The catastrophic dieback of *Typha domingensis* in a drained and restored East Mediterranean wetland: re-examining proposed models

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SUMMARY

We experimentally tested two geochemical models which have been proposed as potential mechanisms leading to the catastrophic dieback of *Typha domingensis* in constructed Lake Agmon within the drained Hula peatland, northern Israel. An elaborate lysimeter station simulating the conditions imposed by sulphide toxicity and P deficiency models was used to test them experimentally. Rhizosphere pH and redox potential were monitored *in situ* in real time throughout the summers of 2007 and 2008. A comparative study of redox-reduction simulation was coupled with periodic sampling and analysis of sulphide and other reducing species. N and P were determined in the plant tissues to compute the N:P nutrient limitation index and evaluate nutrient deficiencies. The sulphide toxicity model was not accepted as a viable mechanism because *Typha domingensis* stands did not show any signs of stress, even when growing in rhizosphere with a sulphide concentration three times that during the actual dieback in 1996. The P limitation model was not supported by the N:P index, which indicated N (<14) rather than P (>16) limitation. Since *Typha* has now returned and is thriving in Lake Agmon and adjacent drainage canals, we suggest a self-thinning mechanism followed by normal succession of macrophytes in this relatively young constructed wetland as the most logical mechanism to explain the observed dieback.

KEY WORDS: geochemical model, Hula peatland, Lake Agmon, P limitation, sulphide toxicity.

INTRODUCTION

The conversion of wetlands for agricultural use is a worldwide phenomenon that has had a dramatic impact on water quality and quantity, both within and downstream of the wetland regions. For example, alteration of parts of the Everglades in the United States for agriculture has had a profound influence on both the Everglades and the near-shore coral reef systems into which the Everglades drain (Davis & Ogden 1994). Alteration of the San Joaquin-Sacramento Delta wetlands in the US has greatly influenced the water quality in neighbouring San Francisco Bay (Deverel *et al*. 1998) and similar phenomena have been observed throughout Europe (Tunney *et al*. 1997). Most of the water-quality issues produced by wetland alteration are a function of the transformation of the wetlands from nutrient sinks which efficiently process and store N and P, to nutrient sources that increase the potential for eutrophication downstream (Richardson 1985, Sharpley & Rekolainen 1997). Other global and regional concerns about wetland alterations include a significant increase in CO_2 efflux (Waddington *et al*. 2002, Billett *et al*. 2004, Lal 2004) and decline in biodiversity. Problems that are commonly encountered in drained wetlands used for agriculture include: loss of soil fertility; diminishing crop yield; and field abandonment leading to colonisation by invasive species, increased salinity and enhanced evapotranspiration.

The drainage of Lake Hula and the surrounding peatland in the 1950s was one of the first major agro-engineering operations undertaken by Israel. The elimination of the old Lake Hula and marshes produced about 6,000 ha of organically rich arable land. However, this drainage resulted in the loss of a very diverse and rare ecosystem that had served as an important phytogeographical meeting zone for holoartic and palaeotropical species. It was an important feeding station for migrating birds, a wintering area for many species and a breeding ground for others. The flora was described as rich, with thickets of *Cyperus papyrus* and clear waters with *Nymphaea alba* and *Nuphar lutea* (Dimentman *et al*. 1992). The transformation of the former marshes to farmland was a difficult agro-technical task because of uncontrolled changes in the peat soils and problems with hydrological management of the altered landscape. The pedological changes included strong oxidation of the exposed organic matter (OM), continuous internal conflagration that changed the texture and structure of the peat layers, decreased water retention, significant land subsidence (2–4 m), increased salinity, and elevated groundwater that prevented profitable farming (Hambright & Zohary 1998). The land-use change transformed the Hula Valley from nutrient sink into nutrient source, with subsequent mobilisation of the nutrients (N and P) from the soils to the waterways and, ultimately, to Lake Kinneret, jeopardising the water quality of Israel's largest freshwater reservoir (Inbar 1982, Rom 1999). Predictions of continuing land subsidence led to initiation (in 1994) of the 'Hula Project', which included the re-flooding of 100 ha in the middle of the valley, creating 'Lake Agmon', and the establishment of 300 ha of meadows and grasslands. The aim of the Hula Project was to rehabilitate the diverse wetland ecology and create an area that was attractive for ecotourism as well as a clear water body which would contribute to purification of the water flow to Lake Kinneret (Gophen *et al*. 2001).

The construction of Lake Agmon was followed by a series of advanced ecological research and monitoring projects. In one of these studies, workers planted *Cyperus papyrus* and monitored the spontaneous colonisation of 53 plant species including *Typha domingensis* and *Phragmites australis* (Kaplan *et al*. 1998). Rapid development of the *Typha domingensis* stands on the south-eastern shore of Lake Agmon in 1995 provided an optimal nesting and roosting habitat for a large heron colony (Ashkenazi & Dimentman 1998). However, towards the end of 1996, these stands started to collapse and the habitat disappeared rapidly. The reasons were hotly debated with two very different conceptual models proposed (Ashkenazi *et al*. 1999, Gophen 2000).

The **sulphide toxicity model** was advanced by Ashkenazi *et al*. (1999), who concluded from an analysis of monitoring data that the *Typha* dieback in Lake Agmon had resulted from a combination of physical, chemical and biological processes that prevented recovery of the *Typha* stands and eventually led to their complete collapse. They suggested that the main mechanism leading to the *Typha* dieback was sulphide toxicity in the transition zone between the anaerobic lower sediment layers and the aerobic upper layer of the rhizosphere, and developed a conceptual model that explained the sulphide formation in terms of numerous interconnected physicochemical processes. The first stage was the transport of large amounts of floating organic debris to the south-eastern corner of Lake Agmon by the prevailing winds. The large increase in floating OM increased the level of dissolved organic carbon (DOC). This enhanced the reduction of SO_4^{2-} to H_2S and Fe(III) to Fe(II), concurrently depleting *Typha* of N because of decreased enzymatic activity, and eventually led to rapid dieback. As the rate of sulphide reduction was higher than that of Fe-S precipitation, it led to increased sulphide concentrations in the rhizosphere and, consequently, sulphide toxicity. The strongly reducing conditions also facilitated intensive denitrification, which created another stress in the form of N deficiency. On the other hand, the reduction of ferrous oxides and hydroxides desorbed P, increasing the level of available P. Hence, according to this model, P deficiency was not the reason for *Typha* dieback in Lake Agmon.

The **P limitation model**, proposed by Gophen (2000), suggested that insufficient storage and uptake of P by the rhizomes of *Typha* during the early years (1994–1996) of Lake Agmon induced the dieback. Gophen (2000) showed a strong correlation between the distribution of *Typha domingensis* habitat and P availability. The *Typha domingensis* stands grew mainly in the marl sediments located on the south-eastern shore of the lake, while very few *Typha domingensis* stands grew on the peaty northern shores. Gophen (2000) argued that the marl sediments are characterised by low P-sorption capacity while the peat sediments exhibit high P-sorption capacity. Support for this assessment was provided by Litaor *et al*. (2003, 2005), who compared the EPC_0 (the point in the isotherm where sorption equals desorption) in the marl and peat layers. The marl sediments exhibited a significantly higher EPC_0 and degree of P saturation than the peat layers, which meant that the marl would release P to water with low P concentrations while the peat layers would adsorb the nutrient. Gophen (2000) claimed that the sulphide toxicity model of Ashkenazi *et al*. (1999) was untenable because the sulphide concentrations did not exceed 8 μM, whereas sulphide toxicity occurs only at concentrations of at least 250 μM (Koch & Mendelsshon 1989, Armstrong *et al*. 1996). He advanced the P deficiency model as an alternative. This was based mainly on studies from the Everglades in Florida where the collapse of submerged plants was linked with P limitation (Davis 1997). It should be noted that different swamp plants exhibit different degrees of sensitivity to P deficiency, and that *Typha domingensis* is extremely susceptible to P limitation. Additional support for the P model given by Gophen (2000) suggested that water-level management was key to the dieback since, once the water level in Lake Agmon decreased, the organic sediments oxidised with subsequent release of P which once again became available for plant uptake.

The above models were based on field observations and routine monitoring of water-quality parameters that were not originally intended to test catastrophic *Typha* dieback processes, and without experimental testing of the impact of changing the geochemical conditions in the rhizosphere. A lack of information from well-designed experiments prevented site managers from adopting either of these models as a basis for the improving the management practices for Lake Agmon. Hence, the main objective of this study was to test the validity and applicability of these models using an experimental approach that simulates sulphide toxicity and P limitation. The experimental design was based on the following hypotheses:

1) The development of extreme reducing conditions led to acute sulphide levels that directly or indirectly brought about the collapse of *Typha domingensis*. Testing sulphide toxicity in the rhizosphere can be achieved by determining N availability under changing redox conditions.

2) The collapse of *Typha domingensis* resulted from nutrient deficiencies, mainly of P, due to efficient utilisation of the labile P fraction in the sediment and pore water, combined with efficient redox-related processes of P depletion in the root zone of these plants following drying and/or re-flooding. This hypothesis can be tested by determining the P content in the macrophyte tissue under changing redox conditions.

METHODS

Study area

The Hula Valley occupies the northernmost part of the Jordan-Arava rift valley, and is approximately 70 m above sea level. It covers about 175 km^2 and is currently drained by a system of artificial canals, which empty into the Jordan River at the southern end of the valley (Figure 1). The climate of the study area is typical East Mediterranean; i.e. hot, dry summers with an average temperature of 28 ºC in July and cool, wet winters with an average temperature of 12 ºC in January. The average annual precipitation in the study area is 400 mm, and the monthly evapotranspiration (ET) rate varies between 90 mm in winter and 240 mm in summer (Tsipris & Meron 1998).

The peat soils of the Hula Valley are predominantly Histosols (~1860 ha). Further classification on the basis of decomposition and the occurrence and quantity of $CaCO_3$ identifies them as Medifibrists, Medihemists, Medisaprists, and 'Conflagrated Histosols' without lime, with minimal lime, and with lime. Following the drainage of Lake Hula and its surrounding peatland in the 1950s, some of the Histosols without lime were highly acidic (pH = 4.0); presently, all the top layers of the Histosols exhibit pHs between 5.0 and 8.0. The high organic matter content of 50–70% observed in 1945 declined steadily after reclamation of the wetlands, to 30–50% in the upper layers of drained peat in 1970 and 25–35% in 1985. A further decline in organic matter is still being observed today (Litaor *et al.* 2011).

Lake Agmon is a shallow water body with a mean depth of < 1 m excavated in deep peat sediments (~ 6 –7 m) at the northern end and shallow peat mixed with marl sediments at the southern end. It has two primary inlets and one outlet. One of the inlets is a waterway that was constructed on the former bed of the Jordan River and now conveys about 2 % of the annual flow of the Jordan River channels system. The second inlet is a ditch that drains most of the peat soils north of the Agmon. The water quality of the reconstructed Jordan River is quite high but the peat drainage inlet is loaded with dissolved organic carbon, nitrates, sulphate, iron, calcium and other nutrients which contribute to the Agmon's eutrophic to hypertrophic state (Zohary *et al.* 1998). The water level fluctuation is no more than few centimetres during the summer and may reach 20 cm during the winter. This water management practice was adapted in order to minimise shore bank flooding or exposure and significant disturbance to nesting birds (Barnea 2011, pers. comm.).

Lysimeter experiment

To test the two models, we built an experiment consisting of 24 lysimeters made of plastic bins (surface area 1 m^2, depth 1.5 m) which were reinforced from the outside with a metal fastening to prevent caving and surrounded with thermal insulation. The substrate in the lysimeters represented the two most common sediments in the study area, namely:

1) an altered peat with ≥ 40 % OM at depths below 1.2 m and approximately 20 % OM in the upper layer, which was taken from the area formerly occupied by the peatland; and

2) organic-rich marl exhibiting small amounts of OM (≤ 5%) and relatively high $CaCO_3$ content(> 65%), which was collected from the area of the former Hula Lake.

The water table was regulated gravimetrically and was held at 10 cm above the surface. The 24 lysimeters were divided into two groups of 12, each

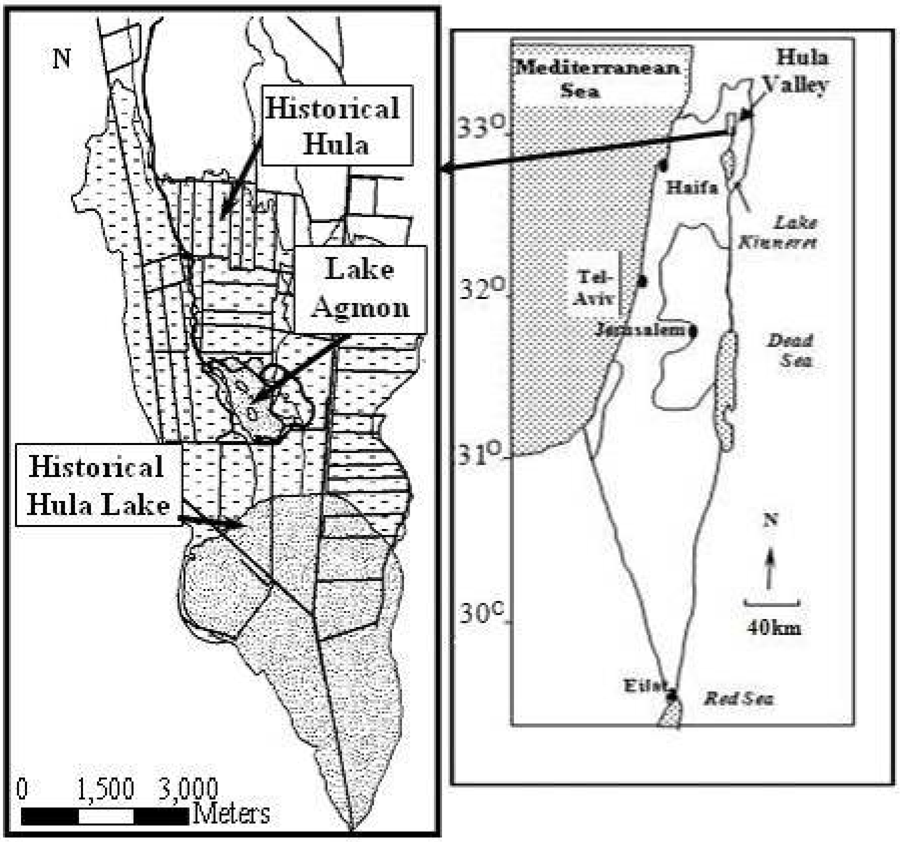

Figure 1. Lake Agmon in relation to the former Hula Lake and wetland (dashed area).

group including six with marl and six with peat substrate. The first group was planted with *Typha domingensis* and the second group was planted with *Phragmites australis*. The latter macrophyte is the most resilient plant in the study area, which showed no signs of stress during the catastrophic dieback episode described earlier.

The sulphide toxicity model was simulated by adding an enriched DOC solution (370 mg l^{-1}) prepared using boiling water with (in 2007) *Sorghum halepense*, a common perennial tropical-subtropical weed or (in 2008) *Ceratophyllum demersum,* a common submerged macrophyte in Lake Agmon and the Hula drainage canals. The enriched DOC solution and the boiled residual plant materials were added to half of the lysimeters in each group twice a week for four weeks during the summers of 2007 and 2008 to create a highly reduced environment similar to the conditions described by Ashkenazi *et al*. (1999). During the experiment, the Eh and pH were measured in selected lysimeters at 10 and 40 cm below the surface using electrodes (5990-55 and 5998-20, respectively, Cole-Pamer, USA). The measured information was collected and stored in a data logger (MultiLog, Fourier, Israel). Plant tissues for nutrient analyses were collected before and after the experiment. Water samples were collected from all 24 lysimeters once every three weeks at the beginning of the experiment and once a week during the final month of the experiment.

After the first year of the experiment some of the macrophytes exhibited difficulty in recovering from their winter dormant state and showed serious nitrogen depletion. In order to encourage a speedy recovery we added liquid N fertiliser (mostly in the forms of NH_4NO_3 & KNO_3) to the lysimeters following the guidelines for common crops in the Hula Valley. The fertiliser was added in three equal portions of 50 mg N l^{-1} per week for three weeks.

The water samples were analysed for major and minor cations using inductively coupled plasma-atomic emission spectrometry (ICP-AES) (Spectro, Kleve, Germany) and anions by ion chromatography (DX-600, Dionex, USA). Soluble reactive P was analysed by the method of Murphy & Riley (1962) while total P was extracted and measured using the ascorbic acid procedure (APHA 2000). Ferrous concentrations were determined using ferrozine solution (Stookey 1970) and sulphide concentrations by a modified Cd-S method, where the sulphide analysis was determined by ICP-AES instead of the specifically equipped IC as described by Montegrossi *et al*. (2006).

Plant tissues from the lysimeter experiment and from selected stands around Lake Agmon were collected, dried at 65 ºC, ground and analysed for total N using an auto Kjeldahl K-370 analyser (Buchi, Switzerland). The ground plant tissues were also extracted by the $NClO_4$ digestion method (Gorsuch 1976) and analysed for major nutrients (P, K, S) and minor elements (Fe, Mn, Ca, Mg, Na, Cu, Mo, Zn) using ICP-AES. The chlorophyll content was determined using the N,N-dimethylformamide extraction described by Moran (1982) and measurement with a spectrophotometer (Genesys 20, Spectronic, UK). We used the N and P concentrations in plant tissues to compute the N:P ratio index suggested by Koerselman & Meuleman (1996) to assess plant response to addition of the limiting nutrient. These authors postulated that, at the community level, the response to addition of the limiting nutrient is an increase in total primary production. They tested this response by using an extensive literature survey and determining whether a given ecosystem was limited by either N or P, or was N + P co-limited.

Statistical and geochemical analyses

Statistical analyses were performed using SPSS Version 17 (SPSS 2002). We opted to use non-parametric tests because the data did not adhere to the requirements of normality and equal variances between groups. Comparisons between three or more groups were performed with a Kruskal-Wallis test while comparison between pairs of groups was accomplished with a Mann-Whitney test. Geochemical modelling to compute species activities and saturation index of various solid phases was conducted with Visual Minteq Version 2.61 (Gustafsson 2009). The redox potential input for the model was derived from the measured SO_4^{2-}/S^{2-} ion pair (Lindsay 1979).

RESULTS

Sulphide toxicity model

The sulphide concentrations in the two groups of lysimeters are summarised in Table 1. In the 2007 and 2008 experiments, no statistical differences in sulphide concentrations were observed between the control plots and the DOC-added plots. The level of sulphide was significantly higher in the peat than in the marl substrate because the peat layers contain more S, mostly in the form of gypsum (Shenker *et al*. 2005). In general, sulphide concentrations in the interstitial water of the root systems were higher in *Typha domingensis* than in *Phragmites australis*. The level of sulphide increased significantly ($P < 0.001$) during the experiment as reducing conditions intensified with time. It was significantly higher in all lysimeters than the 8 μM reported during the catastrophic dieback of the Lake Agmon cattails in 1996 (Markel *et al*. 1998). Moreover it was often higher than the highest level of sulphide (5000 μm) reported in the literature (Koch *et al*. 1990).

Table 1. Summary statistics of sulphide concentration (μM) in the lysimeters during the 2007 and 2008 experiments.

		2007				2008			
		Control (n = 3)		DOC added (n = 3)		Control (n = 8)		DOC added (n = 4)	
	term	Peat	Marl	Peat	Marl	Peat	Marl	Peat	Marl
Typha domingensis	mid	820 ±160	140 ±5	600 ±280	240 ±25	3,830 ±530	955 ±260	2,400 ±1,100	1,400 ±420
	end	8,420 ±430	915 ±230	5,550 ±1720	2,160 ±350	3,700 ±510	780 ±230	1,900 ±515	1,300 ±535
Phragmites australis	mid	800 ±130	170 ±40	540 ±130	275 ±35	405 ±150	440 ±230	1,190 ±470	115 ±60
	end	6,110 ±510	695 ±120	5,430 ±665	1,545 ±150	688 ±310	250 ±110	1,510 ±520	185 ±110

The measured redox potential values in the lysimeter experiment showed that the system is highly reduced and quite close to the lower reduction limit of aqueous ecosystems. The measured redox values were well below the threshold of sulphate reduction to sulphide (-170 mV). Under such conditions, various Fe-S solid phases may precipitate and control the solubility of sulphide in the rhizosphere. We selected plausible reactions that describe the Fe-S system (Table 2) and modelled the saturation index with respect to those solid phases (Figure 2). The modelling results suggest that, under the redox potential reported for Lake Agmon, all the iron oxides and hydroxides will release Fe to solution while FeS_2 may precipitate. Under such conditions, the concentrations of sulphide in the root zone may decrease to a certain extent.

The concentrations of macronutrients in the *Typha domingensis* and *Phragmites australis* growing in peat and marl showed no statistical differences between control plots and DOC-added plots (Table 3). Total N content in the plant tissues of both macrophytes was significantly higher ($P < 0.001$) in the peat substrate than in the marl. No significant difference was observed in P content in the plant tissues, whereas the K level was significantly higher ($P < 0.01$) in the macrophytes growing on marl (Table 3). Release of K under certain conditions from the peat is rather limited due to the poorly understood K-fixation mechanism in the peat OM (Avnimelech *et al*. 1978).

Table 2. Equilibrium constants for various Fe-S reactions.*

No.		Log K
1	$SO_4^{2-} + 8H^+ + 8e^- \Leftrightarrow S^{2-} + 4H_2O$	20.74
2	$CaSO_4 2H_2O_{(gypsum)} \Leftrightarrow Ca^{2+} + SO_4^{2-} + 2H_2O$	-4.64
3	$Ca^{2+} + CO_{2(g)} + H_2O \Leftrightarrow CaCO_{3(calcite)} + 2H^+$	-9.74
4	$Fe(OH)_{3(soil)} + 3H^+ \Leftrightarrow Fe^{3+} + 3H_2O$	2.7
5	$FeCO_{3(sidrite)} + 2H^+ \Leftrightarrow Fe^{2+} + CO_{2(g)} + H_2O$	7.92
6	$Fe_3(OH)_{8(ferrosic\_oxide)} + 8H^+ + 2e^- \Leftrightarrow 3Fe^{2+} + 8H_2O$	43.75
7	$Fe(OH)_{3(amorph)} + 3H^+ \Leftrightarrow Fe^{3+} + 3H_2O$	3.54
8	$FeS_{2(pyrie)} + 2e^- \Leftrightarrow Fe^{2+} + 2S^{2-}$	-42.52
9	$FeS_{(makcinawite)} + H^+ \Leftrightarrow Fe^{2+} + HS^-$	-3.6
10	$Fe^{3+} + e^- \Leftrightarrow Fe^{2+}$	13.04
11	$HS^- \Leftrightarrow H^+ + S^{2-}$	-12.9
12	$Fe_3O_{4(magnetite)} + 8H^+ + 2e^- \Leftrightarrow 3Fe^{2+} + 4H_2O$	35.69
13	$FeS_{(amorph)} + H^+ \Leftrightarrow Fe^{2+} + HS^-$	2.96

*Equations 1–12 taken from Lindsay (1979), equation 13 taken from Langmuir (1997).

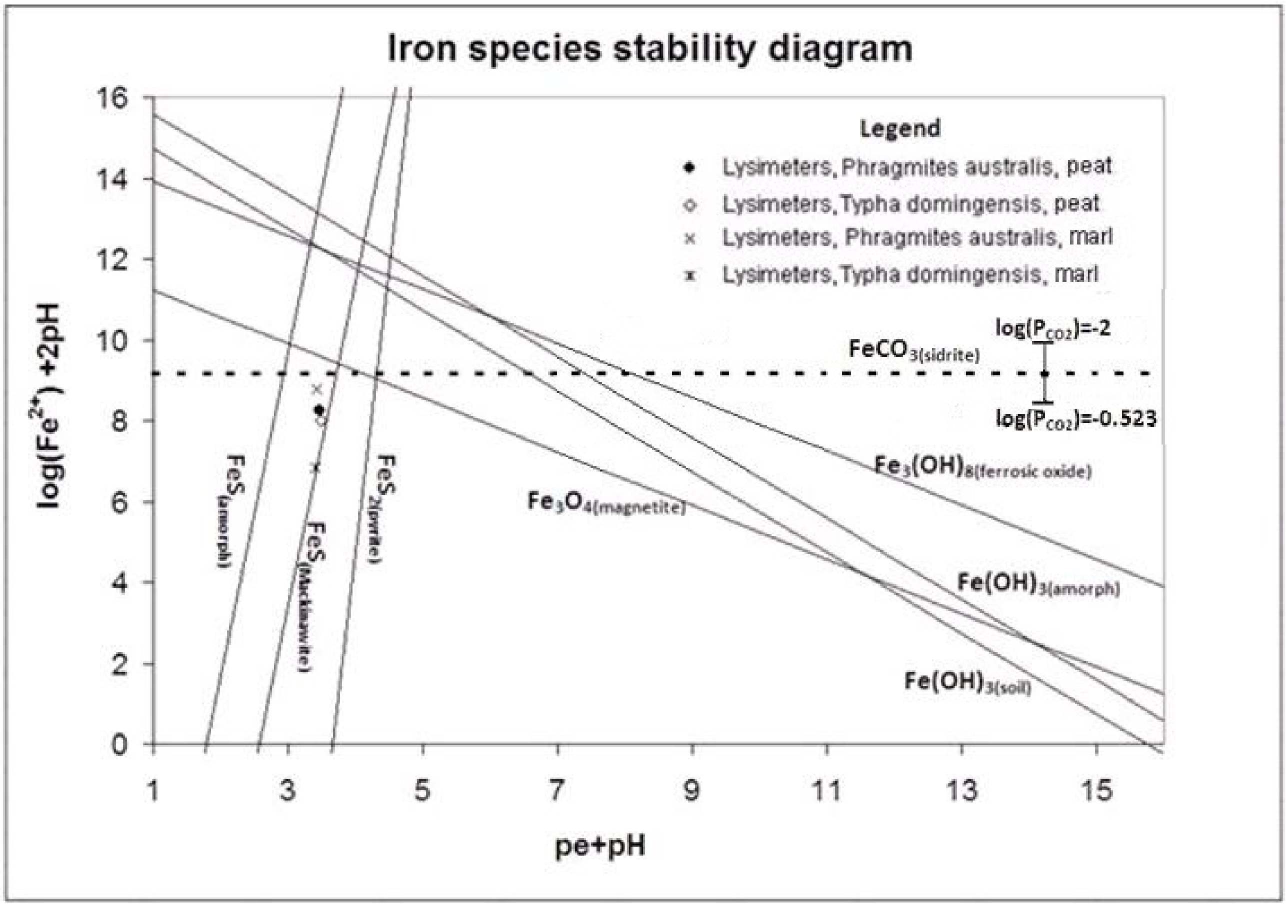

Figure 2. The solubility of selected iron minerals and ferrous iron activity in solutions under highly reducing conditions of the lysimeter experiment supporting *Typha domingensis*.

Table 3. Mean and standard error of macronutrients measured in plant tissues (g kg^{-1}) in control and DOC-added treatments.

	Typha domingensis				*Phragmites australis*			
	Peat		Marl		Peat		Marl	
Nutrient	Control (n = 4)	DOC (n = 2)	Control (n = 4)	DOC (n = 2)	Control (n = 4)	DOC (n = 2)	Control (n = 4)	DOC (n = 2)
N	9.55 ±0.70	10.20 ±0.40	8.65 ±0.85	7.86 ±1.00	12.32 ±0.75	11.35 ±0.35	10.70 ±1.40	10.87 ±2.10
P	2.30 ±0.20	2.00 ±0.05	2.30 ±0.35	1.60 ±0.05	1.35 ±0.10	1.25 ±0.25	1.10 ±0.15	1.25 ±0.15
K	5.70 ±0.40	4.45 ±0.50	7.90 ±0.90	5.60 ±0.55	5.75 ±0.55	7.65 ±3.15	7.40 ±1.75	10.15 ±2.45
S	3.15 ±0.50	2.50 ±0.60	2.80 ±0.35	4.00 ±0.40	2.45 ±0.35	2.45 ±0.40	2.48 ±0.20	2.00 ±0.35

P limitation model

The evaluation of the N:P ratio index to assess nutrient availability and limitation was derived from the N and P contents of the plant tissues. There was no statistical difference in N:P ratio between the control plots and DOC-added plots, thus the N:P ratio summary statistics are given by plant, year and substrate (Table 4). Most N:P ratios were lower than 14, indicating that macrophyte growth is limited by N rather than by P (Koerselman & Meuleman 1996). There was a decrease in N:P ratio between the two years of the experiment, indicating that N availability between years declined in all plots, regardless of treatment or sulphide concentration. Indeed, during the spring of 2008, all macrophytes exhibited difficulty senescing and flowering until N was added at a rate of 50 mg l^{-1} per week for three weeks. All of the macrophytes responded quickly to the added N by greatly improving their general appearance (i.e. colour, height and stem circumference) and flowering began in earnest.

The N:P ratio was also evaluated in macrophyte stands growing around Lake Agmon. The N:P ratios measured in *Typha domingensis* stands in both years (Table 5) were well below the N-limited value computed for *Phragmites australis* (Table 5), indicating co-limitation of N and P. The N concentrations in the *Phragmites australis* around Lake Agmon were significantly (Wilcoxon = 15, $P < 0.02$) higher than those found in the *Typha domingensis* stands (Table 6). No significant difference in P concentration was found between the two macrophytes.

Table 5. Mean and standard error of N:P ratios in the two macrophytes under study at Lake Agmon (n = 3).

Year	*Typha domingensis*	*Phragmites australis*
2007	8.3±0.7	14.9±1.2
2008	6.6±0.3	N/D

Table 6. Mean and standard error of macronutrients measured in plant tissues (g kg^{-1}) at Lake Agmon (n = 3).

Nutrient	*Typha domingensis*	*Phragmites australis*
N	12.00±2.90	20.95±2.10
P	1.45±0.37	1.40±0.04
K	5.10±1.20	4.85±0.20

Table 4. Mean and standard error of N:P ratios in the two macrophytes in the lysimeter experiment.

	2007		2008	
Macrophyte	Peat (n = 6)	Marl (n = 6)	Peat (n = 6)	Marl (n = 5)
Typha domingensis	6.3 ± 0.5	4.0 ± 0.3	4.6 ± 0.3	4.3 ± 0.4
Phragmites australis	12.7 ± 0.8	11.1 ± 0.5	9.4 ± 0.6	9.3 ± 0.3

DISCUSSION

Sulphide toxicity model

Given the neutral pH of the system, the measured redox values were near the reduction limit of aqueous systems, and therefore the lysimeter experiment was considered an adequate surrogate for the conditions observed in Lake Agmon. The mean sulphide concentration in the lysimeters was 600 μM, about two orders of magnitude higher than the values reported in Lake Agmon during the cattail dieback (Markel *et al*. 1998). The N concentration in the macrophyte tissues during the lysimeter experiment did not decrease over time, remaining relatively steady at around 10 g kg^{-1}. These results support the notion that despite the high sulphide concentration in the rhizosphere, there was no impairment in the enzymatic activity of the macrophyte's roots that would affect N uptake, as suggested by Koch *et al*. (1990) and Geurts *et al*. (2009). It is interesting to note that the sulphide concentration in the rhizosphere of *Phragmites australis* was significantly lower ($P < 0.001$) than that found in the rhizosphere of *Typha domingensis*

(900 and 3,100 μM, respectively). This suggests that some macrophytes have developed better ways to deal with extremely reduced environments. *Phragmites australis* uses sulphide to produce gluten, a key protein for its development (Fürtig *et al*. 1996). Indeed, in the current experiment, the average sulphur concentration in the plant tissue of *Phragmites australis* was somewhat higher (3.4 g kg^{-1}) than in the plant tissue of *Typha domingensis* (2.9 g kg^{-1}). Similar results were reported by Li *et al.* (2009) who studied the impact of sulphate enrichment in the Florida Everglades. They found species-specific differences in physiology and growth between *Typha domingensis* and *Cladium jamaicense*. The *Typha* appeared healthy even up to 690 μm sulphide while the *Cladium* was less tolerant.

The geochemical modelling suggested that the activity of ferrous iron and sulphide in the lysimeter experiment was partially governed by precipitation of pyrite (FeS_2). The formation of pyrite is a slow and continuous process (Doner & Lynn 1989) and its existence in the Hula peat and hydromorphic soils has long been known (Department of Agriculture 1986). Hence, it is reasonable to assume that during the two years before the *Typha* collapse, similar geochemical conditions existed, whereby the solubility of sulphide was somewhat moderated by FeS_2 precipitation with little or no impact on the macrophyte's health. In view of all of the above findings, the sulphide toxicity model is probably not the preferred mechanism to explain *Typha domingensis* dieback in Lake Agmon.

P limitation model

Koersleman & Meuleman (1996) suggested that N:P ratios below 14 indicate N limitation, ratios higher than 16 indicate P limitation, and ratios between 14 and 16 indicate N and P co-limitation. We sampled six *Typha domingensis* stands around Lake Agmon in 2007 and 2008 and 23 stands in the lysimeter experiment and the mean N:P ratio index was 7.5, which strongly implied N limitation. Similar results were reported elsewhere (Güsewell & Koerselman, 2002, Güsewell *et al.* 2003, Venterink *et al*. 2003). On the other hand, the N:P ratio index in *Phragmites australis* was around 14.9 (Table 5), while this macrophyte exhibited significantly higher N concentrations and similar P concentrations (20.9 and 1.4 g kg^{-1}, respectively) compared to *Typha domingensis* (11.9 and 1.45 g kg^{-1}, respectively). The ability of *Phragmites australis* to take up NH_4^+ rather than NO_3^- in environments characterised by N deficiency was established by Romero *et al*. (1999) and Tylova-Munzarova *et al*. (2005). This mechanism is even more efficient if P is sufficiently available, which gives *Phragmites australis* an advantage over other macrophytes in highly reducing environments with limited N supply. Field observations in the Hula Valley indicated that *Phragmites australis* has increased in areas where other macrophytes collapsed. On the basis of these observations, it is reasonable to assume that neither the P limitation nor the sulphide toxicity models are good candidates to explain the *Typha domingensis* dieback. Thus we show that neither of the proposed models can account for the *Typha* dieback; however, a field survey showed that *Typha domingensis* has returned and is thriving in Lake Agmon and adjacent drainage canals. This current observation raises the possibility that the dieback was a self-thinning mechanism followed by return of the *Typha domingensis* in a normal succession process. The self-thinning mechanism was invoked by Macek *et al.* (2010) while studying the responses of macrophytes to nutrient addition in an oligotrophic tropical wetland. They observed a decrease of *Typha domingensis* ramet number in P-enriched plots and assumed that density dependent mortality occurred in response to limitation of resources, mostly light, in very dense plant stands. The succession interpretation is supported by several studies which have shown that macrophyte structure and diversity typically exhibit many changes over time in areas of re-flooding (Mitsch *et al*. 2005). *Typha domingensis* is known as a pioneer plant in artificial water bodies (Smith 1967, Fiala & Kvet 1971), and is thus expected to be among the first plants to colonise a freshly re-flooded area. During the first stage of the colonisation, *Typha* creates fairly homogeneous stands, but these stands die out with time *via* succession that leads to a more diverse plant community (Fraga & Kvet 1993). *Typha* may return later and re-colonise as part of mature diversified stands (Van der Valk 1981).

CONCLUDING REMARKS

The main goal of this work was to critically test two published geochemical models that have been proposed as potential mechanisms leading to the catastrophic dieback of *Typha domingensis* in Lake Agmon. The sulphide toxicity model was not accepted as a viable mechanism because *Typha* stands did not show any signs of stress when growing in a highly reduced rhizosphere characterised by sulphide concentrations that were three times the values reported during the cattail dieback. The P deficiency model was not supported by the N:P ratio index, which indicated N limitation rather than P limitation. New survey data indicate that *Typha* has returned and is thriving, and we therefore suggest that periodic succession of macrophytes in this relatively young constructed wetland is probably the mechanism that most logically explains the dieback in 1996.

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