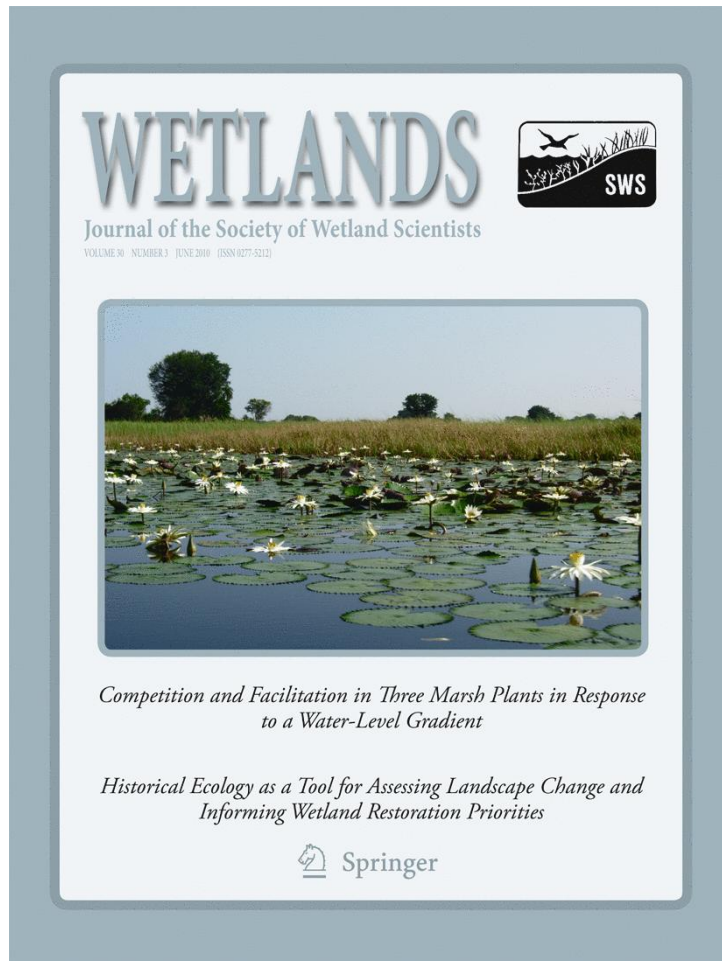


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# Competition and Facilitation in Three Marsh Plants in Response to a Water-Level Gradient

Wenbo Luo · Yonghong Xie · Xinsheng Chen · Feng Li · Xianyan Qin

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**Abstract** Biomass accumulation and neighbor effects (measured with a relative neighbor effect index, NEI) were investigated in three marsh plant species (*Carex lasiocarpa*, *Glyceria spiculosa*, and *Deyeuxia angustifolia*) grown at three water levels (0, 20, and 40 cm relative to the soil surface). The three species occur naturally along a water-level gradient in the Sanjiang Plain, the largest freshwater marsh in China. Both intraspecific and interspecific competition were measured using a target-neighbor design, which subjected the three species to different intensities of inter- and intra-specific competition. Biomass accumulation and NEI differences among water levels and competition treatments suggested that intra- and inter-specific competition was strongest at 0 cm inundation. In contrast, neighboring plants stimulated the growth of *C. lasiocarpa* and *D. angustifolia* at the 40 cm water level. These results indicate that the strength of intra- and inter-specific competition decreases and the strength of facilitation increases with increasing water levels. Our results support the prediction of the stress-gradient hypothesis (SGH) that

plant-plant interactions should switch from competition to facilitation along an increasing water-level stress gradient.

**Keywords** Interspecific competition · Intraspecific competition · Stress-gradient hypothesis · Wetlands

## Introduction

Plant-plant interactions can be negative (competition) or positive (facilitation) (Brooker et al. 2008). Competition involves a struggle to preempt resources, such as light, water, and nutrients, and should be most intense under resource-limiting conditions. Severe abiotic conditions, on the other hand, may restrict the ability of plants to acquire resources, so competition intensities usually decrease with increasing abiotic stress (Bertness and Callaway 1994). The importance of competition in structuring vegetation communities has been long documented (Brooker et al. 2008), but the importance of facilitation has only been recognized recently (Callaway and Pugnaire 1999; Bruno et al. 2003). Facilitative interactions can be defined as any direct or indirect interaction among organisms that stimulates the growth or reproduction of one or more organisms without negative effects on the other(s) (Bertness and Leonard 1997). In severe abiotic environments, facilitation may be as, if not more, important as competition in determining community dynamics and ecosystem processes (Bertness and Callaway 1994; Brooker and Callaghan 1998; Bruno et al. 2003).

The relative importance of competition and facilitation may depend on the intensity of abiotic stress. The stress-gradient hypothesis (SGH) predicts a shift from net negative interactions in benign environments towards net positive in harsh environments (Bertness and Callaway 1994). Facilitation in plant communities may be more

W. Luo · Y. Xie (✉) · X. Chen · F. Li · X. Qin  
Dongting Lake Station for Wetland Ecosystem Observation  
and Research, Key Laboratory of Agro-ecological Processes  
in Subtropical Region, Institute of Subtropical Agriculture,  
The Chinese Academy of Sciences,  
Hunan 410125, China  
e-mail: yonghongxie@163.com

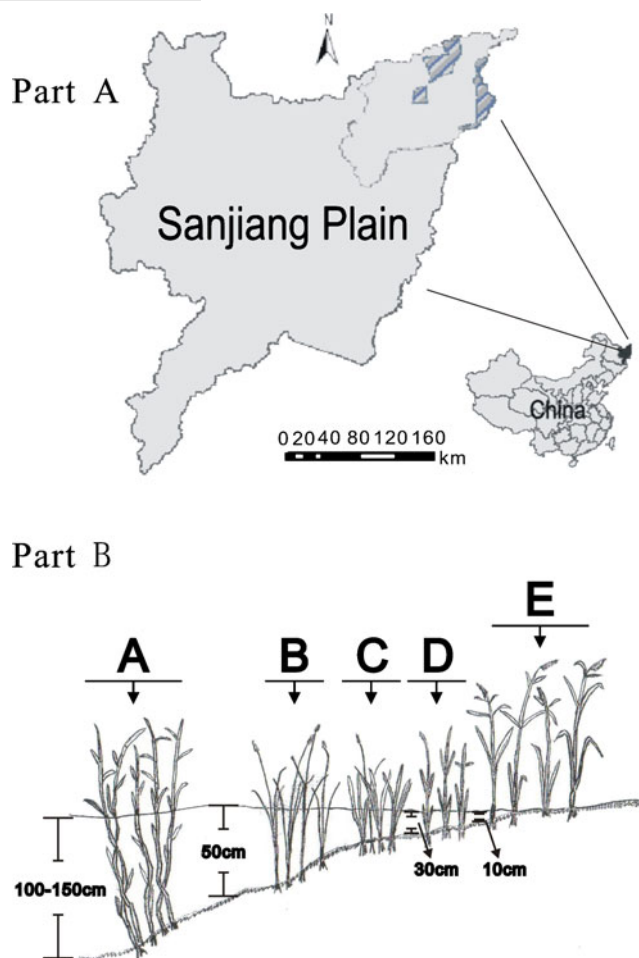
W. Luo  
Key Laboratory for Wetland Ecology and Vegetation Restoration  
of National Environmental Protection,  
Northeast Normal University,  
Changchun 130024, China

W. Luo · F. Li · X. Qin  
Graduate School of the Chinese Academy of Sciences,  
Beijing 100049, China

important under high abiotic stress if neighbors buffer one another from extremes of the abiotic environment. Conversely, competition may be more important in low-stress environments if neighbors deplete limiting resources (Bertness and Callaway 1994). Broad approaches have been taken to examine the SGH in semi-arid regions, alpine ecosystems, and salt marshes. Maestre and Cortina (2004) observed a switch from competition to facilitation and back to competition along a gradient of decreasing rainfall in a semi-arid steppe ecosystem. Callaway et al. (2002) confirmed the SGH in 11 alpine sites around the globe. Bertness and Ewanchuk (2002) found facilitative interactions in warmer, higher salinity areas in New England salt marshes. Pennings et al. (2003), however, failed to find support for the SGH over a large-scale geographical gradient in salt marshes. Therefore, more experiments at different scales and in different ecosystems are still needed to test the generality of the SGH. To date, no studies have tested the stress-gradient hypothesis in freshwater wetlands.

In freshwater wetlands, flooding is the fundamental factor affecting plant growth and species distribution patterns (Voisenek et al. 2004). Tolerance to flooding of terrestrial grassland species or marsh plant species is correlated with distribution patterns in floodplains (Vervuren et al. 2003; van Eck et al. 2004; Luo et al. 2008). Water level is also an important factor influencing competition and facilitation between species (Ervin 2007; Hopfensperger and Engelhardt 2007). Some flood-tolerant wetland plants can alleviate soil anoxia by releasing oxygen into the soil in flooded environments (Mitsch and Gosselink 1986), and this can enable adjacent species to perform better (Callaway and King 1996). Thus, flood-sensitive species should grow well under high water levels when neighboring plants are flood-tolerant.

In order to explore how the strength and direction of species interactions is affected by water level, we conducted an experiment using a target-neighbor design. Three common wetland species, *Carex lasiocarpa*, *Glyceria spiculosa*, and *Deyeuxia angustifolia*, were investigated in the Sanjiang Plain, the largest freshwater marsh in China (Fig. 1). In the Sanjiang Plain, *Carex lasiocarpa* grows in 10–50 cm water depths, *Glyceria spiculosa* in 10–30 cm depths, and *Deyeuxia angustifolia* in 0–10 cm depths (Yi et al. 1985; Luo et al. 2008; Fig. 1). We predicted that (1) plant-plant interactions should switch from competition to facilitation along an increasing water-level gradient, and (2) facilitation would be dependent on the tolerance to flooding of neighboring plants relative to target plants. Thus, at high water levels, the mid-elevation species *G. spiculosa* should facilitate the growth of the flood-sensitive species *D. angustifolia* but restrain the growth of the flood-tolerant species *C. lasiocarpa*.



**Fig. 1** a Location map of the Sanjiang Plain within the China, scale bar applies to inset. b Distribution patterns of common plants along a water level gradient in the Sanjiang plain. A is *Carex pseudocurica*, B is *C. lasiocarpa*, C is *C. limosa*, D is *Glyceria spiculosa*, E is *Deyeuxia angustifolia*

## Materials and Methods

### Plant Materials

Ramets of *C. lasiocarpa*, *G. spiculosa*, and *D. angustifolia* (field density 1,144–1,484 shoots/m<sup>2</sup>) were collected in June 2007 from the Sanjiang Freshwater Marsh Field Observation Station (N 47°35', E 133°31'). Plants were collected in small blocks (15 cm×15 cm×20 cm, the total vegetation area per species was about 25–30 m<sup>2</sup>), and transported to an experimental field outside the station where the temperature ranged from 16 to 24°C during the experimental period. Plant cuttings were then placed into plastic buckets, which contained 10 cm of marsh soil and 2 cm of water to germinate new ramets. Soil used in this study was collected from areas dominated by *D. angustifolia*, and averaged 16.7% organic matter, 231.2 μg g<sup>-1</sup> exchangeable N, 26.1 μg g<sup>-1</sup> exchangeable P, and 270.2 μg g<sup>-1</sup> total K. Water

used in this study was collected from the Sanjiang Freshwater Marsh Field Observation Station, and averaged  $0.649 \mu\text{g L}^{-1}$   $\text{NH}_4^+\text{-N}$ ,  $0.536 \mu\text{g L}^{-1}$   $\text{NO}_3\text{-N}$ , and  $5.467 \mu\text{g L}^{-1}$  total K.

### Experimental Design

In the Sanjiang Plain, the maximal depth of surface water is about 10–50 cm (Yi et al. 1985). Considering the different water depths where the three plants occur, we chose 0 cm, 20 cm, and 40 cm water levels as experimental flooding levels. Both intraspecific and interspecific competition was measured in a target-neighbor design. The experiment included eight treatments: three single-individual treatments (one plant of each species per treatment), three multi-individual treatments (35 plants of each species arranged in a  $7 \times 5$  rectangular array, with the center individual designated as the target plant), and two mixed-species treatments (one plant of *C. lasiocarpa* or *D. angustifolia* as the target plants, and 34 plants of *G. spiculosa* as the neighboring plants). Each treatment was replicated four times.

A total of 2,136 ramets (444 *C. lasiocarpa*, 1,248 *G. spiculosa*, and 444 *D. angustifolia*) of similar size (3–4 leaves, about 25 cm in height) were cut from plant cultures. They were planted in plastic containers (20 cm in height and 25 cm in diameter), which were filled with marsh soil. Eight containers (one container per treatment) were placed into each of four bigger plastic basins (100 cm deep; 80 cm diameter) and supplied with pond water as needed to control water depth. All target plants were harvested after 42 days. After collection, plants were divided into above- and below-ground parts to determine weights, respectively. Plants were oven dried at  $85^\circ\text{C}$  for 48 h, and dry weight recorded. Total biomass was the sum of above- and below-ground weight. At the beginning of our experiments, six plants per species were oven dried at  $80^\circ\text{C}$  for 48 h, and the dry mass was used to estimate initial biomass.

### Relative Neighbor Effect Index (NEI)

Both interspecific and intraspecific interactions were quantified using the relative neighbor effect index (NEI):  $\text{NEI} = (\text{P}_{-N} - \text{P}_{+N}) / X$  (Markham and Chanway 1996), where P is

the final biomass in the presence (+N) and absence (–N) of neighbors, and X the larger value of  $\text{P}_{-N}$  or  $\text{P}_{+N}$ . Calculations were performed using  $\ln(x+1)$ -transformed biomass data (Belcher et al. 1995). NEI is an improved version of the relative competitive intensity index (Wilson and Keddy 1986; Belcher et al. 1995). The NEI enables both competitive and facilitative interactions to be quantified without bias on a scale of 1 to –1. A value of 0 indicates no interaction, a negative value indicates facilitation and a positive value indicates competition.

### Statistical Analysis

Treatment effects on biomass accumulation and NEI were tested using one-way ANOVA. Multiple comparisons of means were performed by Tukey's test at the 0.05 significance level. Data were  $\log_{10}$ -transformed if necessary to reduce heterogeneity of variances, and heterogeneity was tested using Levene's test (Table 1).

### Results

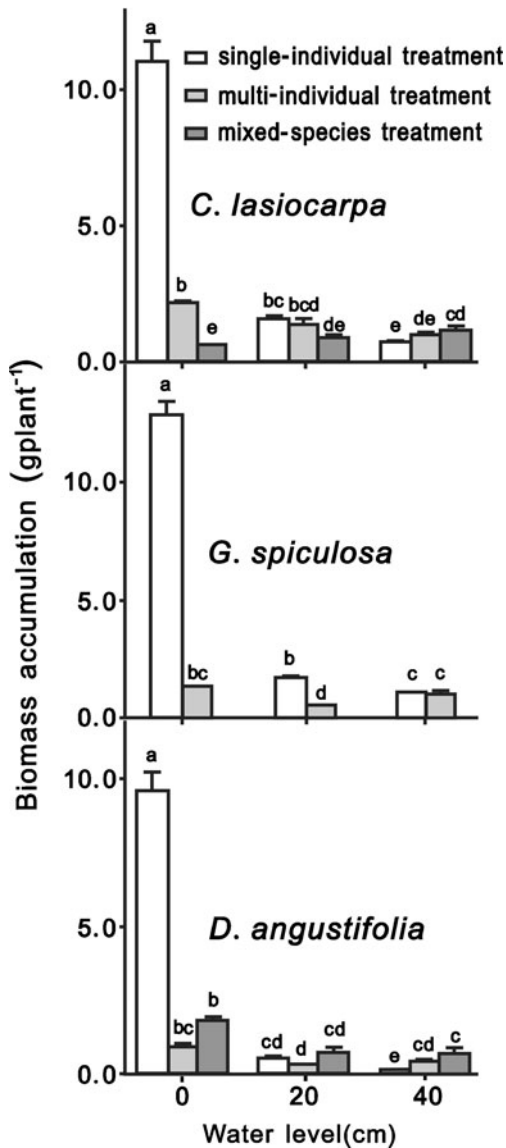
Biomass was generally lower with versus without neighbors at 0 cm water levels (Fig. 2). *Carex lasiocarpa* had a higher and *D. angustifolia* a lower biomass in the mixed species treatment than in the multi-individual treatments at the 0 cm water level. In the 20 cm water-level treatments, *C. lasiocarpa* biomass was higher in single-individual and multi-individual treatments (1.59 versus 1.41 g per plant), and lower in the mixed species treatments (0.91 g per plant). For *G. spiculosa*, biomass was higher in the single-individual treatment than in the multi-individual treatments (1.73 versus 0.58 g per plant). For *D. angustifolia*, biomass in the multi-individual treatments was lower than those in the single-individual treatment or mixed species treatments (0.34 versus 0.56–0.75 g per plant). Under 40 cm water-level conditions, however, biomass of *C. lasiocarpa* and *D. angustifolia* was higher with versus without neighboring plants.

The NEI of *G. spiculosa* was positive or close to zero in the multi-individual treatments. *Carex lasiocarpa* had a

**Table 1** Summary of two-way ANOVAs for biomass accumulation and NEI of *Carex lasiocarpa*, *Glyceria spiculosa*, and *Deyeuxia angustifolia* growing in single-individual, multi-individual and mixed-species treatments under three water-level conditions (*F*-values)

|             | Target species         | n | Water level (W)      | Competition (C)      | W × C               |
|-------------|------------------------|---|----------------------|----------------------|---------------------|
| Biomass (g) | <i>C. lasiocarpa</i>   | 4 | 66.5 <sup>***</sup>  | 71.3 <sup>***</sup>  | 79.4 <sup>***</sup> |
|             | <i>G. spiculosa</i>    | 4 | 376.8 <sup>***</sup> | 571.6 <sup>***</sup> | 98.0 <sup>***</sup> |
|             | <i>D. angustifolia</i> | 4 | 140.5 <sup>***</sup> | 12.7 <sup>**</sup>   | 55.4 <sup>***</sup> |
| NEI         | <i>C. lasiocarpa</i>   | 4 | 162.4 <sup>***</sup> | 6.4 <sup>*</sup>     | 9.9 <sup>**</sup>   |
|             | <i>D. angustifolia</i> | 4 | 293.6 <sup>***</sup> | 25.7 <sup>***</sup>  | 8.8 <sup>**</sup>   |

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

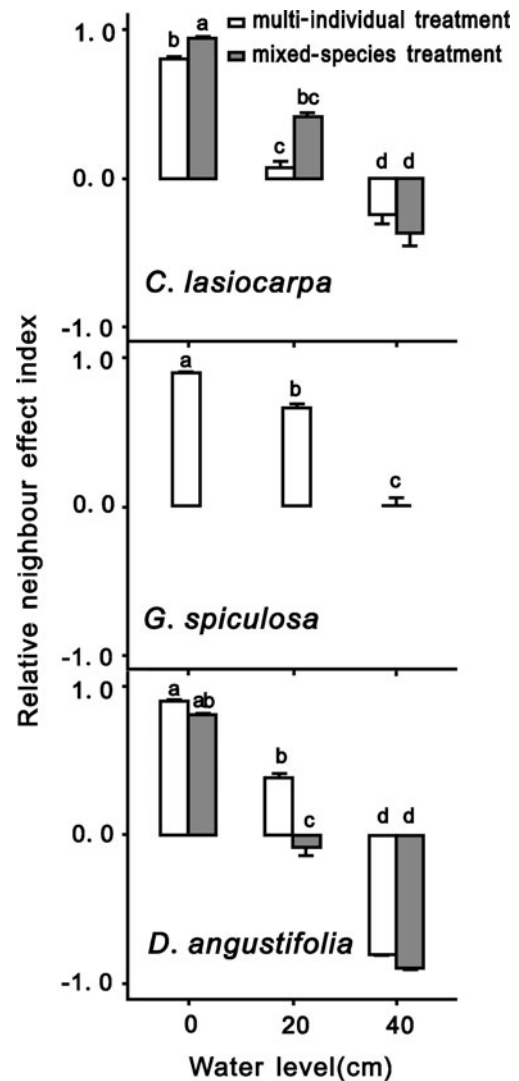


**Fig. 2** Biomass (above + belowground summed) accumulation (means±SE,  $n=4$ ) of *Carex lasiocarpa*, *Glyceria spiculosa*, and *Deyeuxia angustifolia* growing in single-individual, multi-individual, and mixed species treatments under three water-level conditions. Different letters indicate significant differences among treatments based on Tukey's test at the 0.05 significance level

negative NEI (indicating facilitation) only at 40 cm water levels (Fig. 2), but the NEI of *D. angustifolia* was negative under 20 cm and 40 cm water-level conditions (Fig. 3). In the 0 or 20 cm water-level environments, the NEI of *C. lasiocarpa* in the mixed species treatments was significantly higher than that in the multi-individual treatments (0.94 versus 0.80), whereas the NEI of *D. angustifolia* showed an opposite tendency as that of *C. lasiocarpa* (0.81 versus 0.90). In the 40 cm water-level environments, *C. lasiocarpa* and *D. angustifolia* had similar NEI values in the interspecific and multi-individual treatments.

## Discussion

The stress-gradient hypothesis predicts that the intensity of intraspecific and interspecific competition should decrease with increasing abiotic stress (Bertness and Callaway 1994). Lower biomass accumulation of the three species with neighboring plants compared to the single-individual treatments indicated that competition restrained plant growth at 0 cm water levels. In contrast, the higher biomass accumulation of *C. lasiocarpa* and *D. angustifolia* with neighbors compared to single individuals at 40 cm water levels indicated that neighboring plants stimulated the



**Fig. 3** Relative neighbour effect index (NEI, means±SE,  $n=4$ ) of *Carex lasiocarpa*, *Glyceria spiculosa*, and *Deyeuxia angustifolia* growing in multi-individual and mixed species treatments under three water-level conditions. Different letters indicate significant differences among treatments based on Tukey's test at the 0.05 significance level. A value of 0 indicates no interaction, a negative value facilitation, and a positive value competition

growth of both species in deeper water. In the intraspecific and mixed-species treatments, the changes of NEI values of *C. lasiocarpa* and *D. angustifolia* from positive to negative with increasing water levels supported the prediction that competition would shift to facilitation with increasing water levels. This result is also consistent with some previous studies performed in other ecosystems that have confirmed predictions of the SGH (Callaway 1997; Bertness and Ewanchuk 2002; Callaway et al. 2002; Michalet 2006). In contrast, we did not observe facilitation of *G. spiculosa* at the highest water level, perhaps because the depth used (40 cm) may have been too shallow to trigger a facilitative response. However, the NEI for *G. spiculosa* did decline from strong positive values to almost zero. Therefore, our results support the SGH that plant-plant interactions would switch from competition to facilitation along an increasing water-level gradient.

Across environmental gradients, plant-plant interactions among primary space holders are predicted to shift from positive to negative, then back to positive due to opposing gradients in stress and consequent positive group benefits at extremes in abiotic stress (Bertness and Callaway 1994). In harsh physical environments, facilitative interactions could predominate due to neighbor buffering, which could ameliorate abiotic stress (Callaway et al. 2002). The highest biomass accumulation in the single-individual treatments indicated that 0-cm water level was the least stressful condition for the growth of the three species. However, competition was also most intense in this environment, likely due to increased resource acquisition by plants. The negative impact of flooding on wetland plants is closely related to the low diffusion rates of gases and the relatively low solubility of oxygen in water, which jointly lead to anoxia or hypoxia in soil and plant tissues (Armstrong and Drew 2002). Therefore, one likely mechanism of facilitation in deeper water is the amelioration of anoxic rhizosphere environments by oxygen leakage from neighboring plants. However, we did not determine whether this mechanism was operating in our study.

Biomass accumulation and NEI differed between intraspecific and mixed species treatments at 40 cm water levels in *D. angustifolia* but not in *C. lasiocarpa*, indicating that *G. spiculosa* only stimulated the growth of *D. angustifolia*. These data partly support the second hypothesis, which predicts that mid-elevation species *G. spiculosa* will facilitate the growth of the flood-sensitive species *D. angustifolia* but restrain the growth of the flood-tolerant species *C. lasiocarpa* at higher water levels. The different interactive effects between *D. angustifolia* and *C. lasiocarpa* in response to high water-level stresses might be closely related to the different biological characteristics of both species relative to the neighbor species *G. spiculosa*. The differences in biological characteristics among species

in their lowest position along a water-level gradient might indicate that plant species differ in their ability to cope with flooding (Blom and Voeselek 1996). The porosity (relative volume of internal gas spaces in plant tissues, an indicator of the capacity to deliver oxygen to below-ground tissues) is an important characteristic determining tolerance to flooding or anoxia by transporting oxygen to root parts in order to alleviate anoxic stresses in the flooding environments (Mitsch and Gosselink 1986; Armstrong et al. 1992; Xie et al. 2007; Xie et al. 2008), which is an important indicative index of flood-tolerance ability for some wetland species (Laan et al. 1989). Callaway and King (1996) found that other marsh plants growing with *Typha latifolia*, a species with highly effective whole-plant aeration system (Bendix et al. 1994), survived longer and grew larger than in pots without *T. latifolia*, suggesting that porosity might be an important biological characteristics accounting for the mechanism of facilitation. The root porosity in the high water-level species *D. angustifolia* is about 7% (Xie et al. 2008), but root porosity of some wetland plants such as *Carex* and *Rumex* species is usually higher than 20% (Colmer 2003). Therefore, the aeration ability of *D. angustifolia* is relatively low, but *C. lasiocarpa* has a higher ability to deliver oxygen to root tissues, which is also supported by the response of alcohol dehydrogenase activity to flooding in both species (Luo et al. 2008).

In the Sanjiang Plain, *D. angustifolia* usually occurs in seasonal ponds or in wetlands with little surface water, whereas *C. lasiocarpa* and *G. spiculosa* generally occur in permanently flooded habitats (Yi et al. 1985; Xu et al. 2007). The fact that the latter two species are both well adapted to high water-level environments may explain the insignificant facilitative effects of *G. spiculosa* on the growth of *C. lasiocarpa* at higher water levels. Conversely, the lower porosity of *D. angustifolia* might indicate that the growth of species with low aeration ability would be stimulated by neighboring species with high porosity due to amelioration of soil oxidation-reduction status. The low root porosity of *D. angustifolia* may explain why it occurs only in small and sparse populations in the high water-level environments in the Sanjiang Plain (Yi et al. 1985; Xie et al. 2008). Therefore, differences among species in root porosity might be an important predictor of whether plants will interact positively or negatively under flooded conditions, and we encourage more studies linking measurements of root porosity to interspecific interactions.

In sum, biomass and NEI data in this experiment confirm the SGH that plant-plant interactions should switch from competition to facilitation along an increasing water-level stress gradient. In freshwater wetlands, facilitation may be just as important as competition for structuring ecological communities, but the mechanism of facilitation still needs further study.

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## References

- Armstrong W, Drew MC (2002) Root growth and metabolism under oxygen deficiency. In: Waisel Y (ed) *Plant roots: the hidden half*. Dekker, New York
- Armstrong J, Armstrong W, Beckett PM (1992) *Phragmites australis*: verturi- and humidity-induced convections enhance rhizome aeration and rhizosphere oxidation. *The New Phytologist* 120:197–207
- Belcher JW, Keddy PA, Twolan-Strutt L (1995) Root and shoot competition intensity along a soil depth gradient. *Journal of Ecology* 83:673–682
- Bendix M, Tornbjerg T, Brix H (1994) Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L. 1. Humidity-induced pressurisation and convective through flow. *Aquatic Botany* 49:75–89
- Bertness MD, Callaway RM (1994) Positive interactions in communities. *Trends in Ecology & Evolution* 9:191–193
- Bertness MD, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976–1989
- Bertness M, Ewanchuk PJ (2002) Latitudinal and climate driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia* 132:392–401
- Blom CMPW, Voesenek LACJ (1996) Flooding: the survival strategies of plants. *Trends in Ecology & Evolution* 11:290–295
- Brooker RW, Callaghan TV (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81:196–207
- Brooker RW, Maester FT, Callaway RM, Lortie CL, Cavieres LA et al (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96:18–34
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18:119–125
- Callaway RM (1997) Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112:143–149
- Callaway RM, King L (1996) Temperature-driven variation in substrate oxygenation and the balance of competition and facilitation. *Ecology* 77:1189–1195
- Callaway RM, Pugnaire FI (1999) Facilitation in plant communities. In: Pugnaire F, Valladares F (eds) *Handbook of functional plant ecology*. Dekker, New York
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie C et al (2002) Positive interactions among alpine plants increase with stress. *Nature* 417:844–848
- Colmer TD (2003) Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant, Cell & Environment* 26:17–36
- Ervin GN (2007) An experimental study on the facilitative effects of tussock structure among wetland plants. *Wetlands* 27:620–630
- Hopfensperger KN, Engelhardt KAM (2007) Coexistence of *Typha angustifolia* and *Impatiens capensis* in a tidal freshwater marsh. *Wetlands* 27:561–569
- Laan P, Berrevoets MJ, Lythe S, Armstrong W, Blom CWPM et al (1989) Root morphology and aerenchyma formation as indicators of the flood-tolerance of *Rumex* species. *Journal of Ecology* 77:693–703
- Luo W, Song F, Xie Y (2008) Trade-off between tolerance to drought and tolerance to flooding in three wetland plants. *Wetlands* 28:866–873
- Maestre FT, Cortina J (2004) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London B Supplement* 271:S331–S333
- Markham JH, Chanway CP (1996) Measuring plant neighbour effects. *Functional Ecology* 10:548–549
- Michalet R (2006) Is facilitation in arid environments the result of direct or complex interactions? *The New Phytologist* 169:3–6
- Mitsch WJ, Gosselink JG (1986) *Wetlands*. Van Nostrand Reinhold, New York
- Pennings SC, Seling ER, Houser LT, Bertness AM (2003) Geographic variation in positive and negative interactions among salt marsh plants. *Ecology* 84:1527–1538
- van Eck WHJM, van de Steeg HM, Blom CWPM, de Kroon H (2004) Is tolerance to summer flooding correlated with distribution patterns in river floodplains? A comparative study of 20 terrestrial grassland species. *Oikos* 107:393–405
- Vervuren PJA, Blom CWPM, de Kroon H (2003) Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. *Journal of Ecology* 91:135–146
- Voesenek LACJ, Rijnders JHGM, Peeters AJM, Van de Steeg HMV, De Kroon H (2004) Plant hormones regulate fast shoot elongation under water: from genes to communities. *Ecology* 85:16–27
- Wilson SD, Keddy PA (1986) Species competitive ability and position along a natural stress/disturbance gradient. *Ecology* 67:1236–1242
- Xie Y, Luo W, Ren B, Li F (2007) Morphological and physiological responses to sediment type and light availability in roots of the submerged plant *Myriophyllum spicatum*. *Annals of Botany* 100:1517–1523
- Xie Y, Luo W, Wang K, Ren B (2008) Root growth dynamics of *Deyeuxia angustifolia* seedlings in response to water level. *Aquatic Botany* 89:292–296
- Xu ZG, He Y, Yan BX, Song CC (2007) Niche characteristics of typical marsh wetland populations in Sanjiang Plain. *Chinese Journal of Applied Ecology* 18:783–787 (in Chinese with English abstract)
- Yi FK, Li CH, Zhao KY, Ding SQ (1985) Study on vegetation type in the Sanjiang Plain. In: Huang XT (ed) *Study on marsh in China*. Science, Beijing (in Chinese)