



The Effects of Soil Drying on the Growth of a Dominant Peatland Species, *Carex lasiocarpa*

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Abstract The drying of wetlands due to natural and anthropogenic factors has become a serious problem globally. Understanding the tolerance of the dominant hygrophytic plants to drought would help in establishing effective management for the maintenance, protection and restoration of wetlands. We conducted a greenhouse experiment to explore the effect of soil drought on the growth of *Carex lasiocarpa*, a dominant species in peatlands in northeastern China. Three different drought treatments were included. The soil water contents were measured. Results showed that there was little impact of shorter drying treatment on the morphological and physiological characteristics of *C. lasiocarpa*, but significant impact of longer drying treatment on it. The negative effects of longer drying treatment on belowground growth were much higher than aboveground. Drying not only decreased the biomass but also changed the resource allocation, decreasing the root:shoot ratio. The rhizome length of *C. lasiocarpa* significantly decreased, and the tiller number also showed a decreasing trend. Our results suggest that this species could resist soil drying. But continuous soil drying would reduce carbon accumulation and increase carbon allocation aboveground,

which would result in a decline in carbon storage in *C. lasiocarpa* peatlands.

Keywords Biomass allocation · Root length · Specific leaf area · Wetland degradation

Introduction

Extreme climate events such as warming, flooding and drought are increasing in frequency because of global and/or regional climate change (Goswami et al. 2006; Smith 2011). Wetland ecosystems are reported to rapidly degrade due to water shortage caused by the increasing drought (Kim et al. 2008). Furthermore, other natural factors, such as tectonic movement of the earth's crust, environmental change of frozen soil etc. (Zámolyi et al. 2010), as well as the anthropogenic effects such as drainage and harvesting of peat (Chimney and Goforth 2006), have resulted in extensive drying of wetlands throughout the world (Han et al. 2012).

The structure and function of wetland ecosystems are highly dependent on water levels, so the effects of drying may be detrimental (Haapalehto et al. 2014). As flooding is reduced, changes in wetland ecosystems occur not only because of the altered hydrologic process themselves, but also from degradation of the dominant species (Hou et al. 2009). Mesophytes and even xerophytes invade wetland ecosystems (Li et al. 2012), replacing hygrophytes and accelerating the succession of wetlands to grasslands or forests. The invasion of shrub and tree seedlings is now regarded as a common and major problem for herbaceous wetlands (Pellerin et al. 2009). The species diversity of a degraded wetland can increase (Maanaviilja et al. 2014) or decrease (Pellerin et al. 2009), but it is clear that many endemic species of wetlands have disappeared because of degradation (Hou et al. 2009). In addition, the soil carbon

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sequestration capacity of wetlands decreases due to drying, which ultimately led to these ecosystems transform from stable carbon pools to a major carbon source, further contributing to global warming (Dommain et al. 2014). Degradation of wetlands may lower the ability of the regional ecosystems to self-regulate, resulting in an increasing occurrence of extreme environmental events, such as flooding or drought (Dixon 2002).

The dominant species is one of the most important factors in maintaining the structure and function of a wetland ecosystem, and the wetland function may change completely if the dominant species disappears. Some intervention measures have been performed to prevent and/or reverse wetland degradation (Haapalehto et al. 2014). Greater economic resources are required to restore a similar functional community if the dominant species has been already replaced, creating financial obstacles, which often restrict the wetland restoration projects in developing counties.

During the process of soil drying, plants show morphological and physiological responses, some of which reduce the damage caused by drought. Under even drier conditions, plant survival will be threatened (Li et al. 2014). Since the disappearance of dominant species can only occur if the drought continues, applying appropriate human intervention before the disappearance of a dominant species can greatly reduce the restoration effort needed. Understanding the tolerance of the dominant wetland plants to drought and their responses to soil drying will help us to understand the mechanism of wetland succession under a changing hydrological environment and contribute to the development of effective management regimes for the maintenance, protection and restoration of wetlands.

Carex lasiocarpa Ehrh., a rhizomatous perennial herb, is widely distributed in northern temperate and subarctic wetland areas, and is a dominant species of peatlands in northeastern China (Zhao 1999). As this species plays an important role in the succession of peatlands, many studies have been conducted in the *C. lasiocarpa* community, including soil characteristics (Gao and Lu 2002), litter decomposition (He 2003; Hou et al. 2012) and nutrient cycling (He and Zhao 2001; Hou et al. 2012). The ability of *C. lasiocarpa* to respond to environmental change, especially soil drying, is likely to be limited. As an indicator species for hydrological condition in wetland (Godwin et al. 2002), *C. lasiocarpa* is sensitive to the changes of water environment (Luo et al. 2008). The degeneration of *C. lasiocarpa* could reduce the species diversity of the community and ultimately alter the ecological balance of peatland ecosystems (Ji et al. 2004; Lou and Zhao 2008).

We conducted a greenhouse experiment to investigate the biomass, clonal growth (tiller number and rhizome length) as well as morphological and physiological responses to simulated drought on *C. lasiocarpa*. The objectives of this study were (1) to determine what degree of soil drought

C. lasiocarpa could endure under our experimental conditions, (2) how the morphological and physiological traits of this species respond to different drought intensities. Results from our experiment could help making effective approaches for maintaining and restoring peatlands dominated by this or similar species.

Materials and Methods

Plant Collection and Experiment Site

Seedlings of *C. lasiocarpa* were collected in May 2014 from Longwan National Nature Reserve (42°22'N, 126°25'E), Jilin province, China. The plants were cut from peat soil, separated into individual seedlings with roots, and transported to a greenhouse located in Northeast Normal University, Changchun (43°49'N, 125°25'E). Plants were transplanted individually into plastic pots (6.5 cm in length × 6.5 cm in width × 6.5 cm in height). All the original shoots were cut to help establish a new tiller and roots. The soil was kept moist for the following 70 days, and the temperature in the greenhouse was between 22 and 30 °C. Light mainly come from high-pressure sodium lamps (GE LU400/HO/T/40) producing 400–700nm spectrum suitable for plant growth.

Experiment Design

After 60 days, a total of 75 plants of similar size were chosen and transplanted individually into pots (6 cm in length × 6 cm in width × 15.5 cm in height) filled with 1:1 volumetric mixture of field peat and commercial peat soil. After 10 days growth, all 75 plants were randomly divided into 3 groups of 25 plants. There were three different drought treatments: flooded for 60 days (control; CR), dried for 20 days after 40 days flooding (D20), dried 40 days after 20 days flooding (D40). After water drainage, four pots of the D20 and D40 treatments were weighed every 3 to 5 days. At the end of experiment, we measured the weight of soil after drying at 120 °C for a minimum 24 h. Changes in soil water content in D20 and D40 treatments were then calculated with the plant weight excluded.

The water level of the *C. lasiocarpa* natural communities in Longwan National Nature Reserve is 0–10 cm (unpublished data). Since the goal of our study was to explore the effect of drying stress, not flooding, on plant growth, the water level of all flooded treatments was kept at 2 cm above soil surface.

Measurements

After 60 days, the average height of vegetative tillers (no reproductive tiller were formed over the course of the experiment during the experiment), tiller number and leaf number

were recorded for all plants. Ten plants within each treatment were randomly selected for the morphological measurements. The aboveground parts were cut and the roots washed and cleaned. Three or four mature leaves per plant, as well as all the rhizome and non-rhizome roots, were scanned. Leaf area, root length and root surface area were determined by Winrhizo and Winfolia software (Gu et al. 2010). All material was then dried for at least 48 h at 65 °C and weighed to obtain aboveground biomass (AB, including biomass of scanned leaves and other aboveground materials), belowground biomass (BB, including rhizome and non-rhizome root biomass). Then total biomass, root:shoot ratio, specific leaf area and rhizome: non-rhizome root biomass ratio of each plant was calculated.

In order to understand the physiological response of *C. lasiocarpa* to continuous drying after water drainage, 5 randomly selected plants were used to measure leaf chlorophyll content (Zhang et al. 2013), 5 plants were used to measure leaf proline content (Xiao et al. 2005), and 5 plants were used to measure the contents of malondialdehyde (MDA) and soluble sugar (Lin et al. 2012) for both leaves and roots. All physiological measurements were performed on five replicate plants.

Data Analysis and Statistics

Data were log-transformed when necessary to achieve homogeneity of variances. A series of one-way ANOVA tests were used to explore whether the differences in the variables were significant among the treatments. Mean comparisons were tested with LSD method. Significance level is 0.05. All analyses were conducted with SPSS version 17.0 software.

Results

Soil Water Content

The soil water content decreased continually with the increase in drying days. When the plants were harvested, the soil water content of D20 treatment ($55.84 \pm 0.83\%$) was significantly higher than that of D40 treatment ($49.44 \pm 1.19\%$); $t = 6.749$, $P = 0.007$ (Fig. 1).

Biomass and Root:Shoot Ratio

The total, aboveground and belowground biomass of *C. lasiocarpa* decreased with drying after water drainage. There were significant differences in total, aboveground and belowground biomass between flooded and D40 treatments, but the D40 treatment was not significantly lower than D20 (Table 1, Fig. 2a). The root:shoot ratio of *C. lasiocarpa* was also decreased by drying (Table 1, Fig. 2b).

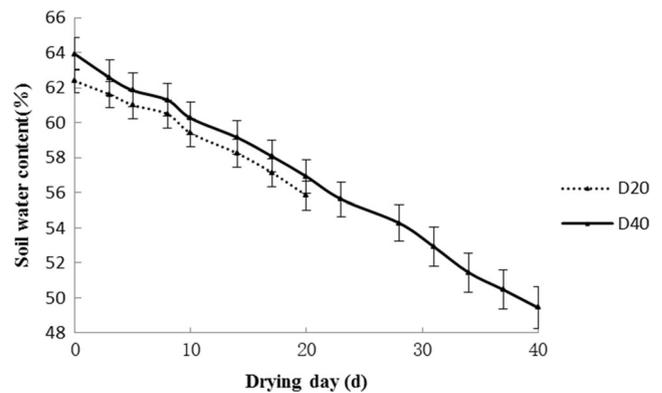


Fig. 1 Changes in soil moisture content over 20 (dotted line) and 40 (solid line) days after water drainage. Data were shown as mean \pm 1.0 SE

Morphological Variables

Drying significantly decreased plant height, although there was no significant difference between the D20 and D40 treatments (Table 1, Fig. 3a). The specific leaf area of plant increased in drying treatments, but a significant difference compared to the control only occurred in the D40 treatment (Fig. 3b). Compared to the control, the leaf number and tiller number increased in D20 treatment but decreased in D40 treatment, and caused a significant differences between the two drying treatments. The changes in both showed little difference from the flooded plants, however (Fig. 3c, d).

The root length and root surface area of *C. lasiocarpa* in the control treatment were similar to plants in D20 treatment, but significantly higher than plants in the D40 treatment (Fig. 4a, b). D40 drying treatment markedly decreased the growth of rhizomes, but the difference of rhizome length between D20 and control treatment was not significant due to the large variation among replicates ($t = 1.915$, $P = 0.092$). There were no significant differences of the ratio of rhizome to non-rhizome roots among treatments when one-way ANOVA was analyzed (Table 1). However, the ratio of rhizome to non-rhizome roots in D20 drying treatments was significantly lower than that in control plants when t -test was analyzed ($t = 2.608$, $P = 0.031$, Fig. 4d).

Physiological Measurements

Both the chlorophyll and the proline content of fresh leaves in plants from D40 treatment were significantly higher than those of control plants. There were no significant differences between D20 and control treatment (Table 1, Fig. 5a, b).

The soluble sugar content of leaves was significantly higher than those of roots for all treatments (CR: $t = 5.231$, $P = 0.006$; D20: $t = 12.107$, $P < 0.001$; D40: $t = 4.086$, $P = 0.015$). Leaf and root soluble sugar content of D40 were

Table 1 One-way ANOVA on the effect of drying on biomass, morphological and physiological attributes of *C. lasiocarpa*

Index		MS	F	P	
Biomass	Aboveground biomass (g)	0.042	4.414	0.022	
	Belowground biomass (g)	0.166	6.296	0.006	
	Total biomass (g)	0.069	5.564	0.009	
	root:shoot ratio	0.040	4.462	0.021	
Morphological indices	Plant height (cm)	570.233	8.614	0.001	
	Specific leaf area (cm ² /g)	294.265	3.413	0.067	
	Leaf number	50.800	2.834	0.076	
	Tiller number	11.233	4.272	0.024	
	Root length (m)	0.368	8.263	0.006	
	Root surface area (cm ²)	0.310	8.209	0.006	
	Rhizome length (cm)	0.852	4.132	0.043	
Physiological indices	Leaf	Chlorophyll content (mg/g)	1.033	8.024	0.006
		Proline content (μg/g)	1.535	21.794	<0.001
		Malondialdehyde content (μmol/g)	0.465	7.644	0.007
	Root	Soluble sugar content (mmol/g)	0.148	10.095	0.003
		Malondialdehyde content (μmol/g)	0.038	4.589	0.033
		Soluble sugar content (mmol/g)	0.020	23.471	<0.001

both markedly higher than those of the other two treatments. There were no significant differences in leaf soluble sugar contents between D20 and control treatment, but the root soluble sugar content of D20 was lower than roots of the control (Fig. 5c). Malondialdehyde content of the roots in both drying treatments was lower than that of the flooded plants. The malondialdehyde content of leaf under D20 was markedly lower than the control, but increased in D40 treatment. The difference between the D40 and control treatment was not significant. The malondialdehyde contents of leaf were similar to those of roots in CR and D20 treatments (CR: $t = -0.680$, $P = 0.534$; D20: $t = -2.568$, $P = 0.062$), and significantly different in the D40 treatment ($t = 2.894$, $P = 0.044$; Fig. 5d).

Discussion

Drying Not Only Decreased Biomass but Also Changed Resource Allocation

Compared with the two drying treatments, the aboveground, belowground and total biomass of *C. lasiocarpa* were highest in control (continuous flooding) treatment (Fig. 2a), which indicates the importance of flooding for the growth of this species. Only when the water level is very high for a prolonged period, creating low soil oxygen levels, is the growth of *C. lasiocarpa* inhibited (Zhang et al. 2014). Short-term water deficiency had little effect on the biomass

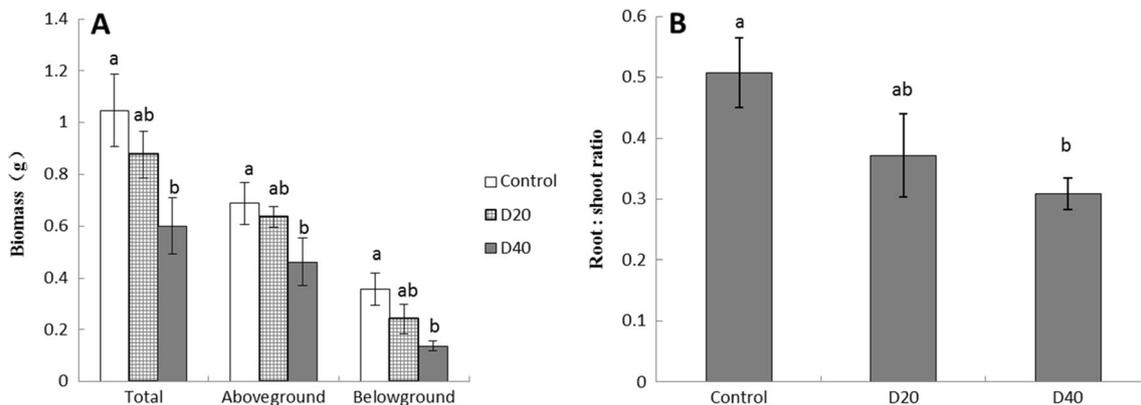


Fig. 2 Total (TB), aboveground (AB) and belowground (BB) biomass (a) and root:shoot ratio (b) of *C. lasiocarpa* in flooded (Control), drying for 20 (D20) and 40 (D40) days after water drainage. Different letters indicate significant differences among treatments. Error bars represent ± 1.0 SE

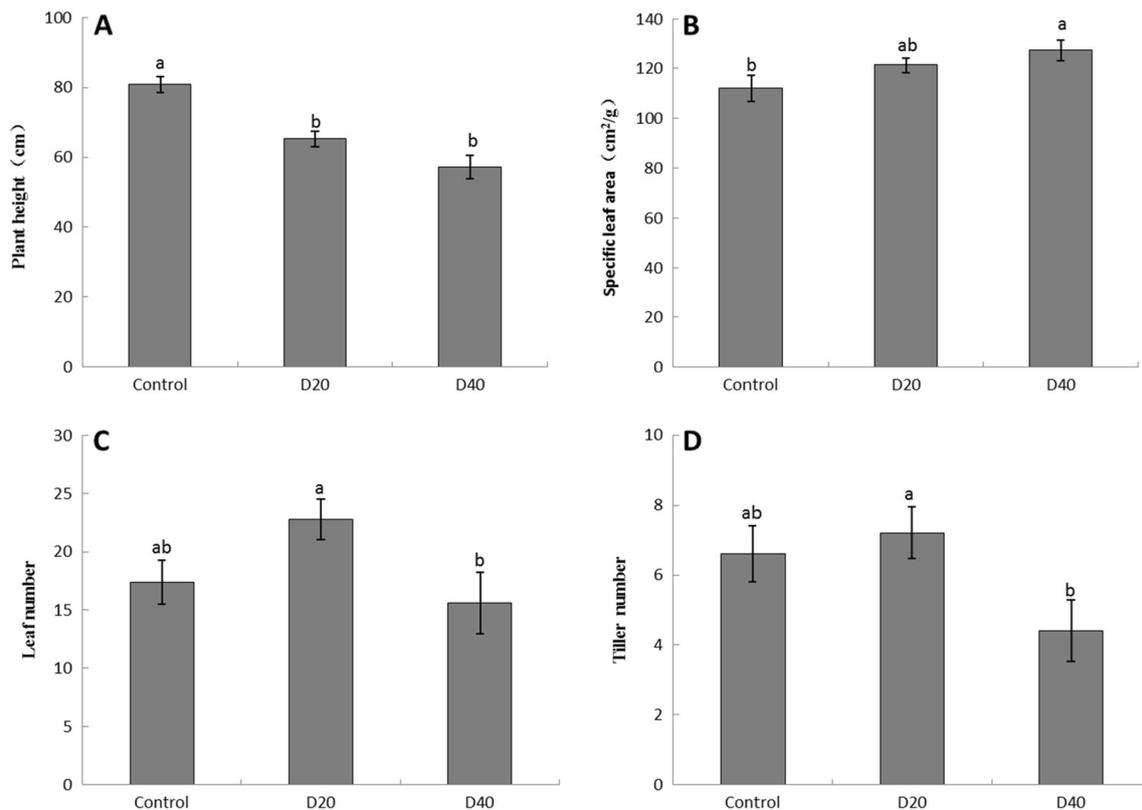


Fig. 3 Plant height (a), specific leaf area (b), leaf number (c) and tiller number (d) of *C. lasiocarpa* in flooded (Control), drying for 20 (D20) and 40 (D40) days after water drainage. Different letters indicate significant differences among treatments. Error bars represent ± 1.0 SE

accumulation of *C. lasiocarpa* (Fig. 2a), indicating that this species had the ability to tolerate soil drying to some extent. The aboveground, belowground and total biomass of *C. lasiocarpa*, was not affected by short-term drying process (Fig. 2a) although plant height was affected (Fig. 3a). The growth of the *C. lasiocarpa* was severely inhibited when drying continued for 40 days and the soil water content decreased to $49.44 \pm 1.19\%$. Even though the soil water content remained higher than the wilting point, which is 37.81% for sedge peat (Feustel and Byers 1936), both biomass and plant height decreased significantly (Figs. 2a, 3a). The negative effect of 40 days drying on belowground growth was much higher than that aboveground as the root: shoot ratio decreased significantly (Fig. 2b), which means that relatively more photosynthate was allocated to the aboveground parts. Compared with the organic carbon in roots, the organic carbon in leaves usually decomposes more easily and quickly into dissolvable or suspended forms, which can leave the ecosystem (Fujii and Takeda 2010).

C. lasiocarpa is a dominant species in many boreal wetlands, especially in peatlands where huge amounts of carbon are stored (Zhao 1999). If the flooding environments disappear because of extreme droughts or management, the carbon sequestration and storage abilities of the entire system will decline due to respiration by microorganisms (Jaatinen et al. 2008), the weakened carbon accumulation by the dominant

species (Dinsmore et al. 2009) and greater carbon allocation to easily decomposed aboveground organs (Wang et al. 1999). The carbon fixed by photosynthesis will be released more quickly as CO_2 due to decomposition, or leave the systems through leaching (Sulzman et al. 2005), further reducing the function of the peatland as a carbon sink.

The root:shoot ratio was highest in control flooding environment (Fig. 2b), which was consistent with the previous conclusion that flood-enduring plants would allocate more biomass to roots under flooding conditions (Ye et al. 2003). Optimal allocation theory predicts that plants normally tend to allocate more resources to the organs which could capture the most limited resource. For example, more biomass will be allocated to leaves when plants growing under shaded conditions, which results in decreased root:shoot ratio. While more biomass will be allocated to roots when plants growing in nutrients and/or water restricted condition (Touchette et al. 2008). However, for this hydrophytic plant, the limiting factor for roots in aquatic environment is not nutrients but oxygen (Koop-Jakobsen and Wenzhöfer 2014). As an important part of the convective gas-through flow system to supply oxygen (Huang et al. 2012), the rhizome of flooding plants grew longer than those suffering drought (Fig. 4c), indicating more resources were allocated to increase the amount of aerenchyma (Zou et al. 2007). Compared with fine roots capturing nutrients and water, rhizomatic roots are much heavier,

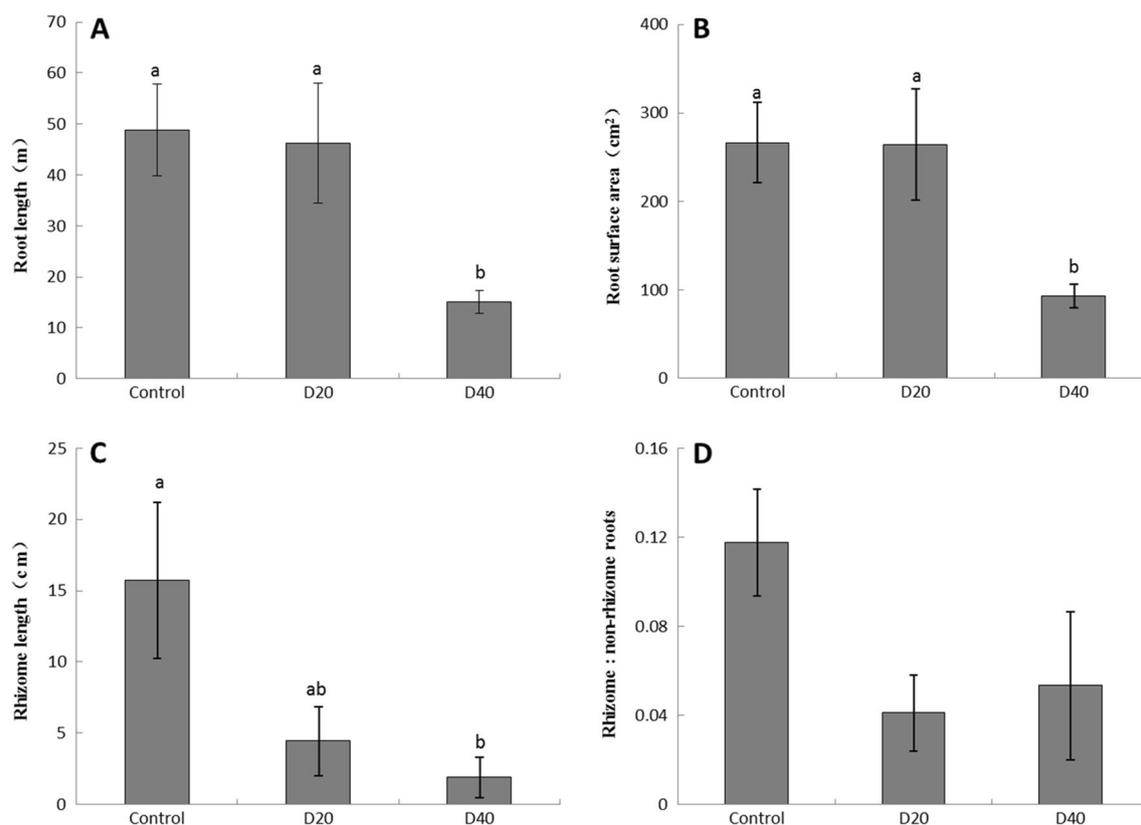


Fig. 4 Root length (a), root surface area (b), rhizome length (c), and rhizome: non-rhizome roots (d) of *C. lasiocarpa* in flooded (CR), drying for 20 (D20) and 40 (D40) days after water drainage. Different letters indicate significant differences among the treatment. Error bars represent ± 1.0 SE

resulting in the high root:shoot ratio of plants in the control treatment (Fig. 2b).

Drying Reduced Clonal Growth

The rhizome length of *C. lasiocarpa* significantly decreased after 40 days of drying (Fig. 4c), and the tiller number also showed a decreasing trend (Fig. 3d), suggesting suppressed clonal growth of this species under drought. In boreal peatland ecosystems, clonal growth via rhizomes maintains plant communities, as recruitment from seeds is very rare (Infante Mata and Moreno-Casasola 2005). Inhibition of rhizome growth under drying will reduce the maintenance and renewal of *C. lasiocarpa* populations. One of the most common consequences for peatlands after drainage is the degradation of the hygrophytic vegetation followed by invasion by several xericspecies (Li et al. 2012). With the help of seed or vegetative reproduction, these species could outcompete the weakening hygrophyte species and/or occupy the empty patches where the hygrophytes fail to maintain themselves. Reduced clonal growth of *C. lasiocarpa* under drought suggests that a reduction of this dominant species' population size may accelerate successional changes in the species composition and community structure.

Drying Changed Morphological and Physiological Characteristics

After 40 days of drying, most morphological and physiological variables changed significantly, and the root growth of *C. lasiocarpa* was severely inhibited (Fig. 4a–c). The contents of proline and soluble sugar in leaves as well as soluble sugar content of root were significantly higher in the D40 treatment than in the other treatments, suggesting that the physiological activities of *C. lasiocarpa* had been affected by drought stress, with a positive response after 40 days drying. The most effective way for plants to response to drought stress is to maintain their osmotic potential. As effective osmotic adjustment substances, the proline and soluble sugar were often directly involved in osmotic regulation to improve the cell osmotic potential and maintain cell turgor (Li et al. 2014).

The malondialdehyde content of leaves was higher than that of roots after 40 days drying, indicating a stronger negative effect of drought on leaf function. This could be because of increased difficulty in water transportation from root to leaf due to decreasing osmotic pressure gap in D40 than in D20 and CR (Li et al. 2014). As a product of membrane lipid peroxidation, the increasing MDA content of leaves can influence the growth of plants greatly. MDA can reduce the

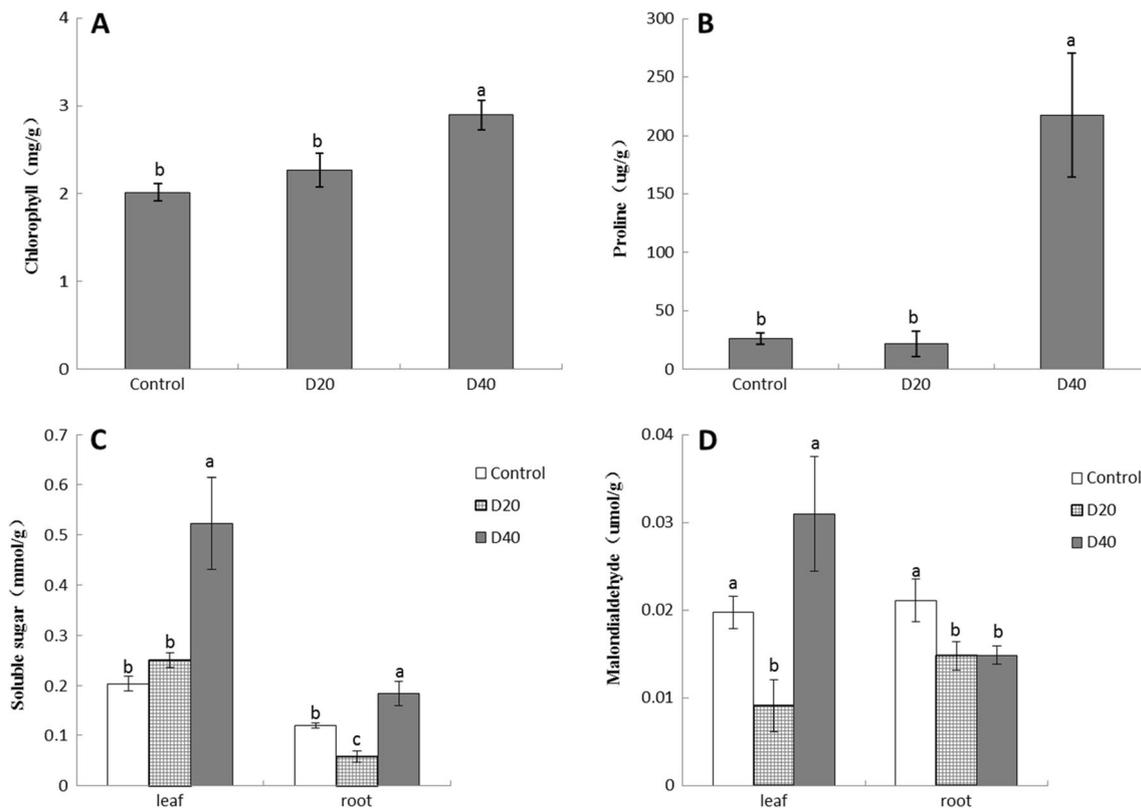


Fig. 5 The chlorophyll (a), proline (b), soluble sugar (c) and malondialdehyde (d) contents of *C. lasiocarpa* in flooded (CR), drying for 20 (D20) and 40 (D40) days after water drainage. Different letters indicate significant differences among treatment. Error bars represent ± 1.0 SE

photosynthetic carboxylase activity (Lin et al. 1989), inhibit photosynthesis (Zeng and Wang 1989), and promote the dark respiration rate (Li et al. 1988). Therefore, even though specific leaf area of plants in D40 treatments increased significantly (Fig. 3b), decreasing the cost of making photosynthetic area, and the chlorophyll content increased significantly (Fig. 5a), biomass production did not increase (Fig. 2a). Although some studies suggest that plant chlorophyll content is positively related to photosynthesis rate (El-Hendawy et al. 2005), the photosynthetic ability and biomass accumulation of plants cannot be predicted from leaf chlorophyll content when the plant is under stress (Zhou et al. 2010).

Unlike the D40 treatment, twenty days of drying had little impact on the morphological (Fig. 3a) and physiological (Fig. 5c, d) characteristics of *C. lasiocarpa*. As we mentioned above, malondialdehyde is a product of membrane lipid peroxidation when plants are growing in a sub-optimal environment. Lower malondialdehyde content of D20 treatment than control indicated that short drying period or lower flooding level might do less damage on membrane. But it would not be appropriate to conclude that a short drying period is advantageous for the survival and growth of this species, as there was no positive effects of D20 on any other measure of growth. Compared with D20, the higher malondialdehyde content in leaves of flooding plants suggests that this species is sensitive

to the change of hydrological environment, especially the degree of flooding. More detailed studies on the effect of flooding and drought conditions on the survival and growth of this species are needed (Luo et al. 2008).

Conclusions

The growth of *C. lasiocarpa* was highly affected by a reduction in flooding which will result in a degradation of peatlands in northeastern China. Results from our greenhouse experiment showed that the biomass, clonal growth as well as morphological and physiological characteristics were all affected by the simulated drought treatments. This species has some resistance to soil drying. If soil drying continues, reduced carbon accumulation and increased partitioning of carbon to aboveground growth might promote a decline of carbon storage capability in peatland dominated by *C. lasiocarpa*. The inhibition of clonal growth of this dominant species due to soil drying will accelerate successional change in the community. Further field studies and the effect of different flooding/or drying regimes on the survival, growth and reproduction of this species will help us better understanding the response of peatlands to drought and other extreme climate events.

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