

Does a Widespread Species Have a Higher Competition Ability Than an Endemic Species? A Case Study in the Dongting Lake Wetlands

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Abstract

This study aimed to compare the competition abilities of *Phragmites australis* (*PA*), a widespread species, and *Triarrhena lutarioriparia* (*TL*), an endemic species, in the Dongting Lake wetlands. Field monitoring indicated that during flooding, the two plant species showed decreased survival percentage, which did not differ noticeably between them. Control experiment indicated that *PA* exhibited higher survival percentage than *TL*. In the field monitoring, *PA* showed higher aboveground biomass before flooding and higher relative elongation rate, whereas *TL* showed higher aboveground biomass after flooding and higher relative growth rate. However, in the control experiment, plant biomass, relative growth rate, and relative elongation rate were not obviously different between the two species, and *PA* showed higher competition ability than *TL* in the early stage and lower competition ability than those of *TL* in the middle and later stages. The relative yield total in both the field monitoring and control experiment were greater than one, indicating that the two plant species occupied different niches. Compared to *TL*, *PA* had higher competition ability in non-submergence habitat and lower competition ability in water submergence habitat. Niche difference between the two species enabled their coexistence in the Dongting Lake wetlands under the influence of seasonal flooding.

1. Introduction

The distribution of a plant can reflect its adaptation to different environmental conditions. Some plant species are widely distributed and are called widespread species. For example, *Stemona tuberosa*, a traditional medicinal plant, is distributed across more than ten countries in Asia¹, and *Menziesia pentandra*, a shrub plant, is distributed across Japan, Sakhalin, and Southern Kuril Islands². However, some plant species have narrow distributions and are called endemic species^{3,4}. For instance, *Cinnamomum kanehirae* is endemic to Taiwan at an elevation range of 200–2,000 m³, and *Pilea carautae* is endemic to Cabo Frio region in the State of Rio de Janeiro, Southern Brazil⁵. Therefore, widespread plant species appear to have wider adaptations to different environments than endemic plant species.

Plant competition has long been considered to be a major driver of plant adaptation to the environment as it reflects their ability to obtain resources (i.e., light, water, and nutrients) and their tolerance to resource stress⁶. For example, under the conditions of water and nitrogen deficiency, the higher competition ability of the invasive plant *Xanthium italicum* compared to that of the native plant *X. sibiricum* was main reason for the replacement of the latter by the former⁷. Plant competition includes intra- and interspecific competition, and is determined by competition intensity, effects, and outcomes^{8,9}. Some researchers have used competitive effects to analyze and predict changes in plant population and community structure^{10,11}. With an increase in nitrogen levels, *Suaeda salsa* was found to have higher competition ability than a congeneric species *Suaeda glauca*, and the former gradually dominated their mixed communities¹². However, few studies have compared the competition ability of widespread and endemic species^{2,13}.

Phragmites australis is a widespread species that widely distributed in North America^{14,15}, Europe^{16,17}, and Asia^{18,19}. *Triarrhena lutarioriparia* is an endemic species that is only distributed in the middle and lower reaches of the Yangtze River, China^{20,21}. These plant species have similar morphological, growth, and propagation characteristics and are distributed at the same latitude on beaches of the Dongting Lake, the largest freshwater lake in China^{22,23}. In recent years, we found that the area occupied by *P. australis* in the lake gradually expanded. With the aim of investigating the reasons for this change, we conducted an experiment to compare the intensity, effect, and outcomes of competition between the two species. We wanted to answer the question: Do widespread plant species have a higher competition ability than endemic plant species?

2. Results

2.1 Survival percentage

In the field monitoring experiment, number of living individuals of both plant species decreased after flood retreat (Table 1). There was an obvious difference in the survival percentage between the two plant species, except in the boxes with the planting ratio of 14:1. With the increase in individual number, the survival percentage of *P. australis* increased, whereas that of *T. lutarioriparia* did not obviously change.

Table 1

Individual numbers of *Triarrhena lutarioriparia* (*TL*) and *Phragmites australis* (*PA*) in 1 m² areas before and after flooding (BF and AF, respectively) in the five fixed communities in East Dongting Lake wetlands.

Time	9:0		14:1		10:5		7:6		0:11	
	<i>TL</i>	<i>PA</i>								
BF	9	1	14		10	5	7	6		11
AF	8	0	6		5	3	5	4		9

Note: The ratios 9:0, 14:1, 10:5, 7:6, and 0:11 are the ratios of individual numbers of *TL* to *PA* in a square meter.

In the control experiment, both species had decreased survival percentage during the experiment, except for *P. australis* in boxes with the planting patterns of 3:1, 1:3, and 0:4 (Table 2). At the same harvest time, *T. lutarioriparia* showed a lower survival percentage than *P. australis*, except in boxes with the planting pattern of 1:3 on the 60th day.

Table 2
Survival percentages (%) of *Triarrhena lutarioriparia* (TL) and *Phragmites australis* (PA) on the 60th, 120th, and 180th days of plant transplantation.

Day	4:0		3:1		2:2		1:3		0:4	
	TL	PA	TL	PA	TL	PA	TL	PA	PA	
60	90.6	95.8	100.0		93.8	100.0	100.0	95.8	100.0	
120	87.5	79.2	100.0		68.8	93.8	50.0	95.8	100.0	
180	75.0	58.3	100.0		68.8	87.5	37.5	95.8	100.0	

Note: The ratios 4:0, 3:1, 2:2, 1:3, and 0:4 are the planting patterns described in Fig. 1.

2.2 Plant biomass, relative growth rate, and relative elongation rate

In the field monitoring experiment, *T. lutarioriparia* showed relatively higher aboveground biomass than *P. australis* before flooding and lower aboveground biomass than *P. australis* after flood retreat (Fig. 2). During the flooding period, *T. lutarioriparia* had a higher relative growth rate and lower relative elongation rate than *P. australis*.

In the control experiment, *T. lutarioriparia* showed relatively higher biomass than *P. australis* in the early growth stage, whereas no obvious difference in the biomass between these two species was observed in the later growth stage (Fig. 3). In addition, plant biomass showed different change trends with the changes in planting patterns. On the 60th day, there was no significant difference in plant biomass between the two species in any of the four patterns. On the 120th day, the biomass of *T. lutarioriparia* was higher in boxes with the 1:3 planting pattern than in boxes with the other three patterns, and that of *P. australis* was higher in boxes with the 3:1 planting pattern than in boxes with the 2:2 planting pattern. On the 180th day, the biomass of *T. lutarioriparia* was higher in boxes with the 2:2 planting pattern than in boxes with the 4:0 and 3:1 planting pattern, whereas the biomass of *P. australis* did not show significant differences among the four planting patterns.

In the control experiment, the relative growth and elongation rates were lower in *T. lutarioriparia* than in *P. australis* in the period of 60–120 days, whereas they were not significantly different between the two plant species in the periods of 0–60 and 120–180 days. In the period of 0–60 days, there were no significant differences in the relative growth and elongation rates between the two species in any of the four patterns. In the period of 60–120 days, the relative growth rate of *T. lutarioriparia* was lower in boxes with the 3:1 planting pattern and higher in boxes with the 1:3 planting pattern, and that of *P. australis* was not significantly different in boxes with any of the four patterns. Furthermore, the relative elongation rate of either species did not differ among the four patterns. In the period of 120–180 days, the relative growth and elongation rates of *T. lutarioriparia* were lower in boxes with the 1:3 planting pattern than in boxes

with the other patterns, and those of *P. australis* were lower in boxes with the 3:1 planting pattern than in boxes with the other patterns.

2.3 Relative competition intensity and relative yield

In the field monitoring experiment, the relative competition intensity of the two plant species was different between two time points (before and after flooding) and three mixed communities (Table 3). In *T. lutarioriparia*, flooding increased the relative competition intensity in boxes with the 14:1 and 10:5 patterns and decreased in boxes with the 7:6 pattern. In *P. australis*, flooding increased the relative competition intensity in boxes with the 14:1 and 7:6 patterns and decreased in boxes with the 10:5 pattern. The relative competition intensity of *T. lutarioriparia* was higher than that of *P. australis*. The relative yield of the two plant species also differed between two time points (before and after flooding) and three mixed communities. The relative yield of *T. lutarioriparia* (≤ 1) was lower than that of *P. australis* (≥ 1). Generally, the relative yield total in the three mixed communities and at the two time points was greater than one, indicating that the plants had different niches in the different communities.

Table 3

Relative competition intensity (RCI), relative yield (RY), and relative yield total (RYT) of *Triarrhena lutarioriparia* (TL) and *Phragmites australis* (PA) before and after flooding (BF and AF, respectively).

Time	Communities	RCI		RY		RYT
		TL	PA	TL	PA	
BF	14:1	0.02	-0.53	0.98	1.53	1.26
	10:5	-0.03	-0.13	1.03	1.13	1.08
	7:6	0.31	-0.34	0.70	1.34	1.02
AF	14:1	0.53	0.01	0.47	0.99	0.73
	10:5	0.06	-1.45	0.94	2.46	1.70
	7:6	0.30	-1.78	0.70	2.78	1.74

Note: The ratios 14:1, 10:5, and 7:6 are the individual numbers of TL to PA in a square meter.

In the control experiment, the relative competition intensity of *T. lutarioriparia* decreased in boxes with the 3:1 and 2:2 planting patterns and increased in boxes with the 1:3 planting pattern over time (Table 3). However, the relative competition intensity of *P. australis* decreased in boxes with the 3:1 and 1:3 planting patterns and increased in boxes with the 2:2 planting pattern. In general, *T. lutarioriparia* had lower relative competition intensity than *P. australis* in boxes with the 1:3 planting pattern on the 60th day and in boxes with the 2:2 planting pattern on the 120th day, and higher relative competition intensity than *P. australis* did in boxes with the other patterns. The relative yield of *T. lutarioriparia* increased in boxes with the 3:1, 2:2, and 1:3 planting patterns over time (Table 4). However, the relative yield of *P. australis* decreased in boxes with the 2:2 planting pattern and increased in boxes with the 3:1 and 1:3 planting

patterns over time. In general, *T. lutarioriparia* showed lower relative yield than *P. australis* in boxes with the 1:3 and 2:2 planting patterns on the 60th day and in boxes with the 1:3 planting pattern on the 120th day, and higher relative yield than *P. australis* did in boxes with the other patterns. Relative yield total of both plants in all three patterns and three harvest times was greater than one, indicating that the plants had different niches in different planting patterns.

Table 4

Relative competition intensity (*RCI*), relative yield (*RY*), and relative yield total (*RYT*) of *Triarrhenes lutarioriparia* (*TL*) and *Phragmites australis* (*PA*) on the 60th, 120th, and 180th days of plant transplantation. The ratios 4:0, 3:1, 2:2, 1:3, and 0:4 are the planting patterns described in Fig. 1.

Days	Patterns	<i>RCI</i>		<i>RY</i>		<i>RYT</i>
		<i>TL</i>	<i>PA</i>	<i>TL</i>	<i>PA</i>	
60	3:1	0.14	-0.31 *	0.86 e	1.31 a	1.09
	2:2	0.07	-0.08 *	0.93 e	1.08 a	1.01
	1:3	-0.37 *	0.22	1.37 a	0.78 e	1.08
120	3:1	0.21	-0.92 *	0.79 e	1.92 a	1.36
	2:2	-0.42 *	0.14	1.42 a	0.86 e	1.14
	1:3	-1.80 *	0.05	2.80 a	0.95 e	1.88
180	3:1	-0.25 *	-0.07	1.25 a	1.07 a	1.16
	2:2	-0.87 *	0.14	1.87 a	0.86 e	1.37
	1:3	-0.40 *	-0.08	1.40 a	1.08 a	1.24

Note: * indicates that the competition ability was strong; a indicates that intraspecific competition was higher than interspecific competition; e indicates that intraspecific competition was lower than interspecific competition.

2.4 Relative efficiency index and expected relative efficiency index

In the field monitoring experiment, relative efficiency index was lower than expected relative efficiency index, indicating that *P. australis* would be the dominant species over time (Table 5). In the period of 0–60 days, the relative efficiency index was lower than expected in boxes with the 3:1 and 2:2 patterns and higher than expected in boxes with the 1:3 pattern; indicating that in this period, *P. australis* would be the dominant species in boxes with the former patterns and *T. lutarioriparia* would be the dominant species in boxes with the latter pattern (Table 6). In the same way, in the period of 60–120 days, *P. australis* would be the dominant species in boxes with the 3:1 pattern, and *T. lutarioriparia* would be the dominant species in boxes with the 2:2 and 1:3 patterns. In the period of 120–180 days, *T. lutarioriparia* would be the

dominant species in boxes with the 3:1 and 2:2 patterns, and *P. australis* would be the dominant species in boxes with the 1:3 pattern. During the whole experimental period (0–180 days), *T. lutarioriparia* would be the dominant species in boxes with mixed patterns.

Table 5

Relative efficiency index (REI) and expected relative efficiency index (REI_{exp}) during flooding.

REI	REI_{exp}
14:1 0.89 P	10:5 0.31 P
7:6 0.47 P	Single communities 1.19

Note: The ratios 14:1, 10:5, and 7:6 are the individual numbers of *TL* to *PA* in a square meter; P indicates that *Phragmites australis* would be the dominant species.

Table 6

Relative efficiency index (REI) and expected relative efficiency index (REI_{exp}) in the periods of 0–60, 60–120, 120–180, and 0–180 days.

Days	REI			REI_{exp} Single planting
	3:1	2:2	1:3	
0–60	-0.03 P	0.25 P	0.96 T	0.39
60–120	-1.08 P	0.04 T	-0.10 T	-0.61
120–180	0.78 T	0.01 T	-1.09 P	-0.28
0–180	-0.33 T	0.29 T	-0.23 T	-0.49

Note: The ratios 3:1, 2:2, and 1:3 are the planting patterns described in Fig. 1; T indicates that *Triarrhena lutarioriparia* would be the dominant species; P indicates that means *Phragmites australis* would be the dominant species.

3. Discussion

Plant survival is one of the most direct reflections of plant adaptation, especially under environmental stress. In our field monitoring experiment, both investigated plant species showed decreased survival percentage during flooding, and this decreased survival percentage was not obviously different between the species. However, in the control experiment, the survival percentage of *T. lutarioriparia* decreased greatly and that of *P. australis* did not vary obviously over time, indicating that *P. australis* exhibited higher survival percentage than *T. lutarioriparia*. The possible reason for this is that *P. australis*, which is a widespread species, has higher ability of adaptation to environmental changes than *T. lutarioriparia*, an endemic species, does¹⁵.

Plant growth also can reflect plant adaptation to environmental stress. In our field monitoring experiment, *P. australis* had higher aboveground biomass before flooding and higher relative elongation rate, whereas *T. lutarioriparia* had higher aboveground biomass after flooding and higher relative growth rate. However, in the control experiment, plant biomass, relative growth rate, and relative elongation rate were not obviously different between the two species. These different results in plant growth between the field monitoring experiment and the control experiment may be because of flooding. In the field experiment, five-month flooding caused different response patterns in the plants: the well-developed stem porosity in *T. lutarioriparia* led to increased oxygen transmission from the aboveground parts to the belowground parts and resulted in increased growth, whereas the relatively lower stem porosity in *P. australis* forced rapid vertical stem elongation so that stems are able to reach the water surface and access oxygen from the air^{24,25}. In the control experiment, the two plants showed similar growth characteristics because of the absence of flooding stress.

Plant competition can be determined by competition intensity and is associated with community characteristics, such as biomass, density, and proportion²⁶. Similar to the growth performance, the competition performance of the two species also differed between the field monitoring experiment and the control experiment. In the control experiment, *P. australis* showed a higher competition ability than *T. lutarioriparia* in the early growth stage and lower competition ability than *T. lutarioriparia* in the middle and later growth stages. However, in the field monitoring experiment, *P. australis* showed higher competition ability than *T. lutarioriparia* both before and after flooding. These differences may be related to flooding stress; in the field monitoring experiment, five-month flooding reduced the competition ability of *T. lutarioriparia* and improved the competition ability of *P. australis*.

Plant competition ability includes the ability of intraspecific and interspecific competition^{8,9}. In the field monitoring experiment, intraspecific competition was higher in *P. australis*, and interspecific competition was higher in *T. lutarioriparia*. However, over time, the competition changed from intraspecific to interspecific in *P. australis* and from intraspecific to interspecific in *T. lutarioriparia*. Competition often leads to species occupying different ecological niches²⁷. Relative yield total in both the field monitoring and the control experiment were greater than one, indicating that the two plant species had different niches. We found that *P. australis* would become the dominant species in the field monitoring experiment, and *T. lutarioriparia* would become the dominant species in the control experiment.

Altogether, the present study showed that the competition ability of plant species varied depending on environmental conditions. In the non-submergence habitat, the competition ability of *P. australis* was higher than that of *T. lutarioriparia*, whereas the opposite was true in the water submergence habitat. In the Dongting Lake wetlands, the five-month flooding period led to *P. australis* becoming the dominant species, and the seven-month non-flooding period led to *T. lutarioriparia* becoming the dominant species. Therefore, niche differences between the two species enable their coexistence in the Dongting Lake wetlands under the influence of seasonal flooding.

4. Methods

4.1 Study site

The Yangtze River is connected to Dongting Lake through three inlets (Songzikou, Taipingkou, Ouchikou) and one outlet (Chenglingji). Dongting Lake covers an area of 2625 km² (28°38'–29°45' N, 111°40'–113°10' E) and is divided into East, South, and West Dongting Lake. The lake is characterized by a subtropical monsoon climate, with an average annual temperature of 16.2–17.8°C and 259–277 frost-free days. The mean annual precipitation ranges from 1,200 to 1,415 mm, with the rainy season lasting from May to September. The average humidity is 80%, and the average evaporation is 1,270 mm. The annual mean wind speed is 2.0–3.0 m s⁻¹ and the elevation is 28–35 m above sea level.

4.2 Field monitoring

4.2.1 Fixed plot selection

In May 2018, five fixed plots consisting of three mixed and two single communities were selected in the beach of the Dongting Lake wetlands. The plots are submerged due to flooding from May to September and exposed from October to April of the next year. The fixed plot area was 25 m² (5×5 m), and the basic characteristics of the plots are provided in Table 1.

4.2.2 Fixed plot monitoring

In the fixed plots, the height and number of living individuals was recorded before flooding and after flood retreat. Simultaneously, six individuals were selected from each of the five plots, and their aboveground parts (leaves and stems) were collected and taken to the laboratory where they were dried until they reached a constant weight.

4.3 Control experiment

4.3.1 Seed collection and germination

In December 2017, seeds of *T. lutarioparia* and *P. australis* were collected from the bottomland (29°15'15"N, 112°49'20"E) of the East Dongting Lake wetlands and brought back to the laboratory at Hunan Agricultural University. The weight of thousand seeds was 0.350 ± 0.018 g (mean ± standard error) for *T. lutarioparia* and 0.280 ± 0.004 g for *P. australis*. Seed length was 2.33 ± 0.034 mm for *T. lutarioparia* and 2.030 ± 0.037 mm for *P. australis*, and seed width was 0.540 ± 0.014 mm for *T. lutarioparia* and 0.570 ± 0.013 mm for *P. australis*. In March 2018, the seeds were sown in the field and germinated.

4.3.2 Seedling transplantation

In April 2018, seedlings with aboveground height of 6–8 cm were transplanted into basins (12 cm length, 12 cm width, and 15 cm height) containing 14 cm of soil (21 g kg^{-1} organic matter, 141 mg kg^{-1}

exchangeable N, and 11.4 mg kg^{-1} exchangeable P). Four seedlings were planted in each basin, and five planting patterns ($TL:PA = 4:0$, $TL:PA = 3:1$, $TL:PA = 2:2$, $TL:PA = 1:3$, and $TL:PA = 0:4$) were used (Fig. 1). For example, the pattern of 3:1 indicated that there were three TL seedlings and one PA seedling in the basin. There were 24 basins for each pattern, with a total of 120 basins. Subsequently, 15 basins were placed into a bucket (68 cm length, 47 cm width, and 41 cm height) in the outdoors, and a total of eight buckets were used for the experiment (Fig. 1). Meanwhile, 12 plants of each species were collected initially and their dry weights were measured. Following seedling transplantation, water was added into the buckets until it reached the soil surface in the basin. This was the only time that water was added artificially into the bucket in order to simulate the natural environment.

4.3.3 Seedling harvest

After transplanting into basins, the plants were grown for 60 days, 120 days, and 180 days and harvested. For a specific planting pattern, eight basins were selected for harvesting. The plants were dug out of the soil and separated to maintain their integrity. The number of living plants, buds, and tillers for each species in a planting pattern were recorded. Dry biomass of their leaves, stems, roots, and buds was determined after drying at 80°C until reaching constant weight.

4.4 Data calculation and analysis

4.4.1 Plant growth parameters

Survival percentage was calculated as the number of living plants divided by the initial number of plants.

Relative growth rate (RGR) was calculated using the following Eq. 2⁸:

$$RGR = \frac{\ln Y_2 - \ln Y_1}{t_2 - t_1} \quad (1)$$

where Y_1 is biomass at harvest time t_1 , and Y_2 is biomass at harvest time t_2 .

Relative elongation rate (RER) was calculated using the following Eq. 2⁸:

$$RER = \frac{\ln h_2 - \ln h_1}{t_2 - t_1} \quad (2)$$

where h_1 is plant height at harvest time t_1 , and h_2 is plant height at harvest time t_2 .

4.4.2 Plant competition parameters

Relative competition intensity (RCI) can reflect plant competition ability in three mixed communities (14:1, 10:5, and 7:6) in field monitoring and three mixed planting patterns (3:1, 2:2, and 1:3) in control experiment and was calculated using the following equations²⁹:

$$RCI_i = (Y_i - Y_{ij})/Y_i \quad (3)$$

$$RCI_j = (Y_j - Y_{ji})/Y_j \quad (4)$$

where Y_i and Y_j are biomasses of species i and species j in two single communities (9:0 and 0:11) in field monitoring and two single planting patterns (4:0 and 0:4) in control experiment, respectively; Y_{ij} and Y_{ji} are biomasses of species i and species j in mixed communities or planting patterns, respectively. $RCI_i > RCI_j$ indicates that species j has a higher competition ability than species i ; $RCI_i = RCI_j$ indicates that species j and i have the same competition ability; and $RCI_i < RCI_j$ indicates that species i has a higher competition ability than species j . The known trend is that the lower the relative competition intensity (RCI), the greater the competition ability.

Relative yield (RY) and relative yield total (RYT) can reflect plant interspecific or intraspecific competition, and they were calculated using the following equations^{28,30}:

$$RY_i = Y_{ij}/Y_i \quad (5)$$

$$RY_j = Y_{ji}/Y_j \quad (6)$$

$$RYT = (RY_i + RY_j)/2 \quad (7)$$

where $RY < 1$ indicates that plants have higher interspecific competition than intraspecific competition; $RY = 1$ indicates that plants have the same interspecific and intraspecific competition; and $RY > 1$ indicates that plants have lower interspecific competition than intraspecific competition. $RYT < 1$ indicates that plants inhabit the same niches; $RYT = 1$ indicates that plants have partially the same niches; $RYT > 1$ indicates that plants have different niches.

Relative efficiency index (REI) and expected relative efficiency index (REI_{exp}) are used to predict the dynamic changes in plant species in mixed communities or patterns, and were calculated using the following equations (Shipley, 1993; Grace, 1995):

$$REI = (\ln Y_{ij2} - \ln Y_{ij1}) - (\ln Y_{ji2} - \ln Y_{ji1}) \quad (8)$$

$$REI_{exp} = (\ln Y_{i2} - \ln Y_{i1}) - (\ln Y_{j2} - \ln Y_{j1}) \quad (9)$$

where Y_{ij1} and Y_{ij2} is the biomass of species i in mixed communities or planting patterns at harvest times t_1 and t_2 , respectively; Y_{ji1} and Y_{ji2} is the biomass of species j in mixed communities or planting patterns at harvest times t_1 and t_2 , respectively. Y_{i1} and Y_{i2} is the biomass of species i in single communities or planting patterns at harvest times t_1 and t_2 , respectively; Y_{j1} and Y_{j2} is the biomass of species j in single communities or planting patterns at harvest times t_1 and t_2 , respectively. $REI < REI_{exp}$ indicates that in

mixed communities or planting patterns, species j will show increasing dominance over time; $REI = REI_{exp}$ indicates that in mixed communities or planting patterns, species j will show stable dominance over time; and $REI > REI_{exp}$ indicates that in mixed communities or planting patterns, species j will show decreasing dominance over time.

Multiple comparisons at the significance level of 0.05 were used to analyze the difference in biomass, relative growth rate, relative elongation rate, tiller number, and bud number among different species and planting patterns. For these analyses, the IBM SPSS Statistics Version 22.0 software was used.

Declarations

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Author contributions

Y L designed the study. Y D, Q Z, and Z P performed the field monitoring. Q Z and L X conducted the control experiment. All authors wrote the manuscript.

Competing financial interests: The authors declare no competing financial interests.

All authors declare that experimental research and field studies on plants (either cultivated or wild), including the collection of plant material complied with relevant institutional, national, and international guidelines and legislation.

All authors indicate that the datasets used and/or analyzed during the current study available from the corresponding author on reasonable request.

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Figures

Figure 1

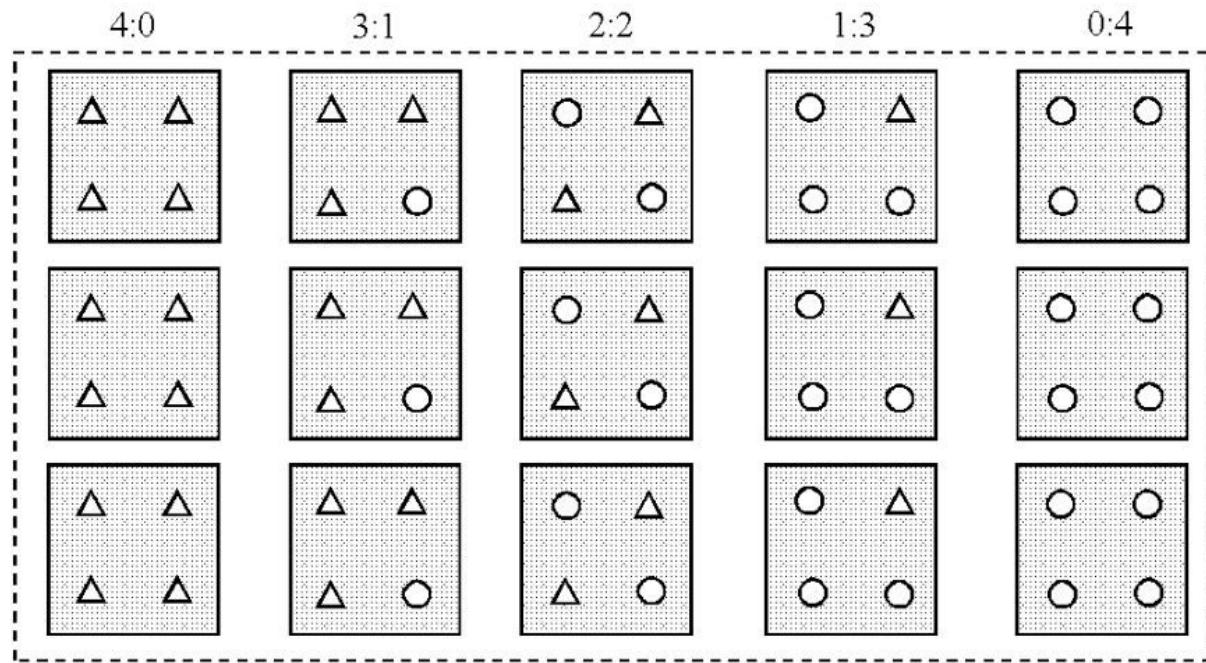


Figure 1

Planting patterns of the two species in each bucket in the control experiment (◻ : bucket, □: basin, Δ: *Triarrhena lutarioriparia*, ●: *Phragmites australis*).

Figure 2

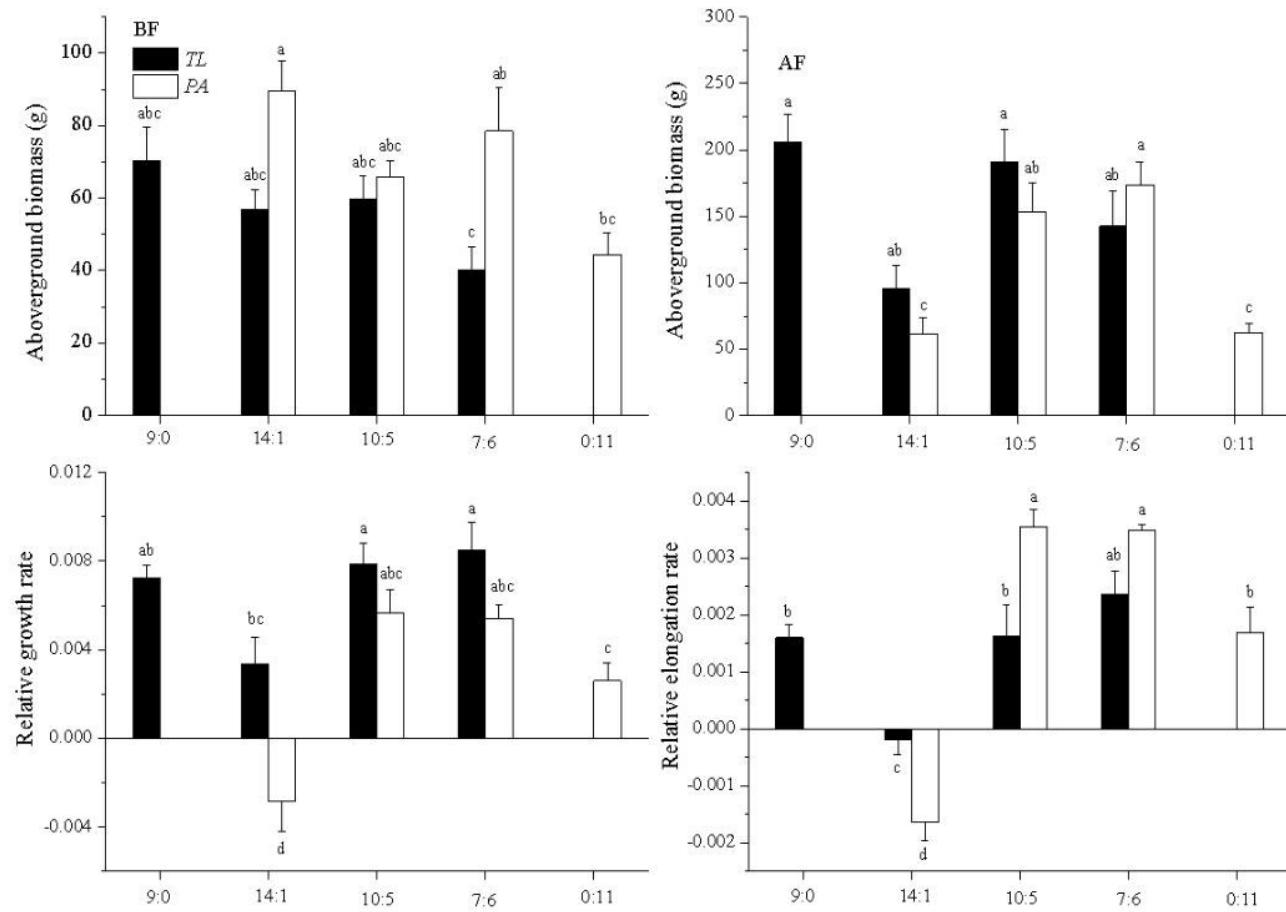


Figure 2

Aboveground biomass of *Triarrhena lutarioparia* (TL) and *Phragmites australis* (PA) before and after flooding (BF and AF, respectively), and their relative growth and elongation rates during the flooding period. The ratios 9:0, 14:1, 10:5, 7:6, and 0:11 are the ratios of individual number of TL to PA in a square meter. Different lowercase letters indicate significant differences among planting patterns at the 0.05 significance level.

Figure 3

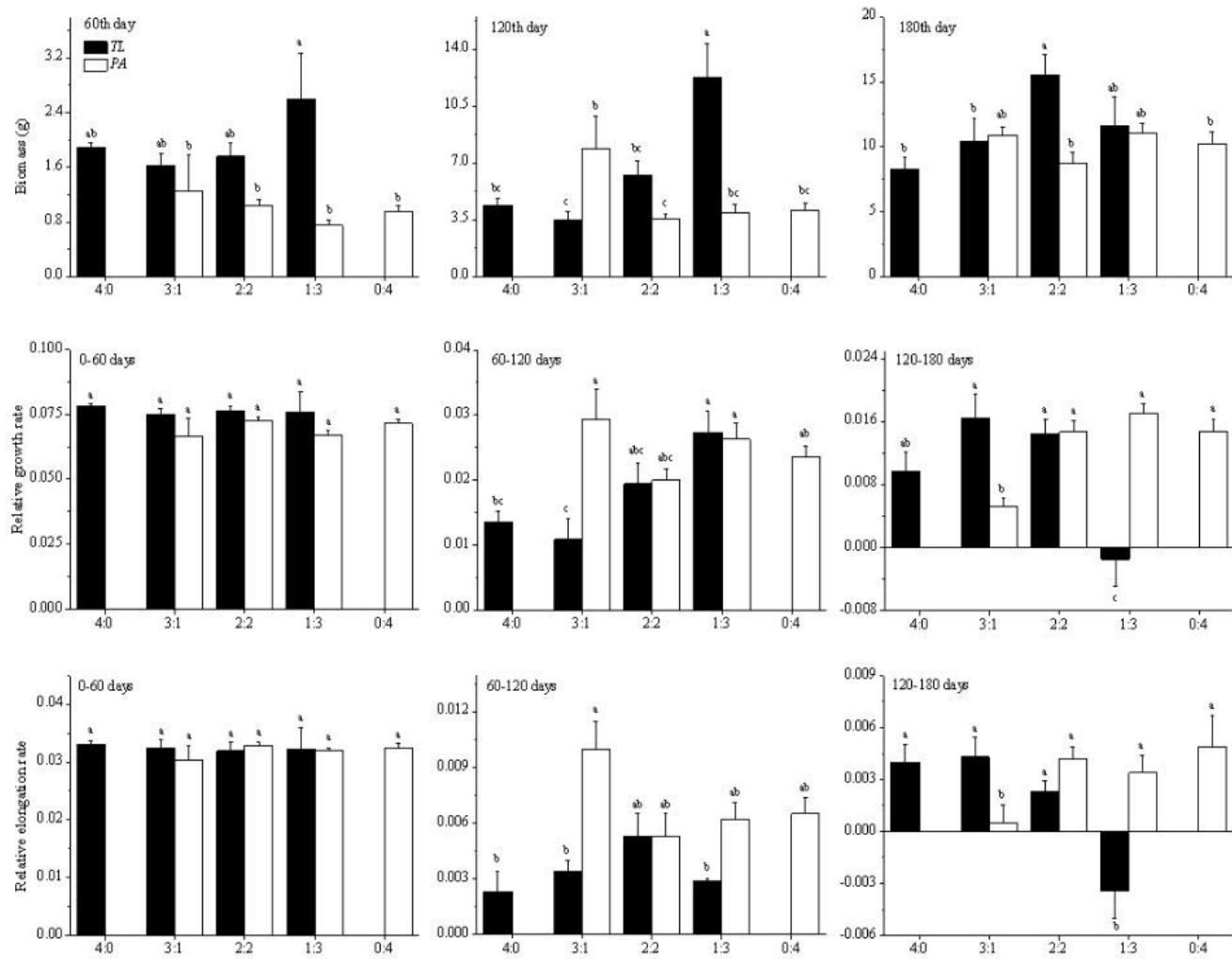


Figure 3

Biomass of *Triarrhena lutarioriparia* (TL) and *Phragmites australis* (PA) on the 60th, 120th, and 180th days of plant transplantation, and their relative growth and elongation rates in the periods of 0–60, 60–120, and 120–180 days. The ratios 4:0, 3:1, 2:2, 1:3, and 0:4 are the planting patterns described in Figure 1. Different lowercase letters indicate significant differences among planting patterns at the 0.05 significance level.