Introduction

Genetic diversity, ecophysiology and growth dynamics of reed (*Phragmites australis*)

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The common reed, *Phragmites australis* (Cav.) Trin ex Steudel, is among the most widespread and productive plant species in the world, and is one of the few species that can truly be regarded as cosmopolitan (den Hartog et al., 1989). It is a robust, perennial emergent aquatic plant up to 6 m high, belonging to the family Poaceae. The annual stems develop from a system of vertical and horizontal perennial rhizomes (Fig. 1) that also function in the vegetative spread of the plant.

*P. australis* usually forms dense, nearly monospecific stands in littoral zones of lakes, along rivers and irrigation/drainage canals and in shallow, freshwater swamps. Its geographical distribution extends from cold temperate regions to the tropics. Some of the largest *Phragmites*-dominated ecosystems in the world are found in Europe (e.g., the Danube Delta and Lake Fertó), where the stems of the reeds have been used for centuries for roofing and fencing. In Romania, the harvesting of reed has been developed to the extent that thousands of tonnes of the plant have been used for manufacturing cardboard, printing paper, insulation and thatching material. Thus, in some parts of the world, many people depend economically and socially on reed culture.

*Phragmites* also plays an important role in preventing wave and current erosion of river and lake banks, and in providing a habitat for wild fowl and other fauna. Many bird reservations are wetlands in which *P. australis* is the dominant species. These areas have a great economic value for tourism (bird watching and hunting) and often support fisheries of local importance.

It is, therefore, not surprising that *P. australis* is one of the most extensively studied wetland species in the world. A dissertation on the species was prepared as early as 1795 by M. Lundén at Åbo Academy, Finland (Björk, 1967). Since then, several monographs and reports have been published, of which I will mention only a few. The dissertation by Hürlimann (1951) summarises most of the earlier knowledge on the biology of *P. australis*. 
The monographs by Rudescu et al. (1965) and Rodewald-Rudescu (1974) focus on the propagation, management and industrial utilisation of *P. australis*, as well as describing the general ecology of the plant. The thesis by Björk (1967), based on 15 years’ study largely in Scandinavia, describes the variation and variability within *P. australis* and its relation to the environmental growth conditions. There was also a report by van der Toorn (1972) on the polymorphism of *P. australis* in the Netherlands.

In more recent times, numerous papers have been published on *P. australis*. A search for the genus *Phragmites* in electronic literature databases produces lists of nearly one thousand references published since 1981. In 1989, a special issue of *Aquatic Botany* was
dedicated to reed and reed decline in Europe (den Hartog et al., 1989), and in 1993 and 1999, special editions of *Limnology Aktuell* (Ostendorp and Krumpscheid-Plankert, 1993) and *Limnologica* (Melzer et al., 1999) were published on the importance of reed communities, including the use of reeds for lake shore protection and wastewater treatment.

In this special issue, sixteen papers on various aspects of the ecology and ecophysiology of *Phragmites* are brought together in an attempt to elucidate the present state of the art in *Phragmites* research. The focus of about half of the papers is directly or indirectly on genetic diversity and genetic differences between clones. The paper by Clevering and Lissner (1999) reviews current knowledge and presents new data on genetic diversity, including ploidy levels, found in *Phragmites*. Part of this paper is concerned with a population dynamic view on the development of healthy and declining populations and the importance of clonal diversity for the stability of *Phragmites* populations. The genetic diversity of *Phragmites* populations in European wetlands is also the topic of the paper by Koppitz (1999). It was found that both monoclonal and polyclonal stands exist and that the diversity of clones in littoral stands was generally higher on or near the shore, compared with stands at greater water depth. This observation supports the hypothesis that the colonisation of lake shores starts with a variety of new clones originating from seeds because the conditions for seed germination and seedling establishment are favourable there. Colonisation continues with the spreading of only a few of the clones into deeper water. As a consequence of this selection process, clones with different ecophysiological characteristics may occur along a depth gradient in the littoral zone of lakes. Different clones may react differently to changing environmental conditions and this could be important in relation to the observed decline of reed population in littoral zones of European lakes. The papers by Paucă-Comănescu et al. (1999) and Kühl et al. (1999) clearly document large morphological differences between different clones irrespective of site conditions, and the paper by Rolletschek et al. (1999a) documents that morphologically different clones growing under identical site conditions also differ in physiological characteristics. Different clones possessing different growth strategies may, therefore, react differently to changing site conditions. In North America, *Phragmites* is spreading rapidly, especially in tidal wetlands along the Atlantic coast (Chambers et al., 1999), and it has been suggested that the expansion may be caused by an aggressive genotype introduced from Europe sometime in the last 200 years. Although it has been demonstrated that specific genetic types dominate within localised areas, no genetics research to date has provided an adequate test of the aggressive genotype hypothesis. The expansion of *Phragmites*, however, has huge impacts on ecosystem processes and generally decreases biodiversity.

Several of the papers of this special issue deal with different ecophysiological aspects of *Phragmites* and the effects of various types of stress on plant performance. The paper by Armstrong et al. (1999) documents that seedling growth, root aeration and rhizosphere oxygenation of *Phragmites* can be detrimentally affected by shallow submergence of shoots, and that algae growing in the water can reduce the growth of submerged seedlings and jeopardise their chances of becoming emergent. Concentrations of phytotoxins, such as low-molecular organic acids, may reach toxic levels in organic reed sediments, especially at eutrophic sites (Čížková et al., 1999). Therefore, in order to enhance recolonisation in reed die-back areas, it might be beneficial to lower the water level to facilitate the oxidation or escape of these phytotoxic compounds. This would also assist the seedling establishment, particularly if
the water level were raised again to secure the moist sediment conditions needed for seed germination. The oxygen demand of the roots of *Phragmites* is met by transport from the atmosphere through the internal airspaces in the plant (Brix et al., 1992). The transport in the roots themselves occurs by passive diffusion, but in stems and rhizomes the transport is accelerated by a convective through-flow mechanism. The paper by Rolletschek et al. (1999b) documents that the efficiency of the internal ventilation is dependent on stand structure. The differences found in ventilation efficiency are also reflected in the contents of amino acids in the basal internodes of the plants indicating more hypoxic conditions at those stands with lower ventilation efficiency.

*P. australis* is a species with a broad ecological amplitude and is able to acclimate to a wide range of growth conditions. The study by Romero et al. (1999) investigated the interactive effects of nitrogen and phosphorus on growth and ammonium uptake kinetics by *P. australis*. The plants grew best at high and balanced nutrient supply rates (molar N : P ratios between 10 and 33), but the uptake kinetics were modified in response to growth at low nutrient levels. The broad ecological amplitude of *P. australis* is also documented in a number of studies on the effect of climate on the salt tolerance of different *P. australis* populations (Lisnner et al., 1999a, 1999b). It was found that the populations differed significantly in salt tolerance, and that the salt tolerance was higher in a Mediterranean climate, compared with a temperate climate. *P. australis* tolerates salinity mainly by two mechanisms, namely, cation adjustment, i.e., an active exclusion of Na⁺ ions, and a mechanism known as water loss (Glenn, 1987), whereby the concentrations of solutes in the cells increase. The authors speculate that the salt tolerance of *P. australis* may increase under conditions favouring high transpiration, contrary to what is observed for most other halophytes. *P. australis* may be found in estuaries with water salinities up to 35 ppt. However, the root systems of the plants usually experience much lower salinities, and the study by Adams and Bate (1999) shows that the plants will probably not survive flushing with sea water unless the roots and rhizomes are located in water with salinities <20 ppt. Genetic differences may affect this conclusion. The study by Hanganu et al. (1999) shows that the octoploid ‘giant’ reeds growing in the Danube Delta are more strongly affected by saline conditions than the tetraploid ‘fine’ reeds. As the salinity presently is increasing in certain parts of the delta, this may lead to a change in the distribution of the two ecotypes in the delta. Salinity also affects the decomposition processes in *Phragmites* sediments, although the study by Mendelssohn et al. (1999) concludes that soil fertility, primarily nitrogen and phosphorus, is the major environmental factor determining decomposition rates in sediments along a salinity gradient.

The last paper of this issue is devoted to endophagous insects attacking *P. australis* and the impact of herbivory on shoot growth (Tscharntke, 1999). Insects affect the growth, shoot architecture, competitive ability and population dynamics of the plant. The attacks of the insects may cause considerable damage to the shoots, but may also enhance growth, e.g., due to the parasitic influence of gall makers which induce shoot elongation. Insect damage is sometimes reported to promote the die-back process in European wetlands. However, only few of the insects that are specialised on *P. australis* occur in the New World, and the paper discusses the possibilities of introducing European insects as a means of biological control of invasive *P. australis* populations in the New World.
Acknowledgements

I thank the authors for preparing the papers for this special issue. I also thank the anonymous referees, who did a great job helping me in the review process, Prof. C. den Hartog for letting me produce this special issue, and Dr. Brian Sorrell for linguistic improvements. This work was funded by the Environment and Climate Programme of the European Commission, contract no. ENV4-CT95-0147 (EUREED).

References


