

The effect of long-term submergence on functional properties of *Eleocharis cellulosa* Torr.

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Abstract

Eleocharis cellulosa Torr., a macrophyte dominating marshes of northern Belize, often experiences great water level fluctuations varying from dry conditions to prolonged submergence. We investigated morphological and ecophysiological responses (shoot length, biomass, CO₂ exchange, chlorophyll content and regeneration) to partial and complete submergence followed by emergence in two field experiments. Submergence greatly enhanced shoot elongation, but it also resulted in a low number of viable shoots, lower biomass and consequently in lower plant fitness. The decline in live shoot length started after 3 months of submergence. The shoots produced by submerged plants were thin and would break easily if the water level decreased fast. Photosynthetic activity, as well as respiration rate, was highly reduced in shoots just emerged from complete submergence. The ability of *E. cellulosa* to retain some level of photosynthesis after emergence is undoubtedly a useful trait in coping with seasonal floods. Submerged plants produced chlorophyll, especially Ch *a*, for at least a period of 3 months. Shoot regeneration was significantly slower in the case of plants submerged for a longer time, probably due to depleted energy reserves, but there were no significant differences in the total shoot length among treatments after 2 months following the emergence. *E. cellulosa* demonstrated high tolerance to long-term (more than 4 months) complete submergence and resulting anoxic conditions and showed rather fast recovery after emergence. This can be viewed as an advantageous trait in habitats of rapid and prolonged increases of water level and also after water recedes, when vegetation starts to colonize newly opened space. Published by Elsevier B.V.

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1. Introduction

Water is essential for plant life; its surplus, however, may create stressful conditions that most plants are not able to tolerate. Seasonally flooded wetlands represent a habitat of the two extremes of water availability (Kirkman and Sharitz, 1993; Santos and Esteves, 2004). During high water levels, these wetlands become harsh environments where only plants able to adapt to low oxygen supply and to protect their tissues against phytotoxins can survive (Brändle et al., 1996). Marshes of northern Belize, where water level can increase rapidly by well over 1.5 m (pers. obs.) and then drop close to zero over a period of several months, represent an excellent system to study this

phenomenon. We investigated the responses of the dominant emergent macrophyte, *Eleocharis cellulosa*, to submergence and consequent emergence.

To cope with water stress, plants developed various adaptive strategies of either avoidance in time or space or of tolerance by metabolic changes. The most common morphological responses to flooding are shoot elongation, either by cell growth or by cell division (Kende et al., 1998; Cooling et al., 2001), and formation of aerenchyma, in both roots and shoots (Justin and Armstrong, 1987; Kende et al., 1998). Anoxic conditions may eventually result in the reduction of growth and total biomass (Mauchamp et al., 2001; Sorrell et al., 2002; Edwards et al., 2003). An important strategy is conservation of energy, e.g. death of older shoots and their replacement by new ones (Cooling et al., 2001) or a switch to anaerobic respiration (Armstrong et al., 1994). When submerged, plants usually produce thinner shoots or leaves, which are more susceptible to

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mechanical failure (Sorrell et al., 2002; Edwards et al., 2003). For more details on plant adaptations to flooding see Pfister-Sieber and Brändle (1994), Blom and Voeselek (1996) and Crawford (2003).

Reemergence after flooding represents additional problems because oxygen radicals and acetaldehyde formed under the submergence start oxidative chain reactions leading to a lipidic membrane destruction and consequent death of plant tissues in a process called “post-anoxic injury” (Wollenweber-Ratzer and Crawford, 1994; Crawford, 1996).

The effect of elevated water level either on plant morphology (Grace, 1989; Santos and Esteves, 2002; Busch et al., 2004) or on community composition was investigated in a number of studies (McKee and Mendelssohn, 1989; Weiher and Keddy, 1995). However, studies investigating the response of typical emergent macrophytes to complete submergence are rather scarce (Crawford, 1996). Furthermore, while tolerance to flooding is expected in the case of emergent macrophytes, there has not been any report of tolerance to long-term complete submergence for *E. cellulosa* yet.

Field observations of *E. cellulosa* surviving prolonged submergence have raised several questions that we try to answer in this paper. (1) What are the morphological responses of *E. cellulosa* to flooding? (2) How long can *E. cellulosa* survive complete submergence? (3) What are the morphological and physiological responses of *E. cellulosa* to re-aeration after prolonged submergence? (4) How fast does it regenerate after emergence? Two consecutive field experiments were established to answer these questions.

We predicted that *E. cellulosa* will invest into shoot elongation rather than shoot number in an effort to reach the water table and maintain air contact. The survival of plants under water will probably be no longer than 2 months. The submergence will lead to production of weak shoots that will die after emergence. Photosynthetic activity will decrease under submergence, but will reach the pre-submergence values in regenerated shoots. We expected an increased amount of photosynthetic pigments in the shoots grown under the submergence. The overall regeneration of plants will decrease with the length of submergence. Shoot length and number were recorded as morphological responses, aboveground biomass was assessed as a growth response. Physiological responses were measured by CO₂ exchange and chlorophyll content. These characteristics also serve to illustrate plant fitness under submergence and after emergence.

2. Material and methods

2.1. Study species

E. cellulosa is a perennial rhizomatous sedge usually from 30 to 80 cm tall. Its terete shoots are formed by one elongated green spike-like terminal internode and undeveloped leaves. The shoots have no septa and are filled with spongy aerenchyma. The species is distributed from the southern part of the USA, throughout Central America and the West Indies. It

usually grows in fresh to brackish marshes forming large, often monospecific stands (Godfrey and Wootn, 1979).

2.2. Study site

Both experiments were conducted in a small marsh located 20 km east of Orange Walk, northern Belize, CA. The location is a part of a larger complex of seasonally flooded wetlands on alluvial sand deposits covered by a moderate layer of peaty marl. The water level fluctuates according to precipitation and consequently the water salinity also varies (at the time of the experiments, the conductivity was $\sim 600 \mu\text{S cm}^{-1}$). The species poor communities are dominated by *E. cellulosa* and *Eleocharis interstincta* (Vahl) Roemer & J.A. Schultes and submerged *Utricularia* species. An important component of these marshes are species rich cyanobacterial communities dominated by *Leptolyngbya* spp. that form benthic and floating mats or periphyton on shoots of higher plants. Sediments at the study site are peaty marls with total N and P content of 7.87 and 0.18 mg g⁻¹, respectively, indicating a strong P limitation. For a more detailed description of soil, hydrology, climate and vegetation of marshes of northern Belize, see Rejmankova et al. (1996).

2.3. Experimental design and sampling

In the first experiment (April–July 2002) we transplanted 72 young ramets of *E. cellulosa* into pots filled with a soil mixture consisting of the equal parts of peat, marl and clay. Uniformly looking plants consisting of two shoots were selected (shoot length 22.3 ± 5.5 cm; shoot number 2 ± 0.6 shoots). The plants in pots were gradually submerged into three different water levels: low (L), water at the soil surface; medium (M), the water level 50 cm above soil surface; high (H), the water level 90 cm above the soil surface. Each treatment was replicated 24 times. Twelve plants of each treatment were harvested 42 days after the start of the experiment, the remaining plants were harvested after 119 days of experiment. The water level had risen during the course of the experiment by ~ 25 cm. At both harvest days, we recorded the number and length of shoots of each plant. Then the aboveground biomass was harvested, dried at 60 °C and weighed. The number of newly produced shoots (plant regeneration) was also recorded 2 months after harvest.

In the second experiment (December 2002–May 2003) we transplanted 140 *E. cellulosa* ramets (shoot length 16.8 ± 3.7 cm; shoot number 2.5 ± 0.5 shoots) into the pots filled with the same soil mixture. Plants were completely submerged. During the experiment, the water level was always kept above the experimental plants to avoid any shoot contact with the air. Plants were grown under complete submergence in anoxic soil for 46, 60, 73, 88, 101 and 130 days (treatments A, B, C, D, E and F, respectively). Plants in the saturated soil served as control. The mean values of redox potential in the soil at the time of the emergence were: A 133 mV; B 188 mV; C 184 mV; D 202 mV; E -52 mV; F -65 mV.

We recorded shoot lengths and their conditions (estimated as dead and live shoot lengths), photosynthesis and respiration of

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