

根茎克隆植物羊草体内可溶性碳水化合物的时间变异及其对去叶干扰的响应

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摘要 本研究针对根茎型克隆植物羊草(*Leymus chinensis*)考察了以下内容:1)地上枝条和根茎中可溶性碳水化合物含量的时间动态及其对去叶干扰的响应;2)特定阶段植物体内一定部位的可溶性碳水化合物浓度差异;3)植物体各部分(地上部分、直立茎地下部分及根茎)间可溶性碳水化合物浓度变化之间的关联。基于上述研究结果,作者试图弄清碳水化合物对于羊草克隆分株和整个基株生长和存活的意义。实验共有4个处理:1)个对照和3个不同频度(在整个实验进行期间分别去叶1次、3次和5次)的去叶处理。所有去叶处理都采取一个统一的强度,即留茬15 cm。地上枝条和根茎的取样频次为每10 d 1次。植物体各部分可溶性碳水化合物浓度以高效液相色谱法(HPLC)测定。对不同去叶频度处理间的碳水化合物含量差异显著性进行ANOVA分析。结果表明:不去叶对照处理在生长季盛期可溶性碳水化合物浓度的显著下降归因于植物体快速的生长而引起植物叶片旺盛的呼吸消耗,而去叶处理中植物的可溶性碳水化合物浓度并没有大的降低甚至在最频繁的去叶处理下还略有上升,主要是由于去叶处理减少叶片而造成地上部分总呼吸量下降所致。一次性去叶处理并没有影响植物地上部分最终的可溶性碳水化合物浓度,但是连续数次的去叶处理对地上部分可溶性碳水化合物浓度产生了一定的影响。在秋季气温下降时,碳水化合物自地上向地下的转移在去叶频度越大的处理下表现越为迅速。这表明当植物体接受到气温降低的信号后,去叶干扰加速碳水化合物自地上向地下的转移。可能由于地下枝条存在一定的贮藏功能,在实验过程中地下枝条中可溶性碳水化合物浓度比地上枝条中表现的更加稳定。根茎中的可溶性碳水化合物必要时会转移到地上以供应地上枝条的生长,而旺盛的生长会消耗可溶性碳水化合物,然而从未接受去叶处理的分株向接受去叶处理的分株的克隆整合(常常在较高频次的去叶处理中发生)可能会在一定程度上缓解这种消耗所造成的影响。

关键词 去叶 羊草 贮藏 可溶性碳水化合物

TEMPORAL VARIATION OF WATER-SOLUBLE CARBOHYDRATE IN THE RHIZOME CLONAL GRASS *LEYMUS CHINENSIS* IN RESPONSE TO DEFOLIATION

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Abstract **Aims** This study of the rhizomatous clonal grass *Leymus chinensis* examines: 1) temporal variations of water-soluble carbohydrate (WSC) in shoots and rhizomes and their responses to defoliation; 2) WSC concentrations in different plant parts at specific growth stages; 3) links between variations of WSC concentration in aboveground shoots, belowground shoots and rhizomes; and 4) the significance of carbohydrate reserves for the growth and survival of ramets and the whole genet of the plant.

Methods A control (intact) and three treatments as one, three and five defoliations were used in a field experiment. All defoliations left plants 15 cm high. Shoots and rhizomes were sampled in different quadrats every 10 days. WSC carbohydrate concentrations in different plant parts were determined with HPLC (high performance liquid chromatography). ANOVA was used to detect differences among treatments in temporal dynamics of WSC contents.

Important findings The marked reduction of WSC concentration in the control in a stage of rapid growth was attributed to higher growth rate and thus higher respiration rate in the carbon metabolism of leaves, while WSC concentrations in defoliation treatments were less reduced or increased under frequent defoliation, mainly due

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to reduction of total respiration with leaf loss. Single defoliation did not affect the final WSC concentration in aboveground shoots, but successive defoliations did. The more frequent the defoliations, the more rapid the transfer of carbohydrate from aboveground shoots to belowground shoots or rhizomes in response to declining air temperature. WSC concentrations in belowground shoots were slightly more stable than in aboveground shoots, probably because belowground shoots functioned as storage organs for tiller buds and partly for some nutrient or assimilate. WSC in rhizomes must be transported into aboveground shoots to supply them, and intensive growth depletes WSC; however, such depletion can be mitigated when clonal integration in intact neighborhood ramets results in replenishment of defoliated ramets (usually at the frequent defoliation treatment).

Key words defoliation, *Leymus chinensis*, storage, water-soluble carbohydrate

Carbohydrate is major photosynthate in plants, and exists in two forms: structural carbohydrate and non-structural carbohydrate (NSC). There is ample evidence that the availability of NSC in temperate grasses, comprising water-soluble carbohydrate (WSC) and starch, has a marked effect on the regrowth potential and persistence of plants (Fulkerson & Donaghy, 2001). Since carbohydrate metabolism is one of basic metabolic courses in plant body, there have been quite a few studies dealing with the mechanisms of how NSC metabolism respond to the changes of environmental factors (Jeong & Housley, 1990; Guy *et al.*, 1992; Garnier & Vancaeyzeele, 1994; Atkin *et al.*, 1996; Livingston, 1996; Loewe *et al.*, 2000). However, these studies were concentrated on two factors: water and temperature. WSC contents in plant would rise in response to the stress of cold and drought (Sanada *et al.*, 2006), because the WSC participates in the osmotic adjustment of plant cell, and more importantly, many WSC formats are signal substances of plants to physiologically adapt to the environment (Yu, 1999; Gibson, 2000; Palacio *et al.*, 2007). In grassland ecosystem, carbohydrate is the substantial foundation of primary productivity. The actual level of WSC in harvestable biomass during herbage growth depends on CO₂-assimilation and demand for these assimilates, mainly for respiration and production of protein and structural carbohydrates (White, 1973). WSC content is therefore subject to great fluctuations during growth, due to phenological development of grass species, modified by species, season and management factors like cutting regime and nitrogen application rate, and the short-term influence of weather factors (Wulfes *et al.*, 1999). Starch is a dominant carbohydrate reserve in many plant species, which may be almost absent in the storage organs in some grasses. Conversion of starch to sugar occurs when reserves are used for active growth. Starch appears to be the most readily available and osmotically inert reserve carbohydrate in perennial plants.

Storage of resources is a widespread phenomenon in clonal plant species. Rhizomes often serve as storage or-

gans. Resource storage can be regarded as a safety measure against temporal changes in the growing conditions of plants (Suzuki & Stuefer, 1999), for storage of carbohydrates reduces the risk of mortality after damage (Iwasa & Kubo, 1997; Veneklaasa & den Oudena, 2005). Optimization model suggested that the amount of stored resources should be related to disturbance frequency and intensity that occurred in a given environment (Iwasa & Kubo, 1997). However, the ecologic significance of storage in clonal plant structures remains partly unclear. Carbohydrate reserves including WSC play a particularly important role in plant regrowth after a period of inactivity and in recovery after disturbance (Veneklaasa & den Oudena, 2005; Handa *et al.*, 2005). In addition, they are used to meet carbon demands for respiration and reproduction. At a smaller time scale, the storage is needed to cover expenses during the bad weather and the night when photosynthesis is reduced or interrupted (Chapin *et al.*, 1990). Moreover, WSC also plays a significant role in freezing tolerance (Chatterton *et al.*, 1989; Klimeš & Klimešová, 2002).

Grazing and mowing are two major ways of utilizing grassland ecosystems. There have been many studies on the effects of mowing and grazing on carbohydrate metabolisms. Davies (1965) found that the capacity of forage regrowth was closely related to carbohydrate level in stubbles and roots of the plants. But more deep exploration into the issue commenced from the 1990s (Johansson, 1993; Fulkerson & Slack, 1994; Donaghy & Fulkerson, 1998; Vanderklein & Reich, 1999; Vallius & Salonen, 2000). But to date, people are uncertain about how the regrowth and performance of grasses are related to temporal dynamics of carbohydrate contents in plant body especially under the stress of defoliation caused by grazing and mowing.

However, our current knowledge about functional responses of clonal plants to habitat patchiness is biased towards spatial aspects of environmental heterogeneity, but temporal changes in biotic and abiotic conditions do occur in most natural habitats, and they are very likely to affect

plant growth and performance, and to create positive selection pressures on traits that can buffer plants against unfavorable consequences of this variability (Suzuki & Stuefer, 1999).

The present study is intended to examine: 1) the temporal variations of WSC in shoots and rhizomes and their responses to defoliations; 2) the discrepancy of WSC concentration in certain part of the plant at a specific stage; 3) the links between variations of WSC concentration in aboveground shoots, belowground shoots and rhizomes. Based on the above-mentioned information, we try to ascertain the significances of carbohydrate reserve for the growth and survival of both ramets and whole genet of the plant.

1 Materials and Methods

Leymus chinensis is a perennial graminaceous plant species distributed in the eastern region of the Eurasian steppe zone, including the outer Baikal Area of Russia, the northern and eastern parts of the People's Republic of Mongolia, the Northeast China Plain, the Northern China Plain, and the Inner Mongolia Plateau of China. The plant is highly tolerant to drought, low fertility and high pH values. It is highly palatable and generally used for grazing livestock (Zhu *et al.*, 1981). Therefore, it is of considerable economic value. The plant has strong rhizomes and vigorous vegetative propagation, and often forms monodominant stands. Its rhizomes lie horizontally about 10 cm beneath the ground surface, and are highly branched. The plant multiplies itself mainly by clonal propagation. The rhizomes have long internodes between ramets, giving rise to extensively spreading clones.

The experiment was carried out in Duolun County of Xilingol League, Inner Mongolia (41°46' - 42°36' N, 115°51' - 116°54' E), 180 km north of Beijing, and situated across the southern edge of Hunshandake Sand. The topography is dominated by low foothills with an elevation of 1 150 - 1 800 m. The main soil type is chestnut soil, accounting for 70% of the total area, and other soil types are aeolian sandy soil, meadow soil and chernozem. This area has a typical middle temperate semiarid continental monsoon climate, with an annual mean air temperature of 1.6 °C and a frost-free period of about 100 days. The accumulated temperature of ≥ 10 °C is 1 917.9 °C, and the mean temperature of the warmest month (July) is 18.7 °C, while that of the coldest month (January) is - 18.3 °C. Annual mean precipitation is 386 mm, while mean potential evaporation is 1 748 mm.

In late June of 2003, we selected and then enclosed

an uniform *L. chinensis* predominant site as experimental plot. Within the plot, 120 experimental quadrats, each 0.25 m × 0.25 m in area, were set up. The four vertexes of each experimental quadrat were pegged with wooden pegs, and a cotton thread was fastened to the four vertex pegs, to delimit the quadrat. Four different defoliation regimes, including control (intact) were imposed upon all the 120 experimental quadrats. The defoliation was imposed at a single intensity: the shoots were cut to 15 cm high left. All the 120 quadrats will then be randomly assigned to the following treatments, 30 for each: Intact, as a control (D₀); Subject to defoliation only once (D₁); Subject to defoliations three times with the interval of 20 days (D₃); Subject to defoliations five times with the interval of 10 days (D₅). The dates of these defoliations are shown as “ + ” in Table 1.

Table 1 The dates of defoliations and samplings

Dates	Treatments				Samplings
	D ₀	D ₁	D ₃	D ₅	
Jun. 30					\$
Jul. 10		+	+	+	\$
Jul. 20				+	#
Jul. 30			+	+	#
Aug. 9				+	#
Aug. 19			+	+	#
Aug. 29					#
Sep. 8					#

The earliest twice samplings (shown as “ \$ ” in Table 1) were conducted outside all the 120 quadrats as the initial twice samplings, altogether 5 quadrats sized as experimental quadrat were sampled at each time as replicates. The 30 quadrats of same defoliation regime would be sampled successively six times (shown as “ # ” in Table 1), so 5 quadrats will be sampled at a time as replicates. When sampling, the quadrates were excavated out to 0.2 m deep with all the aboveground shoots, and all the rhizomes, which would be taken into laboratory after abandoning earth.

The aboveground shoots on each earth core were clipped off, counted, dried and weighed. The earth was rinsed away, and the roots were clipped off, until only rhizomes and belowground culms were left. For each sample, we counted the number of rhizomes, number of vegetative buds (discriminating tiller buds, rhizome buds and apical buds), and determined the biomass of all the aboveground shoots, belowground culms and rhizomes for every quadrat after drying at 70 °C for 24 hours. WSC concentrations in different parts of the plant were deter-

mined with HPLC (high performance liquid chromatography) method .

2 Results

2.1 WSC concentrations in aboveground shoots

The WSC in aboveground shoots sampled on July 20 were insignificantly different among treatments ($p > 0.05$), probably because the plants had not responded to defoliations , for this sampling was conducted only 10 days after the first defoliation applied on July 10. But from July 20 to July 30 , the differences in WSC concentrations for all the treatments kept increasing , so that WSC concentrations of three defoliated treatments were higher than

that of control , and the WSC concentration of D_5 , defoliated twice by then , were still higher than those of D_1 and D_3 (Table 2) , which had been defoliated only once on July 30 .

From August 29 to September 8 , WSC concentrations in aboveground shoots of D_0 , D_3 and D_5 treatments declined while that of D_1 treatment ascended . On September 8 , the WSC concentration of D_1 was slightly higher than that of D_0 ($p > 0.05$) , while those of D_3 and D_5 were significantly lower than that of D_0 or D_1 ($p < 0.05$) , and that of D_5 was also lower than that of D_3 ($p < 0.05$). That is , the WSC concentration at the end of the experiment was reduced with the increase of defoliation frequency .

Table 2 Temporal dynamics of water-soluble carbohydrate (WSC) contents in aboveground shoots , rhizomes and belowground culms (means with the same letter are not significantly different)

[WSC]	Treatments	Sampling dates					
		Jul. 20	Jul. 30	Aug. 9	Aug. 19	Aug. 29	Sep. 8
Aboveground shoots	D_0	18.31 ± 0.65^a	19.84 ± 1.20^a	19.33 ± 1.88^a	18.34 ± 0.83^a	19.56 ± 1.52^a	18.43 ± 0.36^a
	D_1	17.77 ± 1.10^a	13.67 ± 0.88^b	18.04 ± 1.00^a	21.00 ± 0.55^a	19.04 ± 1.08^a	19.85 ± 0.66^a
	D_3	18.82 ± 0.62^a	17.58 ± 1.06^b	18.26 ± 2.93^a	18.86 ± 1.09^a	18.99 ± 1.05^a	16.87 ± 0.32^b
	D_5	17.98 ± 1.38^a	21.49 ± 0.13^c	15.43 ± 0.96^a	18.69 ± 0.69^a	18.84 ± 0.80^a	13.51 ± 0.46^c
Belowground culms	D_0	19.60 ± 0.72^a	22.72 ± 0.86^a	21.01 ± 0.55^a	23.52 ± 1.35^a	18.30 ± 1.88^a	18.67 ± 2.30^a
	D_1	17.71 ± 1.46^a	19.84 ± 1.25^a	19.44 ± 2.53^a	22.17 ± 1.05^a	16.07 ± 0.29^a	19.21 ± 0.19^a
	D_3	20.75 ± 1.11^a	20.60 ± 1.76^a	16.96 ± 0.45^a	21.46 ± 0.61^a	17.21 ± 0.98^a	17.97 ± 1.33^a
	D_5	18.72 ± 1.78^a	18.80 ± 0.99^a	17.50 ± 0.87^a	20.30 ± 1.71^a	19.06 ± 2.17^a	17.45 ± 0.17^a
Rhizomes	D_0	33.37 ± 3.63^a	34.10 ± 3.45^a	26.18 ± 1.21^a	28.44 ± 2.05^a	33.74 ± 1.14^a	34.36 ± 2.94^a
	D_1	31.20 ± 0.87^a	33.17 ± 1.34^a	27.72 ± 3.39^a	31.65 ± 1.31^a	31.37 ± 1.49^a	30.01 ± 0.31^a
	D_3	26.72 ± 1.16^a	33.55 ± 3.40^a	30.13 ± 1.85^a	32.96 ± 1.19^a	35.19 ± 0.57^a	32.91 ± 1.64^a
	D_5	29.96 ± 0.30^a	33.53 ± 3.38^a	32.05 ± 2.41^a	27.84 ± 3.79^a	32.68 ± 3.07^a	31.17 ± 1.23^a

2.2 WSC concentrations in belowground culms

As shown in Table 2 , only the D_1 treatment was similar to D_0 in the “ rising and declining ” temporal dynamic pattern in WSC concentrations in belowground shoots . However , the other two treatments , D_3 and D_5 , were similar to each other in WSC concentrations in belowground shoots . D_0 , D_1 , D_3 and D_5 are not significantly different all the time in the experiment (Table 2).

2.3 WSC concentrations in rhizomes

From July 20 to July 30 , WSC concentrations in rhizomes were kept increasing and almost at the same level for all the treatments . The effects of defoliation might have not been displayed in this period . From July 30 , the treatments began to differ in WSC concentrations in rhizomes . From August 9 to August 19 , the WSC concentrations in the rhizomes of D_0 , D_1 and D_3 treatments increased , while that of D_5 declined . However , from August 9 , the differences between the WSC concentrations of the four treatments were not significant , probably because

the rhizomes of the plant function as carbohydrate storage organs and as the buffer or pool of carbohydrate of the whole plant . From Table 2 we can find that D_0 , D_1 , D_3 and D_5 are not significantly different all the time in the experiment .

3 Discussion

Concentration of carbohydrates in plant storage organs changes with the input of photosynthetic products and translocation of materials from various portions of the plants . The rate of carbohydrate use and export from storage to other areas of the plants also alters this concentration . Thus , any factor affecting the photosynthesis or utilization of carbohydrates for respiration or growth may affect the level and makeup of plant reserves . The marked reduction of WSC concentration of D_0 treatment on July 30 probably could be explained by following fact : the stage is a boom period for the plant growth , for the air temperature was almost at the peak of the growing season (Fig.

2), and the accumulated precipitation was relatively high (Fig. 3), so that the respiration rate of leaves was suspected to be much higher than photosynthetic rate in terms of carbohydrate metabolism, as to provide enough energy for plant growth. Indeed, it has been reported that 40% – 60% of non-structural carbohydrate produced from photosynthesis is consumed by respiration process, and respiration exhibits an exponential increase with the increasing temperature (Fulkerson & Donaghy, 2001). Consequently, a considerable amount of carbohydrate would be consumed. However, WSC concentrations of D₁ and D₃ reduced not so much as D₀ on July 30, and that of D₅ even increased, mainly due to the reduction of the total respiration of shoots on account of leaf loss caused by defoliation.

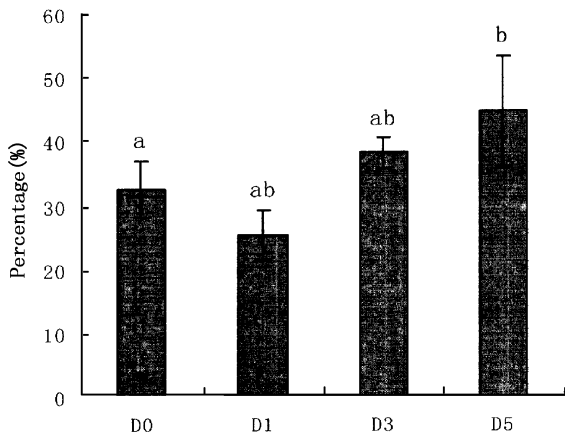


Fig. 1 The percentages of standing litter over total aboveground biomass

Values are shown as means \pm SE. The bars sharing the same letter are not significantly different

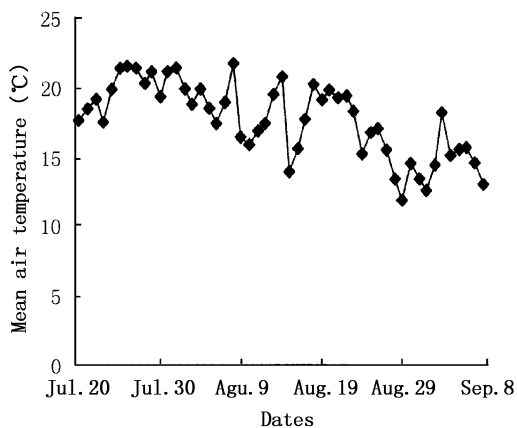


Fig. 2 The diurnal mean air temperature during experimental period

At the end of the experiment, the WSC concentrations of three defoliated treatments displayed significant

differences between one another, and showed a decreasing tendency with the increasing defoliation frequency. However D₁ showed no difference with D₀ in WSC concentration. We thought one-off defoliation did not affect the final WSC concentration in aboveground shoots of the plant, but several successive defoliations would. This was probably related to the promptness of WSC transfer from aboveground shoots to belowground shoots or rhizomes in response to the signal of air temperature decline. The transferring rate of the aboveground shoots of D₅ treatment was higher than those of D₃ and D₀ treatments. The increase of WSC concentration in aboveground shoots of D₁ treatment could be ascribed to smaller portion of standing litter while greater portion of green shoots compared with the other treatments (Fig. 1), because aboveground shoots of D₁ would produce more photosynthate. The more frequent the defoliation, the more prompt the transfer, so it could be concluded that the defoliation accelerated the carbohydrate transfer from aboveground towards belowground when prompted by air temperature decline. The earliest frost of the year at our study site was on September 5, and our last sampling was conducted on September 8. The low temperature or even the frost probably functioned as a signal for carbohydrate transfer from aboveground towards belowground. Maybe the discrepancy of carbohydrate transfer could account for the comparison between the treatments in standing litter at the end of the experiment.

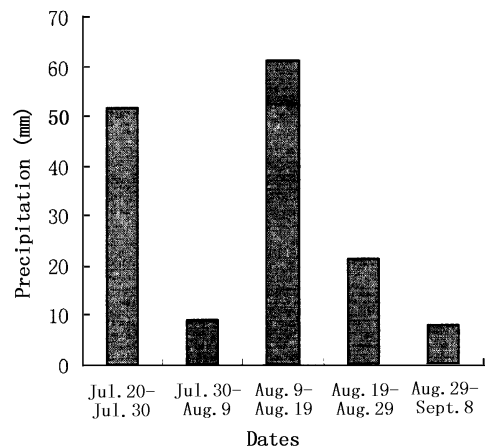


Fig. 3 Accumulated precipitation during the experiment

WSC concentrations in belowground shoots were a little more stable than in aboveground shoots during the experiment. Belowground parts of shoots probably functioned as storage organ for tiller buds and at least in part for some nutrient or assimilate, and as the intermediate for transfer of substances or signals between aboveground parts of shoots and rhizomes and even roots.

The noticeable declines of WSC concentrations in D₀

and D_1 in rhizomes on August 9 were possibly resulted by the rapid growth of the aboveground shoots of plants, for it was just in the boom season for plant growth. A sink-source system might have formed between aboveground shoots and belowground rhizomes. We inferred that WSC in rhizomes must be transported upwards into the aboveground shoots to supply them. A major use of non-structural carbohydrate in plants is for growth (Fulkerson & Donaghy, 2001), and intensive growth depletes non-structural carbohydrate. After the energy requirements of the plant for respiration and growth have been met, the remainder is available for storage as plant reserves (Fulkerson & Slack, 1994). In general, storage of carbohydrates can be understood as a precaution against variability in the growing conditions of plants (Suzuki & Stuefer, 1999; Veneklaasa & den Oudena, 2005). Therefore, allocation to storage may bear on the lifetime fitness of the plant.

To ascertain the ecological functions and implications of storage, comparative studies involving plant species with and without storage organs are called for. Such comparisons should be done with structurally similar and closely related species. It is likely that the ecological functions and implications of carbohydrate reserves in clonal plants can be displayed if their inter-annual variations especially in response to disturbance such as defoliation and shading are incorporated. Therefore, longer-term studies on the temporal variations of carbohydrate reserves in plants under the pressure of disturbance of different intensities, timing, and frequencies may uncover implications of plant storage in terms of evolution and adaptation.

References

- Atkin OK, Botman B, Lambers H (1996). The causes of inherently slow growth in alpine plants: an analysis based on the underlying carbon economies of alpine and lowland *Poa* species. *Functional Ecology*, 10, 698–707.
- Chapin FS III, Schulze ED, Mooney HA (1990). The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics*, 21, 423–447.
- Chatterton NJ, Harrison PA, Bennett JH, Asay KH (1989). Carbohydrate partitioning in 185 accessions of Gramineae grown under warm and cool temperatures. *Journal of Plant Physiology*, 134, 169–179.
- Davies A (1965). Carbohydrate levels and regrowth in perennial ryegrass. *Journal of Agricultural Science*, 65, 213–221.
- Donaghy DJ, Fulkerson WJ (1998). Priority for allocation of water-soluble carbohydrate reserves during regrowth of *Lolium perenne*. *Grass and Forage Science*, 53, 211–218.
- Fulkerson WJ, Donaghy DJ (2001). Plant-soluble carbohydrate re-serves and senescence—key criteria for developing an effective grazing management system for ryegrass-based pastures: a review. *Australian Journal of Experimental Agriculture*, 41, 261–275.
- Fulkerson WJ, Slack K (1994). Leaf number as a criterion for determining defoliation time for *Lolium perenne*. 1. Effect of water-soluble carbohydrates and senescence. *Grass and Forage Science*, 49, 373–377.
- Garnier E, Vancaeyzeele S (1994). Carbon and nitrogen content of congeneric annual and perennial grass species: relationships with growth. *Plant, Cell and Environment*, 17, 399–407.
- Gibson SI (2000). Plant sugar-response pathway. Part of a complex regulatory web. *Plant Physiology*, 124, 1532–1539.
- Guy CL, Huber JLA, Huber SC (1992). Sucrose phosphate synthase and sucrose accumulation at low temperature. *Plant Physiology*, 100, 502–508.
- Handa IT, Körner C, Hättenschwiller S (2005). A test of the tree-line carbon limitation hypothesis by *in situ* CO₂ enrichment and defoliation. *Ecology*, 86, 1288–1300.
- Iwasa Y, Kubo T (1997). Optimal size of storage for recovery after unpredictable disturbances. *Evolutionary Ecology*, 11, 41–65.
- Jeong BR, Housley TL (1990). Fructan metabolism in wheat in alternating warm and cold temperatures. *Plant Physiology*, 93, 902–906.
- Johansson G (1993). Carbon distribution in grass (*Festuca pratensis* L.) during regrowth after cutting-utilization of stored and newly assimilated carbon. *Plant and Soil*, 15, 11–20.
- Klimeš L, Klimešová J (2002). The effects of mowing and fertilization on carbohydrate reserves and regrowth of grasses: do they promote plant coexistence in species-rich meadows? *Evolutionary Ecology*, 15, 363–382.
- Livingston DP (1996). The second phase of cold hardening: freezing tolerance and fructan isomer changes in winter cereal crowns. *Crop Science*, 36, 1568–1573.
- Loewe A, Einig W, Shi L, Dizengremel P, Hopp R (2000). Mycorrhiza formation and elevated CO₂ both increase the capacity for sucrose synthesis in source leaves of spruce and aspen. *New Phytologist*, 145, 565–574.
- Palacio S, Maestro M, Montserrat-Martí G (2007). Seasonal dynamics of non-structural carbohydrates in two species of mediterranean sub-shrubs with different leaf phenology. *Environmental and Experimental Botany*, 59, 34–42.
- Sanada Y, Takai T, Yamada T (2006). Ecotypic variation of water-soluble carbohydrate concentration and winter hardiness in cocksfoot (*Dactylis glomerata* L.). *Euphytica*, doi: 10.1007/s10681-006-9262-9.

- Suzuki J-I, Stuefer JF (1999). On the ecological and evolutionary significance of storage in clonal plants. *Plant Species Biology*, 14, 11 – 17.
- Vallius E, Salonen V (2000). Effects of defoliation on male and female reproductive traits of a perennial orchid, *Dactylorhiza maculata*. *Functional Ecology*, 14, 668 – 674.
- Vanderklein DW, Reich PB (1999). The effect of defoliation intensity and history on photosynthesis, growth and carbon reserves of two conifers with contrasting leaf lifespans and growth habits. *New Phytologist*, 144, 121 – 132.
- Veneklaasa EJ, den Oudena F (2005). Dynamics of non-structural carbohydrates in two *Ficus* species after transfer to deep shade. *Environmental and Experimental Botany*, 54, 148 – 154.
- White LM (1973). Carbohydrate reserves of grasses: a review. *Journal of Range Management*, 26, 13 – 18.
- Wulfes R, Nyman P, Kornher A (1999). Modelling non-structural carbohydrates in forage grasses with weather data. *Agricultural Systems*, 61, 1 – 16.
- Yu SM (1999). Cellular and genetic response of plants to sugar starvation. *Plant Physiology*, 121, 687 – 693.
- Zhu TC, Li JD, Yang DC (1981). A study of the ecology of yangcao (*Leymus chinensis*) grassland in northern China. *Proceedings X IV International Grassland Congress*, 429 – 431.

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