of the same species. Error bars are standard errors.

Table 1. Results of one-way ANOVA testing the effects of interspecific interaction treatment on seed germination percentage of invasive *Spartina alterniflora* (Sa) and four native species (*Scirpus mariqueter*, Sm, *Phragmites australis*, Pa, *Suaeda glauca*, Sg, and *Tripolium vulgare*, Tv) seeds in different species combinations. The abbreviations in brackets after species combinations denote the target species considered. Significant *p* values are in bold.

Source of Variation	Sa + Sm (Sa)			Sa + Pa (Sa)			Sa + Sg (Sa)			Sa + Tv (Sa)		
	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>
treatment	2	11.86	0.003	2	2.55	0.133	2	2.11	0.177	2	0.30	0.746
Source of variation	Sa + Sm (Sm)			Sa + Pa (Pa)			Sa + Sg (Sg)			Sa + Tv (Tv)		
	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>
treatment	2	14.35	0.002	2	4.52	0.044	2	1.91	0.204	2	1.28	0.325

Table 2. Results of one-way ANOVA testing the effects of interspecific interaction treatment on the mean time to seed germination of invasive *Spartina alterniflora* (Sa) and four native species (*Scirpus mariqueter*, Sm, *Phragmites australis*, Pa, *Suaeda glauca*, Sg, and *Tripolium vulgare*, Tv) in different species combinations. The abbreviations in brackets after species combinations denote the target species considered. Significant *p* values are in bold.

Source of Variation	Sa + Sm (Sa)			Sa + Pa (Sa)			Sa + Sg (Sa)			Sa + Tv (Sa)		
	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>
treatment	2	5.40	0.029	2	8.03	0.010	2	4.51	0.044	2	5.27	0.030
Source of variation	Sa + Sm (Sm)			Sa + Pa (Pa)			Sa + Sg (Sg)			Sa + Tv (Tv)		
	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>
treatment	2	8.31	0.026	2	1.60	0.291	2	5.32	0.030	2	11.02	0.005

3.3. Salinity Modification during Germination

The final salinity of the solution in Petri dishes after germination differed significantly among different interspecific interaction treatments for *Spartina alterniflora* in species combinations of Sa + Sm and Sa + Sg, and for *Scirpus mariqueter*, *Phragmites australis* and *Tripolium vulgare* (Table 3). In most species combinations, final salinity was significantly lower in competition treatment than in control and allelopathy treatments, except for *Spartina alterniflora* in species combinations of Sa + Pa and Sa + Tv, and for *Suaeda glauca* in species combination of Sa + Sg (Figure 4).

Table 3. Results of one-way ANOVA, testing the effects of interspecific interaction treatment on the final salinity of the solution in Petri dishes after seed germination in different species combinations. The abbreviations in brackets after species combinations denote the target species considered. Significant *p* values are in bold.

Source of Variation	Sa + Sm (Sa)			Sa + Pa (Sa)			Sa + Sg (Sa)			Sa + Tv (Sa)		
	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>
treatment	2	16.49	0.001	2	3.82	0.063	2	7.09	0.014	2	1.85	0.212
Source of variation	Sa + Sm (Sm)			Sa + Pa (Pa)			Sa + Sg (Sg)			Sa + Tv (Tv)		
	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>	Df	F	<i>p</i>
treatment	2	78.77	<0.001	2	30.89	<0.001	2	2.00	0.191	2	13.33	0.002

Sa: *Spartina alterniflora*, Sm: *Scirpus mariqueter*, Pa: *Phragmites australis*, Sg: *Suaeda glauca*, Tv: *Tripolium vulgare*.

In all species combinations, the final salinity of the solution in Petri dishes after germination significantly decreased with an increasing total germinated seed number (Figure 5).

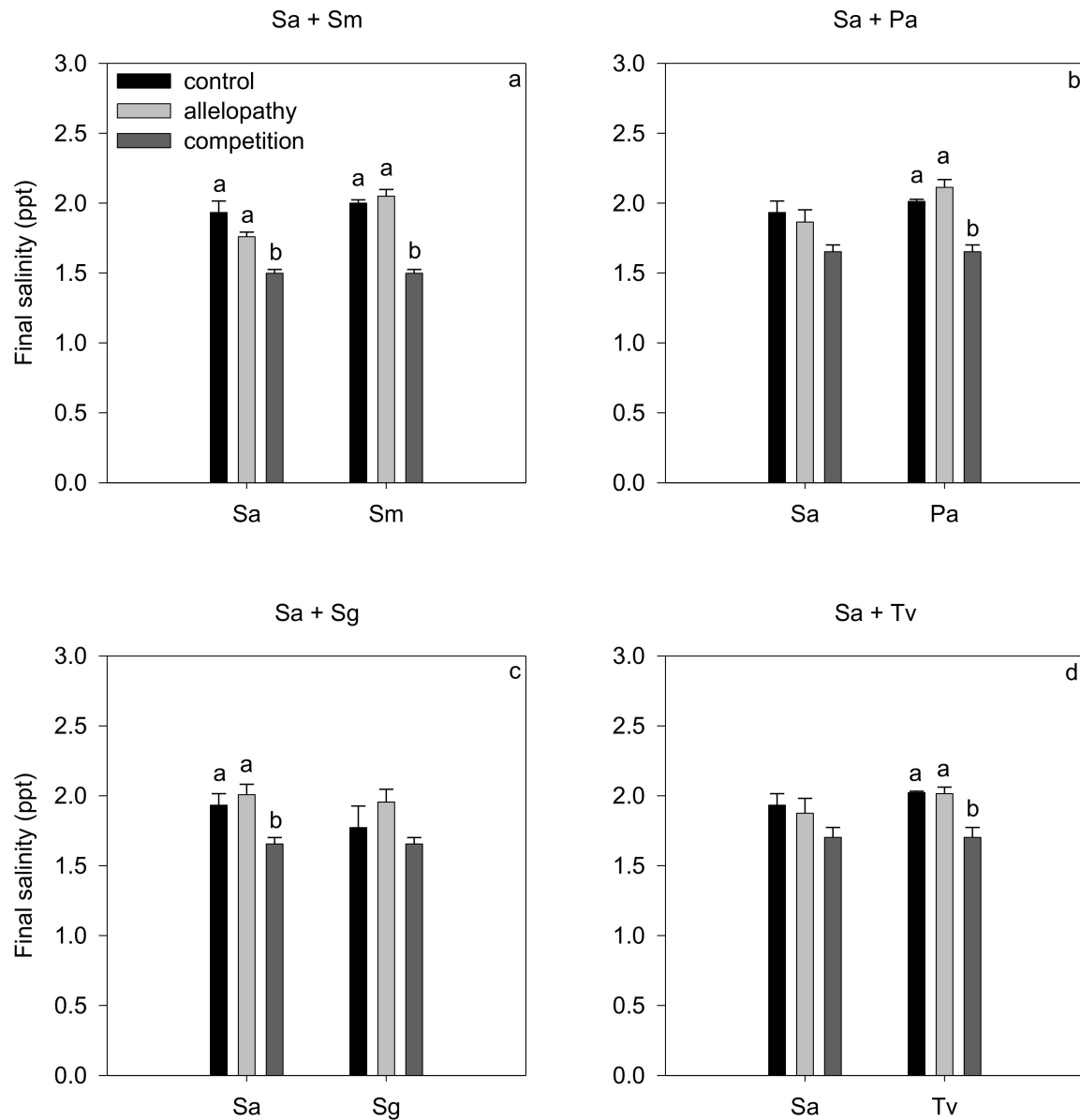


Figure 4. Final salinity of the solution in Petri dishes after germination in different interspecific interaction treatments (control: target species in monoculture, allelopathy: target species seeds + competitor seeds leachate, competition: target species seeds + competitor seeds in mixture). (a) Species combination of Sa + Sm, (b) Species combination of Sa + Pa, (c) Species combination of Sa + Sg, (d) Species combination of Sa + Tv. Sa: *Spartina alterniflora*, Sm: *Scirpus mariqueter*, Pa: *Phragmites australis*, Sg: *Suaeda glauca*, Tv: *Tripolium vulgare*. Different lower cases denote significant differences among different interspecific interaction treatments of the same species. Error bars are standard errors.

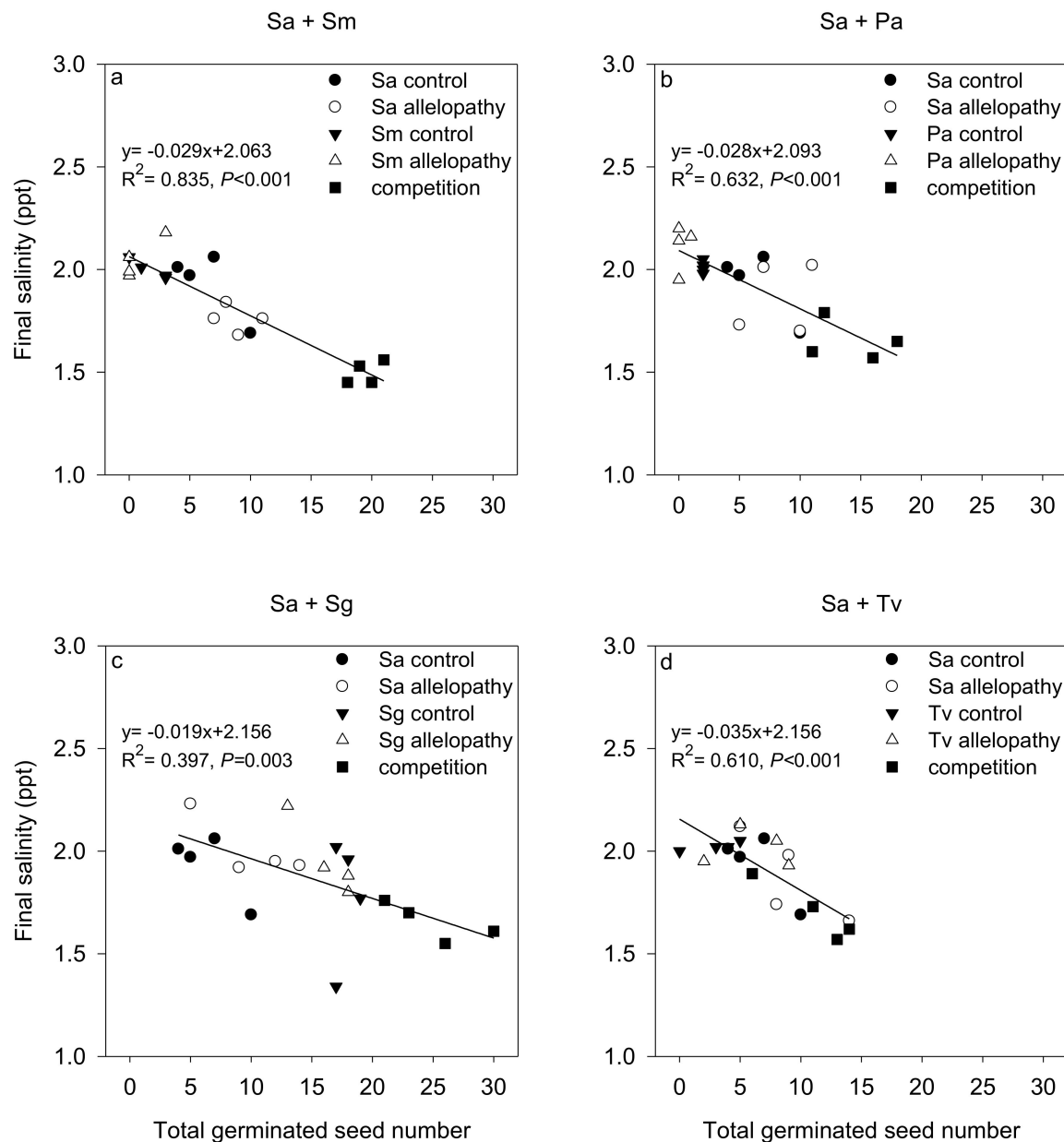


Figure 5. Relationship between final salinity of the solution in Petri dishes after germination and total germinated seed number in different interspecific interaction treatments (control: target species in monoculture, allelopathy: target species seeds + competitor seeds leachate, competition: target species seeds + competitor seeds in mixture). (a) Species combination of Sa + Sm, (b) Species combination of Sa + Pa, (c) Species combination of Sa + Sg, (d) Species combination of Sa + Tv. Sa: *Spartina alterniflora*, Sm: *Scirpus mariqueter*, Pa: *Phragmites australis*, Sg: *Suaeda glauca*, Tv: *Tripolium vulgare*.

4. Discussion

Seed germination is an irreversible process and the weakest stage in the life cycle of plants [48], which plays important roles in maintaining plant populations and communities. The findings in this and previous studies [41] suggested that the interaction between seeds is more complicated than we realized before. Our study indicated that the leachate of competitor seeds and the entire competitor seeds had inconsistent effects on germination of target species. This, together with the reduction of solution salinity in Petri dishes, implied that seeds could affect germination performance of neighbors through both allelochemical release and microenvironment modification.

4.1. Effects of Allelopathy on Seed Germination

In a natural environment, soil seed banks usually consist of seeds of different species, which makes seed-to-seed interactions ubiquitous. Adult plants can affect neighbors in a number of ways (e.g., resource competition and direct interference), whereas seeds interact with each other primarily through allelopathy [49]. In addition, the nature and magnitude of interspecific interactions among seeds usually vary with different types and concentration of allelochemicals [50].

In our experiment, the leachate of invasive *Spartina alterniflora* seeds slightly reduced (but not significantly) both the germination percentage and germination speed of native *Scirpus mariqueter* and *Phragmites australis* (Figures 2a,b and 3a,b). That is to say, only a small part of seeds of these species germinated slowly, while the others failed. This effect was probably caused by allelochemicals released from *Spartina alterniflora* seeds. As the shape and anatomical structure of seeds (e.g., seed coat thickness, wax content and embryo position) play important roles in seed response to external conditions [48,51], seed leachate will have different effects on different species. That might be the reason why the germination process of *Suaeda glauca* and *Tripolium vulgare* was significantly accelerated (Figure 3c,d).

The leachate of native *Scirpus mariqueter* and *Phragmites australis* seeds altered the microenvironment and significantly reduced the germination speed of invasive *Spartina alterniflora* seeds (Figure 3a,b). That means that more *Spartina alterniflora* seeds (especially those with poor germination ability) were activated to germination. These asymmetric effects between invasive and native seeds may be due to their substantial mass difference [35,52–54]. During germination, all the seeds may absorb allelochemicals from surrounding leachate, but accumulate them in different concentration, and the allelopathic effects of these chemicals usually depend on the concentration [31,50]. We are not clear what kind of allelochemical was released in the seed leachate of these species and how the interaction effects vary with their concentration, which needs further validation.

4.2. Effects of Salinity Modification on Seed Germination

During germination, seeds can absorb ions from the surrounding solution, which allow them to regulate osmotic potential [55,56]. We found a decrease in salinity after germination in most species combinations in competition treatment (Figure 4), which indicated the importance of microenvironment modification in mediating seed-to-seed interactions. Under the additive design, seed density in competition treatment was twice that of other treatments, which might be the main cause of decreased salinity in mixture. However, the change of total density is also a part of the influence of competing species. Future research following a response surface design can help us understand the effects of both intraspecific and interspecific interactions in different species proportion and total density levels. Notably, seeds in the mixture treatment are affected by allelopathy and microenvironment modification simultaneously, and we are not able to separate them from each other.

In our experiment, invasive *Spartina alterniflora* seeds had inconsistent effects compared with seed leachate and promoted the germination percentage of *Scirpus mariqueter* seeds (Figure 2a,b). Meanwhile, the germination speed of *Scirpus mariqueter* was significantly slowed down (Figure 3a), whereas that of *Phragmites australis* was not affected (Figure 3b). This can be explained by the positive effects of decrease in solution salinity in mixture. *Scirpus mariqueter* seeds are salt sensitive [13]. When the seeds of this native species germinate alone in 1% NaCl treatment, they will suffer from high osmotic and ion-toxicity stress, and only a small proportion of seeds successfully germinate. As *Spartina alterniflora* seeds are more salt tolerant, a great deal of salt ions will be absorbed during germination when this invasive plant is present, which led to a significant decrease in solution salinity. The positive effect of salinity modification by *Spartina alterniflora* on native species seemed to be stronger than the negative effect of its seed leachate, as the germination percentage of *Scirpus mariqueter* seeds was the highest in the mixture (Figure 2a). Conversely, halophyte

Suaeda glauca and *Tripolium vulgare* seeds are much more salt tolerant, and require a certain concentration of salt during germination. Hence, alleviation of salt stress by competing *Spartina alterniflora* seeds in mixture had minor effects, which did not significantly affect the germination percentage (Figure 2c,d) and germination speed of these two species (Figure 3c,d).

For *Spartina alterniflora*, salt-sensitive *Scirpus mariqueter* seeds significantly promoted its germination percentage (Figure 2a), whereas the seeds of halophyte *Suaeda glauca* and *Tripolium vulgare* significantly delayed its germination process (Figure 3c,d). The net effects of microenvironment modification (i.e., regulation of salinity) on this invasive plant differed in different combinations with native species, which was also related to their salt preference. Despite of different species combinations and treatments, the extent of solution salinity decrease in Petri dishes after seed germination is all significantly correlated with the number of total germinated seeds (Figure 5), indicating that the salinity modification effect by competing seeds was mainly due to the change of total density level rather than the biological attributes of competitors. Surprisingly, the Sa + Sg combination had the lowest efficiency of salt absorption per single seed (Figure 5c), even though these two species were the most salt tolerant ones among the five species used in our study. Whether there is another interaction mechanism during seed germination needs further investigation.

4.3. Implications for Community Assembly

Interspecific interactions play important roles in species coexistence and biodiversity. As seeds of different species coexist universally in the field, they may interact with each other through leachate or the modification of microenvironment in the soil. Seeds that germinate earlier usually have an advantage over those germinate later in competition [57]. For invasive plants, high seed yield, high germination percentage and short germination time are important traits which facilitate their invasion into native plant communities [58]. However, sometimes, rapid germination causes seeds to be exposed to a stressful environment, and is bad for subsequent plant survival [59]. Previous studies found that there exists a special mechanism for seeds to “sense” the surrounding environment via allelochemicals, which allow them to assess the optimal germination timing for more competitive advantages [57,60,61]. Among the five species used in our study, *Phragmites australis* had the shortest germination period (Figure 1b), and hence, the lowest potential of germination timing regulation. On the contrary, *Tripolium vulgare* had the longest germination period (Figure 1b), which may improve its adaptability to changing environments. It should be noted that due to the difference in germination timing, seeds that germinate later will not only affected by neighboring seeds, but also by seedlings from early germinated seeds [62]. Future research on the interaction between seeds and seedlings will contribute to our understanding of the role of the germination process in community assembly.

Our study found inconsistent effects of seed leachate and salinity modification on germination of both invasive and native species in Chongming Dongtan. On the whole, *Spartina alterniflora* had more positive effects on *Scirpus mariqueter* and *Phragmites australis* seeds during germination than on halophyte *Suaeda glauca* and *Tripolium vulgare*, and vice versa. Although invasive *Spartina alterniflora* promoted the germination percentage of *Scirpus mariqueter* seeds, it may still gain competitive advantage over native *Scirpus mariqueter*, *Tripolium vulgare* and *Phragmites australis* due to its short time lag (Figure 1a) and high germination index (Figure 1c). Besides, the strong competitive ability of *Spartina alterniflora* in subsequent life stages would promote its invasion into these native plant communities and had caused a series of negative ecosystem impacts [37,63,64]. The competitive mechanisms between invasive *Spartina alterniflora* and native species during germination stage were quite different from those between adult individuals, which highlighted the importance of including regeneration into the framework of community assembly.

In Chongming Dongtan, perennial clonal plants *Spartina alterniflora*, *Phragmites australis* and *Scirpus mariqueter* are heavily dependent on vegetative reproduction in mature patches, whereas seed dispersal and germination play important roles in new habitat

colonization [13]. Therefore, eradication of both the aboveground and belowground part of *Spartina alterniflora* before its florescence is critical for control of this invasive species. After the elimination of *Spartina alterniflora*, transplantation of *Phragmites australis* should be implemented due to its relatively low seed vigor in saline water, whereas *Scirpus mariqueter* has the potential to recover from its persistent seed bank [65]. Artificial reduction of sediment salinity will be an effective measure to facilitate the recovery of these native species, but the cost is too high under current conditions. On the other hand, seed dispersal and germination are crucial for the recruitment of annual *Suaeda glauca* and *Tripolium vulgare*, but they are less affected by invasive *Spartina alterniflora* in their hypersaline habitats. Seed addition of these halophytes may also be beneficial to community biodiversity, as there is intransitive competition among the dominant species in Chongming Dongtan during germination stage [66].

Seed-to-seed interactions are an important perspective to understand the underlying mechanisms of community dynamics, species diversity maintenance and invasion of alien species and can improve the effectiveness in the management of invaded coastal wetlands. However, it should be noted that due to the frequent scouring of tide in the field, the concentration of allelochemicals in the soil will be much lower than in laboratory treatment, and seeds will have minor effects of salinity modification. We need to be very careful to extrapolate our laboratory results to natural ecosystems.

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