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Carbohydrate storage in rhizomes of *Phragmites australis*: the effects of altitude and rhizome age

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Abstract

Starch, glucose, fructose and sucrose were measured in nodes and internodes of horizontal rhizomes of *Phragmites australis* in two localities, at 400 and 1350 m above sea level respectively, before spring growth started. In the respective localities, five and four age categories of rhizomes were distinguished. Rhizomes of lowland plants, harvested on March 21, contained more starch (17.6%), glucose (2.5%) and total non-structural carbohydrates (35.2%) per gram dry mass than rhizomes of plants collected at the tree line on June 3 (11.8, 1.7 and 30.5%, repectively). The proportion of water soluble carbohydrates to total non-structural carbohydrates, as an indication of acclimatisation to a cold climate, was higher in the mountain locality (60 and 49%, respectively). Glucose and starch concentrations increased with rhizome age in both localities. All other carbohydrate fractions were independent of locality. Water soluble carbohydrates were preferentially accumulated in internodes whereas starch was accumulated in nodes.

Keywords: Common reed; Storage carbohydrates; Extreme altitude; Lowland

1. Introduction

The role of storage is one of the neglected topics in population ecology of clonal plants (Chapin et al., 1990; de Kroon and van Groenendael, 1997). Carbohydrates in the form of sugars (sucrose, glucose and fructose), starch or fructosans (Ho, 1988) are deposited in specialised tissues of stems, rhizomes, tubers, and roots. The storage is especially important in perennial plants occurring in regions with cold winters. Spring growth of these plants

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strongly depends on the reserves accumulated during the previous season (Shaver et al., 1976; Klimeš et al., 1993; Kubín and Melzer, 1996).

The dynamics of non-structural carbohydrates has been studied in clonal wetland plants mostly in relation to their tolerance of flooding (Barclay and Crawford, 1982; Monk et al., 1984; Brändle, 1985). In addition, the non-structural carbohydrates are involved also in the tolerance of cold climatic conditions, but this aspect has attained little attention as yet in wetland plants. Cold climates involve two major hazards for perennial plants: (1) a danger of damage by frosts and (2) a long winter, which implies a short vegetation period with low temperatures, which limit carbon assimilation. Accumulation of non-structural carbohydrates represent a solution to both problems: (1) the frost resistance is increased by accumulation of soluble carbohydrates, and (2) large carbohydrate reserves subsidise the fast spring growth in addition to photosynthesis.

Phragmites australis (Cav.) Trin. ex Steud. is well suited for studies of effect of cold climate as it occurs over a range of climatic conditions and its accumulation of carbohydrates is well understood for typical, i.e. lowland habitats (Fiala, 1976; Granéli et al., 1992; Kubín and Melzer, 1996). Studies of carbohydrate accumulation are, however, complicated by the fact that *Phragmites* rhizomes live for several years and their age affects both accumulation (Fiala, 1976) and use (Čížková and Bauer, 1998) of the carbohydrates. Moreover, the nodal diaphragma of *Phragmites* rhizomes comprises more parenchymatous tissue than internodia with pith cavities so that there may be great differences in storage content within a rhizome.

We studied storage accumulation at a marginal (mountain) and a typical (lowland) habitat of *P. australis* in relation to rhizome morphology, particularly, in rhizome fragments of different age and separately for nodes and internodes. We aimed at answering the following questions: (1) What is the effect of rhizome age and rhizome morphology on the storage of carbohydrates? (2) Is there any difference between storage carbohydrates and the ratio between starch and WSC in lowland and mountain localities at the beginning of spring growth?

1.1. Study sites

The maximum altitude of *P. australis* in the Czech Republic in natural plant communities has been reported from the Velká and Malá kotlina cirques (Hrubý Jeseník Mts.) where it occurs at altitudes from 1150 to 1350 m above sea level. These records were reported first in 1843 (Jeník et al., 1983), indicating that the species was not introduced to these localities recently.

The mountain population was compared with one in lowland, studied on the eastern bank of Rožmberk fishpond (423 m a.s.l.) near the town of Třeboň, South Bohemia, Czech Republic. The latter population is not so stressed by eutrophication, which affects most lowland populations that colonize fishpond banks in the Czech Republic. In both localities, the water level fluctuates during the vegetative season between about 10 cm above and 10 cm below ground level.

2. Methods

Rhizome samples were collected in the studied localities at the end of winter before carbohydrate mobilisation for the spring growth started. Due to the difference in altitude of

the two localities the date of plant collection differed. At the Rožmberk fishpond the plants were collected on March 21, 1995, in the Velká Kotlina cirque June 3, 1995. At the time of collection the soil surface in the lowland locality was still frozen, but without snow cover. The mountain locality was inaccessible at the corresponding time (when the soil was still frozen) because of avalanche danger. Therefore, the plants were collected later, at the time of snow melting, when 5–10 cm of snow covered the soil surface.

In each locality six randomly selected sites were chosen. The *Phragmites* rhizomes were excavated from a single soil block at each site. The sample was partly washed out in the field. Final washing of the rhizomes was carried out in the laboratory. The horizontal rhizomes were arranged according to age category and then divided into nodes and internodes, weighed and dried at 80°C in a drying chamber to constant weight. Age categories of rhizomes cannot be exactly defined in *P. australis*. However, it is possible to define relative rhizome age categories which need not exactly correspond to the absolute age. These categories are defined as follows: (1) white rhizomes with preserved scale leaves, roots missing; (2) ivory white rhizomes without scale leaves and with preserved adventitious roots; (3) light brown rhizomes, sometimes with darker brown spots, cortex of adventitious roots often disturbed; (4) dark brown rhizomes with darker patches, usually without roots; (5) dark brown rhizomes with rusty-coloured short lines at the nodes, without roots (at Rožmberk fishpond only). Only non-disturbed rhizomes were used for the analysis. The dry samples were ground and weighed. Two grams of the ground tissue were used for starch and WSC estimation. Carbohydrate fractions were estimated using HPLC chromatography and starch was determined in a supernatant with the anthrone method using glucose as a standard. For methodological details see Čížková et al. (1996).

All values of both WSC and starch are given in relation to rhizome dry mass. For statistical analysis two-way ANOVA was used (Wilkinson et al., 1992). Percentage data were arcsin transformed before testing.

3. Results

Glucose and starch concentrations increased with rhizome age ($P < 0.05$), whereas fructose and sucrose concentrations were independent of it. Neither TNC nor WSC concentrations depended on relative rhizome age.

Concentrations of all carbohydrate fractions, WSC and TNC differed between nodes and internodes ($P < 0.001$). Starch was accumulated mainly in nodes whereas higher concentrations of WSC were found in internodes. The concentration of WSC in nodes was higher in the mountains than in the lowlands ($P < 0.05$).

Starch and glucose concentrations differed between the localities ($P < 0.001$), whereas concentrations of sucrose and fructose did not (Fig. 1). The TNC (total non-structural carbohydrates) was higher in the lowland locality ($P < 0.01$), but WSC was the same in both localities. The WSC/TNC ratio was higher in the mountains than in the lowlands ($P < 0.001$, Fig. 1).

Significant interactions between locality and storage content in nodes versus internodes was found for glucose, sucrose, WSC, TNC and WSC/TNC ratio ($P < 0.05$). The differences between nodes and internodes were much higher at the higher altitude than at the lower

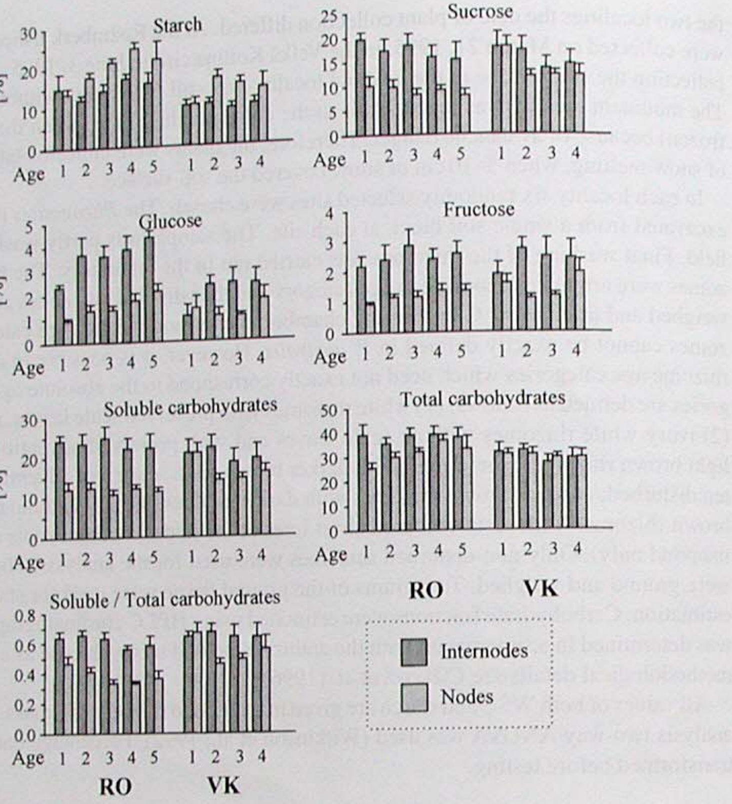

Fig. 1. Starch, water soluble carbohydrates (WSC), total non-structural carbohydrates (TNC) and WSC/TNC in nodes and internodes of horizontal rhizomes of *Phragmites australis* in a lowland community (RO-Rožmberk fishpond, 400 m above sea level) and at the tree line (VK - Velká Kotlina cirque, 1350 m above sea level), measured before the spring growth started (mean + S.E.), in relation to relative age of the rhizome segments.

altitude for these variables. Significant interactions were found also between locality and relative rhizome age, and between relative rhizome age and nodes versus internodes, but only for starch ($P < 0.05$). At the higher altitude, its concentration increased with relative rhizome age much steeper than at the lower altitude. Also, the age-dependent increase of starch concentration was steeper in internodes than in the nodes.

4. Discussion

The concentration of all fractions of carbohydrates and TNC differed between nodes and internodes of *P. australis* rhizomes. These differences were probably related to the extensive parenchymatous tissue in the nodes, where starch may be stored in plastids. The percentage of the nodes in the total biomass was however low and therefore hardly affected the TNC storage per plant.

Though the proportion of glucose and starch differed among the rhizome age categories, no difference was found for TNC, fructose and sucrose. This contrasts with results from other species showing that TNC concentration changes with rhizome age, with either the oldest (Fiala, 1976; Shaver and Billings, 1976; Masuzawa and Hogetsu, 1977) or the youngest (Ralph et al., 1992; Klimešová and Klimeš, 1996) tissue exhibiting the lowest values. However, these trends may not be seasonally stable. In *Polygonatum officinale*, rhizome storage increased with age in summer but was independent of it in autumn (Ljubarskij, 1972).

The TNC concentration in rhizomes of *P. australis* was higher at the lowland site than in the mountains. However, the difference was only about 5% for most age categories. Small differences in TNC concentrations between the Velká Kotlina cirque and a locality at the foot of the mountains were found also in another rhizomatous plant, *Phalaris arundinacea* (Klimešová, 1996). The TNC levels in horizontal segments of *P. australis* rhizomes reported in literature are usually similar to the ones we observed (Čížková et al., 1996) or slightly higher (Granéli et al., 1992; Kubín et al., 1994) than we found. The WSC/TNC ratio was higher in the mountains than in the lowland, which may contribute to frost tolerance of plants adapted to the cold mountain climate.

It is a pertinent question as to what extent the stored carbohydrates limit spring growth of *P. australis* in the mountain locality. It has been shown that in plants growing in localities with a water level of about 5 cm above the ground level, 25–30% of TNC is mobilised in spring (Granéli et al., 1992). The decrease of TNC concentration in rhizomes of *P. australis*, however, continues until June in lowland localities (Granéli et al., 1992; Čížková et al., 1996; Kubín and Melzer, 1996). As a result the amount of stored TNC may decrease to about one half. Therefore, the 5% lower TNC storage that we found in the mountain locality does not limit spring growth. If extensive and prolonged flooding takes place or the stand is mown, the demand for stored carbohydrates further increases and TNC reserves may be nearly exhausted (Klimeš et al., 1993; Clevering et al., 1995). However, the soils in the mountain locality are flooded only temporarily in spring, when snow cover is melting, so additional demand for carbohydrates due to prolonged flooding or anaerobiosis is unlikely.

5. Conclusions

Rhizome nodes had higher concentrations of starch and lower concentrations of WSC than internodes. The effect of rhizome age on carbohydrates was significant only for starch and glucose concentrations, which increased with rhizome age. The proportion of WSC was higher at the mountain site than in the lowland. Stored carbohydrates were only 5% lower at the mountain site than at the lowland and was therefore unlikely to limit spring growth.

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