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*Full Length Research Paper*

# Growth and morphological responses to water level variations in two *Carex* species from Sanjiang Plain, China

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**Sanjiang Plain is the largest freshwater marsh wetland in China. *Carex lasiocarpa* and *Carex limosa* are two dominant species in the area. The niche of *C. limosa* is similar with *C. lasiocarpa* and both species always distribute in the same region. However, the distribution area of *C. limosa* is far smaller than that of *C. lasiocarpa*. The aim of the study is to determine whether *C. lasiocarpa* had superiority in plant growth than *C. limosa* in the condition of submergence. To this end, plant growth and root morphologies were investigated in two *Carex* species. Experimental treatments included three water levels (0, 10 and 20 cm) . Relative growth rates in *C. lasiocarpa* (0.038 g g $^{-1}$ d$^{-1}$) were much higher than that in *C. limosa* (0.030 g$^{-1}$ d$^{-1}$) under 20 cm water level. There existed more severe effects in biomass accumulations in *C. limosa* (dropped 77%) than that in *C. lasiocarpa* (dropped 52%) when comparing 20 cm water level to 0 cm water level. Enhanced water level could enhance root porosity (*C. lasiocarpa* 20.4%** and *C.* ***limosa* 21.5%) in both species but form shorter roots in *C. limosa*. Higher relative shoot growth rate could be found** in ***C. lasiocarpa* under deep water conditions. These data could explain why the two species had the same niche but different distribution areas in Sanjiang plain.**

**Key words:** Flooding, morphological, responses, growth, root porosity.

## INTRODUCTION

Sanjiang Plain is the largest freshwater marsh wetland in China, about 10.89×10$^6$ km$^2$ (Ma, 1995), served by Songhua River, Heilong River and Wusuli River. *Carex lasiocarpa* and *Carex limosa* are aquatic plants in the plain, and they share similar niche. *C. lasiocarpa* bears erect stems which may exceed a meter in height and very long, very thin leaves from a rhizome. *C. limosa* has a large rhizome and hairy roots, and produces a stem which is generally just less than half a meter in height and has a few basal leaves which are long and threadlike. *C. lasiocarpa* Fhrh, the dominant species in the plain, usually distributes in the lowly elevated sites, which area is about 2642 km $^2$. While another kind of grass, *C. limosa* Linn, whose niche is similar with *C. lasiocarpa*, but had far smaller distribution area than the *C. lasiocarpa*, this indicates that *C. lasiocarpa* had higher competitive ability than *C. limosa* when flooding.

In wetlands, flooding is the key factor for determining plant distribution (Andrews and Pomeroy, 1989; Klimesova, 1994; Siebel, 1998; Sparks et al., 1998; Johansson and Nilsson, 2002; Luo et al., 2008), since flooding usually leads to oxygen deficiency in physiological activity (Crawford and Brandle, 1996; Vartapetian and Jackson, 1997; Xie et al., 2007). Under flooding conditions, the air diffusion rate is 10×10$^4$ times lower than that in the atmosphere. As a result, many flood-sensitive species can not endure the soil-oxygen deficiency and then they are replaced by the flood-tolerant species, or their distribution area is reduced. Many wetland plants are able to adapt to inundation through physiological and morphological changes (Blom and Voesenek, 1996; He et al., 1999; Vervuren et al., 1999; Voesenek et al., 2003; Colmer and Flowers, 2008), such as high growth rate (Nichol and Biondini, 2002; Mediavilla and Escudero, 2003), shortening root length, forming parenchyma (Laan et al., 1989; Visser et al., 1997; Jackson and Armstrong, 1999), producing adventitious roots, changing biomass allocation patterns (Blom and Voesenek, 1996), enhancing shoot height, forming shallow root systems (Kozlowski, 1984; Rubio et al., 1995; Pezeshki et al., 1996; Blom and Voesenek, 1996). These changes are considered to increase the capacity of oxygen transportation to root rhizosphere, which greatly enhances the adaptive abilities to inundation (Blom et al., 1990; Naidoo and Naidoo, 1992; Blom and Voesenek, 1996). Therefore, the differences in growth and morphological responses between *C. lasiocarpa* and *C. limosa* under flooding conditions, for example higher RGR, higher shoot height or higher root porosity of *C. lasiocarpa*, may explain why *C. limosa* had similar niche with *C. lasiocarpa*, whereas had far smaller distributed area than *C. lasiocarpa*.

The objective of this research is to study growth and root morphological responses to different water level, and thereby to make sure whether *C. lasiocarpa* had higher adaptive ability than *C. limosa* in flooding conditions, by studying growth and root morphological responses to different water level. We hypothesized that (1) root porosity in *C. lasiocarpa* was higher than that in *C. limosa* when inundated; (2) Relative growth rate (RGR) in *C. lasiocarpa* was higher than that in *C. limosa* in submergence conditions.

## MATERIALS AND METHODS

### Plant materials

Vegetations of *C. lasiocarpa* and *C. limosa* were collected in October 2007, from Sanjiang plain freshwater marsh experimental station (N 47º35', E 133º31'), Chinese Academy of Sciences. The vegetations were cut into small blocks (15 × 15 × 20 cm), and transplanted to a greenhouse in the Northeast Institute of Geography and Agricultural Ecology, Chinese Academy of Sciences, where the temperature was controlled at 25 ± 2ºC in the day and 17± 2ºC at night and the light was provided by 400 watt SON-T ARGO sodium lamps (Philip, Guildford, UK) at a photon flux density of 600 $\mu$mol $m^{-2}$ $s^{-1}$ (PAR) in a 14 h light/10 h dark cycle. The blocks of vegetations were placed in the plastic buckets filled with water about 20 cm in height, to germinate new ramets.

### Experimental design

Two months later, new ramets of both species with similar size (about 15 cm in height) were taken from the plant blocks and planted in plastic pots (15 cm in diameter, 12 cm in height), which were filled with soil collected from Sanjiang plain in October 2007. The soil contained 0.81% organic matter, 54.5 g $g^{-1}$ exchangeable N and 21.1 g $g^{-1}$ exchangeable P. After weighing, each plant was planted in one pot containing 2.5 kg of soil. Six pots were randomly placed into one bigger plastic bucket (100 × 80 × 80 cm) to control water level (one pot per species per treatment). A total of four buckets were used in the experiment. So each treatment was repeated four times. The treatments contained three water levels: 0, 10 and 20 cm water level relative to the soil surface. Tap water was daily supplied to maintain the water level.

### Plant growth

During the experimental period, shoot length and the number of ramets of both species were measured and recorded every two weeks. The plants were harvested after 12 weeks. After removal from soil, the plants were carefully washed using tap water, divided into shoots and roots, and fresh weight was recorded. For each treatment, 10 typical roots in each plant were chosen to measure root length using a steel meter-ruler. Plants were oven dried at 80ºC for 48 h. All fresh weights were transformed into dry weights. Relative growth rate (RGR) was calculated as follow: RGR= ($ln w_2$-$ln w_1$)/($t_2$-$t_1$). Where $w_2$ and $w_1$ indicate the final and initial plant dry weight, respectively, and ($t_2$ - $t_1$) indicated the experimental time (day). Relative shoot growth rate and relative ramets number increase rate were also used in this equation. Root: shoot ratio was calculated as the ratio of root mass to shoot mass.

### Root porosity

Roots from different treatments were examined for porosity (percentage of air -filled volume) by the pycnometer method (Jensen et al., 1969). The porosity of roots is usually used as an indicator of the capacity of the lacunar system to deliver oxygen to below-ground tissues. Representative fresh adventitious roots (> 5 cm in length) were removed intact, and were separated into main roots and laterals by tweezers. Main roots were cut into 1 - 2 mm segments. The porosity of main roots was then determined using 0.1 - 0.3 g of root tissue and a 25 mL pycnometer. Three determinants per treatment were made using a vacuum pump.

### Statistical analysis

Treatment effects were tested by the analysis of variance (ANOVA) using the software SPSS 13.0. Multiple comparisons of means were performed using Duncan’s test at 0.05 significance level. Data were $log_{10}$-transformed if necessary to reduce the heterogeneity of variances, and homogeneity was tested using Levene’s test. A two-way ANOVA, with species and water level as main factors, was used to evaluate the effects on biomass accumulation, biomass allocation and root characteristics of the two *Carex* species.

## RESULTS

### Biomass accumulation and biomass allocation

Shoot biomass, root biomass and total biomass were generally decreased with increase in water level for both species ($P$<0.001 Table 1, Figure 1). At the same treatment, biomass accumulation was relatively higher in *C. lasiocarpa* (18.2 - 37.6 g per plant) and lower in *C. limosa* (6.6 - 28.5 g per plant), indicating that the response of plants to high water level is dependent on species. Biomass allocation in the two species was significantly affected by water level ($P$<0.001 Table 1) and were significantly decreased with enhanced water level,

**Table 1.** Two-way ANOVAs for biomass accumulation, biomass allocation and root characteristics of **C. *lasiocarpa*** and **C.** *limosa* growing in three water levels. (F-values).

| | Species(S) | Water level (W) | S×W |
|---|---|---|---|
| Total biomass (g) | 14.432$^{***}$ | 25.584$^{***}$ | 0.331$^{ns}$ |
| Shoot mass (g) | 15.903$^{***}$ | 15.449$^{***}$ | 0.791$^{ns}$ |
| Root mass (g) | 13.600$^{***}$ | 23.007$^{***}$ | 3.816* |
| Root: Shoot ratio | 0.320$^{ns}$ | 19.049$^{***}$ | 2.541$^{ns}$ |
| Shoot length (cm) | 1136.134$^{***}$ | 50.120$^{***}$ | 98.828$^{***}$ |
| Relative shoot growth rate (cm $cm^{-1}d^{-1}$) | 52.929$^{***}$ | 0.946$^{ns}$ | 1.639$^{ns}$ |
| Relative ramets number increase rate | 0.000$^{ns}$ | 7.424$^{**}$ | 0.158$^{ns}$ |
| Relative growth rate (g $g^{-1}d^{-1}$) | 1.721$^{ns}$ | 30.283$^{***}$ | 6.149$^{**}$ |
| Porosity (%) | 0.118$^{ns}$ | 17.283$^{***}$ | 0.329$^{ns}$ |
| Root length (cm) | 3.226$^{ns}$ | 5.815$^{**}$ | 1.756$^{ns}$ |

$^{ns}$ $P$>0.05; $^{*}$ $P$ < 0.05; $^{**}$ $P$ < 0.01; $^{***}$ $P$ < 0.001

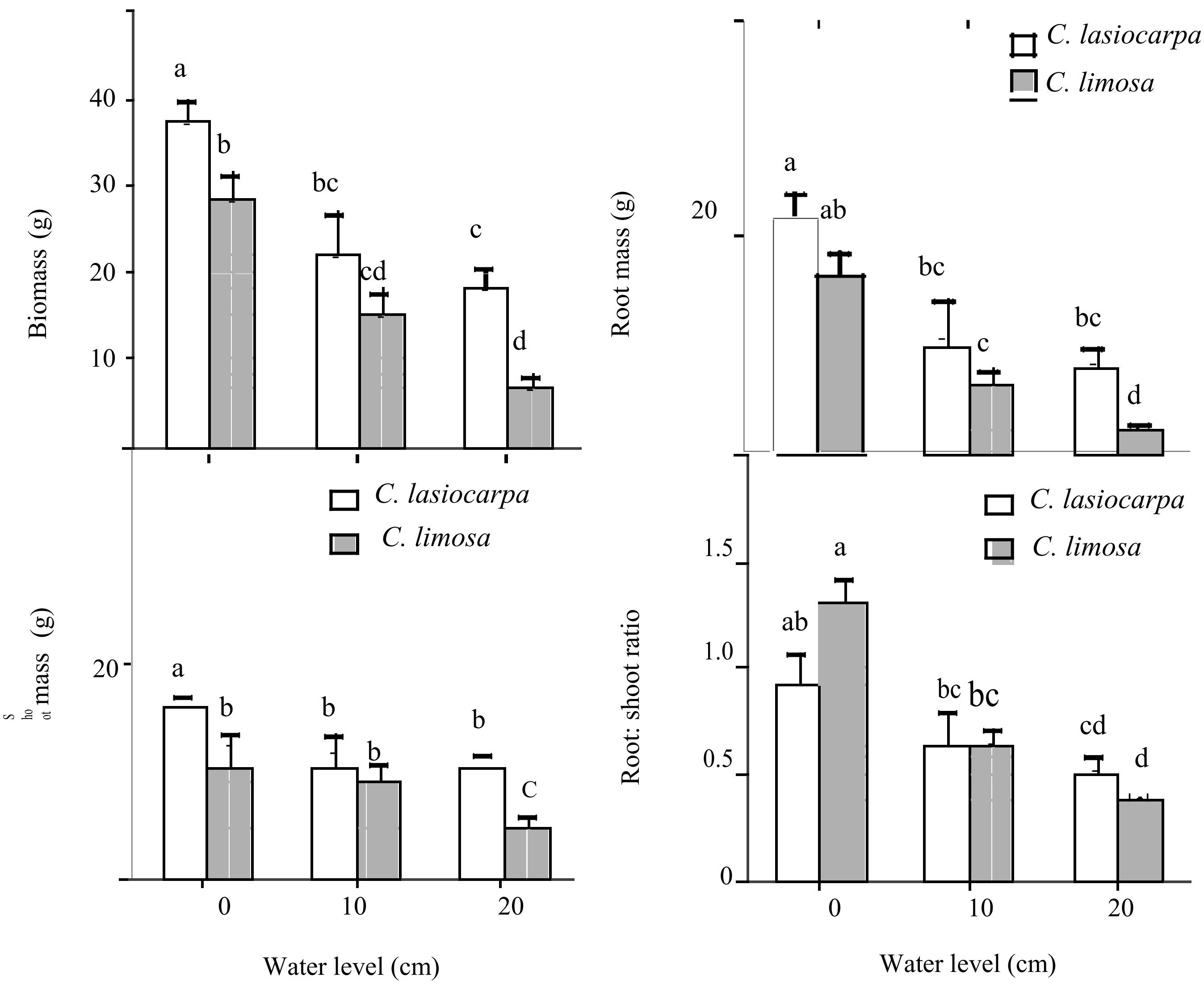


**Figure 1.** Biomass accumulation, Shoot mass, root mass and root: shoot ratio (means ± SE, n = 4) of *C. lasiocarpa* and C. *limosa* growing under three water levels. Different letters indicate significant differences between both species among treatments ($P$<0.05).

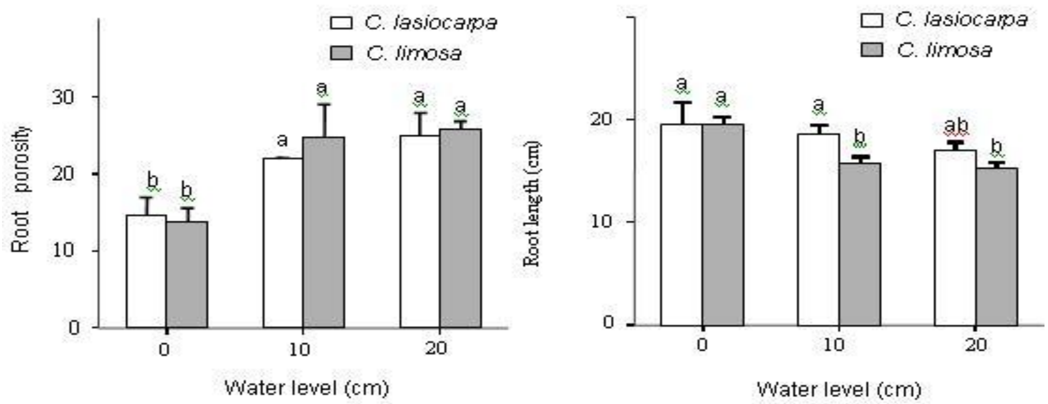


**Figure 2.** Root porosity and root length (means ± SE, n = 4) of C. *lasiocarpa* and C. *limosa* growing in three water levels. Different letters indicate significant differences among treatments ($P$<0.05).

but there was no significant difference between the two species ($P$>0.05 Table 1 and Figure 1).

### Root characteristics

Water level had significant effects on root length and porosity in both species ($P$<0.01 Table 1). Enhanced water level usually led to shorter roots and increased root porosity in both species ($P$<0.01 Table 1 and Figure 2). There was a tendency that root length of *C. lasiocarpa* was generally higher than that of *C. limosa* in the high water-level treatments. However, there were insignificant differences in root porosity between *C. lasiocarpa* (20.44%) and *C. limosa* (21.45%).

### The characteristics of plant growth

Water level had dramatic effects on shoot length and the number of ramets in both species ($P$<0.001 Table 1). Enhanced water level usually results in higher shoot length and less ramets (Figure 3). There exist a significant difference in relative shoot growth rate between the two species ($P$<0.05 Table 1 and Figure 4), and shoot length in *C. lasiocarpa* was much higher than that in *C. limosa* in the same treatment (Figure 3). However, relative ramets increase rate showed no difference between the two species ($P$>0.05 Table 1 and Figure 4) . RGR decrease with enhanced water level, and in the 20 cm water-level treatment, RGR in *C. lasiocarpa* (0.038 g $g^{-1}d^{-1}$) was higher than that in *C. limosa* (0.030 g $g^{-1}d^{-1}$) ($P$<0.05 Figure 4)

## DISCUSSION

Flood tolerance is determined by the ability of a plant to grow and survival in soils with water content above field capacity (Rowe and Beardsell, 1973). In our experiment, biomass accumulation of the two species decreased significantly with enhanced water level. For *C. limosa*, biomass accumulation decreased 77% in 20 cm water level compared to that in 0 cm water level, whereas for *C. lasiocarpa*, it was only 52%. Thus, deeper water had more severe influences in *C. limosa* than in *C. lasiocarpa*. Moreover, RGR of *C. lasiocarpa* was much higher than that of *C. limosa* in 20 cm water level ($P$<0.05 Figure 4). Higher growth rate was advantageous in rapidly occupying the limited space and to acquire more resources (Nichol and Biondini, 2002; Mediavilla and Escudero, 2003). These data indicated that *C. lasiocarpa* had more superiority in plant growth than *C. limosa* in the condition of submergence, which could explain that why *C. limosa* had smaller distribution areas than *C. lasiocarpa* in Sanjiang Plain.

Biomass allocation showed the same tendency as biomass accumulation, and enhanced water level significantly decreased root: shoot ratio in both species. Similar results were found in the study of Rubio and Lavado (1999), significant changes in root/shoot ratio were reported in many wetland plants such as *Phalaris* or *Spartina* might decrease biomass and oxygen demand of the root system when flooded, which was important adjustment in most wetland plants during flooding period. But enhanced water level had different impacts between two species. When compared 20 cm water to 0-cm water, root/shoot ratio of *C. limosa* dropped 61.9%, whereas it dropped 43.9% in *C. lasiocarpa*. So *C. limosa* had more drastic adjustments in deep water than *C. lasiocarpa*, and these data may indicate that the latter was more suitable to grow under deep water than the former, which also could explain why *C. limosa* had smaller distribution areas than *C. lasiocarpa* in the Sanjiang plain.

Soil flooding usually reduces plant growth by decreasing the availability of oxygen to roots

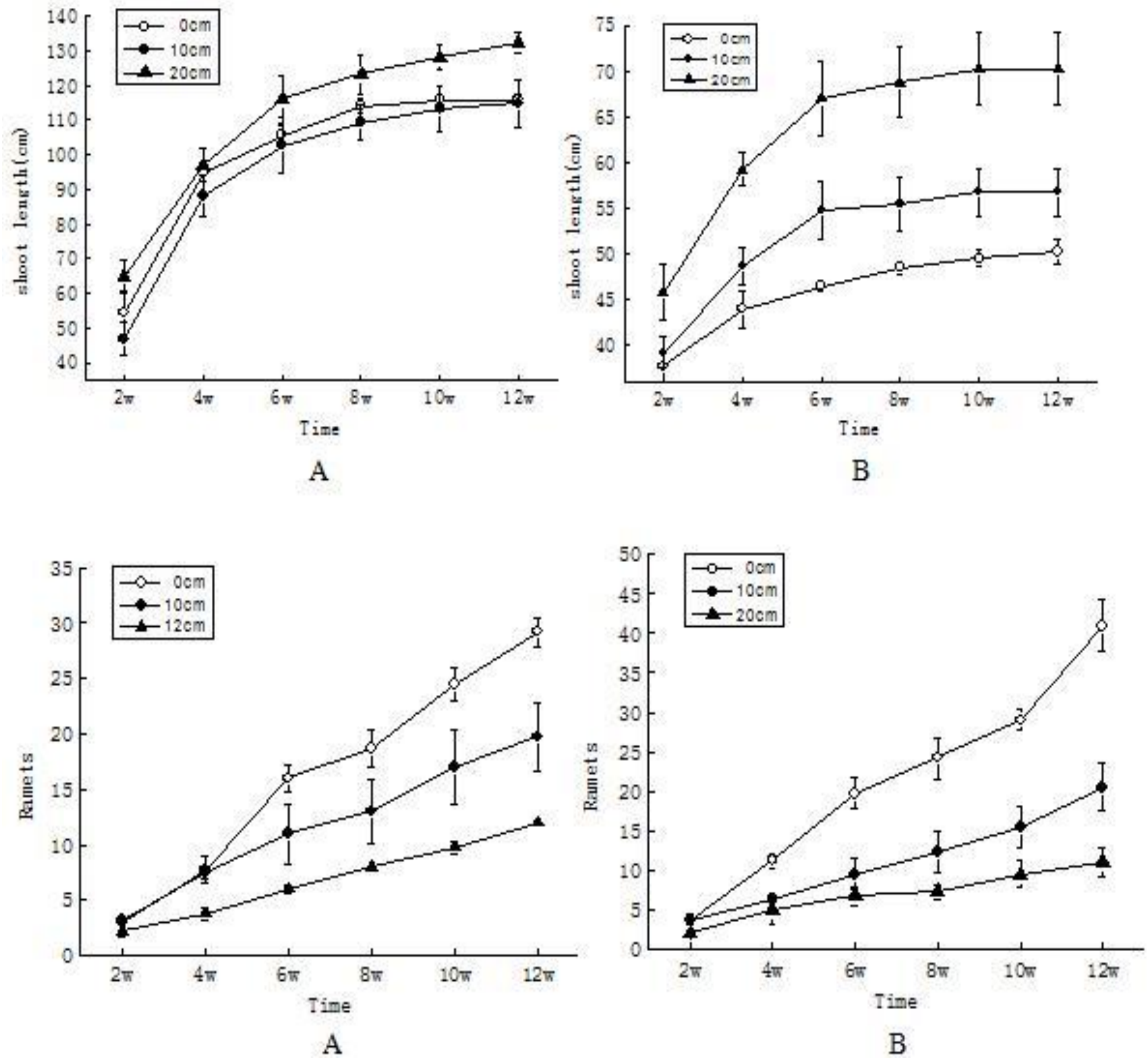


**Figure 3.** Changes of shoot length (cm) and ramets (means ± SE, n = 4) of C. *lasiocarpa* (A) and C. *limosa* (B) growing in three water levels during 12 weeks.

(Clevering et al., 1996; Sorrell et al., 2000; Striker et al., 2008). Root characteristics, which were beneficial for long-distance transportation of gases, were considered to be important for wetland species to acclimate to anoxic soil environments (Sorrell et al., 2000; Colmer, 2003). In our experiments enhanced water level could significantly increase root porosity in both species, which indicates that more extensive root lacunar systems were developed in the deep water-level in two species and this was an important adaptive adjustment in oxygen-deficiency environments (Laan and Blom, 1990; Maricle and Lee, 2007). Therefore *C*. *lasiocarpa* and *C. limosa* were suitable to grow in high water level environments and they had very similar niche in Sanjiang plain. But there were no differences in porosity between two species ($P$>0.05 Table 1, Figure 2), indicating that they had the same capacity of transportation oxygen, which is inconsistent with the authors hypothesis 1.

Shoot length and relative shoot growth rate in *C***.** *lasiocarpa* were much higher than those in *C*. *limosa* ($P$<0.05 Figure 4). Higher shoot length and higher relative shoot growth rate could help the plant recontact with the atmosphere more quickly, and hence allowing internal oxygen transport to submerged organs during flooding

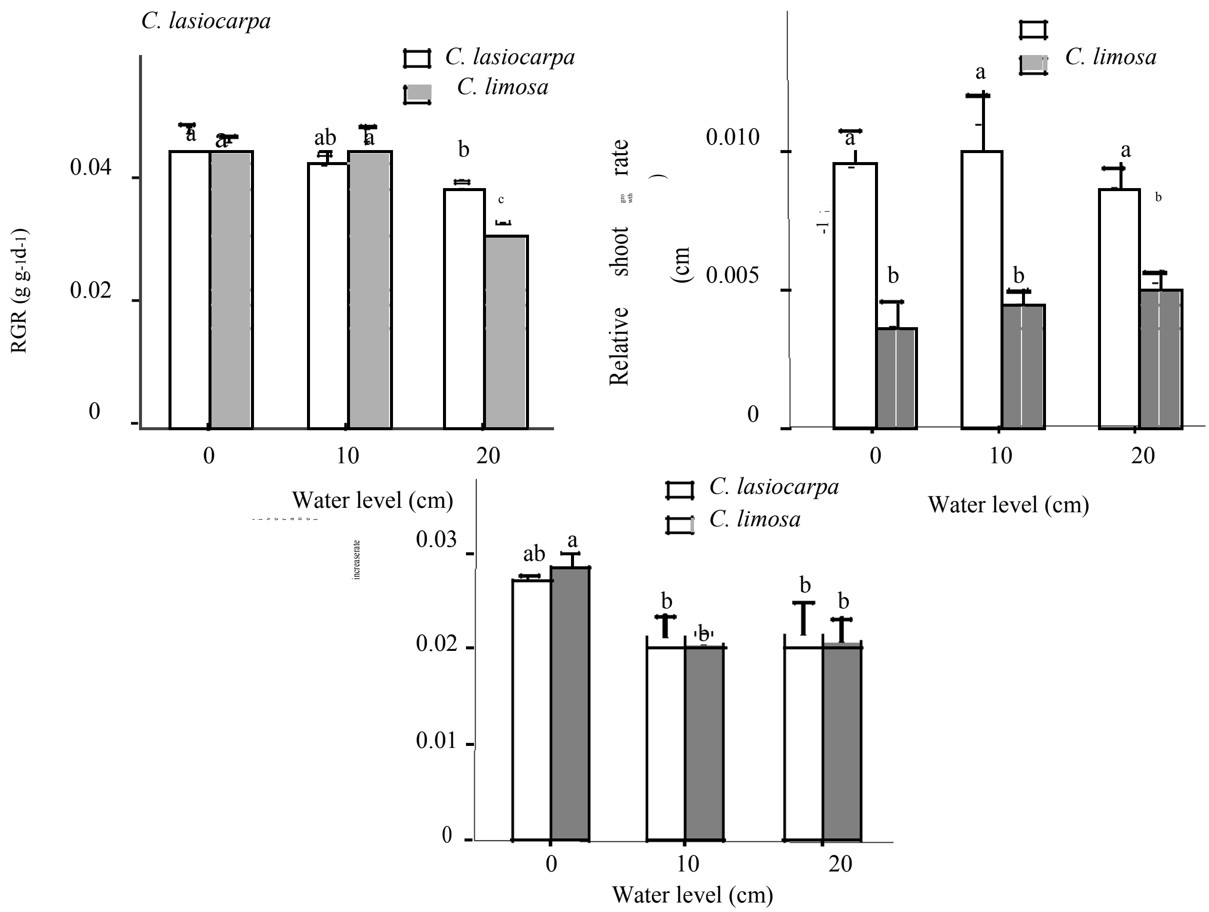


**Figure 4.** Relative growth rate (g g $^{-1}$d$^{-1}$), Relative shoot growth rate (cm cm$^{-1}$d$^{-1}$ ) and Relative ramets number increase rate (means ± SE, n = 4) of **C. *lasiocarpa* and C. *limosa*** growing in three water levels. Different letters indicate significant differences among treatments (*P*<0.05).

periods (Blom and Voesenek, 1996). Therefore, these traits may help *C*. *lasiocarpa* growth well especially under deep water conditions than *C*. *limosa*, so *C*. *lasiocarpa* had more extensive distribution areas than *C*. *limosa* in Sanjiang plain. In conclusion, higher root porosity of *C*. *lasiocarpa* and *C*. *limosa* might suggest that both species were beneficial to supply oxygen to root system, so these species were suitable to grow in deep water and they had the very similar niche. In 20 cm water level, higher biomass accumulation, relative growth rate, shoot length and relative shoot growth rate in *C*. *lasiocarpa* suggested that this species was more suitable to growth under deep water conditions than *C*. *limosa*. Thus, *C* . *lasiocarpa* might have higher competitive ability than *C*. *limosa*, and it could explain why the distribution area of *C*. *lasiocarpa* was larger than *C*. *limosa*.

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