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Different genotypes of *Phragmites australis* show distinct phenotypic plasticity in response to nutrient availability and temperature

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ABSTRACT

We studied the phenotypic plasticity of physiological and growth traits in two distinct clones of common reed (*Phragmites australis* (Cav.) Trin. Ex Steud.). Replicates of a clone from Denmark (DK clone) belonging to the European temperate *P. australis* and a clone from Algeria (ALG clone) belonging to the African-Mediterranean gene pool of *P. australis* were grown in phytotrons in a factorial block design at 15 °C or 25 °C daytime temperature and high or low fertilization level. Plant growth, tissue nutrient concentrations, photosynthetic pigments and photosynthetic characteristics were measured. Phenotypic plasticity was quantified for the measured traits as plasticity indices in relation to temperature and fertilization. The plasticity index was calculated as the difference between the maximum and the minimum mean value divided by the maximum mean value of a parameter within a treatment. The functional significance of the plasticity and its contribution to plant fitness was assessed by correlation of the plant traits to plant biomass as a proxy for fitness.

The DK clone responded much more to temperature than the ALG clone, which responded more to fertilization, and both clones responded to high fertilization with lower allocation of biomass to roots and rhizomes. The ALG clone had a higher nutrient demand due to its large and fast biomass development. Hence, for most traits, the calculated plasticity indices for fertilization were highest for the ALG clone, especially within photosynthetic parameters and pigments, and the plasticity indices for temperature were highest for the DK clone, especially within growth parameters. In both clones, photosynthetic pigments, biomass allocation to leaf blades and rhizomes, the shoot:root ratio as well as leaf and shoot production rates were highly correlated to fitness. These traits also had a relatively high degree of plasticity, indicating a functional significance of plasticity, but several traits that showed high plasticity did not correlate with fitness (e.g. P_{max}). We conclude that the responses of the two contrasting *P. australis* genotypes to temperature and fertilization are genetically determined and related to the climatic conditions at the site of their origin. Although phenotypic plasticity per se is not a precondition for plant fitness, the genetically determined differences in the degree of phenotypic plasticity of distinct *P. australis* genotypes to temperature and nutrient availability affect fitness and may influence how the genotypes will respond to global environmental change.

1. Introduction

Plants of the same species with several distinct genotypes are capable of growing in different habitats of high environmental heterogeneity. As a consequence, they may possess a high phenotypic variation (Lehmann and Rebele, 2005; Sultan, 1995). Phenotypic plasticity is generally defined as the capacity of a genotype to produce distinct phenotypes when exposed to different environmental conditions, and phenotypic plasticity has been suggested important for adaptation to temporal environmental changes and spatial heterogeneity (Bradshaw, 1965; Sultan, 2000). Adaptive phenotypic plasticity is the phenotypic response to an environment that enhances plant performance. This phenotypic variation is often considered to be a functional response maximizing fitness in the particular environment (Sultan, 1995). Sudden environmental changes might put species lacking sufficient plasticity at risk of extinction, not being able to withstand unfavorable conditions (Coleman et al., 1994; Sultan, 2000).

Plasticity is trait-specific, as genotypes are not plastic but can disclose plastic traits when exposed to contrasting environmental conditions. An example is a rapid change in growth characteristics and morphology that can provide greater access to limiting resources (Grime and Mackey, 2002; Haraguchi, 1993). Thus, to compensate for biomass reduction occurring under resource limitation, plants increase biomass allocation to roots in low-nutrient soils. Such functional plasticity can allow the genetic individual to

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grow and reproduce successfully in different environments (Sultan, 2000).

Plants encounter multiple environmental factors and the effects on plant growth often interact. Nutrient availability and temperature are key environmental forces to which plants respond phenotypically. For instance, simulated warming changed the biomass allocation among developmental stages and types of ramets of *Carex bigelowii* as well as the nutrient concentrations in the aboveground tissues (Jonsdottir et al., 2005). Also, in *Calamagrostis epigejos*, the highest plasticity was found for the belowground biomass allocation as an adjustment to variable soil fertility (Lehmann and Rebele, 2005). In spring and winter wheat a change of the growth temperature resulted in the adjustment of the root:shoot ratio and the carbohydrate content (Equiza and Tognetti, 2002).

Phenotypic plasticity has been investigated in both annual and perennial plants (Dong et al., 1996; Funk, 2008; Sultan, 1995). Clonal perennials reproduce both vegetatively and by sexual reproduction. By clonal spread, the plants are able to respond rapidly to environmental heterogeneity whereas sexual reproduction enables the maintenance of genetic variability for natural selection. Santamaria (2002) pointed out that the generality of broad plastic responses, promoted by the clonal growth of aquatic vascular plants, favors a wide spatial distribution.

The common reed (*Phragmites australis*) is a dominant clonal wetland plant with a worldwide geographical distribution. The occurrence of this perennial grass ranges from cold temperate to tropical regions, in oligotrophic as well as eutrophic habitats. It relies both on sexual and vegetative spreading, with annual shoots emerging from perennial horizontal and vertical rhizomes (Brix, 1999; Haslam, 1968). Several studies have shown that *P. australis* has a high genetic variability both between and within populations, which is augmented by its clonal growth form and cosmopolitan distribution (Brix, 1999; Clevering and Lissner, 1999; Hansen et al., 2007; Kuhl et al., 1999; Rolletschek et al., 1999). Also, genetically determined differences in the timing of flowering, length of growing seasons, biomass allocation and morphology have been found in different *P. australis* clones from a latitudinal gradient (Bastlova et al., 2006; Clevering et al., 2001). These differences have been proposed to have developed as adaptations to growth in various climatic habitats (Clevering et al., 2001; Hansen et al., 2007). However, the significance of genetic determinacy and external constraints for *P. australis* stand structure and growth may vary from habitat to habitat (Engloner, 2009). In *P. australis* clones growing adjacent to each other, clone-specific differences in morphology and physiological parameters have been found, even after transplantation to a common environment, indicating that different genotypes may respond differently to changing site conditions, and that different genotypes may use different ecophysiological strategies (Rolletschek et al., 1999). Also, a strong effect of the geographical gradient on the growth and phenology of different *P. australis* populations has been found by Bastlova et al. (2004). *P. australis* has been shown to be a highly plastic plant in several studies. Vretare et al. (2001) found that *P. australis* exhibited phenotypic plasticity as a functional response to different water depths, and Bellavance and Brisson (2010) reported that *P. australis* had a competitive advantage over *Typha* sp. due to its high morphological plasticity. Moreover, Clevering (1999) showed that clones of *P. australis* originating from infertile habitats were less plastic than those from fertile and eutrophicated habitats.

Although *P. australis* is one of the most intensively studied wetland plants, to our knowledge, a comparison and quantification of the phenotypic plasticity of distinct genotypes, and an assessment of the functional significance of their plastic responses, has never been made. In this study, the plasticity of physiological and growth traits in two phylogeographically distinct clones of *P. australis* subjected to different growth temperatures and nutrient availabilities was measured. The effects of growth temperature and nutrient availability on the contribution of plant trait plasticity to fitness were investigated in order to assess the extent to which differences in genotypes may lead to a different functional significance of plasticity. We hypothesize that the genetic background of the clone determines which plant traits contribute mainly to fitness in different environments.

2. Materials and methods

2.1. Plant material and experimental setup

The plants used in this study were chosen from a large collection of live *P. australis* clones, kept in a common environment at Aarhus University, Denmark (56°13′N; 10°07′E), for at least five years prior to the study. Each clone of the collection is the progeny of a single plant and represents a different genotype. Two clones were compared based on their phylogeographic relationship: a clone from a coastal stand close to Aarhus, Denmark (56°12′N; 10°29′E) (DK clone), and a clone from an oasis in the Sahara desert close to Guebbour, Algeria (28°29′N; 6°41′E) (ALG clone). The DK clone possesses the alleles of the European temperate *P. australis*, whereas the ALG clone belongs to the African-Mediterranean gene pool of *P. australis*. The differences between the clones are therefore assumed to be driven by different evolutionary pressures in their native distribution ranges. The phylogeographic groups within *P. australis* were identified and described in Lambertini et al. (2006).

The clones were propagated by layering of shoots horizontally in shallow water for five weeks to initiate adventitious shoot growth at the stem nodes. When adventitious shoots were 15–20 cm high and had developed roots, the stems were cut at both sides of the nodes and the resulting genetically identical replicates were planted in 3.5 L pots containing a commercial peat. Each potted plant was placed in its own outer container to allow separate treatment. The plants were then placed in two 2.0 m × 0.8 m × 1.7 m ($L \times W \times H$) indoor growth cabinets (BIO 2000S, Weiss Umwelttechnik GmbH, Lindensruth, Germany) at a relative air humidity of 65%, a light:dark cycle of 16:8 h, and at an irradiance of approximately 400 μmol m^{-2} s^{-1} (PAR) at the base of the plants, provided by metal halide bulbs. After an acclimatization period of two weeks with a 20 °C:17 °C day:night temperature cycle, the plants were distributed between two growth cabinets: one with a 15 °C:12 °C day:night temperature cycle (Low Temp treatment; 15 °C), the other with a 25 °C:22 °C day:night temperature cycle (High Temp treatment; 25 °C). The ability of the growth cabinets to control the air temperature and relative humidity was generally better than 0.5 °C and 3% RH, respectively. However, during photoperiods, gradients in temperature and humidity develop in the chambers. Hence, plants were rotated at random in each of the growth chambers once a week to minimize undesired chamber effects.

The plants were fertilized twice per week with 250 mL of a nutrient solution prepared from tap water containing either 1‰ (High Fert treatment) or 0.1‰ (Low Fert treatment) of a commercial macronutrient solution (Pioner NPK Makro 10-4-25 + Mg, Brøste, Denmark). The 1‰ nutrient solution contained (in mM): 6.1 NO_3, 0.9 NH_4, 1.3 P, 6.5 K, 1.8 Mg and 1.8 S. Micronutrients were supplied at the same level (in μM: 0.02 B, 2.2 Cu, 24 Fe, 9.1 Mn, 0.5 Mo and 2.8 Zn) in all treatments from a commercial micronutrient stock solution (Pioner Mikro + Fe, Brøste, Denmark). The pH was adjusted to pH 6.7 and additional iron (approximately 0.6 mM of $Fe(II)SO_4$) was added right before every fertilization. Between fertilizations, the plants were watered with demineralized water. The plants were placed such as to largely avoid shading by adjacent taller plants.