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Flooding tolerance and horizontal expansion of wetland plants: Facilitation by floating mats?

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ABSTRACT

Water level fluctuations (WLF) can be important disturbances promoting the diversity of riparian plant communities, but are currently absent from many managed aquatic ecosystems. A lack of WLF is thought to reduce plant diversity and hamper hydrosere succession. However, a positive impact of WLF on plant diversity may crucially depend on nutrient availability and the presence of a potential ecosystem engineer, the floating plant *Stratiotes aloides*, that may provide structural support to riparian plants. We tested the interactive effects of 40 cm flooding, presence of *S. aloides* and sediment nutrient availability (N and P) on growth and horizontal expansion of eight wetland plant species in a 10 week experiment. Seven out of eight species showed a significant elongation response to flooding. Compared to stagnant water levels, flooding in combination with high nutrient availability decreased horizontal expansion in two short species and increased it in two tall species, whereas flooding decreased horizontal expansion in two other short species under both nutrient levels. In this 10 week experiment, we observed no effect of *S. aloides* on the measured plant parameters. This experiment shows short-term negative effects of flooding on most of the short species. On the long-term, we hypothesize that improvements in water quality and seedling recruitment due to drawdown may result in net positive effects of WLF in the riparian zone, but as the species that were rare in the field happened to be short, care should be taken to maintain rare species when allowing more WLF.

1. Introduction

Disturbances are thought to potentially enhance species diversity in communities because at a moderate level of disturbance species with different responses to such disturbances may coexist (Connell, 1978; Roxburgh et al., 2004). Recruitment of subordinate species can be facilitated by disturbances (Bakker and Olff, 2003; Hidding et al., 2010b) while dominants can persist. Disturbances may be generated biotically, for instance by disease, bioturbation or herbivory, or they may be generated abiotically, through fire, drought or flooding. In (semi-) aquatic habitats water level fluctuations (WLF) may form such type of disturbance and therefore the diversity of wetland vegetation may be enhanced through intra-annual variation in water levels (Riis and Hawes, 2002; Van Geest et al., 2005a; Jansson et al., 2005). Lack of water level fluctuations may under some circumstances promote hypoxia of the water column and of the sediment (Bunch et al., 2010). Water drawdown may provide oxygen to the sediment and promote the establishment of submerged aquatic vegetation (Van Geest et al., 2007). In addition, the disturbance dynamics related to WLF may favor coexistence between competing wetland species (Bonis et al., 1995; Van Eck et al., 2004) and create windows of opportunity for the recruitment from seeds (Casanova and Brock, 2000). The natural variation in water level, which often exhibits a seasonal pattern with low water levels in summer and high water level in winter may promote lake-ward expansion of fringing vegetation, as established from paleorecords (Korhola, 1992).

However, WLF may have negative consequences for wetland plant diversity as well (Zohary and Ostrovsky, 2011). The flip-side of positive drawdown effects is the possibility of flooding in spring or summer. Such scenario can be common with excessive precipitation in spring and/or when lakes are influenced by water levels in rivers (Van Geest et al., 2005b). Under such a scenario, plants may experience CO_2 and O_2 shortage (e.g. Mommer and Visser, 2005; Perata et al., 2011) and a changed light climate, in particular when the flooding water is turbid. Plants growing in frequently flooded areas have evolved mechanisms of flooding mitigation such as shoot elongation or quiescence (Voesenek et al., 2006), which ultimately affects their distribution along flooding gradients (Mommer et al., 2007) and subsequently community composition.

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In many managed aquatic systems, including those in the Netherlands, water levels are fixed at a target level and strictly controlled by sluice drainage, such that WLF type disturbances are absent (Coops and Hosper, 2002). Together with eutrophication, the low frequency and intensity of WLF has been hypothesized to be a cause of the lack of expansion of riparian vegetation and reduced biodiversity (Lamers et al., 2002; Sarneel and Soons, 2012; Van der Putten, 1997). In particular, floating mat vegetation has become rare, although it was once a common component of peat lakes in the Netherlands (Lamers et al., 2002; Sarneel et al., 2011). This highly valued habitat type, considered to be an important stage in hydrosere succession (succession of aquatic habitats toward terrestrial systems, sensu Tutin (1941)) has now frequently been replaced by less diverse, tall reed and *Thypha* vegetation.

Stratiotes aloides L., suspected to be a vital component in the formation of floating mats in peat lakes (Sarneel et al., 2011) has particularly declined (Smolders et al., 2003). The plant has been associated with high diversity of wetland plants (Sugier et al., 2010), and may be an important constituent of floating mats because the sturdy leaves in *S. aloides* mats may facilitate horizontal expansion of marsh plants by providing physical support. Facilitation has been shown to be important under adverse conditions in salt marshes (Bertness and Hacker, 1994), and more recently also in submerged macrophytes (Le Bagousse-Pinguet et al., 2012). Similarly, for emergent wetland plants facilitation by floating plants may be an important factor in the expansion of helophytes, as was shown in Lake Victoria (Azza et al., 2006). In this sense, floating plants may be ecosystem engineers (sensu Jones et al., 1994). In the Netherlands, a lack of dense *S. aloides* beds has been hypothesized to contribute to decreased horizontal expansion of wetland plants in peatlands (Lamers et al., 2002; Beltman et al., 2008; Sarneel et al., 2011). Facilitation through physical support from floating plant species such as *S. aloides* may mitigate the potential negative effects of flooding.

Here, we experimentally test the resistance of both tall and short emergent wetland species from fen systems to flooding, with one treatment consisting of submergence and subsequent drawdown and a control treatment with a stable water level but waterlogged sediments. This treatment was performed at two nutrient levels (high and low). We also test whether the presence of *S. aloides* may mitigate negative effects of flooding and may facilitate horizontal expansion of these plants. To this end we performed an experiment using 12 experimental ponds and measured horizontal, and vertical growth and biomass development during 10 weeks. We hypothesized (1) that tall plant species (*Typha*, *Phragmites*) would be better at resisting water level fluctuations than short plants, as tall plants may continue to photosynthesize effectively and provide the root system with oxygen at high water levels. We hypothesized (2) nutrient availability to positively affect biomass mitigating the negative effects of the flooding period while stimulating growth during drawdown. We hypothesized that (3) the presence of *S. aloides* would mitigate negative flooding effects on horizontally expanding plants as they facilitate their expansion by offering physical support. We measured the plant response to the treatments in total biomass, aboveground biomass, root shoot ratio and horizontal and vertical expansions.

2. Methods

2.1. Study system

Peat lakes in the Netherlands are mostly the result of peat excavations that date back to the middle ages (Lamers et al., 2002). Peat lake vegetation is characterized by extensive reed fields and the submerged vegetation, if at all present, is dominated by *Potamogeton* species. The drier areas that represent later successional stages, are characterized by alder forest. In such systems, floating mat vegetation used to be rather common until the 1970s (Beltman et al., 2008). However, nowadays these vegetation types have become rare. In attempting to meet Natura 2000 and Water Framework Directive requirements, water managers in the Netherlands aim at reinstalling flexible water levels in a range of wetlands in order to promote natural disturbance regimes.

2.2. Field survey

To obtain an idea about the abundance of the focal plant species that potentially colonize floating mats, ten wetlands in the west of the Netherlands that were candidate for WLF type management were surveyed (Appendix A). To this end, depending on wetland size, three to six transects with a surface area of 200 m^2 were established in mid-August to mid-September 2010. Length was 50 m along the bank and width 4 m across the slope from dry to wet conditions. In ditches however, that have narrower fringes, transects were 100 m long and 2 m wide across the slope. At each transect, percent cover of our focal species (Table 1) was estimated per species following the Dutch Water Framework Directive standards (Bijkerk et al., 2010) which is derived from the Braun Blanquet method (Barkman et al., 1964) (Table 1).

2.3. Experimental design

We tested the effect of flooding, nutrient availability and of *S. aloides* presence on plant performance parameters of a set of eight wetland species that occur in floating mats. To this end, we set up a large full factorial mesocosm experiment using twelve experimental ponds (5 m × 5 m) at the Loenderveen experimental pond facility owned by the water board Waternet (52°12′41″ N, 5°2′18″ E). Water was taken from a nearby lake that contained dephosphatized water (water properties after introduction in the ponds: N–NH_4^+ = 0.09 mg/L, N–NO_3^- = 0.03 mg/L and P–PO_4^{3-} = 0.01 mg/L). Alkalinity was 3.5 meq and the pH varied between 8.0 and 8.9. Such pH is high but not uncommon in our focal peat lakes (Smolders et al., 2012). Based on these values we estimated CO_2 concentrations to fluctuate between 0.01 and 0.09 mM (Stumm and Morgan, 1996). Hence, underwater

Table 1
Percentage presence of the eight focal species in ten wetland systems in the west of the Netherlands in areas, transects and mean cover respectively.

Latin name	Code name	Height (cm)[b]	Perc. areas	Perc. transects	Mean cover if present	Max. cover
Calla palustris L.	CalPal	15	10	1	≪1	≪1
Menyanthes trifoliata L.	MenTri[a]	20	20	3	<1	1
Comarum palustre (L.)	ComPal[a]	30	30	4	<1	1–5
Berula erecta (Huds.) Coville	BerEre	48	90	33	<1	5–15
Cicuta virosa L.	CicVir	83	70	19	1	15–20
Ranunculus lingua L.	RanLin	85	40	10	<1	15–25
Typha angustifolia L.	TypAng	150	80	34	1	50–75
Phragmites australis (Cav.) Steud.	PhrAus	250	100	73	5–15	75–100

[a] Red list status in the Netherlands according to Van der Meijden, 2005.
[b] Data from the LEDA trait base. Median value was taken if more than one record was present.