



Strong divergence in quantitative traits and plastic behavior in response to nitrogen availability among provenances of a common wetland plant



Jennifer Born*, Stefan G. Michalski

Department of Community Ecology, Helmholtz Centre for Environmental Research—UFZ, Halle, Germany

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ABSTRACT

Wetland ecosystems provide important ecosystem services such as the degradation and retention of excessive nutrient loadings. Plants may affect these processes directly or indirectly via the interaction with the rhizosphere community. Many studies on the impact of plant functional traits on ecosystem processes in wetlands focused on variability among species, neglecting the importance of intraspecific variability. Here we assessed the intraspecific genetically based variability of a common wetland plant for traits, potentially relevant for the removal of nitrogen compounds from the soil. We asked whether and how quantitative genetic variation is expressed differently depending on nitrogen availability and how it is structured within and among natural European populations of *Juncus effusus*. We partitioned the observed genetic variation into within- (broad-sense heritability) and among (Q_{ST}) population components for mean traits and plasticities. We found a strong plastic behavior for all measured traits in response to nitrogen availability. Genetic variation for mean traits differed strongly among populations but was very low at population level. We could not demonstrate a general effect of nitrogen availability on genetic trait expression. Our results suggest that basic and applied studies on wetland ecosystem processes will benefit from a deeper understanding of intraspecific genetic variation for traits and plastic behavior which is also fundamental for breeding approaches or to predict evolutionary responses.

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1. Introduction

Progressive agricultural intensification as well as ongoing urbanization result in immense nutrient loading in both freshwater and coastal ecosystems (Tilman et al., 2002). The eutrophication of natural communities by an increased input of nitrogen via fertilizers and wastewaters can entail substantial risks for biodiversity (Smith et al., 1999; Stevens et al., 2004). Wetland ecosystems provide an important service by the natural decomposition and retention of such excessive substances (Millennium Ecosystem Assessment, 2005). Two ecosystem processes have primarily been described to be relevant for nitrogen removal in wetlands. Firstly, plant uptake associated with incorporation into biomass and secondly, denitrification by anaerobic microorganisms in the soil (Sutton-Grier et al., 2013). These processes are not independent from each other because of the close interaction between plants and the rhizosphere community. For example, among other exu-

dates, roots of wetland plants release oxygen into the rhizosphere via aerenchymatous tissues (Armstrong, 1967), which can affect the redox potential of the soil (Blossfeld et al., 2011) and microbial communities both supporting mineralization and nitrification processes. Products of the microbial activity can in turn be resorbed by the plants (Rydin and Jeglum, 2006; White and Reddy, 2009). In general, this interaction between plant and rhizosphere has an immense potential to affect the accumulation, metabolization and hence, the removal of contaminants from the environment (Dhir et al., 2009). Although these processes and involved functional plant traits still remain poorly understood, there is a strong scientific and practical interest in the utilization of wetland plants and associated microorganisms to remediate contaminated waters, soils and sediments.

Understanding patterns of intraspecific trait diversity within and among populations is fundamental for both the prediction of evolutionary pathways under changing environmental conditions, and targeted selection of lines with particular properties. In the past, the variability of functional traits relevant for removal of contaminants in wetland ecosystems has mostly been assessed among species. For example, significant differences among species have

* Corresponding author.

E-mail address: jennifer.born@ufz.de (J. Born).

Table 1Location of studied *Juncus effusus* populations, sample sizes used in the common garden experiment and soil nitrogen content at population origin.

ID	country	population	latitude (°N)	longitude (°E)	nr. of seed families/total nr. of plants	Soil N content (g/kg)
KP	Estonia	Kõpu	58.3367	25.2650	8/160	1.95
GR	Germany	Groß Rosenburg	51.9124	11.9178	8/160	1.25
OB	Germany	Offenbach	49.2029	8.2123	8/160	1.05
PS	Germany	Pressel	51.5655	12.7322	8/160	2.50
SF	Germany	Siptenfelde	51.6605	11.0484	8/160	1.80
DL	United Kingdom	Dunfermline	56.0598	-3.3866	3/35	2.05
FD	United Kingdom	Findochty	57.6989	-2.8902	7/111	2.90

been described for nitrogen uptake efficiency (Borin and Salvato, 2012), root traits such as length, longevity or porosity (Lai et al., 2011), and organic matter decomposition (Gingerich and Anderson, 2011) all of which are linked to many wetland processes. However, the extent of intraspecific variability for these functional traits is less well known. This is surprising, since intraspecific variability may be as important as interspecific variability with respect to ecosystem function (Silfver et al., 2007; Lecerf and Chauvet, 2008).

Observed intraspecific phenotypic variation is the result of heritable differences in genetic architecture (Linhart and Grant, 1996) and the ability of genotypes to express different phenotypes (trait means) in different environments, known as phenotypic plasticity (Miner et al., 2005). At the population-level both, genetic diversity and plasticity, are subject to neutral evolution and adaptive evolutionary changes in response to the local environment that both can lead to a diversification in traits and reaction norms across populations. Assessing genetic diversity in quantitative traits is a challenging task. Often, this is realized in common garden studies using a seed family design with individuals of known relatedness. Trait heritability is then defined as the proportion of phenotypic variance that is attributable to genetic variation, i.e. explained by relatedness (Falconer, 1989). However, heritability may differ depending on the environment in which it is expressed (Hoffmann and Merilä, 1999; Sgrò and Hoffmann, 2004). Various hypotheses with contrasting expectations have been formulated for the relation between environment and genetic variation expressed (see Hoffmann and Merilä, 1999 for details). On the one hand, heritability is predicted to increase under rare, stressful conditions due to the expression of genes behaving neutral in normal environments and which hence are not affected by natural selection (Holloway et al., 1990; Pigliucci et al., 1995). In contrast, decreased values for heritability under stressful conditions could be expected if environmental and phenotypic variation increase while genetic variation remains constant (Charmantier and Garant, 2005). Assessing trait variability under a range of experimental treatments will hence allow a more general assessment of expressed genetic variability and plastic behavior.

Juncus effusus, the soft rush, has been established as a model plant in basic and applied research on wetland ecosystems. It is well characterized ecologically by a number of studies, e.g. on seed production (Ervin and Wetzel, 2001), germination and establishment (Lazenby, 1955), growth rates and production of biomass (Wetzel and Howe, 1999), litter decomposition (Gingerich and Anderson, 2011) or the interaction with co-occurring plant species (Ervin, 2005). In respect of contaminant removal it has been studied, e.g. on metal accumulation (Mays and Edwards, 2001), wastewater remediation (Borin and Salvato, 2012) and microbial activity in the rhizosphere (Nikolaus et al., 2008). However, potentially related intraspecific trait variation within and among natural populations has not been described so far.

Like many other species in this genus, *J. effusus* has been described as predominantly selfing (Buchenau, 1892) and its high seed production (Stockey and Hunt, 1994) makes the species an efficient colonizer. Consequently, molecular marker studies found

large inbreeding coefficients and a strong degree of genetic structuring within the species (Michalski and Durka, 2012, 2015) which is expected for selfing species (Hamrick and Godt, 1996).

Here we assess intraspecific variability for functional traits of *Juncus effusus* putatively related to the removal of excessive nitrogen in the soil, and ask how this variability changes depending on nitrogen availability, how it is genetically structured within and among populations and whether it relates to soil nitrogen availability of the site of origin as a signature of adaptation. We hypothesize that, (1) as a consequence of the mating system and other life history traits of *J. effusus*, genetic variation for quantitative traits will be more strongly expressed among than within populations; (2) under nitrogen deficiency, genetically based variation of traits will differ from that expressed under higher nitrogen availability, and (3) expressed trait variability related to nitrogen acquisition varies with soil nitrogen of sample origin revealing signatures of adaptation.

2. Material and methods

2.1. Study species and experimental design

Juncus effusus L. (Juncaceae) is a perennial herb and widespread in temperate wetland ecosystems. It has been described to vary substantially in morphological traits across its worldwide distributional range (Kirschner et al., 2002). In Europe only *J. effusus* ssp. *effusus* has been described (Kirschner et al., 2002). Between 2010 and 2012, we collected seed families, i.e. offspring from a single maternal individual, from seven locations in Europe (Table 1). From each location (all with population sizes $N > 100$), individuals were selected arbitrarily across the whole site. As the species is highly selfing (Michalski and Durka, 2012, 2015) seed families were assumed to represent the maternal genotype. Before the start of the experiment seeds from all families were stored in paper bags at room temperature. In December 2012, we germinated seeds in quickpots (96 cells, 4 cm diameter \times 8 cm deep; Hermann Meyer KG, Rellingen, Germany) filled with a mixture of sand and commercial soil (1:2, vol/vol; Fruhstorfer soil type P) in a climatic chamber with a 12 h photoperiod and mean day and night temperature of 30 °C and 20 °C, respectively. Germination success was high and did not vary with the year of collection (J. Born; pers. obs.). Eight weeks after sowing, trays with seedlings were placed in a greenhouse under frost-free conditions. In May 2013, we planted individual seedlings, all approximately of the same size, in 31 pots (17 cm diameter \times 18.5 cm deep) filled with a mixture of sand and unfertilized commercial soil (1:2, vol/vol; Fruhstorfer soil type 0). Sample extracts ($N = 10$) from 10 g air-dried soil mixture suspended in 40 ml 1 M potassium chloride gave average concentrations of 2.37 NO_3^- – N mg/kg and 3.08 NH_4^+ – N mg/kg detected by flow-rate injection analyzer FIAStar™ 5000 Analyzer (FOSS Analytical, Denmark).

Each of the seven populations was represented by three to eight seed families (mean: 7.1 seed families per population) with up to 20 individuals per seed family (Table 1). Because of a low initial seed number and insufficient establishment rate, not enough off-

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