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ScienceDirect
Aquatic Botany 86 (2007) 269–279
Aquatic botany
www.elsevier.com/locate/aquabot

Clone-specific differences in *Phragmites australis*: Effects of ploidy level and geographic origin

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Received 7 June 2006; received in revised form 27 October 2006; accepted 10 November 2006

Abstract

Phragmites australis (Cav.) Trin. ex Steud. is virtually cosmopolitan and shows substantial variation in euploidy level and morphology. The aim of this study was to assess clone-specific differences in morphological, anatomical, physiological and biochemical traits of *P. australis* as affected by the geographic origin, the euploidy level (4*x*, 6*x*, 8*x* and 12*x*), and to assess differences between native and introduced clones in North America. Growth, morphology, photosynthetic characteristics, photosynthetic pigments and enzymes were measured on 11 geographically distinct clones propagated in a common environment in Denmark. Any differences between the measured parameters were caused by genetic differences between clones.

Overall, the largest differences between clones were found in ontogeny, shoot morphology and leaf anatomy. The North Swedish clone was adapted to short growing seasons and sprouted very early in the spring but senesced early in July. In contrast, clones from southern regions were adapted to warmer and longer growing seasons and failed to complete the whole growth-cycle in Denmark. Some clones from oceanic habitats with climatic conditions that do not differ much from conditions at the Danish growth site did flower in the common environment.

The octoploid genotype in general had larger dimensions of leaves, taller and thicker shoots and larger cell sizes than did the hexaploid and tetraploid clones. The dodecaploid clone was neither bigger than the octoploid, nor significantly different from tetraploid and hexaploid clones in most of the morphological characters observed. Stomatal density decreased with increasing ploidy level, while length of guard cells increased. Tetraploid clones generally had morphometric dimensions, similar to hexaploids. Hence, polyploidy did not always result in an increase in plant size, probably because the number of cell divisions during development is reduced.

Four North American clones were included in the study. The clone from the Atlantic Coast and the supposed invasive European clone resembled each other. The Gulf Coast clone differed from the rest of the clones in having leaf characters resembling *Phragmites mauritianus* Kunth. Thus, morphological characters are not unmistakable parameters that can be used to discriminate between introduced and native clones.

The physiological and biochemical processes also differed between clones, but these processes showed considerable phenotypic plasticity and were therefore very difficult to evaluate conclusively.

It is concluded that *P. australis* is a species with very high genetic variability which is augmented by its cosmopolitan distribution, clonal growth form and the large variation in chromosome numbers. It is therefore not surprising that large genetically determined differences in ontogeny, shoot morphology and leaf anatomy occur between clones.

Keywords: Common reed; Exotic; Genotypic variation; Invasion; Phenotypic plasticity; Photosynthesis; *Phragmites australis*; Polyploidy; Wetland

1. Introduction

The common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) is a perennial grass with perhaps the largest geographical distribution of any flowering plant in the World (Brix, 1999; Clevering and Lissner, 1999). *P. australis* is a clonal plant with annual stems that develop from a system of rhizomes which also function in the vegetative spreading of the plant. The species has a wide ecological amplitude and is very variable in morphology and shows plastic responses to growth conditions (Hanganu et al., 1999; Kühl et al., 1999; Lessmann et al., 2001). Significant morphological differences have been found both between different populations of *P. australis* and between different clones within the same population, irrespective of site conditions (Björk, 1967; Clevering, 1999; Rolletschek et al., 1999; Pauca-Comanescu et al., 1999; Clevering et al., 2001). Part of the

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doi:10.1016/j.aquabot.2006.11.005

clone-specific variability in *P. australis* can be attributable to differences in chromosome number. A euploid range of 3*x*, 4*x*, 6*x*, 7*x*, 8*x*, 10*x*, 11*x* and 12*x* (with $x = 12$) has been found for this species, with tetraploids ($2n = 48$) and octoploids ($2n = 96$) being the most frequently observed (Clevering and Lissner, 1999). Shoots of octoploids are generally longer and thicker and have larger leaves than those of tetraploids. Octoploid reeds sometimes are referred to as 'giant' reeds and tetraploid reeds as 'fine' reeds (Hanganu et al., 1999; Pauca-Comanescu et al., 1999; Clevering et al., 2001). This relationship between euploidy level and morphology is common because the most immediate and universal effect of polyploidy is an increase in cell size. However, polyploidy does not always lead to an overall increase in the plant size, since a common effect of polyploidy is also a reduction in the number of cell divisions during development (Stebbins, 1971).

It has been suggested that genetic variation among populations from different geographic regions has arisen as a result of growth in different climatic environments (Clevering et al., 2001). Along a latitudinal gradient gradual change occur in the relative day length, amount of solar radiation and air temperature. Also, differences occur between oceanic and continental habitats. In oceanic habitats, differences between summer and winter are generally smaller than in continental habitats. *Phragmites australis* populations originating from different geographic regions along a latitudinal gradient from Northern Sweden to Spain differ in time of cessation of growth, shoot morphology and biomass allocation (Clevering et al., 2001). Grown under the same environmental conditions *P. australis* originating from higher latitudes started to grow earlier than southern populations, but finished growth early in the season. The southern populations failed to complete the whole growth-cycle before the first frost and did not develop mature seeds.

Phragmites australis is considered native to North America; however, over the last 200 years an aggressive expansion has occurred in coastal wetland communities where it has out-competed other native species of the wetland communities. The invasion is taking place particularly along the Atlantic Coast and in the Mississippi delta region of the Gulf of Mexico (Chambers et al., 1999). This invasion can be attributable to the effective vegetative spread of *P. australis*, colonizing habitats it is unable to invade directly with seeds or rhizomes (Amsberry et al., 2000). Studies by Saltonstall (2002) have however, documented that a non-native type of *P. australis* is responsible for the observed spread. Based on genetic studies of *P. australis* populations from all over the world, 11 haplotypes were found to be unique to North America and were therefore considered to be native to this part of the continent. Two haplotypes (I and M) had a wide distribution on multiple continents, and haplotype M is the most common type in North America today. Haplotype I was distributed along the Gulf Coast. Comparing herbarium samples collected before 1910 with modern samples revealed that haplotype M has spread along the Atlantic Coast and westward displacing native types and expanding to regions previously not known to have *P. australis* (Saltonstall, 2002). Genetic analyses have shown that this introduced clone is more closely related to European clones than to native North American groups (Saltonstall, 2003), and it is therefore considered to be introduced from European populations.

The aim of the present study was to assess clone-specific differences in morphological, anatomical, physiological and biochemical parameters of *P. australis* in order to identify and quantify differences in traits that can be associated with the

Table 1
Designation of *Phragmites australis* clones used in the study and information about their origin, ploidy level, colour of stem, time of flowering and leaf sheaths during senescence

Clone	Sample label[a]	Origin	Group[b]	Ploidy level	Colour of stem	Time of flowering	Leaf sheaths during senescence
RO4*x*	Pa 657 RO	Romania, Lake Razim		4*x*	Green, green and red to brown at stem base	–	Lower sheaths fall off
RO6*x*	Pa 650 RO	Romania, Lake Razim		6*x*	Green, red to brown at stem base.	–	Stay on stem
RO8*x*	Pa 661 RO	Romania, Lake Obretin		8*x*	Green.	–	Stay on stem
RO12*x*	Pa 660 RO	Romania, Lake Razim		12*x*	Green, red to brown at stem base	–	Lower sheaths fall off
SE	Pa 637 SE	Sweden, Gammelstaden		4*x*	Green	–	Stay on stem
IL	Pa 90 IL	Israel, Yerokham, Negev Highlands		4*x*	Green	–	Stay on stem
ES	Pa 72 ES	Spain, Gallocanta N		4*x*	Green	Middle of August	Stay on stem
US-MW	Pa 111 US	United States, Utah, Green River	Midwest	4*x*	Green and red to brown. Red to brown at stem base	–	Lower sheaths fall off
US-AC	Pa 190 US	United States, NY, Buffalo, Orchard Park	Atlantic Coast	4*x*	Green, green and red to brown at stem base	Beginning of September	Lower sheaths fall off
US-GC	Pa 100 US	United States, Alabama, Mobile	Gulf Coast	?	Green and red to brown	–	Lower sheaths fall off
US-INTR	Pa 193 US	United States, Virginia, Upshur Creek	Introduced	4*x*	Green, green and red to brown at stem base	Middle of September	Stay on stem

[a] Sample labels as presented by Lambertini et al. (2006).
[b] Group refers to the four American groups (see text).