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Allelopathic effects of invasive *Spartina alterniflora* root exudates in soil on the offspring (seeds) of *Scirpus mariqueter*

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ABSTRACT

Spartina alterniflora Loisel is an invasive species in Jiuduansha Islands and threatens the local biodiversity and the survival of native species *Scirpus mariqueter*. In this study, the resistant and tolerant characteristics of native species *S. mariqueter* against invasive species *S. alterniflora* and the inheritance of these characteristics were examined. Our results showed that due to the invasion of *S. alterniflora*, the germination of *S. mariqueter* seeds and the growth of seedlings in the invaded soil were significantly inhibited. The ultimate germination of *S. mariqueter* decreased from 91.67% (non-invaded) to 5.83% (invaded). Our data indicated that soil of *S. alterniflora* and *S. mariqueter* both contained many compounds. But heneicosanoic acid, hexadecane, octadecane, sulfuric acid, diethyl ester and so on were only found in *S. alterniflora* soil and they might have allelopathic effect on the *S. mariqueter*. *S. mariqueter* would begin to evolve resistant or tolerant characteristics against allelochemicals when invaded by *S. alterniflora*. The resistant or tolerant characteristics were utilized by *S. mariqueter* genetically developed in *S. mariqueter* offspring. However, the growth of *S. mariqueter* was still affected seriously by *S. alterniflora*.

Key Words: Allelopathic effect, invasive plant, *Scirpus mariqueter*, soil, *Spartina alterniflora*

INTRODUTION

Changes in biodiversity are becoming more and more intense due to the changes in atmospheric carbon dioxide, climate, vegetation and other factors (27). With the development of trade globalization, biological invasion is becoming more and more serious and is one of the most severe environmental problems (27). Biological invasion may be considered as a form of biological pollution and a significant component of the human-induced global environmental change (15,22,32). The invasion of foreign species is primary cause of biodiversity loss and cause environmental or harm to human health (10).

Spartina alterniflora Loisel is a rhizomatous perennial, native to the Atlantic and Gulf coasts of North America and it was introduced into China in 1979 based on its potential value to coastal engineering and agriculture (7,29,34,38). Due to its strong survival and reproductive potential, *S. alterniflora* is expanding rapidly and now colonizes across the islands after being introduced in 1997 in Jiuduansha Islands. It threatens the

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local biodiversity and ecosystems and threatens the survival of the native species *S. mariqueter.*

S. alterniflora growth characteristics, strong environmental adaptation and salt tolerance have been well documented (1,2,8,5,25). It is known that some plants have allelopathic potential by releasing allelochemicals to their surroundings that have either deleterious or beneficial effects on other plants in the vicinity (23). Although most plant tissues may also contain allelochemicals, only the compounds released from the plants into the environments can inhibit the germination and growth of neighbouring plant species and, thus, act as allelochemicals in natural ecosystems (25). Some allelochemicals have been identified in root exudates of many plants, such as rice (17, 18). In nature communities, allelopathy forms a selection pressure on the one hand and on the other hand a long period of evolution makes some plants develop resistance to allelochemicals so that the impact of allelopathy becomes not so obvious to these plants (11,26).

The objectives of this study were: (i) to determine whether the allelopathic effect was from *S. alternflora* on *S. mariqueter*; (ii) to determine whether the *S. alternflora* invaded soil displayed the allelopathic effect; (iii) to confirm whether *S. mariquete* would form resistant or tolerant characteristics against allelopathic substances released by the *S. alternflora* roots and then if these characteristics really existed whether they would be genetically inherited to its offspring.

METHODS AND MATERIALS

I. Material

The seeds of *S. mariqueter* and soil were obtained from Jiuduansha Islands. Both the seeds and the surface soil (0~20 cm below surface) were collected from monoculture *S. mariqueter* community (N 30°10′12″, E 121°57′40″) and *Scirpus–Spartina* mixture community (N 31°10′29.1″, E 121°57′27.4″). They were labeled as monoculture seed, invaded seed, monoculture soil and invaded soil, respectively. The soil of *S. alterniflora* was collected in *S. alterniflora* monoculture community (N 31°12′35.1″, E 121°58′19.3″). All soil samples were allowed to air-dry at room temperature at the laboratory. Then the dry soil was mixed with grit (dia. 0.65 mm~0.85 mm) [soil: grit= 4:1(volume)]. All seeds were imbibed in 0.4% NaCl solution and kept in refrigerator at 4^{o}C to break dormancy until use (6).

II. Effects of *S. alterniflora* invaded soil on *S. mariqueter* seed germination

The two kinds of seeds were sown in plastic pots (dia. 15×12cm) containing monoculture soil and invaded soil respectively. So there were four treatments: (I) monoculture seed + monoculture soil; (II) monoculture seed + invaded soil; (III) invaded seed + monoculture soil; (IV) invaded seed + invaded soil. 40 seeds were sown in each pot covered with a thin layer of sand (6). All pots were put in 0.4% NaCl solution to keep the moist and salinity (3~4‰) so as to keep the environment similar to the field soil conditions. All treatments were replicated four times. The experiment was conducted in an artificial climate chamber at 25 ℃/28 ℃ (dark/light) and with a 12 photoperiod (light intensity was 6000 lux) and 80% relative humidity. Germination was determined by counting the number of seeds germinated every 24 h until there was no new seed germinated for five consecutive days (6).

III. Effects of *S. alterniflora* invaded soil on *S. mariqueter* seedling growth

The two kinds of seeds were placed in Petri dishes on filter paper saturated with distilled water. When the seed radical emerged, the germinated seeds were transferred in the two types of soil respectively. Namely, the four treatments were set: (V) monoculture seedling + monoculture soil; (VI) monoculture seedling + invaded soil; (VII) invaded seedling + monoculture soil; (VIII) invaded seedling + invaded soil. All treatments were replicated three times.

All plants were grown in an artificial climate chamber at 25 ℃/28 ℃ (dark/light) and with a 12 h photoperiod (light intensity was 6000 lux) and 80% relative humidity. Thirty days after planting, the seedlings of *S. mariqueter* were harvested to measure growth indices such as total root length, total projected root area, average root diameter, total root surface area, total root volume, number of tips with the Regent WinRHIZO root analysis system (Regent Instruments, Inc, Canada) and EPSON Perfection 3200 scanner (EPSON, Inc, USA). The seedlings were separated into aboveground and underground parts to measure the dry weight (dried for 48h under 80 ℃).

IV. Soil extraction

The soil of *S. mariqueter* and *S. alterniflora* (200 g) were respectively soaked in a mixed liquid [dichloromethane : methanol= 1:1 (volume)] (500 ml) with oscillation 2 h and ultrasonic extraction 1 hr. After soaking, the liquid was removed by filtration and the liquid was evaporated out using a rotary evaporator (Shensheng R-205, Shanghai, China) at 35℃. Samples of extracts from two soils were methyl esterification by a solution [methanol : boron trifluoride diethyl etherate = 3:1 (volume)].

V. GC-MS

The GC-MS analyses were done using an Agilent 6890N GC system coupled to an Agilent 5975 mass selective detector (MSD) (Agilent, USA). Helium of high purity was used as the carrier gas at a flow-rate of 1 ml/min and the injection volume was 1 μL in splitless mode. The GC column used was DB-5MS (30 m ×0.25 mm, 0.25 μm film thickness, J & W Scientific, USA). The column temperature was initially held at 50℃ increased to 150℃ at a rate of 5℃/min and further increased to 250℃ at a rate of 15℃/min and finally reached 300℃ at a rate of 25℃/min.

Statistical analysis were performed using SPSS 16.0 statistical software program. All data were evaluated by one-way analysis of variance (ANOVA). From the germination counts the following germination parameters were determined.

(1). Ultimate Germination (UG): The maximum number of seeds that germinated during the experiment.

(2). Mean Period of Ultimate Germination (MPUG) = $\sum_{1}^{i} N_i D_i / UG$

(3). Rate of Germination (RG) = $\sum_{1}^{i} N_i / D_i$

Where, N : Daily increase in seedling number, D : Day of seedling germination (28).

RESULTS

Effects of *S. alterniflora* invaded soil on ultimate germination of *S. mariqueter*

Different treatments significantly affected theUGs of *S. mariqueter* (Table 1). A significant difference in UG among the different treatments was found at confidence level of 95%. The monoculture seeds (treatment I) placed in the soil of *S. mariqueter* community had the highest UG 91.67%, suggesting that *S. mariqueter* seeds could germinate and developed normally in their original environment. The UG of monoculture seeds sown in the soil of *Scirpus–Spartina* mixture community (treatment II) was 5.83% only. However, the UGs of invaded seeds in both monoculture soil and invaded soil were inhibited seriously, only 25% and 16.7% of the rate in treatment I, respectively. A significant difference was also found between treatment III and treatment IV. The lowest UG appeared when the monoculture seeds planted in the invaded soil.

Table 1. Effects of different treatments on *S. mariqueter* germination parameters

Treatments	Ultimate germination (%)	Rate of germination (seeds·d^{-1})	Mean period of ultimate germination (d)
I	91.67 a	2.97 a	5.46 a
II	5.83 b	0.33 b	13.80 b
III	18.33 c	0.55 b	12.63 b
IV	13.33 d	0.43 b	12.06 b

Values in column marked with the same letter don't differ significantly at $P \leq 0.05$.

Effects of *S. alterniflora* invaded soil on germination rates of *S. mariqueter*

The MPUG obtained from the different treatments were not consistent with the changes in UG (Table 1). RG and MPUG in treatment I were significantly different from those in other treatments. The average of RG was over 2 seeds·d^{-1} and the average MPUG was 7 days shorter at least in treatment I than in other treatments, while there was no distinct difference in RG and MPUG among other three treatments. MPUG of *S. mariqueter* in treatment I was 5.46 days, 8.34 days longer than in treatment II.

Effects of *S. alterniflora* invaded soil on the growth of *S. mariqueter* seedlings

Seedlings developed from mono- and mixed-culture were planted in the *S. alterniflora* invaded or non invaded soil. Significant differences in seedling growth status were found between the different treatments (Table 2). Similar to the result of seed germination tests, the growth of seedlings was enhanced when grown in the soil of monoculture *S. mariqueter* community compared to the same seedlings grown in the *S. alterniflora* invaded soil. Among the different treatments, treatment V resulted in highest levels of height of seedling, total length and surface area of roots, projected area of roots, bulk volume of roots, the number of tips, dry weight of aerial part and underground part while treatment VI led to the lowest values of seedling growth indices.

The height of seedlings in treatment V was 58.20 mm, i.e. 1.91, 1.59 and 1.62 times more than other 3- groups respectively. However, there was little differences between treatment VII (invaded seedling + monoculture soil) and treatment VIII (invaded seedling + invaded soil). The same was found for root length, dry weight of aerial and underground part.

Table 2. Effects of different treatments on *S. mariqueter* seedling growth

Treat-ments	Hypocotyl length (mm)	Total root length (cm)	Total projected root area (cm^2)	Average root diameter (mm)	Total root surface area (cm^2)	Total root volume (cm^3)	Number of tips	Shoot dry weight (mg/ seedling)	Root dry weight (mg/ seedling)
V	58.20 a	20.21 a	0.72 a	0.36 a	2.27 a	0.020 a	38.00 a	2.20 a	1.91 a
VI	30.43 c	10.41 c	0.36 b	0.41 a	1.14 b	0.012 b	21.33 b	1.03 c	1.08 c
VII	36.53 b	16.99 b	0.60 a	0.39 a	1.90 a	0.019 a	33.33 a	1.40 b	1.17 b
VIII	36.00 b	16.65 b	0.39 b	0.39 a	1.21 b	0.012 b	32.67 a	1.34 b	1.20 b

Values in column marked with the same letter don't differ significantly at $P \leq 0.05$.

For projected area, total surface area and bulk volume of roots, no significant difference was detected between treatment V and treatment VII, also between treatment VI and treatment VIII. However, the levels in treatment V and VII were higher than those in treatment VI and VIII.

The number of root tips represents capabilities of root branching and root system development. Seedlings developed from the monoculture *S. mariqueter* seeds were inhibited significantly when grown in soil invaded by *S. alterniflora*, which suggested allelopathic effect of *S. alterniflora* on *S. mariqueter* might occur through soil media shared by the two plants. However, there was no significant difference in root diameter of *S. mariqueter* seedlings among the four treatments.

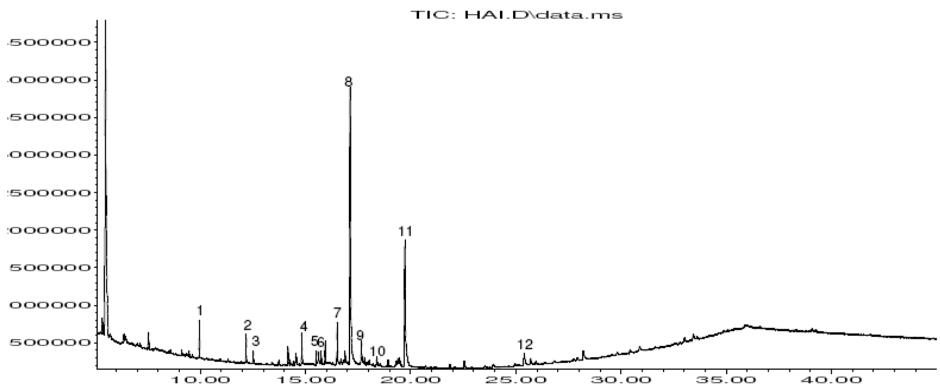

Figure 1. Gas chromatograms of the hydrophobic extracts of *S. mariqueter*

GC-MS analysis

Compared with Fig. 1 and Fig. 2 and according to Table 3, many compounds in Fig. 1 also appeared in Fig. 2, such as No. 4-14 in Fig. 1. But obviously, there were more compounds isolated from the soil of *S. alterniflora* than those from the soil of *S. mariqueter*, such as heneicosanoic acid, hexadecane, octadecane, sulfuric acid, diethyl ester, tetracosanoic acid, tricosanoic acid were only identified in *S. alterniflora* soil. The chemical structures and retention data of the compounds identified were given in Table 3.

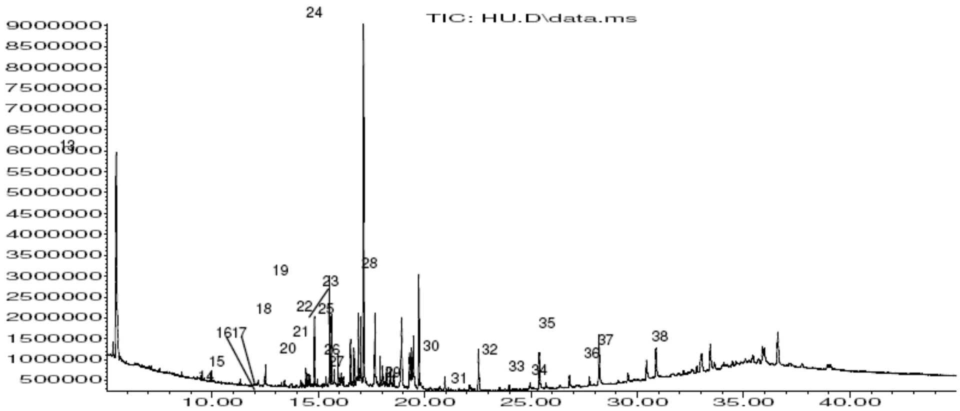

Figure 2. Gas chromatograms of the hydrophobic extracts of *S. alterniflora*

DISCUSSION

Seed germination and seedling stages are the most vulnerable periods of the plant life cycle. Poor germination and weak seedlings often lead to limited individual development and species prosperity. It is highly important in plant biology and agriculture practice to study the propagation and adaptability of seeds and seedlings (31).

Our results showed that when the seeds collected from *S. mariqueter* monoculture community and their seedlings were planted in the soil from the same community, the seed germination and seedling growth were better than those of other treatments. This indicated that the native species had a high capacity of reproduction and growth in its native environment. This was consistent with the research of Callaway *et al.* (4).

In treatment II (monoculture seed + invaded soil), the seed germination was seriously inhibited compared to treatment I (monoculture seed+ monoculture soil), the RG sharply decreased more than 80%. In addition, the MPUG was much longer in treatment II and the RG had decreased. This suggests that invasive plant *S. alterniflora* might release some phytotoxin substances to *S. mariqueter* and according to Vivanco *et al*. (33) mechanisms of *S. mariqueter* to resist or tolerate the phytotoxin had not been evolved out. By determining 9 growth indices of *S. mariqueter* seedling, we found the maximum values of 8 indices appeared in treatment V (monoculture seedling+ monoculture soil), suggesting that the invaded soil inhibited the growth of *S. mariqueter* seedlings. These data confirmed that the soil invaded by *S. alterniflora* may contain its root released compounds, which would inhibit effectively to *S. mariqueter*. Inderjit *et al*. (16) proposed soil communities could have profound effects on invasions of ecosystems by exotic plant species through three main pathways, the one of which was the effect of allelochemicals. Exotic plants produce allelochemicals toxic to native plants that could not be detoxified by local soil communities, or that became more toxic following microbial conversion. That means these compounds might affect the *S. mariqueter* directly or indirectly by changing microorganisms in soil which need further studied.

Table 3. The main components in soil through GC-MS

No.	Name	Retention time min)	Area
	S. mariqueter		
1	Cyclohexasiloxane, dodecamethyl-	9.9621	8001853
2	Cycloheptasiloxane, tetradecamethyl-	12.1879	6263000
3	Dodecanoic acid	12.5255	3201689
4	Methyl tetradecanoate	14.8257	9091300
5	Methyl 13-methyltetradecanoate	15.5238	3840737
6	Eicosane	15.747	3778502
7	Methyl hexadec-9-enoate	16.8914	5173700
8	Pentadecanoic acid	17.126	101183611
9	Dibutyl phthalate	17.6696	8341993
10	Hexadecanoic acid	18.3963	3731077
11	Octadecanoic acid	19.7295	58245196
12	Docosanoic acid	25.4057	6916577
	S. alterniflora		
13	Sulfuric acid, diethyl ester	5.5046	171201339
14	Sulfur	12.4682	4841233
15	Dodecanoic acid	12.5198	9359659
16	Hexadecane	14.5453	6872388
17	Pentadecane, 2,6,10,14-tetramethyl-	14.6083	4472584
18	Methyl tetradecanoate	14.8257	27481392
19	Methyl 13-methyltetradecanoate	15.5181	43965077
20	Pentadecanoic acid	15.9358	14796764
21	Heptadecanoic acid, 16-methyl-	16.6796	17392505
22	9-Hexadecenoic acid, methyl ester, (Z)-	16.8856	33285550
23	Methyl hexadec-9-enoate	16.9371	6756780
24	Hexadecanoic acid	17.1317	168170469
25	Methyl 15-methylhexadecanoate	17.9156	14813228
26	Methyl 14-methylhexadecanoate	18.0300	11245411
27	cis-10-Heptadecenoic acid	18.2188	13665462
28	Octadecanoic acid	19.7294	62284429
29	Methyl 9,10-methylene-octadecanoate	20.9539	8412769
30	Methyl 18-methylnonadecanoate	22.5389	25836315
31	Heneicosanoic acid	23.9694	4096219
32	Docosanoic acid	25.3999	27636330
33	Tricosanoic acid	26.8132	9834760
34	Octadecane	27.7516	6902997
35	Tetracosanoic acid	28.2037	41801754
36	Eicosane	30.4352	21672298
37	Hexacosanoic acid	30.8873	24414158
38	Methyl octacosanoate	33.4278	24817320

The seeds used in treatment III and treatment IV were both collected from the mixed community containing the invasive species, although they were sowed in two different soils, their overall seed germination was worse than that of treatment I. Among all treatments, seed germination in treatment IV was the lowest. In natural communities, allelopathy forms a selection pressure and a long period of evolution makes the receptors in the receiving organism have resistance to allelochemicals so that the impact of allelopathy is not so effective (11,26). Compared with treatment II and treatment IV, the only difference between them was that seeds used in treatment II were monoculture seeds while in treatment IV were invaded seed. But UG between treatment II 5.83% and treatment IV 13.33% was significantly different. So it could be explained that after *S. mariqueter* community was invaded, *S. mariqueter* themselves would become forming characteristics of resistance or tolerance to the allelochemicals released by *S. alterniflora*, then this resistant or tolerant characteristics might be transmitted to their offspring, thereby the sensitivity of *S. mariqueter* to the exudates of *S. alterniflora* was weakened. Inderjit *et al.* (16) proposed plant species that were introduced longest ago had the strongest negative soil feedback. The idea was consistent with the result of our study. However, our data (Table 1) indicated that the overall germination of "invaded seeds" in both soil was low, suggesting that *S. mariqueter* was still sensitive to the allelochemicals released by *S. alterniflora*. Our observations on seedling growth in different treatments also confirmed the above speculation. Ehlers *et al.* (9) studied on *Bromus erectus* adaptability to the soil where the invasive species of *Thymus vulgaris* grew and proposed that there was possibility for native plants to adapt to invasive plants and to co-occurring with them Callaway *et al.* (3) suggested that the invasion of alien species was a kind of selective pressure, some species could adapt to the invasion of alien species and then there would be a coevolution between native and alien species. The evolution of resistance of a native species would result in "biotic resistance" of the species and ultimately achieved the reconstruction of communities and the coexistence of different species; Strauss *et al.* (30) showed that the adaptive capability of native species to allelochemicals released by invasive species would reduce the impact of invasive species on native species, so as to achieve the coexistence pattern of two species. These studies provide us a theoretical basis for the idea to use enhanced natural rehabilitation technology to achieve reconstruction of communities. In natural environment, when an alien species invaded to an area, the indigenous species would definitely be seriously affected, but if suitable measures were taken to enhance the survival competition of indigenous species, the two species may achieve to a balance. Because the production of coevolution is a long co-evolutionary process and it helped *S. mariqueter* evolve the resistance to *S. alterniflora* allelopathic effects. However, to maintain the co-evolution situation of *S. mariqueter* and *S. alterniflora*, the first prerequisite was to ensure that *S. mariqueter* could survive in the survival competition with *S. alterniflor*a and then protected *S. mariqueter* in the invaded region; and on the basis, to promote the competitive symbiosis of *S. mariqueter* with *S. alterniflora.*

S. alterniflora can inhibit sexual reproduction of some plants, which is supported by the findings of Gordon *et al.* (12) and Pavlik *et al.* (24). Under certain genetic background, ecological characteristics (ecological adaptability and their offspring's ability of propagation and spread), especially propagation characteristic play a key role for rapid population establishment (13). So *S. alterniflora* was able to rapidly spread and grow in *S. mariqueter* communities and take an advantageous position in the competition with *S. mariqueter*. This might be the consequence of *S. alterniflora* inhibited sexual reproduction ability of *S. mariqueter*. For *S. mariqueter*, asexual reproduction is the main reproduction way (6,37). However, the mechanisms underlying the inhibition of *S. mariqueter* seed germination and asexual reproduction due to the impact of invasive *S. alterniflora* should be learned in future.

The allelochemicals sometimes serve as defence chemical weapons to help alien species successfully invade to new areas and many invasion species release allelochemicals (39). Putative allelochemicals such as α-pinene, β-pinene, cineole, camphene, spanthueol were identified from underground parts of *Ambrosia artemisiifolia* (36). In ragweed (*Ambrosia trifida*), potent allelochemicals are organic acids, terpenoids and polyenes such as camphor, limonene, cineole, decane and myrcene (5,35). Studies on phytotoxic extracts of *Cynodon dactylon* showed that the weed extracts contained several phenolic compounds such as ferulic, vanillic, p-hydroxybenzoic and p-coumaric acids (14).

GC-MS analysis revealed that the extracts consisted primarily of some long chain fatty acids, alkanes and esters and according to the category of allelochemicals, they were three most important allelochemicals. Heneicosanoic acid, hexadecane, octadecane, sulfuric acid, diethyl ester, tetracosanoic acid, tricosanoic acid and so on were identified in *S. alterniflora* soil, most of which were also isolated from the root exudates of *S. alterniflora* in our previous study. The results of our study were also consistent with that of Ma's, whose study was focus on the identification of volatile components in *S. alterniflora* and fatty acids in leaf of *S. alterniflora* (20,21). The soil of *S. mariqueter* also contained many kinds of compounds and the reason may because i) the root of *S. mariqueter* would also release kinds of compounds from their roots, ii) the effect of tidal may accelerate the exchange of substances in different soils. But according to our results, invaded soil inhibited the germination of seeds and the growth of seedlings while non-invaded soil enhanced them. It might be speculated that compounds isolated only in the soil of *S. alterniflora* had allelopathic effect on *S. mariqueter* and the bioassay of these compounds would be conducted in our future study.

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