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Effects of physical space and nutrients on the growth and intraspecific competition of a floating fern

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Abstract Physical space, defined by its volume and shape, is considered a resource for plant growth, as a plant can be limited by physical space even when other resources (e.g., light, water and nutrients) are unlimited. However, the effect of physical space limitation on intraspecific competition of plants, especially floating plants, is not well understood. Here we tested the hypothesis that physical space affects the growth and intraspecific competition of floating plants, which is further influenced by the volume and surface area of the containers in which these plants are grown. We grew either one or four clonal fragments of a floating clonal fern, *Azolla imbricata*, in cylindrical containers differing in diameter and height (and thus surface area and volume) and filled with solutions containing the same or different nutrient concentrations. Biomass and number of clonal fragments of *A. imbricata* were higher in the container with the larger diameter and thus water surface area, but were not significantly affected by the height/volume of the container. Biomass and number of clonal fragments were reduced by intraspecific competition and tended to increase first and then decreased with increasing nutrient concentration. Increasing nutrient concentration inhibited the growth and then reduced intraspecific competition of *A. imbricata*, but the diameter or height/volume of the container had no effect. Our findings suggest that nutrient levels can alter intraspecific competition of plants, but physical space may not.

Keywords Aquatic plant · *Azolla imbricate* · Clonal plant · Container type · Density effect

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Introduction

Most plants are sessile and complete their life history in one place (Grams and Lüttge 2010; van Loon 2015; Velazquez-Castro and Eichhorn 2017). Some plants, such as floating plants, move from one place to another with the assistance of, e.g., wind and currents (Ngari et al. 2010; Mccann 2016), but their movement is restricted by the size of their habitat (e.g., water surface area). Under limited physical space, the growth of these plants may be restricted by intraspecific competition (Wang et al. 2015). Although many environmental factors can affect intraspecific competition of plants, the role of physical space remains unclear.

Physical space is considered a resource for plants, as plant growth can be limited by physical space even if other resources (e.g., light, water and nutrients) are unlimited (Mcconnaughay and Bazzaz 1991; Nesmith and Duval 1998; Schenk et al. 1999; Poorter et al. 2012). A previous study showed that plants of *Eucalyptus citriodora* grew taller and produced more reproductive tissues, thicker stems and larger canopies when grown in larger space than in smaller space, despite the equal nutrient treatment (Yiftach et al. 2009). Similarly, biomass, number of leaves and leaf area of *Syzygium samarangense* demonstrated a linear increase with increasing volume of containers (Hsu et al. 1996). Moreover, larger space delayed the senescence and shedding of leaves of *Brassica oleracea* (Yang et al. 2000) and increased photosynthetic rate, soluble sugar content and protein content in leaves of *Paeonia suffruticosa* compared to smaller space (Li 2014). However, it remains unclear how physical space affects intraspecific competition of plants, especially floating plants. The surface area of the water in a habitat (or a container) is likely to affect individual crowding of floating plants and thus may greatly affect their intraspecific competition.

Physical space is a complex factor determined by its volume and shape, which are further influenced by its length, width, height and/or diameter (Latimer 1991). When the volume is kept uniform, the shape of the container may affect the surface area of the water in the container, which may then affect crowding and intraspecific competition of floating plants. If the surface area of the water in cylindrical containers is kept uniform, the differences in the height and thus the volume of the containers may have little effect on intraspecific competition of floating plants as it may not affect crowding. In addition, when the surface area of water in the containers is uniform but the volume of the containers differs, the concentrations and the total amount of nutrients in the water in the containers cannot be kept the same simultaneously. Also, different volumes of water are likely associated with different oxygen contents in water, which may also have an effect on the growth and intraspecific competition of floating plants.

We grew one or four clonal fragments of a floating clonal fern, *Azolla imbricata,* in cylindrical containers differing in volume, diameter and/or height, and filled with solutions with the same or different concentrations (or total amounts) of nutrients. We aimed at testing the hypothesis that physical space affects the growth and thus intraspecific competition of floating plants, which is further influenced by the size and shape of the containers. We also tested the roles of nutrient levels in the intraspecific competition of floating plants.

Materials and methods

Plant species and material collection

Azolla imbricata (Roxb.) Nakai (Azollaceae) is a free-floating small aquatic fern (Peters and Meeks 1989) widely distributed in China (Lu and Lu 2018). This species can reproduce clonally by forming prostrate stems on which new ramets and stems can be formed. The stems are slender and brittle and thus easy to break to form clonal fragments of different sizes (Liu and Zheng 1989). Under suitable conditions, number of ramets in a population of *A. imbricata* can double within 3–5 days (Reddy 1985). This species has a high ability to tolerate heavy metal contamination (Zhang et al. 2017) and can grow well in water with extremely low nitrogen due to its association with nitrogen-fixing blue alga (Vermaat and Hanif 1998; Forni et al. 2001).

Plants of *A. imbricata* were collected from a small river in Jiaojiang district, Taizhou, Zhejiang Province, China. They were cultivated for several weeks in a greenhouse (28°39′N, 121°23′E) at Taizhou University in Taizhou, Zhejiang Province, China, before the commencement of the experiment.

Experimental design

To test the effects of physical space, we used three types of containers coded as S (8 cm in diameter × 12 cm in height), W (16 cm in diameter × 12 cm in height) and T (8 cm in diameter × 42 cm in height). The level of nutrient solution for cultivation in each container was maintained 2 cm below the upper edge of the container. Thus, W and T contained the same volume of nutrient solution, which was fourfold that of S. To investigate the effects of intraspecific interactions, in each container, either one or four fragments of *A. imbricata* were grown. To examine effects of nutrient levels, each container was filled with either 1% or 10% of full-strength Hoagland solution (Hoagland and Arnon 1950). These three factors were crossed, making 12 treatment combinations (3 container types × 2 density levels × 2 nutrient levels). In addition, we set up four treatments in which S was filled with 4% or 40% Hoagland solution and either one or four fragments of *A. imbricata* were grown so that the total nutrient level in S was the same as that in the corresponding treatments in W and T. The nutrient levels (1, 4, 10 and 40% Hoagland solution) used are commonly found in lakes with different levels of eutrophication (Reddy 1985; Forni et al. 2001; Zhang et al. 2019), and the initial density of the *A. imbricata* fragments (1 and 4 fragments) is commonly observed in the field (Si personal observation). There were eight replicates for each of the 16 treatments (Table 1), making a total of 128 containers.

The experiment was conducted in the same greenhouse for material cultivation. It started on June 29, 2017, and ended on August 4, 2017, lasting 37 days. During the experiment, mean air temperature in the greenhouse was 24.6 °C, and mean air humidity was 77.3%. The pH of the nutrient solutions was adjusted to 6–7, and distilled water was added to compensate for the loss due to evapotranspiration and absorption. The nutrient solutions were replaced every 10 days.

Measurements and data analysis

At harvest, we counted number of fragments of *A. imbricata* in each container. The plants were then dried at 70 °C for 72 h and weighed. Data on biomass and number of fragments were standardized by dividing by one for the treatments with one initial fragment and by four for the treatments with four initial fragments. These data were used in the following analyses.

We used three-way ANOVA to test the effects of container type (S, W and T), nutrient level (1 and 10% Hoagland solution only), initial density (one and four fragments) and their interactions on biomass and number of fragments of *A. imbricata*. We then used Duncan test to compare the means among the three container types within each of the two nutrient levels under each of the two density treatments. For the plants of *A. imbricata* in the containers of the type S, we further employed two-way ANOVA to examine the effects of nutrient level (1, 4, 10 and 40% Hoagland solution), initial density (one and four fragments) and their interaction on biomass and number of fragments. Duncan test was also used to compare the means among the four nutrient levels within each of the two density treatments.

To measure the intraspecific competitive intensity, we calculated the log response ratio (LnRR) as

Table 1 Treatment setup in the experiment

Container type	Container size (Diameter × height)	Nutrient level (% Hoagland solution)	Density (No. of initial fragments)
S	8 cm × 12 cm	1	1
S	8 cm × 12 cm	1	4
W	16 cm × 12 cm	1	1
W	16 cm × 12 cm	1	4
T	8 cm × 42 cm	1	1
T	8 cm × 42 cm	1	4
S	8 cm × 12 cm	10	1
S	8 cm × 12 cm	10	4
W	16 cm × 12 cm	10	1
W	16 cm × 12 cm	10	4
T	8 cm × 42 cm	10	1
T	8 cm × 42 cm	10	4
S	8 cm × 12 cm	4	1
S	8 cm × 12 cm	4	4
S	8 cm × 12 cm	40	1
S	8 cm × 12 cm	40	4

LnRR = ln (B_i/B_o), where B_o is mean biomass in the treatment with one initial fragment across the eight replicates and B_i is biomass in the treatment with four initial fragments in replicate *i*. Values of LnRR are symmetrical around zero (Hedges et al. 1999; Armas et al. 2004). Positive values indicate facilitation, negative values indicate competition, and zero indicates neutral. We used two-way ANOVA to test the effects of container type and nutrient level (1 and 10% Hoagland solution) on LnRR and also performed one-way ANOVA to test the effects of nutrient level (1, 4, 10 and 40% Hoagland solution) on LnRR in the containers of S. The differences of LnRR among the three container types or among the four nutrient levels were assessed by Duncan test. One replicate was lost in the treatment in which T was filled with 1% nutrient solution and four fragments of *A. imbricate* were grown. All analyses were performed using SPSS 22.0 (Chicago, IL, USA).

Results

Container type, nutrient level, initial density, and their two-way and three-way interactions all significantly affected biomass of *A. imbricata* (Table 2). Container type, nutrient level, initial density, and the interaction of container type and initial density also significantly affected number of fragments of *A. imbricata* (Table 2). Biomass and number of fragments were smaller when number of initial fragments was four than when it was one (Fig. 1). Overall, biomass and number of fragments of *A. imbricata* were significantly greater in W than in S and T (Fig. 1), suggesting that the larger diameter and the resultant larger water surface area increased the growth of *A. imbricata*. By contrast, neither biomass nor number of fragments differed significantly between S and T (Fig. 1), suggesting that the larger height and the resultant larger volume of water had no significant effect on the growth of *A. imbricata*. Based on the plants of *A. imbricata* growing only in S, biomass and number of fragments were significantly higher at 4% than at 40% Hoagland solution when there was only one initial fragment and were significantly higher at 4% than at both 10% and 40% Hoagland solution when there was four initial fragments; number of fragments was also significantly smaller at 1% Hoagland solution than at any of the other three nutrient levels when there were four initial fragments (Fig. 1A, Table 3).

LnRR was significantly smaller at the highest nutrient level (40% Hoagland solution) than at the other three nutrient levels (1, 4 and 10% Hoagland solution) (Fig. 2; $F = 3.652$, $P = 0.025$). However, LnRR did not differ significantly among the three container types (Fig. 2, Table 4).

Table 2 ANOVA results for effects of container type (S, W and T), nutrient level (1 and 10% Hoagland solution only) and initial density (1 and 4 fragments) on biomass and number of fragments of *Azolla imbricata*

Effect	d. f.	Biomass		No. of fragments	
		F	*P*	*F*	*P*
Container (*C*)	2,83	**47.54**	**< 0.001**	**33.70**	**< 0.001**
Nutrient (*N*)	1,83	**42.43**	**< 0.001**	**10.01**	**0.002**
Density (*D*)	1,83	**87.43**	**< 0.001**	**118.27**	**< 0.001**
C × *N*	2,83	**14.47**	**< 0.001**	1.59	0.211
C × *D*	2,83	**5.58**	**0.005**	**3.306**	**0.042**
N × *D*	1,83	**6.73**	**0.011**	0.015	0.902
C × *N* × *D*	2,83	**4.61**	**0.013**	0.305	0.738

Degree of freedom (d. f.), *F* and *P* values are given. Values are in bold when $P < 0.05$

Discussion

As predicted, physical space affected the growth of *A. imbricata*. The larger surface area of water, resulting from the larger diameter of the cylindrical container, increased the growth of *A. imbricata*. In a recent study, Cai et al. (2014) similarly showed that two algae species (*Dunaliella salina* and *Platymonas subcordiformis*) grew faster in flasks with a larger water–air surface and thus a higher air supply than in tubes with a smaller water–air surface and thus a lower air supply. This result is probably because the larger surface area could provide the plant with greater exposure to other limiting resources for its growth (Cai et al. 2014). For instance, the access to light, O_2 and/or CO_2 from the air may greatly increase when the surface area of water increases (Cai et al. 2014), which may greatly improve the efficiency of photosynthesis and thus the growth of the floating plant. In addition, a large surface area of water was more conducive to temperature control because the central part in a large space may warm up

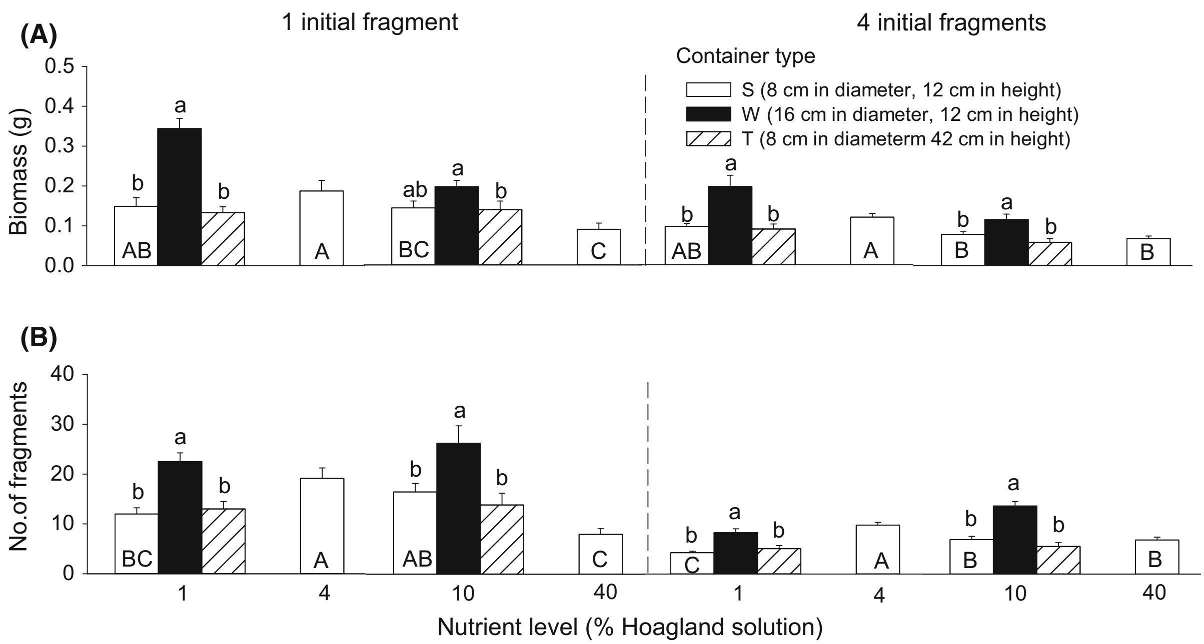

Fig. 1 **A** Biomass and **B** number of fragments of *Azolla imbricata* at each of the four nutrient levels, in each of the three container types and at each of the two initial densities. Bars and vertical lines are means and SE ($n = 8$ except for T with 1% Hoagland solution and 4 initial fragments in which $n = 7$). Different small letters (a, b) above bars indicate significant differences among the three container types within each of the two nutrient levels (1 and 10% Hoagland solution) at each of two initial densities; different capital letters (A–C) inside bars indicate significant differences among the four nutrient levels within each of the two initial densities for the plants growing in the container of S (8 cm in diameter × 12 cm in height)

Table 3 ANOVA results for effects of nutrient level (1, 4, 10 and 40% Hoagland solution) and initial density (1 and 4 fragments) on biomass and number of fragments *Azolla imbricata* in the containers of S (8 cm in diameter × 12 cm in height)

Effect	d. f.	Biomass		No. of fragments	
		F	*P*	*F*	*P*
Nutrient (*N*)	3,56	**10.69**	**< 0.001**	**15.25**	**< 0.001**
Density (*D*)	1,56	**31.96**	**< 0.001**	**68.93**	**< 0.001**
$N \times D$	3,56	2.41	0.077	**5.57**	**0.002**

Degree of freedom (d. f.), *F* and *P* values are given. Values are in bold when $P < 0.05$

and cool down more slowly than that in a small space (Martini et al. 1991; Xu et al. 2001). Thus, larger space can be beneficial to plant growth when the maximum daily temperature is low. However, this explanation may not be the case in our study as our study was conducted in the greenhouse with little temperature fluctuations, and the water surface areas used in the setup may be too small to initiate such effects.

Plants also need more space to propagate (Al-Menaie et al. 2012). Therefore, the limited surface area could directly increase competition in plants and indirectly affect their physiological and morphological characteristics, including root distribution and biomass allocation strategies (Cahill et al. 2010; Chen et al. 2015; Semchenko et al. 2015). However, our current experimental setup does not allow us to separate the pure effect of the water surface area from the area-associated effects of, e.g., light, O_2 and CO_2 on floating plants. Further studies could be designed to maintain the level of light, O_2 and CO_2 and thus to test the pure effect of the water surface area on floating plants.

When the surface area of water was kept the same, the depth/volume of water had no effect on the growth of *A. imbricata*. This was despite the fact that a larger volume of water contained a larger amount of nutrients and likely also O_2 (Cai et al. 2014). This result was in contrast with that of terrestrial plants which can be greatly affected by soil volume (Poorter et al. 2012).

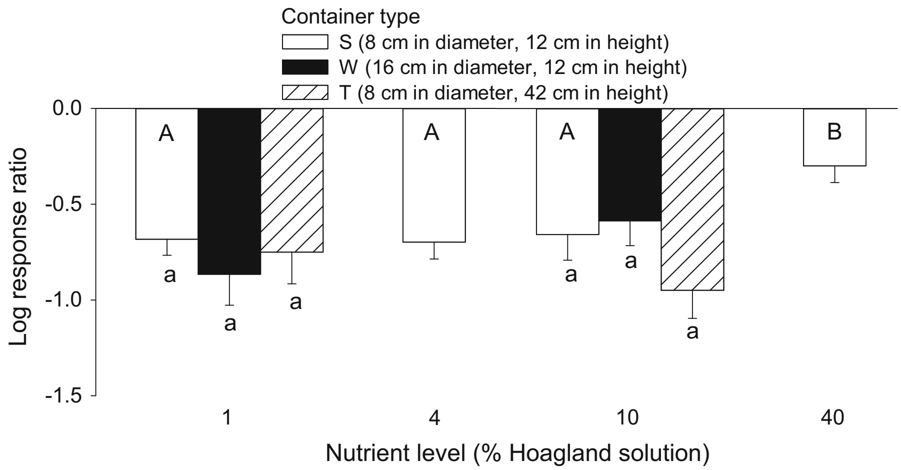

Fig. 2 Competitive intensity as measured by log response ratio of biomass of *Azolla imbricata* at each of the four nutrient levels and each of the two initial densities. Bars and vertical lines are means and SE (n = 8 except for T with 1% Hoagland solution in which n = 7). Different small letters (a, b) below bars indicate significant differences among the three container types within each of the two nutrient levels (1 and 10% Hoagland solution); different capital letters (A, B) inside bars indicate significant differences among the four nutrient levels for the plants growing in the container of S (8 cm in diameter × 12 cm in height)

Table 4 ANOVA results for effects of container type (S, W and T) and nutrient level (1 and 10% Hoagland solution) on log response ratio of *Azolla imbricata*

Effect	d. f.	*F*	*P*
Container (*C*)	2,41	0.861	0.430
Nutrient (*N*)	1,41	0.098	0.756
$C \times N$	2,41	1.477	0.240

Degree of freedom (d. f.), *F* and *P* values are given

The lack of response to the volume of water is likely because *A. imbricata* was distributed only at the water surface and nutrients in this study were sufficient for its growth. However, if nutrients in the water are insufficient for the growth, then changes in the depth/volume of water may alter the growth of floating plants. Future studies could be conducted to test this hypothesis.

Biomass was always smaller when the initial number of fragments was one than when it was four, and also the values of log response ratio were always negative, suggesting the occurrence of intraspecific competition among individuals of *A. imbricata*. Surprisingly, however, we did not find the difference of intraspecific competition among the three container types. The reason may be that the growth reduction due to intraspecific competition was independent of the container types. These results suggest that physical space was not the key factor in shaping intraspecific competition of floating plants.

Not surprisingly, the nutrient level affected the growth of *A. imbricata*. However, the growth of *A. imbricata* was reduced at the highest nutrient level, suggesting that this nutrient level restricted the growth of this floating plant likely due to its toxicity. Similar results have been reported that *A. imbricata* is efficient at removing nitrogen and phosphorus from water, but it is not conducive to its growth when the concentration of phosphorus and/or nitrogen is too high or too low (Liu and Zheng 1989; Costa et al. 2009). The absorption rate of phosphorus and ammonia and total growth of *A. imbricata* declined with increasing nitrogen and phosphorus concentration in the water (Yi 2013).

The log response ratio was significantly smaller when the nutrient level was the highest (40% Hoagland solution) than in the other nutrient levels (1, 4 and 10% Hoagland solution), suggesting that increasing nutrient level greatly reduced intraspecific competition of *A. imbricata*. Similarly, the effects of nutrients on intraspecific competition have been reported in many other studies (He et al. 2012; Zhang et al. 2019). The reason is that the highest nutrient level greatly reduced the growth of *A. imbricata* and such an impact of nutrients was larger when there was no intraspecific competition than when there was.

We conclude that physical space can affect the growth of floating plants, but not their intraspecific competition. However, we still do not know the exact mechanisms underlying the effect of physical space on floating plants. Future studies could focus on the potential mechanisms.

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