

WETLAND PLANTS AS A SUBJECT OF INTERDISCIPLINARY RESEARCH

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Habitats that are prone to flooding usually support a distinctive flora. Rushes, sedges and reed are vernacular terms which convey an image of a wetland plant community even to the non-botanist. What features enable these plants to survive months or even years of flooding while the intolerant plants die under such conditions after several days or even hours? A whole range of niches exists even within the wetland environment (Tab. 1, 2). What strategies underlie this niche differentiation, observed and described by field botanists?

Waterlogged and flooded soils are usually anoxic, except for a thin surface layer. Due to its low diffusivity in water, oxygen is depleted from most soils in several hours to days after the onset of flooding. Anoxia is associated with the accumulation of potential phytotoxins such as ferrous and manganous compounds, hydrogen sulphide and various organic compounds produced by anaerobic microorganisms in the soil (GAMBRELL & PATRICK 1978, PONNAMPERUMA 1984). Thus, wetland plants face the following major problems: (1) to ensure an alternative oxygen supply for the metabolism of their roots and other underground organs (for example rhizomes); (2) to establish an adequate metabolism under oxygen shortage and re-oxygenation; and (3) to protect themselves against the effects of phytotoxins.

Well developed aerenchyma is obviously a solution to the first problem (oxygen supply). Large gas spaces are a characteristic feature of roots and rhizomes of many wetland and aquatic plants (SCULTHORPE 1967, JUSTIN & ARMSTRONG 1987). This system of interconnected gas spaces permits internal aeration, i.e. a supply of oxygen from the atmosphere via aerial shoots down to the rhizomes and roots (ARMSTRONG et al. 1994). In rhizomatous wetland and aquatic plants, a pressure gradient drives the flow of air ("internal wind") through influx shoots down to the rhizomes and roots and up again through efflux shoots (GROSSE et al. 1991, ARMSTRONG & ARMSTRONG 1991). Part of the oxygen present in the gas spaces covers respiration of root/rhizome cells. The other part diffuses across the surface tissues to the anaerobic surroundings and creates an oxidised layer around the buried organs. This oxidised layer is regarded as a protection against contact with the anaerobic phytotoxins (KONČALOVÁ 1990, ARMSTRONG et al. 1994).

Even with a well developed system of gas spaces, wetland plants can suffer from oxygen deficiency. During the growing season, hypoxic conditions can occur within plant roots living

Table 1. Field observations (summarised) on the occurrence, growth and production of selected Central European wetland plant species at four ecophases sensu HEJNÝ (1960, 1971), determining the habitat character during the growing season. Full line denotes optimum conditions, dashes denote sub-optimum conditions. (Based on HEJNÝ 1960, and the authors' own experience.).

ECOPHASES	Hydric	Littoral	Limosal	Terrestrial
<i>Phragmites australis</i> (CAV.) TRIN. ex STEUD.	---	-----	-----	-----
<i>Carex elata</i> ALL.	---	-----	-----	
<i>Molinia caerulea</i> (L.) MOENCH.			-----	-----
<i>Phalaris arundinacea</i> L.		---	-----	-----
<i>Glyceria maxima</i> (HARTM.) HOLMB.	---	-----	-----	-----
<i>Typha latifolia</i> L.		-----	-----	-----
<i>T. angustifolia</i> L.	---	-----	-----	
<i>Sparganium erectum</i> L.	---	-----	-----	
<i>Scirpus lacustris</i> L.		-----	-----	
<i>S. maritimus</i> L.		---	-----	-----
<i>Sparganium emersum</i> REHM.	---	-----	-----	---
<i>Acorus calamus</i> L.	---	-----		---
Nymphaeids	-----	---		
<i>Oenanthe aquatica</i> (L.) POIR.	---	-----	-----	-----
<i>Butomus umbellatus</i> L.	---	-----	-----	
<i>Eleocharis palustris</i> (L.) ROEM. et SCHULT.		---	-----	-----
<i>E. acicularis</i> (L.) ROEM. et SCHULT.	-----	-----	-----	-----

in extremely reducing substrates (MENDELSSOHN et al. 1981). Oxygen deficiency may also be experienced by rhizome cells at the start of the growing season (ARMSTRONG et al. 1994), i.e. before the internal aeration through new shoots is fully established. A range of metabolic adaptations enable plants to endure varying lengths and degrees of anoxia. Rhizomes of *Scirpus maritimus*, one of the most tolerant species, can survive up to two months under strict anoxia and even towards the end of this period are still capable of extending shoots from pre-formed buds. In anoxia-tolerant species, sufficient amounts of ATP are produced by anaerobic fermentation to maintain cell integrity and function. Those species that can survive extended periods of anoxia also have the largest carbohydrate reserves to support the anaerobic fermentation. In addition, such species are able to tolerate high levels of the main fermentation end-product, ethanol, and at the same time, vent it to the surroundings more rapidly than wetland intolerant species (BRAENDLE & CRAWFORD 1987). Last but not least, they are able to protect their tissues against oxygen damage (post-anoxic injury) on the return of aerobic conditions (CRAWFORD & BRÄNDLE 1996).

The perception of flooding and the subsequent metabolic and structural response involve an interplay of plant hormones. Ethylene appears to play a crucial role in many species by

Table 2. Field observations (summarised) on growth and production of selected Central European wetland plant species in oligo-, meso-, eu-, and hyper-eutrophic habitats sensu WETZEL (1975): ++ = very good growth, + = good growth, (+) = poor growth, - = absence. (Based on the authors' own experience.)

Species	Oligo-	Meso-	Eu-	Hyper-
<i>Phragmites australis</i> (CAV.) TRIN. ex STEUD.	(+)	++	++	(+)-
<i>Carex elata</i> ALL.	+	++	-	-
<i>Molinia coerulea</i> (L.) MOENCH	++	+	-	-
<i>Phalaris arundinacea</i> L.	-	+	++	(+)-
<i>Glyceria maxima</i> (HARTM.) HOLMB.	-	+	++	++
<i>Typha latifolia</i> L.	(+)	+	++	++
<i>T. angustifolia</i> L.	-	+	++	+
<i>T. laxmanii</i> LEPECH.	-	+	+	-
<i>Sparganium erectum</i> L.	-	(+)	+	++
<i>Scirpus lacustris</i> L.	+	++	(+)	-
<i>S. maritimus</i> L.	+	+	+	-
<i>Sparganium emersum</i> REHM.	-	+	++	+(+)
<i>Acorus calamus</i> L.	-	+	++	++
Nymphaeids	+	++	(+)	-
<i>Oenanthe aquatica</i> (L.) POIR.	(+)	+	++	++
<i>Butomus umbellatus</i> L.	-	+	++	-
<i>Eleocharis palustris</i> (L.) ROEM. et SCHULT.	-	++	(+)	-
<i>E. acicularis</i> (L.) ROEM. et SCHULT.	(+)	+	+	-

initiating aerenchyma development in roots and petiole elongation in response to submergence (ARMSTRONG et al. 1994).

These are only some of the adaptation mechanisms known to operate in wetland plants. Other relevant features include adaptations in reproduction, morphology and timing of various biological activities. The niche differentiation within the wetland environment is further modified by interacting factors, such as the trophic status of the habitat (Tab. 2). A holistic appreciation of the whole plant performance is emphasised in the first paper of this issue (by R.M.M. Crawford), which focuses on plant adaptations to fluctuating water levels. The article shows that numerous different mechanisms may be involved in adapting plants to survive a period of inundation and the following re-exposure to air, and that no one mechanism on its own may be sufficient to ensure survival.

Many aspects of plant adaptations to wetland habitats are still only partly understood. This issue contains several articles which aim at elucidating more general features of the physiology and performance of wetland plants, using model situations or species. Using mathematical modelling, W. Armstrong et al. address some theoretical aspects of pressurized ventilation in wetland and aquatic plants. The metabolism of *Acorus calamus*, a species of remarkable tolerance to anoxia, is characterized by M. Weber & R. Brändle. L.A.C.J. Voeselek et al. demonstrate differential hormone sensitivity in a range of *Rumex* species, in relation to their differential flooding tolerance. U. Schlüter et al. compare the response to flooding between flood-tolerant and flood-intolerant species within the genera *Senecio* and *Myosotis*. The role of glutathione in prevention of post-anoxic injury, again in *Senecio* and *Myosotis*, is evaluated by S. Biemelt et al.

As with other fields of research, the theoretical knowledge on plant adaptations to wetland conditions should provide a basis for elucidating practical problems. One of the topics of both socio-economic and environmental importance is the decline of *Phragmites australis*, observed in many European lakes (OSTENDORP 1989). Several papers in this issue contribute to this subject. The approaches range from field observations and literature surveys to quantitative anatomical studies of cultivated plants. The topics include the detrimental effects of organic matter on a reed stand in a eutrophic fishpond habitat (H. Čížková et al.), the interference of stabilised high water levels with vegetative and sexual reproduction in reed (N. Rea), oxygen transport distance as a probable factor determining length of horizontal rhizomes (S.E.B. Weisner & J.A. Strand), the dynamics of reserve carbohydrates as affected by sediment chemistry (P. Kubín & A. Melzer, H. Čížková et al.) and anatomical responses of plant roots to super-abundant nitrogen supply (O. Votrubová & A. Pecháčková). The paper by J. Armstrong et al. on the role of phytotoxins in *Phragmites* die-back is an exquisite example of how both the field and experimental approaches can be matched in one single study. In the search for causes of *Phragmites* die-back, the team began by field observations. In subsequent experiments focussed on the effects of potential phytotoxins (sulphide and acetic acid), most of the die-back symptoms were simulated. Finally, the authors proposed a scheme of the die-back syndrome, based on their own findings as well as on other available information. This last study is nicely complemented by the subsequent paper by K. Fürtig et al., who evaluated the short term metabolic responses of reed plants to sulphide, including detoxification capabilities of roots and rhizomes.

The decline of *Alnus glutinosa* along streams is a problem of similar importance as *Phragmites* decline, which has nevertheless received much less attention. S. Struková et al. raise this problem by reviewing the possible role of mycorrhizal and actinorhizal symbionts on *A. glutinosa* performance, and reporting the results of experiments evaluating the effects of these symbionts on alder growth and the effects of eutrophication on these symbionts.

By its nature, the biology of wetland plants is a multidisciplinary field of research. Field botanists, who observe the plants in their natural habitats, provide inspiration for experimental research, which is better suited for investigating causal relationships. The experimental results should, however, be verified again in the field. Thus, the study of plant biology is a constant alternation between field observation and laboratory experimentation. However, what is the degree of mutual communication between the botanists "in rubber boots" and those "in white coats"? They often have different educational background, use different methodologies, speak different jargons and often publish in different journals. The aim of this issue was to confront the observational, "field", with the experimental, "laboratory" approach. The papers are based on lectures presented at the workshop entitled "Plant Survival under Wetland Conditions" held in Třeboň in September 1994, which hosted both "field" and "laboratory" botanists under one roof.

Why was the workshop held at Třeboň? The Třeboň Basin (one of the oldest UNESCO Biosphere Reserves) is an example of a successful landscape transformation which took place in the 13th to 16th centuries, mainly through drainage and construction of fishponds, small and large. The fishponds represent a unique type of wetlands which have replaced former pools, marshes, bogs, wet meadows, etc. Sophisticated networks of canals and ditches allow for the regulation of water levels in the ponds and enable their drawdown at any time. Nowadays, there are more than 500 fishponds in the Třeboň Basin, occupying a total area of

some 75 square kilometres. Some of the ancient large ponds, constructed 400 to 650 years ago, occupy 2 to 5 square kilometres each. Wetlands are also preserved in the watercourses of the Třeboň Basin. Its hydrological backbone, the Lužnice river with its floodplain, has been only little affected by straightening and regulation, so common in Europe in the last two centuries. A variety of small and shallow water bodies (backwaters, oxbows and pools) is present in the river floodplain. There are also about 70 square kilometres of peatlands (transition mires, bogs and acidic fens) in the Třeboň Basin.

The richness and variety of wetlands and of both running and standing shallow waters, has provided a background for wetland research, beginning with the century-old studies on fishponds by the founder of modern Czech fisheries, Josef Šusta (ŠUSTA 1898), through long term observational studies by J. AMBROŽ (1938, 1939), R. NEUHÄUSL (1965) and particularly S. HEJNÝ (1971) to the IBP and MaB programmes (DYKÝJOVÁ & KVĚT 1978, JENÍK & KVĚT 1983, HEJNÝ et al. 1986). In 1992, the Třeboň wetland ecologists joined the EUREED project of the European Union, concentrating on a causal explanation of the decline or dieback of the common reed (*Phragmites australis*) observed in the littorals of numerous European water bodies. At the same time, similarly oriented research was carried out by other European teams not involved in EUREED. The studies into reed performance and various aspects of its decline therefore constitute a large part of this issue.

The research into causes of *Phragmites* decline documents a high degree of mutual understanding and effort of both field and laboratory botanists. It has considerably improved our knowledge not only about this particular problem, but also about some more general aspects of *Phragmites* biology. This example also shows that the traditional belief of field and laboratory biologists "tending not to intermingle" does not hold, at least for wetland research.

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