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# Changes of Photosynthetic Activity and Carbohydrate Content in Resurrection Plant *Caragana korshinskii* during Dehydration and Rehydration

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## ABSTRACT

The effects of extreme drought stress and subsequent re-hydration on photosynthetic activity and carbohydrate content were investigated in resurrection plant *Caragana korshinskii*. Extreme drought stress was imposed by withholding water and covering plants with a polyvinyl chloride sheet during rain 53 days after all leaves had shed. Thereafter, plants were watered at 7-day intervals. Drought-induced leaf abscission and photosynthetic rate drastically decreased, while carbohydrate concentration increased in stems and in leaves prior to leaf abscission. Re-hydration promoted the emergence of new leaves, reactivated photosynthetic machinery function, and reduced soluble carbohydrate, sucrose and fructose concentrations. The results indicate that *C. korshinskii* plants are able to sustain drought stress through leaf abscission and carbohydrate concentration accumulation in stems. The high carbohydrate concentration in stems can stimulate the emergence of new leaves and regrowth if soil moisture reaches a normal level.

**Keywords:** leaf abscission, starch, total nonstructural carbohydrate

## INTRODUCTION

*Caragana korshinskii* is a perennial xerophytic shrub. It is well known for its ability to resist drought (Wang *et al*. 2006). In our study, we found that under severe drought stress, *C. korshinskii* shed all leaves and died away. After re-hydration, this plant can stimulate new leaves and re-growth. This plant is thus a resurrection plant. Many researches have assessed the anatomical, physiological and biochemical characteristics of *C. korshinskii* (Ma *et al*. 2004; Zhao *et al*. 2006), but no reports focus on the resurrection mechanisms after extreme drought.

Perennial plants of seasonal environments allocate a significant fraction of their photosynthetic output to long-term storage (Chapin *et al*. 1990). Perennating organs of these plants contain mobile carbohydrates, the level of which may undergo fluctuation in the course of the growing season (Schulze 1982). Studies of numerous plant species have shown that temporal variation in the level of nonstructural carbohydrates typically reflects a persistent imbalance between photosynthetic carbon gain and the activity of carbon sinks (Tissue and Wright 1995; Mirjam *et al*. 2005). The continued oversupply and accumulation of carbon suggests that storage carbohydrates have an important ecological role. If so, allocation to storage may bear on the lifetime fitness of the plant.

Allocation of photosynthate to long-term storage could fulfill several ecological functions (Chapin *et al*. 1990). The following hypotheses have been proposed to account for the functional significance of storage: (1) support of vegetative regrowth following dormancy (Menke and Trlica 1981), (2) support of sexual or vegetative reproduction during the absence or shortage of photosynthesis (Tissue and Nobel 1990), (3) recovery from herbivory (Danckwerts 1993), (4) survival during dormant periods and under shading (Kobe 1997). Additionally, stored carbohydrates may enable survival of habitat-specific disturbances, such as fire or flooding (Miyanishi and Kellman 1986) or experimental enrichment with atmospheric carbon dioxide ($CO_2$)( Rubén *et al*. 2006).

All of these hypotheses suggest why plants might at times rely on stored, rather than currently fixed carbon. Yet in most species, the degree to which each of these functions depends on stored reserves remains uncertain. Moreover, a number of studies have found little association between the level of available carbohydrates and plant performance with respect to one or more of these functions. Kroon *et al*. (1991) working with *Podophyllum peltatum* found no effect of reduced storage on plant growth and reproduction. Zimmerman and Whigham (1992) found no effect of corm severance in a terrestrial orchid, *Tipularia discolor*, on its ability to recover from defoliation. Similarly, Stenfanie *et al*. (2007) found that *Pinus uncinata* used current carbon compounds to build up new shoot and needle. In fact, a low-starch cultivar of alfalfa showed better re-growth than a high-starch cultivar (Boyce and Volenec 1992). Differences among cultivars in freezing tolerance, a trait related to winter hardiness and frequently attributed to osmotic action of carbohydrates could not be quantitatively explained by the level of soluble carbohydrates for alfalfa (Castonguay *et al*. 1995). In addition, in a number of plant species, carbohydrate mobilization during the period of greatest demand is only partial, leaving a considerable fraction of the storage pool unused (Menke and Trlica 1981).

Taken together, these negative results suggest a non-adaptive nature for carbohydrate storage. Such an explanation would be consistent with storage representing an evolutionary relic in carbon allocation pattern, and/or a temporary imbalance between carbon acquisition and use (Lipson *et al*. 1996) as expected if activity of carbon sinks is limited by other resources (Fichtner *et al*. 1994). It is also possible that a fraction of the storage pool could simply be anatomically sequestered and not available for withdrawal (Nissen and Foley 1986).

Here, by studying the drought stress and re-hydration induced changes in storage carbohydrate levels, we test hypotheses concerning the functional significance of carbo-

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hydrate storage especial of total non-structural carbohydrate (TNC) concentration in the ability of desert resurrection plant *C. korshinski*.

## MATERIALS AND METHODS

### Experimental site and treatments of water stress

The experiment was conducted at the biological plantation, Lanzhou University (latitude 36°01′N and longitude 104°09′E), where the mean annual temperature is 5-9°C and the mean annual precipitation is 324 mm. Three seeds of *C. korshinskii* were sown in each pot (25 cm in diameter and 30 cm deep) which were buried (60 pots were buried, 30 cm deep) under soil with a piece of plastic under the pot's bottom in the spring of 2005. After the emergence of seedlings, the plants were thinned to one per pot. Plants received natural rain from spring of 2005 to 14 May 2006. On 14 May 2006, plants were well watered. Twenty pots were selected for drought treatment (20 replications) and ten pots were selected for control treatment (10 replications). Drought was imposed by withhold water and covering plants with a polyvinyl chloride sheet when it rained during 53 days until all leaves abscised in 20 pots. Thereafter, plants were watered once a week for the next 41 days. The control treatment was natural rain and watering at 7-day intervals during the experiments.

### Soil and leaf relative water content

Samples for leaf relative water content analysis were taken nine times from the 20 study pot plants. Leaves or stems from at least 10 plants were collected. The leaves or stems (about 0.5 g fresh weight) were cut and weighed immediately to obtain the fresh weight (FW), and then placed in a beaker (25 mL), filled with water, and left overnight in the dark. They were then reweighed to obtain the turgid fresh weight (TW) the next morning and dry weight (DW) after drying at 80°C for 24 h in a drying oven. The relative water content (RWC) of the leaves could be calculated as $RWC = [(FW - DW)/(TW - DW)] \times 100\%$.

To monitor soil water content in the pots by the weighing method, we probed the 0-10 cm and 10-25 cm soil layers with a steel cylinder 1.2 cm in diameter and 5 cm in length. The soil samples thus obtained were dried at 80°C, and the soil water content (SWC), was calculated from the difference between the initial and dried soil weights (Mao *et al.* 2004).

### Photosynthesis

Diurnal photosynthetic rate was measured in *C. korshinskii* leaves and stems (after leaf abscission and before emergence of new leaves) during the period of water stress and subsequent re-hydration, with a Li-6400 portable photosynthesis system (LI-COR, Nebraska, USA) from 7:00 am to 19:00 pm.

### Carbohydrate concentration

Samples for carbohydrate analyses were collected at midday. Leaves and stems from at least 10 plants were collected, frozen in liquid nitrogen and lyophilized. Soluble sugar, starch, sucrose and fructose were determined using the method of Ebell (1969). All carbohydrate concentrations were expressed as the percentage dry weight (DW) and TNC data was the sum of the soluble sugars and starch (Thomas *et al.* 1996).

### Statistical analysis

Data management and statistical analyses were performed using SPSS 10.0 software (SPSS for Windows, Version 10.0). Means were expressed with their standard error (means ± SE) and compared by ANOVA using the LSD test at the 0.05 significance level.

## RESULTS

### Leaf and soil water status

To confirm the effectiveness of water stress treatment imposed on *C. korshinskii* plants, leaf and soil water content were determined during the period of water deprivation and subsequent re-hydration. Leaf and soil water content showed large differences: soil water content changed from 87% to 2% at 0-10 cm and from 91% to 13% at 10-25 cm while leaf water content changed from 89% to 10% during the water stress period. Unlike the rapid decrease of soil water content, leaf water content decreased slowly over 42 days after treatment. It should be noted that the reduction of leaf water content was not drastic despite the severity of the stress imposed. Re-watering applied at 54 days after treatment induced a rapid recovery of soil water content, but stem relative water content did not recover until the new leaf budded (**Fig. 1**).

### Photosynthesis

Net assimilation rate (*A*) maintained a high level with the maximum around 20 µmol $m^{-2}$ $s^{-1}$ during 3 days after treatment (**Fig. 2A**). *A* showed bimodal behavior. The first peak was at mid-morning while the second peak was at 13:00 to 14:00 pm. This indicated that *C. korshinskii* has a midday depression phenomenon under normal water conditions. At noon, under saturating photosynthetically active radiation (PAR) and high leaf temperature ($T_L$) (**Fig. 3**), *A* declined. In the afternoon, *A* recovered slightly in association with a decrease in $T_L$. Forty-two days after treatment, there were no significant differences (at 0.05 significance level) between the time of day in the afternoon. The second peak disappeared. Water stress altered $CO_2$ assimilation and induced a progressive decrease of photosynthetic rate in the stem after leaves abscised. Re-watering stimulated gas exchange which showed a normal pattern after 9 days (**Fig. 2B**).

### Soluble carbohydrate

Water stress did not cause a significant increase in soluble sugar content in leaves and stems during the first 42 days after water shortage (**Fig. 4A**). This treatment reduced significantly the increase in soluble sugar content from the 42nd day and reached a maximum after leaf abscission (53 days after treatment). On the contrary, re-hydration caused a

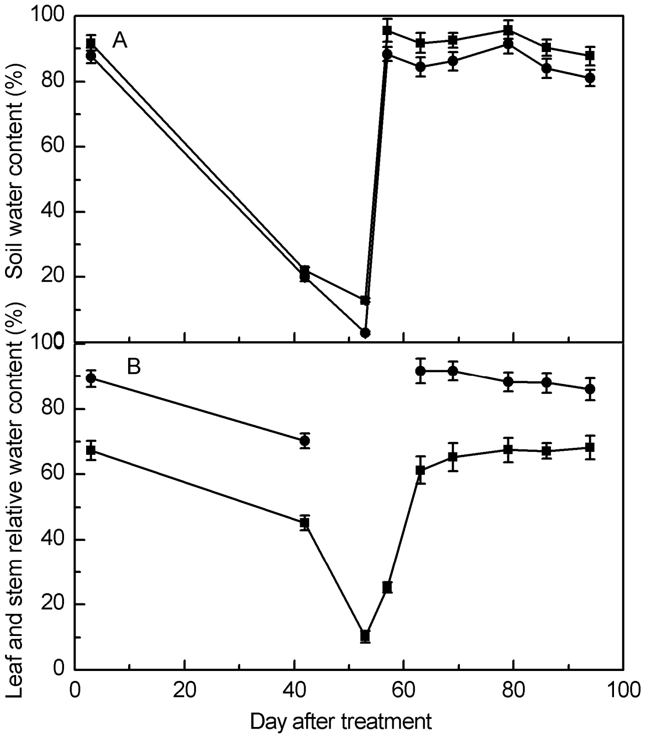

**Fig. 1** Soil water content (**A**) in 0-10 cm (●) and 10-25 cm (■) and leaf (●) and stem (■) relative water content (**B**) during experiment. Data = means ± SE (n = 9).

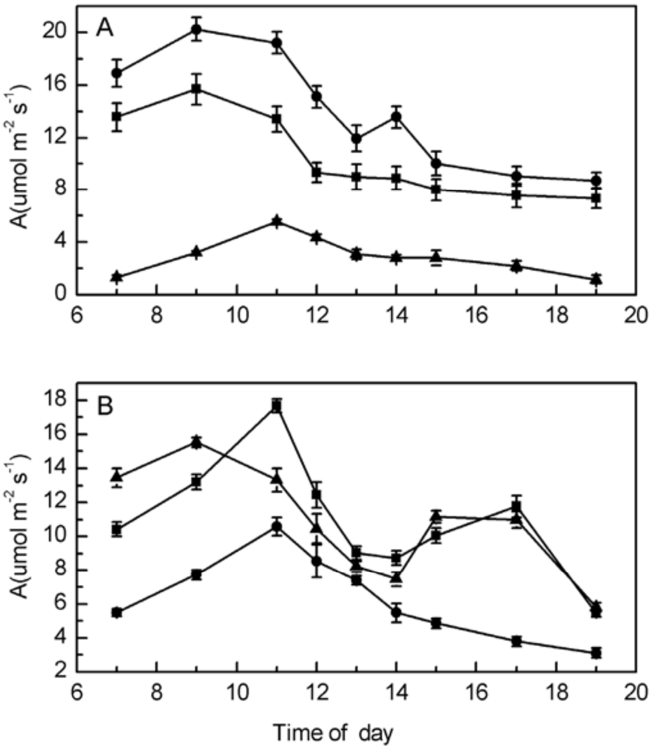

**Fig. 2** Diurnal changes of net photosynthetic rate (A) during water stress (**A**) and re-hydration (**B**), ●, ■ and ▲ indicate 3, 42 and 53 and 57, 63 and 79 days after treatment respectively. Data = means ± SE (n=8).

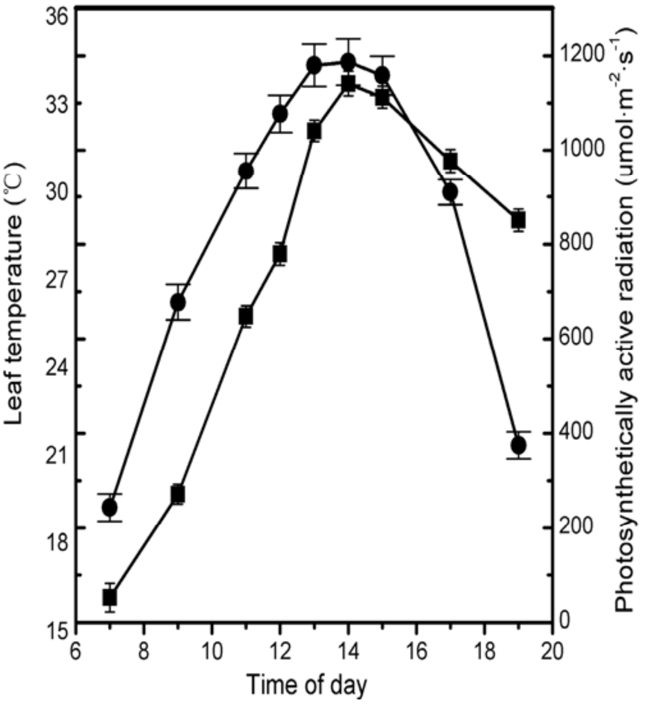

**Fig. 3** Diurnal variations of leaf temperature (■) and photosynthetically active radiation (●) on May 18, 2006 at experimental site. Data = means ± SE (n=8).

significant decrease of soluble sugar in the stem during the first 9 days after re-watering. Compared with the content at the beginning of the 3rd day, this parameter reached constant and normal values at the end of the experimental period.

## Starch and total non-structural carbohydrates (TNC)

Water stress caused a progressive increase in starch and total non-structural carbohydrate content in leaves during the first 42 days and in the stem during the whole water stress period (**Fig. 4B, 4C**). Both starch and total non-structural carbohydrates in the stem reached maximum values on the 3rd day after re-watering. But these parameters decreased rapidly thereafter until 69 days after treatment; from the 69th day on, these two parameters maintained constant values until the end of the experiment. In leaves, the changes in these two parameters were complicatedly after re-hydration. On the 9th day after re-watering, they reached maximum values. Compared with the starch and total non-structural carbohydrate contents at the beginning of the 3rd day after treatment, the increase was by about 60% and 58%, respectively. In this study, more than 60% of TNC was starch in most cases (**Fig. 4B**), while at 3 days after re-hydration, this value reached more than 80%.

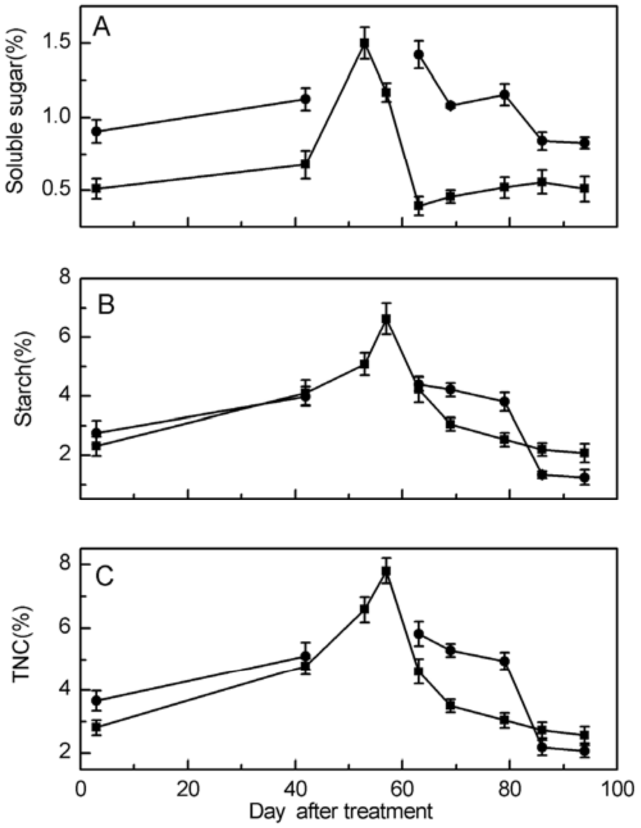

**Fig. 4** Percent of dry weight of soluble sugar (**A**), starch (**B**) and total nonstructural carbohydrate (**C**) content in leaf (●) and stem (■) during experiment. Data = means ± SE (n=6).

## Sucrose

Water stress caused a progressive increase in sucrose content in the stem during the whole water stress period and did not affect the content in leaves during the 42 days after treatment and a high level was observed during the end of this period (**Fig. 5A**). Re-hydration caused this parameter to decrease rapidly in the stem and leaves and to reach normal levels at 25 days and 40 days, respectively in these two organs.

## Fructose

The changing pattern of fructose content in the stem during the water stress and re-watering periods was similarly to that of TNC and starch, with a steady increased during the water stress period and a steady decreased after the emergence of new leaves, attaining normal values by the end of the experiment (**Fig. 5B**). A high level was observed for 3 days following re-hydration. The change in the pattern of fructose content in leaves was very complex, with a steady increase during the water stress period and from the 6-to-32 days period after re-hydration followed by a decrease to normal values.

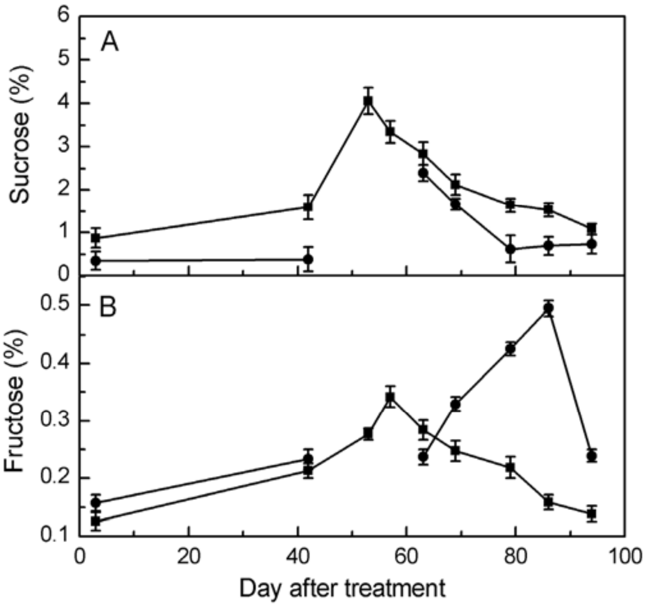

**Fig. 5** Percent of dry weight of sucrose (**A**) and fructose (**B**) content in leaf (●) and stem (■) during experiment. Data = means ± SE (n=6).

## DISCUSSION

A decrease in net assimilation rate (*A*) with water deficit in *C. korshinskii* was observed. Similar results with water deficit have been reported in two other xerophytic species, *Ipomoea carnea* and *Jatropha gossypifolia* (Herrera *et al.* 1994; Tezara *et al.* 1998). Inhibition of *A* by drought is one of the effects that water deficit can have on growth and metabolism of xerophytes. The decline in *A* with decreasing leaf and soil water content was correlated with a reduction in $g_s$. This may indicate that under water deficit stomata were imposing a larger limitation on *A*. Midday depression of *A* must be the result of a combination of stresses (photo inhibition, water stress, heat stress, etc.) and accumulation of assimilates in chloroplasts (Schulze and Hall 1982). On the other hand, after re-watering of the soil and the emergence of a new leaf, photosynthesis was restored to the initial state, a condition that was also observed in general plants such as Norway spruce seedlings and papaya seedlings (Pawełet *et al.* 2005; Jalel *et al.* 2006) and resurrection plant such as *Boea hygrometrica*. Deng *et al.* (2003) found that the levels of net photosynthesis declined rapidly during desiccation, and recovered very quickly during re-hydration in *Boea hygrometrica*. Confirming the view that the photosynthetic apparatus in this plant is very resistant to water stress.

Huber and Huber (1996) suggested that sucrose plays a non-nutritive role as a regulator of cellular metabolism, acting at the level of gene expression. According to Avigad and Dey (1997), there are several examples of enzymes expressed by sucrose. Although limited, our results suggest a distinct involvement of sucrose during leaf abscission and during the process of emergence of new leaf. A reduction in carbohydrate content was observed during leaf emergence to accompany the decrease in sucrose content in stem and leaf and a simultaneous increase in fructose in the leaf, suggesting sucrose cleavage and mobilization for the growing buds. High levels of fructose were detected in the leaves of *C. korshinskii* during the re-hydration process. This level is in agreement with the large amounts of energy expended by meristematic tissues of general plant kiwifruit vines in growth and maintenance (Buwalda 1993).

The changes in carbohydrate content indicate that under water stress conditions *C. korshinskii* increased carbohydrate contents such as starch, soluble carbohydrate, TNC, sucrose and fructose in the stem, especially after a long period of extreme drought. This increase was largely driven by starch accumulation, but effects on soluble sugars were also statistically significant in most cases. The plants studied set aside a large amount of TNC in the stem at very early stages of the drought stress. High concentrations of carbohydrate in the stem, leaves or underground parts have also been found in tropical forest species (*Anacardium excelsum*, *Cecropia longipes*, *Cecropia peltata*, *Ficus insipida*) when those plants encounter unfavorable conditions such as elevated $CO_2$ concentration (Mirjam *et al.* 1998) and in spring wheat (*Triticum aestivum L.*) when salinity level in soil is elevated (Kafi *et al.* 2003). Among the high content, most is total non-structural carbohydrate. In earlier research, Schubert *et al.* (1995) had reported a linear correlation between water stress and dry matter accumulation in *Medicago sativa*. We found that during water stress the resurrection plant *C. korshinskii* accumulated a lot of total non-structural carbohydrate in stems.

The formation of large stem content of TNC appears to play a major role in the noted ability of *C. korshinskii* to withstand disturbance and loss of aboveground tissue. Hough (1968) found that unburned stems of the fire-tolerant saw-palmetto, *Serenoa repens*, contained up to about 40% TNC. Eighty percent of this TNC was starch. McPherson and Williams (1998) observed that starch grains in stem cross-sections suggested that a large portion of storage carbohydrate in *Sabal palmetto* was in the form of starch. In this study, more than 60% of this TNC was starch in most cases and at 3 days after re-hydration this increased to more than 80%. The rapid increase of TNC in the stem indicated that for long-term reserve formation, this is a logical pattern of allocation because, presumably, stem tissue is much longer-lived than leaf-bases in these plants. These stores were drawn upon during the growth of the new leaf bud, and appeared to be necessary for the emergence of new leaves and for regrowth.

Both Chapin *et al.* (1990) and Kobe (1997) noted that, although allocation to TNC stores reduces plant growth rates, such opportunity costs are much smaller in low-resource environments than in high-resource environments. *C. korshinskii* is a long-lived shrub and widely spreads in desert and semi-desert zones and the Loess Plateau in northwestern China (Xia *et al.* 2006). It has important ecological and economic value in this area, including playing a key role in vegetation succession from shifting dune to sandy grassland, helping to restore degraded land by fixing atmospheric nitrogen, forming shrub shelterbelt for crops and artificial grassland, and serving as a supplemental livestock forage (Zheng *et al.* 2004). *C. korshinskii* occurs in habitats and micro sites where unfavorable conditions for photosynthesis may be common. These conditions could include periods of drought, flooding by fresh and salt water, tissue loss due to clips, gnawed by animals, or partial burial by falling sand. Our results suggest that early allocation of carbon to large storage pools helps allow them to tolerate such conditions, despite the growth costs of such storage.

The above results indicated that carbohydrate content is reduced in stems after re-hydration as the plants produce new leaves. A reduction in reserve carbohydrates has also been reported for species as they produce new growth after defoliation, fire, or loss of aboveground parts. Reduced levels of reserve carbohydrates during regrowth have been reported for tea (*Camellia sinensis*) following shoot pruning (Kandiah *et al.* 1984), and for *Cedrela odorata* under shoot damage (Rodgers *et al.* 1995), and two tropical savanna shrubs *Clidemia sericea* and *Miconia albicans* following flooding (Miyanishi and Kellman 1986). The evidence strongly supports the idea that plants mobilize reserve carbohydrates to rebuild photosynthetic tissue after cutting, defoliation, or seasonal loss of foliage. Results from the present study point out that reserve carbohydrates in plants decrease as regrowth occurs after defoliation caused by extreme water stress.

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