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Influence of nutrient supply on growth, carbohydrate, and nitrogen metabolic relations in *Typha angustifolia*

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Abstract

Performance of *Typha angustifolia*, a species common in European wetlands, was studied in connection with wetlands eutrophication. Cultivation in a sand culture was used to follow the effect of nutrient availability per se and to study, in detail, both aboveground as well as belowground organs (rhizomes and roots) of the plant in contrast to the possibilities of field study. A complex study of growth, carbohydrate, and nitrogen metabolic relationships, with respect to tissue age, was done in plants growing in nutrient solutions that differed in their levels of N and P (oligotrophic: 0.026 mM N and 0.001 mM P; eutrophic: 2.635 mM N and 0.0999 mM P; hypertrophic treatment: 9.539 mM N and 0.999 mM P).

In contrast to the poor growth of *Typha* plants under the oligotrophic treatment, *Typha* coped best under the eutrophic treatment. Further increase in nutrient availability to the hypertrophic treatment did not result in additional stimulation of growth, but instead some negative reactions appeared. Changes in the growth and allocation of biomass, in favour of shoots and including rhizomes (as compared with roots) with increasing nutrient availability, were accompanied by an increase in N allocation and content of non-structural carbohydrates in these tissues. Detailed biochemical analysis revealed significant differences between tissues of different ages. These characteristics probably reflect the physiological potential of this species for their successful spreading in natural eutrophic habitats. Moreover, a decrease in the C/N ratio, decreasing proportion of starch/soluble sugars ratio, increasing proportion of hexoses/sucrose ratio (taking into account the type and tissue age of plant organs), with increasing nutrient availability, indicate high metabolic activity of the tissues at the stage of maximum growth.

Keywords: Wetland plant; Nitrogen; Phosphorus; Storage carbohydrates; Starch; C/N balance; Eutrophication

1. Introduction

In intensely managed landscapes, human-induced eutrophication frequently affects not only water bodies, but also adjacent ecosystems, particularly wetlands. Numerous studies have documented a shift in species composition in response to the eutrophication of wetland habitats (Ostendorp, 1989; Newman et al., 1998; Smith et al., 1999). The extreme situation is represented by the large-scale decline of *Phragmites australis*, observed since the 1950s, in numerous shallow water bodies of Europe (Ostendorp, 1989; Van der Putten, 1997). Field observations have indicated that several species cope well in extremely eutrophic habitats (Brändle et al., 1996). Understanding of the underlying mechanisms would not only improve our knowledge of processes associated with eutrophication, but also would facilitate the use of this species in constructed wetlands (Květ et al., 1999) designed for wastewater treatment.

Eutrophication of wetland habitats is associated with two main changes of the wetland soil (Čížková et al., 2001): (1) increased availability of the main nutrients, i.e. nitrogen and phosphorus, and (2) accumulation of organic matter,

Abbreviations: NUE, nitrogen use efficiency; SGF, sum of sucrose, glucose, and fructose; TNC, total non-structural carbohydrates (sum of starch, sucrose, glucose, and fructose)

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which, under flooding, brings about increased oxygen debt and increased concentrations of toxic substances in the rhizosphere, as a result of a shift in microbial metabolism (Čížková et al., 1999; Picek et al., 2000). As the effects of these two factors are difficult to separate in natural habitats, we conducted a series of cultivation experiments with defined nutrition, in order to ascertain the effects of elevated nutrient availability per se. Moreover, the experimental conditions provided the possibility to study both aboveground as well as belowground organs in detail in contrast to the situation in natural habitats, where there are problems to obtain intact belowground organs.

This study is focused on *Typha angustifolia*, a species known to cope well in nutrient-rich littoral habitats (Hejný and Husák, 1978; Brändle et al., 1996), where it could replace other species (Ostendorp, 1989). Up to now, the performance of the *Typha* genus has been mainly studied with respect to growth and tissue nutrient content (e.g. Cary and Weerts, 1984; Ulrich and Burton, 1988; Lorenzen et al., 2001; Miao, 2004). By contrast, the associated metabolic features (e.g. related to carbohydrate metabolism) (Čížková-Končalová et al., 1996; Miao et al., 2000), which could contribute to the understanding of the physiological background of the species performance, have rarely been studied.

The aim of this study was to assess, in detail, the long-term effects of nutrient supply on the main features of plant growth and metabolism, which are considered important for survival in wetland habitats (Brändle and Crawford, 1987; Čížková-Končalová et al., 1992). These features include: (1) the production of biomass and its distribution among various plant organs; (2) the metabolic ability to form and accumulate sufficient carbohydrate reserves, and its synchronization with tissue differentiation; (3) the ability to balance carbon and nitrogen metabolism under a range of nutrient concentrations.

Based on these features, the specific aims of this study were to test the following hypotheses: (1) *T. angustifolia* responds to increased nutrient supply by an increase in growth and biomass production. Its distribution among particular organs contributes to its competitive ability. (2) *T. angustifolia*, contrary to other species, does not respond to increased nutrient supply by the decreased formation of reserve carbohydrates, regardless of tissue age. (3) *T. angustifolia* maintains a balance between carbon and nitrogen metabolism over a range of nutrient concentrations, in accord with the growth of individual organs.

2. Materials and methods

2.1. Plant material

The experimental plants were cultivated from 3–4 cm long rhizome cuttings possessing one shoot. Mother plants originally came from natural habitats (littoral zones of fishponds in South Bohemia, Czech Republic) and were kept and propagated in the Institute of Botany, Academy of Sciences of the Czech Republic in Třeboň, Czech Republic, for several years. The rootless cuttings were pre-cultivated in a mixture of perlite and pure silica sand, and moisturised with tap water until new roots emerged (3–4 weeks). The length of the average cutting's shoot was 65 cm after pre-cultivation at the beginning of the experiment.

2.2. Experimental set-up

The cuttings were planted in plastic pots (33 cm × 20 cm × 29.5 cm, one cutting per pot) filled with pure silica sand. The eight pots per treatment were placed in tanks each filled with 130 L of the nutrient solution. Three treatments were designed. The oligotrophic (NH_4^+, 0.0043 mM; NO_3^-, 0.0219 mM; PO_4^{3-}, 0.001 mM; Ca^{2+}, 0.767 mM; K^+, 0.500 mM; Mg^{2+}, 0.391 mM; SO_4^{2-}, 0.391 mM; Cl^-, 2.014 mM) and eutrophic (NH_4^+, 0.444 mM; NO_3^-, 2.192 mM; PO_4^{3-}, 0.099 mM; Ca^{2+}, 1.096 mM; K^+, 0.105 mM; Mg^{2+}, 0.391 mM; SO_4^{2-}, 0.391 mM; Cl^-, 0.443 mM) treatments resembled the nutrient composition in pore waters in the natural wetland habitats (Třeboň Basin, South Bohemia, CZ), while the hypertrophic treatment (NH_4^+, 4.444 mM; NO_3^-, 5.095 mM; PO_4^{3-}, 0.999 mM; Ca^{2+}, 1.096 mM; K^+, 1.049 mM; Mg^{2+}, 0.391 mM; SO_4^{2-}, 0.391 mM; Cl^-, 0.017 mM) simulated the nutrient levels of constructed wetlands. All three treatments received the same amount of trace elements (BO_3^{3-}, 0.23 μM; Fe^{2+}, 20.42 μM; Mn^{2+}, 0.71 μM; Zn^{2+}, 0.01 μM; Cu^{2-}, 0.003 μM; $Mo_7O_{24}^{2-}$, 0.001 μM). One normal HCl was used to adjust the pH level of the nutrient solutions to 6.8, the value commonly found in littoral sites of South Bohemian ponds (Úlehlová and Přibil, 1978). The nutrient solutions were changed every 3 weeks. The water level was kept up to the surface of the sand. The experiment was performed outdoors under a transparent plastic shelter to prevent dilution of the nutrient solutions by rain. The experiment lasted 4 months (end of April until the end of August).

2.3. Plant harvest

At the end of the experiment, the *Typha* plants were taken out of the pots and the belowground organs were washed with tap water to remove sand. Detailed biometric analysis of aboveground as well as belowground organs was then carried out. Plants were divided into leaves, rhizomes and roots (no plant produced a stem with spadix). The number and length of shoots, number and condition of leaves (green or yellow plus dry leaf), and total length of the rhizome system were determined. Roots were classified into categories according to the length of their main axis and the occurrence of lateral roots (branched roots have developed lateral roots, while unbranched roots did not have any visible lateral roots). Finally, the dry weights of leaves, rhizomes, and