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Habitat diversity along a hydrological gradient in a complex wetland results in high plant species diversity

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ABSTRACT

Plant communities and selected environmental parameters were studied at the intermittent Lake Cerknica. Seventeen plots (16 m^2) were defined down a 600-m transect on a gentle sloping shore with an elevation decrease of 2.7 m, to investigate the different types of wetland vegetation characteristic of the different habitats. Vegetation was investigated using the standard Central European method. Soil samples were measured for pH, electrical conductivity, organic matter, total nitrogen, available phosphorous and potassium, cation exchange capacity, and texture. Large differences in floristic composition of the plant communities were found. Vegetation of mesic meadows was seen for the rarely flooded most elevated plots, with transition downwards to wet grassland communities from the alliance *Molinion* and from the alliance *Deschampsion*. The lower habitats with soils waterlogged until July were colonized by marsh communities, while community of emergent hydrophytes was at the lowest end of transect. Over 100 vascular plant species were recorded in the plots. Species richness increased with elevation and decreased with moisture, with > 50 taxa in three most elevated plots, and 9–15 taxa per plot for the nine most frequently flooded plots. The hydrological gradient corresponded to the elevation gradient, and together with duration of flooding had a crucial role in shaping plant community composition, distribution and diversity. The flooding arose from Ca-rich lake water, while elevated habitats were rainwater fed, which the consequent enhanced nutrient leaching and lowered pH and electrical conductivity. This produced negative correlations between plant community diversity and species richness *versus* pH, Ca^{2+} and electrical conductivity, since these influences were overridden by hydrological gradient.

1. Introduction

Hydrological gradients and diversity within wetland plant communities have been the object of many studies over the years, because the threat to the biodiversity of these ecosystems is very high (*e.g.* Wassen et al., 2003; Zelnik and Čarni, 2008; Chen et al., 2015). One of the most outstanding features of wetlands that are associated with a hydrological gradient is the zonation of the vegetation types, which primarily reflects the species-specific differences in response to flooding (Blom and Voesenek, 1996). Correlation between the hydrological regime and the composition and distribution of the herbaceous wetland plant communities has been shown for instance by Keddy and Ellis (1985), Stromberg (2001) and Dwire et al. (2004).

The hierarchy of the causes that shape the floristic composition and vegetation patterns in wetlands has remained an issue despite numerous studies. Parameters like soil moisture, nutrient content and pH have been shown to be the most important factors that determine the species composition of wet grasslands (Zelnik and Čarni, 2013). However, the water regime or hydrological gradient is generally accepted as the primary environmental factor that determines the growth and survival of different species and the structure and dynamics of wetland plant communities (Wassen et al., 2003; Luo et al., 2008; Keddy, 2010). The hydrological gradient of a wetland (shallow lake) is strongly correlated with the water level, and therefore it can be indirectly defined according to an elevation gradient (Urban, 2005; Zelnik and Čarni, 2008). The increasing elevation of the terrain is accompanied by decreasing water-table level, duration of the flooding and by the soil properties which best explain the presence and abundance of the species in plant communities (Townsend, 2001; Moran et al., 2007).

Water level fluctuation and associated processes shape the plant communities in different ways. The susceptibility to the two extremes of flooding and dry periods has an important role in the distribution and

Abbreviations: N, number of plant species per plot; SWI, Shannon-Wiener diversity index; C:N, ratio between organic carbon and total nitrogen in the soil; P, plant available phosphorous in the soil; OM, organic matter in the soil; AG, above-ground; CCA, canonical correspondence analysis; CSR, intermediate strategists according to Grime CSR-strategies of vascular plants; CS, competitive-stress-tolerant species; C, competitors (highly competitive species)

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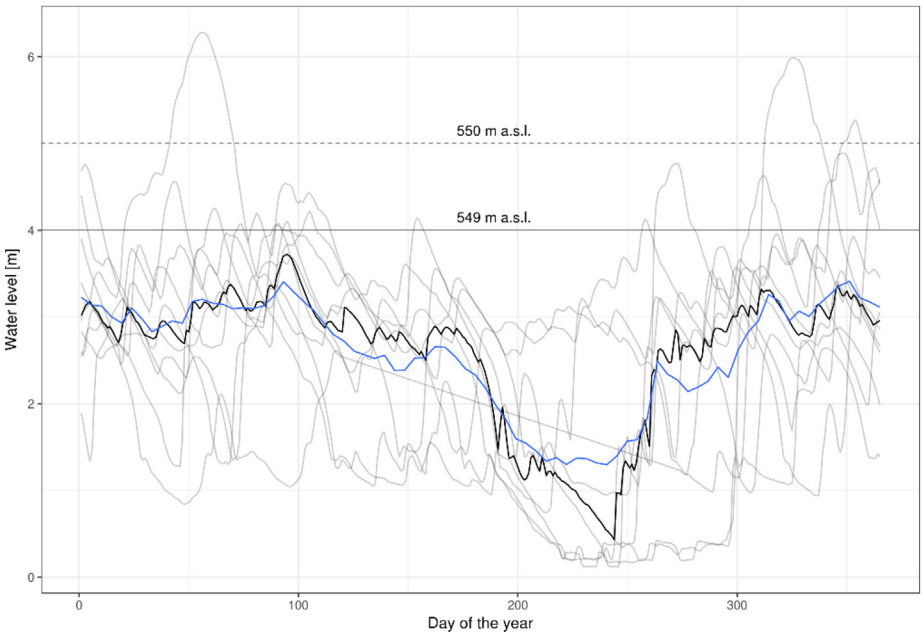

Fig. 1. Water level of Lake Cerknica during the 10-year period from 2005 to 2015. Light grey curves – water levels for specific years; black curve – 10-year mean; dark grey curve – 10-year median; dashed horizontal line – 550 m a.s.l. which is the maximal annual water level according to Drev and Panjan (2011); solid horizontal line – 549 m a.s.l. which delimits the upper section of the transect, while the lower section begins at 548.5 m and further downward. This lower part is more frequently flooded, as the mean and median water levels exceed this altitude for the first 100 days and the last 60 days of the year (Figure created with R program package (R Development Core Team, 2011)).

abundance of species (Dolinar et al., 2010; Moran et al., 2007). The success of plants in such an environment depends primarily on their ability to overcome the stress conditions caused by the water level fluctuations (Germ and Gaberščik, 2003), while the sensitivity is reflected in reduced growth of the plant species (Grime, 1973, 2001). Along the elevation gradient, flood-sensitive species are distributed at the higher elevation sites, whereas flood-tolerant species will occur at the lower elevations (Luo et al., 2008). Higher species richness is usually found in the vegetation types of the elevated, drier sites (Grime, 1973; Wassen et al., 2003; Dwire et al., 2004). In the wetter sites, which are represented by aquatic or marsh vegetation, stress-tolerant species dominate, while in wet meadows, competition has a greater role in determining the species composition (Keddy, 1992; Zelnik and Čarni, 2008).

The water regime and variable microtopography of Lake Cerknica results in a mosaic of habitats, and consequently in species-rich communities (Martinčič and Leskovar, 2003). Several wetland vegetation types alternate in the area of Lake Cerknica, with the most common being marsh and wet meadow vegetation (Ilijanić, 1979; Martinčič, 1991). Some plant communities consist of species from different ecological groups of plants, like aquatic macrophytes, and marsh, fen and grassland species. The shape of the lake basin, and consequently the differences in the durations of the aquatic phases, results in clear zonation of the vegetation (Martinčič and Leskovar, 2003). This is mainly a consequence of the differences in the chemical and physical processes in the plant rhizosphere, such as the microbial activities and the availability of oxygen and nutrients (Urbanc-Berčič and Gaberščik, 2003, 2004; Bailey-Serres and Voesenek, 2008).

Recent changes in worldwide precipitation distribution have also resulted in unpredictable changes in water regimes in different wetlands, and consequently for their associated vegetation structures (Garssen et al., 2015). In comparison to long periods of flooding or dessication, the effects of repeating wet-dry cycles on the processes in the soil are less known (Baldwin and Mitchell, 2000). Therefore, the intermittent water regime of Lake Cerknica can serve as a model system for insight into the changes in vegetation patterns due to sudden extreme changes in the water regime.

The knowledge about structure and function of intermittent aquatic ecosystems may be applied in intermittently loaded vertical subsurface flow constructed wetlands or in shallow surface flow constructed wetlands where water table is regulated and fluctuating in certain rhythm (Põldvere et al., 2009). In addition, new insights into ecology of plant species from these habitats may contribute to better choice of plant species used in these systems (Sehar et al., 2015).

We hypothesized that in the studied wetland complex the variability of hydrological and soil characteristics in habitats along the hydrological gradient will significantly influence the species composition of plant communities and will also result in high γ-diversity of vascular plants. To explain the changes in the vegetation patterns according to the environmental parameters, we measured the elevation gradient, soil properties, and distribution of plant species and communities along transect of Lake Cerknica, and examined the relations between the environmental parameters and the plant species composition and diversity.

2. Methods

2.1. Study area

Lake Cerknica is an intermittent lake in the Dinnaric karst region of southwest Slovenia. The lake appears at the lowest part of Cerknica Polje, which is a karst feature that is the result of chemical weathering of limestone. The mean annual precipitation in this area is relatively high (1700 mm) (Zupančič, 2003).

Cerknica Polje is a floodplain of the Stržen River, which fills the lake during the rainy season. At the highest annual water level, the surface of the lake reaches 550 m above sea level (a.s.l.), with an average water depth of 2.9 m; about 80% of the water that fills Lake Cerknica comes from karst sources, and 20% from surface sources (Kranjc, 2003b). Lake Cerknica usually drains once a year (see Fig. 1), with the average duration of the aquatic phase as 8–10 months per year (Kranjc, 2003b), although this varies greatly across the years. The dry phase is usually from July to September. The bottom of Lake Cerknica is filled with a 4–10-m thick layer of fine sediment (loam, clay, sand) that is covered with a soil layer that is very thin at the drainage area, and much thicker at the edge of Lake Cerknica (Kranjc, 2003a). The wetland plant communities that have developed on Lake Cerknica depend on local environmental conditions and human activities. During dry periods, the vegetation is mown by local farmers and the management staff of the Notranjska Regional Park.

The studied transect was on the very gentle sloping shore of Lake Cerknica in the northern part of Cerknica Polje (45°46′39 N, 14°21′31