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Article

Environment Modification Mediates Seed-to-seed Interactions between Dominant Species in the Yangtze River Estuary

Cheng-huan Wang [1], Zhen-lin Yu [1], Yuerenisha Yasenjiang [1], Long Tang [2], Yang Gao [3] and Chun-jing Zou [1,*]

[1] School of Life Sciences, Shanghai Key Laboratory of Urbanization and Ecological Restoration, East China Normal University, 500 Dongchuan Road, Shanghai 200241 China
[2] School of Human Settlements and Civil Engineering, Xi'an Jiaotong University, 28 Xianning West Road, Xi' an 710049 China
[3] State Key Laboratory of Eco-Hydraulics in Northwest Arid Region, Institute of Water Resources and Hydroelectric Engineering, Xi'an University of Technology, 5 South Jinhua Road, Xi'an 710048 China
* Correspondence: cjzou@bio.ecnu.edu.cn;

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 5 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 neighbours through both allelopathy and microenvironment modification. Salinity of the solution in petri dishes after germination decreased in all treatments, and was negatively correlated with the number of total germinated seeds. Seed leachate of invasive *Spartina alterniflora* inhibited the germination of native *Scirpus mariqueter* and *Phragmites australis*, but not the two halophytes *Suaeda glauca* and *Tripolium vulgare*. The salt absorption by *Spartina alterniflora* seeds had the opposite effects compared with that of its seed leachate. On the other hand, seed leachate of native species promoted the germination of invasive *Spartina alterniflora*. The effect of microenvironment modification of *Scirpus mariqueter* and *Phragmites australis* was positive, whereas that of *Suaeda glauca* and *Tripolium vulgare* was neutral or negative. 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; environment modification; interspecific interactions; salinity; seed germination;

1. Introduction

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 driven 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 neighbours 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 rate 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 neighbouring 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 driven 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 environment modification 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 large amounts 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 (but 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 5 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 environment modification 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 subtropical monsoon climate. Dongtan has the annual average rainfall of 1145 mm and annual average temperature of 15.7℃. The highest temperature is in July with long-term average temperature of 27.3℃, and the lowest temperature is in January with long-term average temperature of 4.2℃ [40]. *Phragmites australis* (Pa) dominates the high marsh with frequently occurred *Suaeda glauca* (Sg) and *Tripolium vulgare* (Tv) in bare patches. Native *Scirpus mariqueter*

(Sm) was the dominant species in sedge communities in middle to low marsh. 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 in these areas [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℃. *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 in early April, 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 piece of filter paper on the bottom. The petri dishes were placed in a light incubator (PGX-600B) for germination, with the setting of 30℃ and 100% light intensity (12000 lux) in the daytime (from 08:00 to 20:00) and 18℃ 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. 400 ml of distilled water was added into each flask. The flasks were sealed and vibrated in a shaker at room temperature for 48h. After that, NaCl was added into the flasks to reach the salinity of 1%, which is close to the condition of their natural habitat.

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 came to 4 species combinations: Sa+Sm, Sa+Pa, Sa+Sg, 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 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 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. Similary, four native species seeds were treated by *Spartina alterniflora* leachate, respectively. In competition treatment (Sa+Sm, Sa+Pa, Sa+Sg, 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. There were 17 treatments in all (5 control + 8 allelopathy + 4 competition) and each treatment was replicated 4 times, making a total of 68 dishes .

Distilled water was added into each petri dish everyday to maintain a shallow layer of water. The number of germinated seeds (those root tips had protruded from its seed coat) of each species was counted and recorded everyday and then randomly rotated its position until no seeds germinated within a week. 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

The germination rate was calculated as the percentage of total germinated seeds of each species. The mean time to germination (MTG) was calculated as follows [41]:

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

where Gi is the number of germinating seeds on the i^{th} day; Di is the number of days.

One-way ANOVA (post hoc Tukey’s HSD test) was used to examine the effects of different treatments on germination rate, 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. 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. Effects of interspecific interaction on germination

In species combination of Sa+Sm, the germintation rate of both species was significantly promoted in competition treatment than in control and allelopathy treatment (Table 1, Figure 1a). The germination rate of *Phragmites australis* seeds was also significantly affected by interspecific interaction (Table 1). Allelopathy treatment inhibited the germination of *Phragmites australis* seeds, resulted in significantly lower germination rate than in competition treatment, which had an opposite promotion effect (Figure 1b). Interspecific interaction between Spartina alterniflora and native halophytes *Suaeda glauca* and *Tripolium vulgare* didn't significantly affect their germination rate (Table 1, Figure 1c, 1d).

Table 1. Results of one-way ANOVA testing the effects of interspecific interaction treatment on the germination rate 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.

Source of variation	**Sa + Sm (Sa)**			**Sa + Pa (Sa)**			**Sa + Sg (Sa)**			**Sa + Tv (Sa)**		
	Df	F	*P*	Df	F	*P*	Df	F	*P*	Df	F	*P*
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	*P*	Df	F	*P*	Df	F	*P*	Df	F	*P*
treatment	2	14.35	**0.002**	2	4.52	**0.044**	2	1.91	0.204	2	1.28	0.325

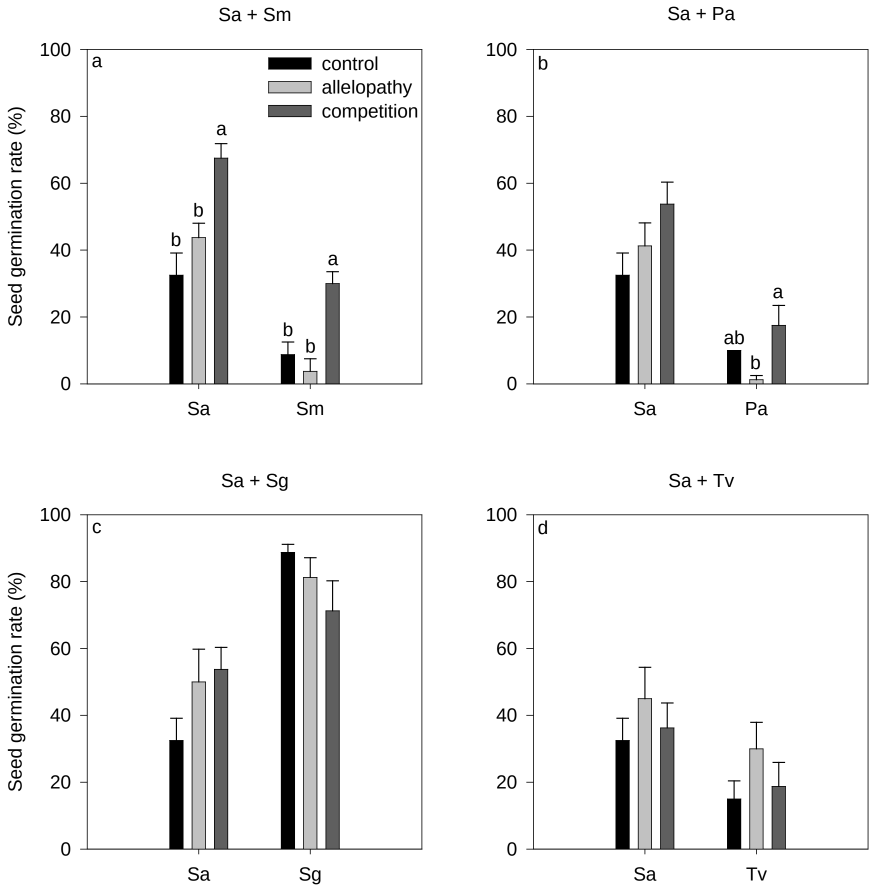

Figure 1. Seed germination rate of invasive *Spartina alterniflora* (Sa) and four native species (*Scirpus mariqueter*, Sm, *Phragmites australis*, Pa, *Suaeda glauca*, Sg and *Tripolium vulgare*, Tv) in different interspecific interaction treatments (control: target species in monoculture, allelopathy: 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* (Figure 2a, 2b) and in competition treatment with *Suaeda glauca* and *Tripolium vulgare* (Figure 2c, 2d). Competition treatment with *Spartina alterniflora* seeds significantly slowed down the germination of *Scirpus mariqueter* (Figure 2a), whereas allelopathy treatment of *Spartina alterniflora* significantly promoted the germination speed of *Suaeda glauca* and *Tripolium vulgare* (Figure 2c, 2d).

Table 2. Results of one-way ANOVA testing the effects of interspecific interaction treatment on the mean time to germination 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.

Source of variation	**Sa + Sm (Sa)**			**Sa + Pa (Sa)**			**Sa + Sg (Sa)**			**Sa + Tv (Sa)**		
	Df	F	*P*	Df	F	*P*	Df	F	*P*	Df	F	*P*
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	*P*	Df	F	*P*	Df	F	*P*	Df	F	*P*
treatment	2	8.31	**0.026**	2	1.60	0.291	2	5.32	**0.030**	2	11.02	**0.005**

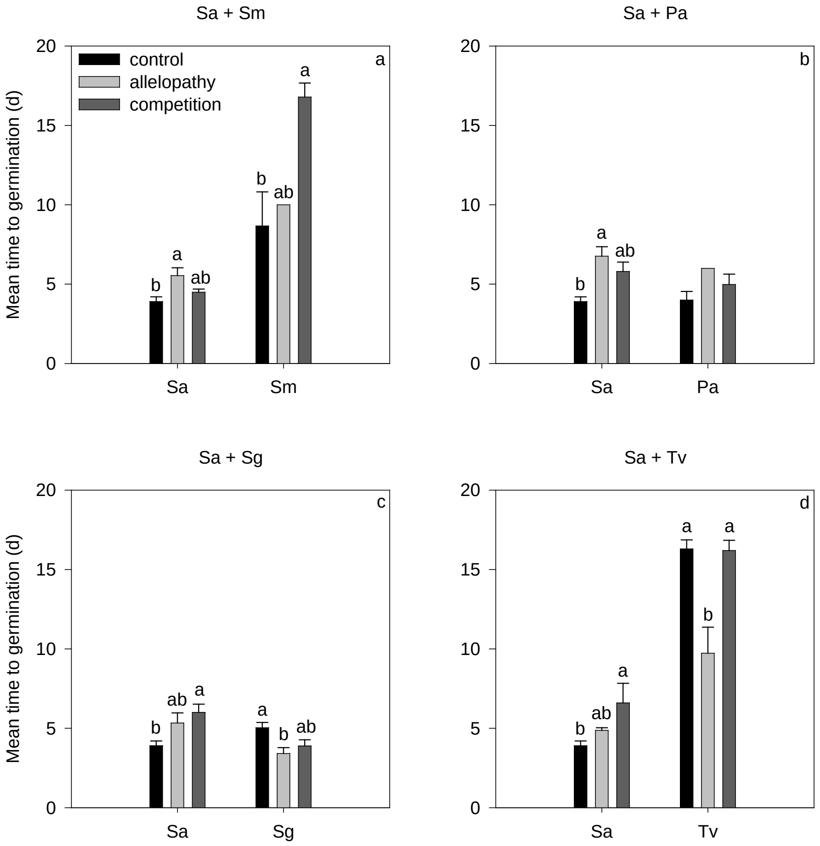

Figure 2. Mean time to germination of invasive *Spartina alterniflora* (Sa) and four native species (*Scirpus mariqueter*, Sm, *Phragmites australis*, Pa, *Suaeda glauca*, Sg and *Tripolium vulgare*, Tv) seeds in different interspecific interaction treatments (control: target species in monoculture, 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.

3.2. 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 combination of Sa+Sm and Sa+Sg, and for *Scirpus mariqueter*, *Phragmites australis* and *Tripolium vulgare* (Table 3). In all species combinations, final salinity was lower in competition treatment than in control and allelopathy treatments, and the differences were significant except for *Spartina alterniflora* in species combination of Sa+Pa and Sa+Tv, and for *Suaeda glauca* (Figure 3).

In all species combinations, final salinity of the solution in petri dishes after germination significantly decreased with increasing total germinated seed number (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 germination in different species combinations.

Source of variation	**Sa + Sm (Sa)**			**Sa + Pa (Sa)**			**Sa + Sg (Sa)**			**Sa + Tv (Sa)**		
	Df	F	*P*	Df	F	*P*	Df	F	*P*	Df	F	*P*
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	*P*	Df	F	*P*	Df	F	*P*	Df	F	*P*
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.

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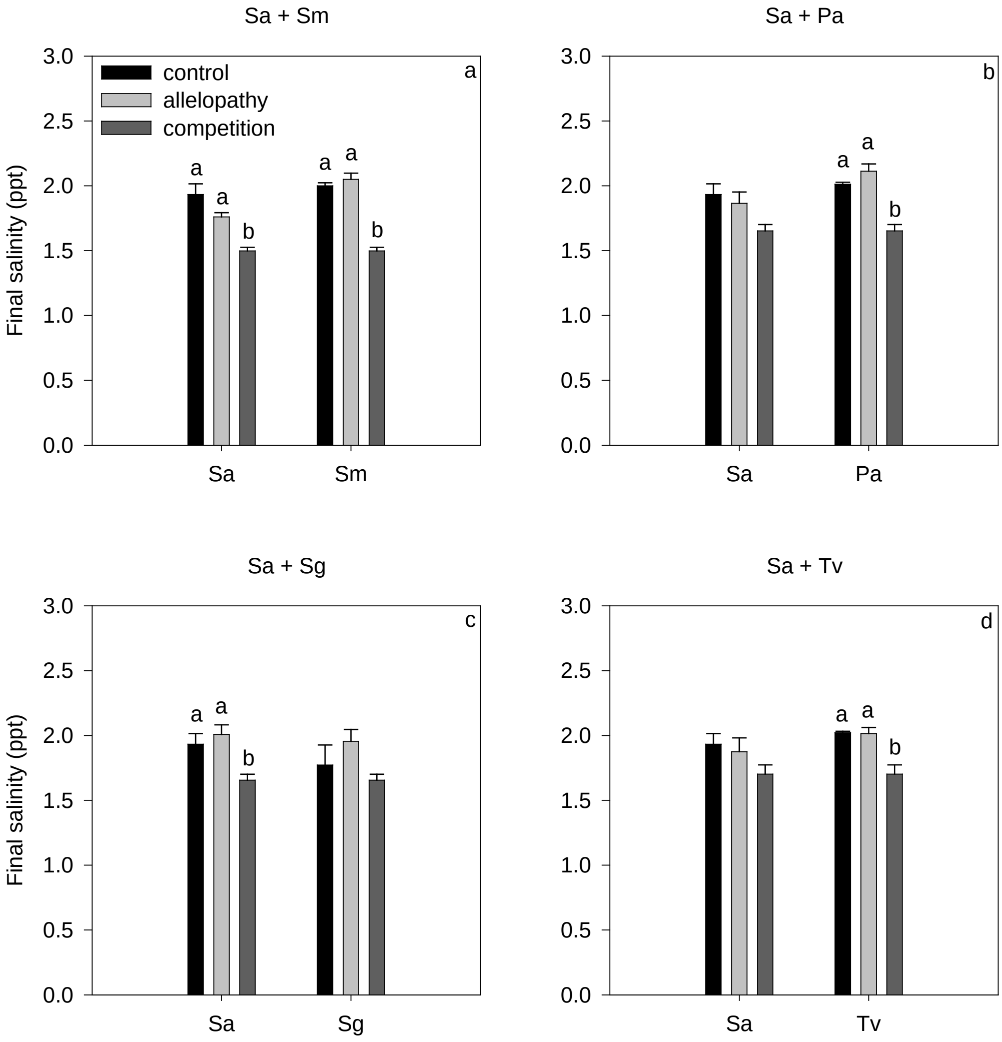

Figure 3. Final salinity of the solution in petri dishes after germination in different interspecific interaction treatments (control: target species in monoculture, allelopathy: target species seeds + competitor seeds leachate, competition: target species seeds + competitor seeds in mixture). a) Species 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.

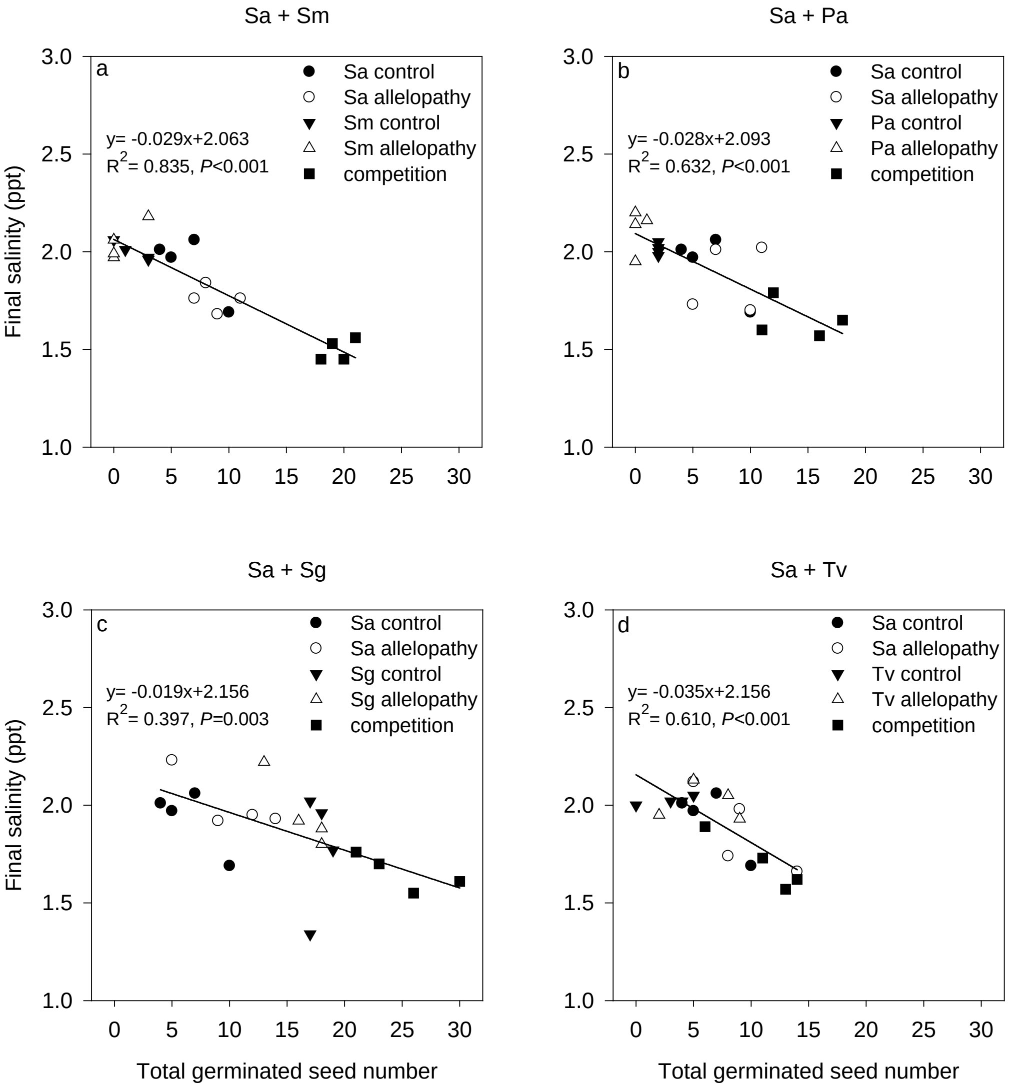

Figure 4. Relationship between final salinity of the solution in petri dishes after germination and total germinated seed number in different interspecific interaction treatments (control: target species in monoculture, allelopathy: target species seeds + competitor seeds leachate, competition: target 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 [42], which plays important roles in maintaining plant populations and communities. The findings in this and previous studies [43] suggested that the interaction between seeds was more complicated than we realized before. Our study indicated that the leachate of competitor seeds and the entire competitor seeds had opposite 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 neighbours through both allelochemical release and microenvironment modification.

4.1. Effects of allelopathy on seed germination

In natural environment, soil seed banks usually consist of seeds of different species, which makes seed-to-seed interactions ubiquitous. Adult plants can affect neighbours in a number of ways (e.g., resource competition and direct interference), whereas seeds interact with each other primarily through allelopathy [44]. In addition, the nature and magnitude of interaction intensity among seeds usually vary with different types and concentration of allelochemicals [45].

In our experiment, the leachate of invasive *Spartina alterniflora* seeds created stressful environment and reduced both the germination rate and germination speed of native *Scirpus mariqueter* and *Phragmites australis* (Figure 1a, 1b, 2a, 2b). 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 [42,46], 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 2c, 2d).

The leachate of all native species seeds might have created favorable conditions and can promote the germination rate (Figure 1) but reduce the germination speed of invasive *Spartina alterniflora* seeds (Figure 2). That means 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 [35,47-49]. 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 [31,45]. We are not clear what kind of allelochemicals 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 microenvironment modification on seed germination

During germination, seeds can absorb ion from surrounding solution, which allow them to regulate osmotic potential [50,51]. We found decrease in salinity after germination in all treatments (Figure 3), which indicated the importance of microenvironment modification in mediating seed-to-seed interactions. 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 the opposite effects compared with seed leachate and promoted the germination rate of *Scirpus mariqueter* and *Phragmites australis* seeds (Figure 1a, 1b). Meanwhile, the germination speed of *Scirpus mariqueter* was slowed down (Figure 2a), whereas that of *Phragmites australis* was less affected (Figure 2b). This can be explained by the positive effects of decrease in solution salinity caused by *Spartina alterniflora* seeds. *Scirpus mariqueter* and *Phragmites australis* seeds are salt sensitive [13]. When the seeds of these 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 significant decrease in solution salinity. The positive effect of microenvironment modification by *Spartina alterniflora* on native species seemed to be stronger than the negative effect of its seed leachate as the germination rate of both *Scirpus mariqueter* and *Phragmites australis* seeds was the highest in mixture (Figure 1a, 1b). 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 didn’t significantly affect the germination rate (Figure 1c, 1d) and even slightly delayed the germination process of these two species (Figure 2c, 2d).

For *Spartina alterniflora*, the existence of native species seeds promoted the germination rate (Figure 1), but delayed its germination process (Figure 2). Actually, the net effects of microenvironment modification (i.e., salt absorption) on this invasive plant differed in different combinations with native species, which was also related to their salt preference. Microenvironment modification by salt sensitive *Scirpus mariqueter* and

Phragmites australis seeds promoted both germination rate (Figure 1a, 1b) and germination speed of *Spartina alterniflora* (Figure 2a, 2b), whereas that by halophyte *Suaeda glauca* and *Tripolium vulgare* seeds delayed the germination process (Figure 2c, 2d) and had neutral or negative effects on germination rate of *Spartina alterniflora* (Figure 1c, 1d). Surprisingly, despite of different species combinations and treatments, the extent of solution salinity decrese in petri dishes after germination is all significantly correlated with the number of total germinated seeds, and Sa+Sg combination had the lowest efficiency of salt absorption per single seed (Figure 4). Whether there is other 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 [52]. For invasive plants, high seed yield, high germination rate and short germination time are important traits which facilitate their invasion into native plant communities [53]. However, sometimes rapid germination makes seeds exposed in stressful environment, and is bad for subsequent plant survival [54]. 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 [52,55,56]. Due to the difference in germination timing, seeds that germinate later will not only affected by neighbouring seeds, but also by seedlings from early germinated seeds [57]. Future research on the interaction between seeds and seedlings will contribute to our understanding of the role of germination process in community assembly.

Our study found adverse effects of seed leachate and microenvironment 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* did not gain competitive advantages over native species during germination and even facilitated the germination of *Scirpus mariqueter*, 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 [37,58,59]. This highlighted the importance of including regeneration stage into the framework of community assembly.

In Chongming Dongtan, perennial clonal plants *Spartina alterniflora*, *Phragmites australis* and *Scirpus mariqueter* are heavily dependent on vegetative reproducion in mature patches, whereas seed dispersal and germination play important roles in new habitat colonization [13]. Therefore, eradication 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 [60]. 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 is 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 [61].

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. However, it should be noted that due to the frequent scouring of tide in the field, concentration of allelochemicals in the soil will be much lower than in laboratory treatment, and seeds will have minor effects of microenvironment modification. We need to be very careful to extrapolate our results in laboratory control experiment to natural ecosystems.

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