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Lake water acidification and temperature have a lagged effect on the population dynamics of *Isoëtes echinospora* via offspring recruitment

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ABSTRACT

The aquatic quillwort, *Isoëtes echinospora*, survived the strong water acidification during 1960s–1990s in Plešné Lake (Bohemian Forest, Central Europe), but failed to reproduce. We studied the relationships between a recent population recovery and an improvement of lake water quality. We used correlation analysis to evaluate lagged seasonal effects of lake water quality on population dynamics during the past decade, and factor analysis to determine the independent factors responsible for population recovery. We also provided a water-quality-based reconstruction of population growth from the beginning of the lake recovery two decades ago, using a partial least squares regression (PLSR) model of population growth. We identified three independent controlling factors: nutrients (nitrate, phosphorus, calcium, potassium, magnesium), stressors (pH, ionic aluminium) and temperature. Of these, nutrient availability did not limit the quillwort growth, but annual mean pH and winter mean concentrations of toxic ionic aluminium influenced population growth through negative effects on sporeling establishment until the age of one year, while cumulative temperature in spring and summer controlled the later plant growth. Thus, water quality in the acidified Plešné Lake mainly controls recruitment success rather than adult survival of *Isoëtes echinospora*. This study provides the first in situ evidence that the recruitment success, namely the annual increment in the adult quillwort population, indicates the degree of recovery from acidification, however further extensive investigation is required to more accurately quantify, and therefore understand, the relationships between recruitment, water quality and other factors.

1. Introduction

Isoetid species are small, slow-growing, evergreen water plants that are highly specialised for life in carbonate poor (weakly buffered) and nutrient poor (oligotrophic) lakes (Hutchinson, 1975; Smolders et al., 2002). During the last century, isoetid vegetation in lakes of the Northern Hemisphere declined or became endangered due to anthropogenic acidification and eutrophication (Arts, 2002; Brouwer et al., 2002; Smolders et al., 2002). Many of the atmospherically acidified lakes have been chemically and biologically recovering since the 1980s (e.g., Stoddard et al., 1999; Graham et al., 2007; Gray and Arnott 2009; Garmo et al., 2014), allowing for unique ecological studies on the ecosystem functioning along rapidly changing temporal gradients of water chemistry. In contrast to fish, plankton and benthos, current knowledge on the environmental stress affecting isoetids in acidified lakes remains fragmented, since long-term quantitative data on their growth under in situ conditions has been missing. The successional changes in plant communities ascribed to lake water acidification are quite common in the literature (for review see Arts 2002), supported by inconsistently surveyed presence-absence data on 'sensitive' species. Only a few transplant (Brandrud and Johansen 1994) or germination (Čtvrtlíková et al., 2009; Čtvrtlíková et al., 2014) experiments focused on the symptoms of plant sensitivity to particular stressors including low pH and toxic ionic aluminium (Al_i). There is, however, no compelling evidence that these stressors within other physico-chemical conditions in situ play a significant role in decline of the original flora in acidified lakes (Arts 2002).

Isoetids obtain both nutrients and carbon from relatively rich sediments through a large root system (for review see Smolders

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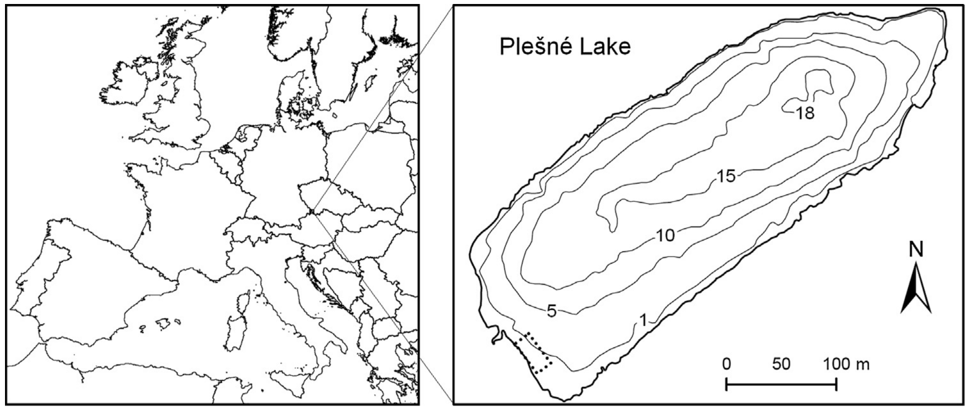

Fig. 1. Situation map of Plešné Lake and study plots (dotted rectangle) of *Isoëtes echinospora* population along the south-west shore.

et al., 2002), while the green aboveground parts of isoetid leaves are covered by thick cuticle, thus, only responsible for light absorbance and photosynthesis but not for nutrient uptake from lake water (Madsen et al., 2002). Isoetid vulnerability to changes in ambient water quality has been generally described in eutrophic lakes, where they are eventually outcompeted by taller rooting macrophytes, epiphytes, floating macrophytes, or phytoplankton (Arts 2002; Brouwer et al., 2002), all better competitors for nutrients dissolved in the water column and ultimately for light. By analogy, the shading effect of expanding acidotolerant macrophytes has also been suspected to be responsible for a large decline of isoetids in acidified lakes (Arts 2002; Brouwer et al., 2002). Since lake water acidification does not affect deeper sediment horizons (Herlihy and Mills 1986; Kopáček et al., 2001), it remains unclear why the isoetids – with impermeable leaves and rooted in those favourable sediment horizons – decline in acidified lakes, even if competitive plants are absent and light conditions are satisfactory for growth (Murphy 2002; Čtvrtlíková et al., 2009).

Quillworts (*Isoëtes*) are representatives of isoetid growth and typically are the dominant species in European unproductive lakes (Rørslett and Brettum 1989; Murphy 2002). Sole, monospecific population of *Isoëtes echinospora* persists as a glacial relic in Plešné Lake (Bohemian Forest), which has been strongly acidified since the 1960s (Majer et al., 2003). Our laboratory experiments on the effects of strong acidity and Al_i toxicity of lake water on spore germination of *I. echinospora* showed that both stressors significantly damaged the fine root system of the quillwort sporelings (Čtvrtlíková et al., 2009). Therefore, we hypothesised that the extreme stress during spring germination of *I. echinospora* has been responsible for the quillwort reproduction failure over the 30 years of severe acidification of Plešné Lake. Nontheless, there is no observed weakness in deeply rooted adult plants in the lake population. In fact, there were approximately 1000–5000 adult plants forming the population until the 2000s (Husák et al., 2000). The resistance of long living adults to lake water stressors most likely allowed for long-term survival of *I. echinospora* in acidified Plešné Lake. Recently we have witnessed remarkable reproduction recovery of the quillwort following improvement of the Plešné Lake water quality due to reduced sulphur and nitrogen deposition (Oulehle et al., 2013). In this study, we aim to elucidate the controlling role of the presumed environmental stressors that affect *I. echinospora* recruitment in Plešné Lake during its recovery from atmospheric acidification. To achieve this aim, the study has four objectives: (1) to assess relationships between population dynamics of *I. echinospora* and ambient lake water conditions in Plešné Lake, (2) to verify controlling roles of still seasonally high acidity and Al_i toxicity in the quillwort renewal in situ, (3) to confirm that the early ontogenetic stages of *I. echinospora* are sensitive to environmental stresses associated with lake water acidification, and (4) to reconstruct the population growth from the beginning of the lake recovery two decades ago.

2. Material and methods

2.1. Study site

The population of *I. echinospora* Durieu has inhabited Plešné Lake situated in the Bohemian Forest, the Czech Republic (48°47′N,13°52′E; 1087 m a.s.l.; Fig. 1) since the end of the last Glacial (~10 kyr BP; Jankovská 2006). The lake is of glacial origin, dimictic, mesotrophic (area of 7.5 ha, volume of 617,000 m^3, maximum depth of 18 m), with small catchment area (66.6 ha) on granitic bedrock forested by Norway spruce (*Picea abies*) (Kopáček et al., 2007). The lake has been acidified by atmospheric deposition of sulphur (S) and nitrogen (N) compounds since the late 1960s. Acidification progressed until the middle 1980s, when pH ranged between 4.4 and 4.7, carbonate buffering system was entirely depleted, and total aluminium (Al_t) and ionic aluminium (Al_i) concentrations reached 1.1 and 0.8 mg l^{-1}, respectively (Kopáček et al., 2009). Since the 1990s, the lake chemistry has been recovering, with a temporary renewal of carbonate buffering capacity and increase of mean pH values to approximately 5 during summer stratification in the early 2000s. A partial lake water re-acidification has occurred since 2004 due to forest dieback in the Plešné catchment due to bark-beetle infestation (Kaňa et al., 2013; Oulehle et al., 2013).

Isoëtes echinospora forms a monospecific plant stand in the inshore area of approximately 0.03 ha, at depths of 0.3–0.5 m (max. 1.0 m; Čtvrtlíková et al., 2009). The lake shore is grown by Bottle Sedge (*Carex rostrata*); its dense stand forms a dynamic inshore border of the quillwort population. The sediment at the quillwort stand is an aqueous sapropel with a high proportion of organic matter. The lake is usually ice-covered from December to April.

2.2. Population dynamics

Population dynamics of *I. echinospora* in Plešné Lake were investigated at 3 adjacent study plots (3 × 10 × 15 m) covering most of the lake population (95% in July 2013). The plant stands outside the study plots were not taken into account as they had been gradually overgrown by the Bottle Sedge. Underwater visual censuses were performed in transitory strip transects (0.5 × 10 m) using snorkelling every June–July from 2004 to 2014 and additionally in October 2013, when a plant stand disturbance occurred. All plant individuals in transects were recorded by the same observer throughout this study.