Genetic differentiation of the endemic grass species *Deschampsia littoralis* at pre-Alpine lakes

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Abstract *Deschampsia littoralis* is an endemic tetraploid Poaceae occurring on the shores of pre-Alpine lakes. It is closely related to the diploid and widespread *D. cespitosa*. Several *D. littoralis* populations from Lake Constance are vegetatively propagating through pseudoviviparous spikelets. These latter populations were formerly described as a separate species, *D. rhenana*. Still, the species status of *D. rhenana* has been questioned since, apart from pseudovivipary, no morphological differentiation from *D. littoralis* is observed. Both species are highly endangered and accurate assessment of taxon status is needed for conservation management. We used amplified fragment length polymorphism fingerprinting to assess whether *D. rhenana* from Lake Constance (43 specimens) was genetically differentiated from *D. littoralis* (11 specimens collected at Lac de Joux, incl. Lac Brenet) and the widespread *D. cespitosa* (48 specimens). An analysis of

molecular variance (AMOVA) showed that 12 % of the genetic diversity occurred among the three species, 7 % occurred among populations within species and 81 % within populations. Principal coordinate analysis and fuzzy c-means clustering showed that *D. rhenana* was genetically distinct from *D. littoralis*. In addition, both species differed in levels of genetic diversity and clustering, with *D. rhenana* being the most divergent and structured species. *D. littoralis* appeared as genetically intermediate between *D. rhenana* and *D. cespitosa*. These results suggested that (1) all species are closely related, (2) genetic variation within populations is high even in the asexually propagating *D. rhenana* and (3) *D. rhenana* is more distinct from *D. cespitosa* than is *D. littoralis*. We therefore suggest to treat *D. rhenana* from Lake Constance and *D. littoralis* from Lac de Joux as independent evolutionary units in conservation management.

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Pseudovivipary

Introduction

Species at high latitudes and altitudes often reproduce vegetatively or through apomixis (Körner 1999). Pseudovivipary may be regarded as a special form of clonal growth (Elmqvist and Cox 1996), because plants produce asexual propagules (proliferating spikelets, bulbils) in inflorescences instead of seeds (Bell 1991). Pseudovivipary is interpreted as an adaptation to short vegetation periods (Lee and Harmer 1980). Indeed, Fischer et al. (2011) have shown for *Poa alpina* that pseudoviviparous reproduction increases with altitude.

In the present article, we focus on the genus *Deschampsia* (Poaceae), which comprises about 40 species (Chiapella 2000) and is distributed in both hemispheres. *Deschampsia* occurs mostly at high latitudes and in harsh environments. For instance, *D. antarctica* Desv. is one of the only two angiosperm species growing in the Antarctic (Crawford 2008). Although diploid species ($2n = 26$) are dominating in the genus, tetraploid *Deschampsia* species ($2n = 52$) are also known (Cardone et al. 2009), notably in the *D. cespitosa* complex. The tetraploid species are often pseudoviviparous (Nygren 1949; Hedberg 1958, 1986; Rothera and Davy 1986). In Central Europe, the only example of pseudoviviparous *Deschampsia* is known from tetraploid populations ($2n = 39$ – 52 ; Albers 1975, 1978) at Lake Constance (Fig. 1), formerly described as *D. rhenana* by Gremlé (1874). This species appears to be morphologically similar to another tetraploid taxon, previously described by Gaudin (1828) as *Aira cespitosa* β *littoralis* [= *D. littoralis* Gaudin (Reut.)], from Lake Geneva. Apart from pseudovivipary, morphological differences between *D. littoralis* and *D. rhenana* are scarce (see below), and several authors considered both taxa as conspecific (Hess et al. 1967; Conert 1998). This latter view is further supported by the low taxonomic value of pseudovivipary as pseudovivipary may respond plastically to environmental changes (Heide 1989; Pierce et al. 2003), although it seems to be mainly genetically determined (Hedberg 1986; Fischer et al. 2011). Little genetic differentiation has been reported between pseudoviviparous and sexual populations within a species (Rudmann-Maurer et al. 2007). We, nevertheless, hereafter refer to “*D. rhenana*” to designate plants from Lake Constance (irrespective of their taxonomic status).

The extent of genetic differentiation between *D. rhenana* and *D. littoralis* is currently unknown and needs to be

Fig. 1 Inflorescence of *Deschampsia rhenana* from Lake Constance (Konstanz-Hörnle) with pseudoviviparous spikelets (photo credit: M. Dienst)

addressed. Both species represent glacial relicts (Lang 1967), endemic to a few pre-Alpine lakes. The two species are considered to be highly endangered (Käsermann and Moser 1999). In fact, *D. littoralis* is now extinct at Lake Geneva (Käsermann and Moser 1999), but the species is still known from two lakes in the Vallée de Joux in the Swiss Jura mountains (Delarze et al. 2004). In contrast, *D. rhenana* is only known from Lake Constance. The status of endangerment asks for an accurate assessment of taxon identity to optimize conservation strategies. If the two species were genetically distinct, they have to be managed as separated evolutionary units; both species having rather small distribution ranges. In the present study, we use AFLP fingerprinting to examine levels of genetic differentiation (1) among species, including *D. littoralis* from the Vallée de Joux, *D. rhenana* from Lake Constance and their closest diploid relative *D. cespitosa* (L.) P. Beauv., and (2) among individuals, to detect clonality, which is expected to predominate at Lake Constance due to the pseudovivipary of the respective populations.

Materials and methods

Plant material

Sampling included three populations of tetraploid *D. rhenana* from Lake Constance (43 specimens), four populations of tetraploid *D. littoralis* from Lac de Joux and Lac Brenet (11 specimens) and two populations of the close diploid *D. cespitosa* (48 specimens) at locations in the area between Lake Constance and the Vallée de Joux (Table 1). Sampling effort varied according to population size and ranged between 2 and 26 specimens per population. Specimens were collected at least 2 m distant from each other. Fresh leaves were sampled and immediately dried in silica gel. The three species were identified based on morphology: *D. littoralis* and *D. rhenana* are characterized by the absence of prickly hairs on the abaxial (lower) side of the leaf (Fig. 2a) and by the presence of small papillae on the adaxial (upper) side of the leaf (Fig. 2b; Conert 1998; Ziltener 1998). In contrast, papillae are absent in *D. cespitosa*, but prickly hairs occur in high density on the lower side of the leaf (Fig. 2c, d).

Deschampsia rhenana is a characteristic species of the *Deschampsietum rhenanae* (Lang 1967), an amphibious plant community occurring on exposed gravel shores of Lake Constance (400 m a.s.l.). This community includes other pre-Alpine endemics such as *Myosotis rehsteineri* Wartm., the now extinct *Saxifraga oppositifolia* L. subsp. *amphibia* (Sünd.) Braun-Blanq. or *Armeria maritima* Willd. subsp. *purpurea* (Koch) A. Löve and D. Löve (Dienst et al. 2004), which is now extinct in the wild, along with

Table 1 Sampled populations, their locations, sampling size (N) and geographic coordinates (Swiss grid) of the three studied species of the *Deschampsia cespitosa* complex

Population	Municipality and Canton (Switzerland) or Federal State (Germany)	Swiss coordinates	Altitude (m a.s.l.)	N
<i>D. rhenana</i> —Lake Constance				
Hörnle	Konstanz, Baden-Württemberg	733.480/281.350	400	26
Wallhausen	Konstanz, Baden-Württemberg	727.826/289.933	400	11
Mutschellern	Reichenau, Baden-Württemberg	720.490/284.844	400	6
<i>D. littoralis</i> —Vallée de Joux (Lac de Joux and Lac Brenet)				
Lac Brenet	L'Abbaye, Canton Vaud	515.101/170.364	1,000	2
Le Pont	L'Abbaye, Canton Vaud	514.770/169.055	1,005	3
Le Sentier	Le Chenit, Canton Vaud	508.567/162.750	1,005	4
Les Bioux	L'Abbaye, Canton Vaud	510.310/164.049	1,005	2
<i>D. cespitosa</i>				
Tägerst	Stallikon, Canton Zürich	679.327/239.166	590	14
Sous le Chateau	Goumois, Canton Jura	562.760/233.689	500	19
Combe de la Valouse	Bassins, Canton Vaud	503.016/150.211	1,200	15

Fig. 2 Morphology of **a** lower leaf side and **b** papillae at the upper leaf side of *Deschampsia rhenana* (Lake Constance-Reichenau, Germany) and of **c**, **d** prickly hairs at the lower side of *D. cespitosa*

(Allensbach; Germany; SEM photos by R. Ziltener and R. Rutishauser, University of Zürich, Zürich)

widespread amphibious plants such as *Littorella uniflora* (L.) Asch. or *Ranunculus reptans* L. This shore community is flooded regularly during the vegetation period, because the water regime of Lake Constance is (almost) unregulated and varies seasonally with an amplitude of about 2 m (Lang 1967; Peintinger et al. 2007). *Deschampsia littoralis* s.str. is currently only known from Lac de Joux and Lac Brenet, two lakes of the Vallée de Joux in the Swiss Jura mountains (Albers 1978; Conert 1998; Delarze et al. 2004). Both lakes are much smaller (8.77 and 0.8 km², respectively) than Lake Constance (535 km²) and are located at higher altitudes (about 1,000 m a.s.l.) and therefore experience much harsher climatic conditions. Although the water level fluctuates with an altitude of about 2 m, the seasonal changes are less pronounced than at Lake Constance (http://www.hydrodaten.admin.ch/fr/2007.html#historische_daten). The lakeshore sediments consists of calcareous gravel. At the lakeside *D. littoralis* mainly co-occurs with *Carex acuta* L. and *Phalaris arundinacea* L. Finally, *D. cespitosa* s.str. is a common, wind pollinated and self-incompatible species, mainly inhabiting wet meadows (Davy 1980).

Molecular fingerprinting

DNA was extracted with the DNeasy Kit (single columns or 96 well format; Qiagen) according to the manufacturer's instructions. AFLP fingerprinting followed the methods detailed in Gugerli et al. (2008). In brief, we used the restriction enzymes EcoRI and MseI, ligation with EcoRI- and MseI-adaptors, preselective amplification with an additional A (EcoRI) and additional C (MseI) and selective amplification with three additional bases for EcoRI and MseI (EAGC-MCTT; EACA-MCTT; EAGC-MCAG; Holderegger et al. 2003; Van de Wouw et al. 2008). Analysis of fragment lengths was done on an ABI3130 automated sequencer (Applied Biosystems). The selective amplifications of all samples were performed twice: the complete set of AFLP reactions was replicated. Peaks were detected and sized using PeakScanner 1.0 (Applied Biosystems). RawGeno 2.0-0 (Arrigo et al. 2009) was then used for quality control and automated stringent scoring of reproducible AFLP markers in a presence/absence matrix containing all three studied species.

Data analysis

The presence of genetic clones was assessed using the methods implemented in AFLPdat (Ehrich 2006). Genotypes were considered as non-identical if they differed from each other in more than 6.5 % of AFLP bands (i.e., the observed AFLP genotyping error rate). The proportion of identical genotypes ($P_{\text{ClonalGen}}$) was computed per species. Genetic structure was investigated using analysis of

molecular variance (AMOVA; Excoffier et al. 1992) to assess the proportion of genetic variation occurring among species, among populations within species and within populations. In addition, a principal coordinate analysis (PCoA) based on pairwise Euclidean genetic distances between specimens, as implemented in GENALEX 6 (Peakall and Smouse 2006) was calculated. Finally, a non-model based c-means fuzzy clustering (for details see Supplementary Material) was used to quantify the levels of phylogeographic structure and potential admixture of species, as described in Arrigo et al. (2011). In brief, fuzzy c-means clustering uses an iterative approach to (1) classify individuals into a pre-defined number of groups (K), to minimize the intra-group variance and (2) compute the memberships of individuals to each group. The memberships can be understood as assignment probabilities and are used here as proxies of genetic admixture (for details see Supplementary Material). The analysis requires the optimization of two parameters: the number of groups, K , and the sensitivity level applied during membership computation (i.e., r , also called “fuzzification” parameter). The optimal number of groups, K , was determined following a strategy adapted from Evanno et al. (2005). The appropriate sensitivity level was determined empirically (for details see Supplementary Material), by exploring r values covering the complete spectrum of sensitivity and ranging from non-fuzzy (i.e., using $r = 1$, where memberships take values of either zero or one) to over-fuzzy clustering (i.e., using $r > 1$ increases fuzziness, until eventually reaching an over-fitting limit where all individuals are assigned to every group).

Results

A total of 153 polymorphic AFLP bands was obtained, with an average genotyping error rate of 6.5 %. The mean number of bands per specimen was almost identical for the three species studied (*D. rhenana*: 114.7, *D. littoralis*: 111.1 and *D. cespitosa*: 118.2), which implied no influence of ploidy level on observed AFLP patterns.

None of the 102 specimens showed identical AFLP banding patterns. Still, six pairs of specimens differed from each other with less than 6.5 % of mismatching AFLP bands and could thus potentially represent clonal genotypes (*D. rhenana*, five potential clones, $P_{\text{ClonalGen}} = 14$ %; *D. littoralis*, one potential clone, $P_{\text{ClonalGen}} = 19$ %). Most of these putative clones occurred within a single population; Hörnle: three clones; Wallhausen: one clone; Mutschellern: one clone; Lac Brenet: one clone. In contrast, no putative clones were detected in *D. cespitosa*.

AMOVA showed that *D. rhenana*, *D. littoralis* and *D. cespitosa* were closely related, with only 12 % of molecular variance being observed among the three species

Table 2 Results of analysis of molecular variance (AMOVA) for AFLP variation of *Deschampsia rhenana* (Lake Constance), *D. littoralis* (Vallée de Joux) and *D. cespitosa*

Source of variation	df	Sum of squares	% of variation	Significance
Among species	2	164.627	12	$P < 0.001$
Among populations	7	156.527	7	$P < 0.001$
Within populations	92	1,190.405	81	

(Table 2). Differentiation among populations within species was low (7 %), but high within populations (81 %). Overall genetic differentiation (F_{st}) equalled 0.186.

The first three PCoA axes explained 65 % of the total genetic variation (33, 16.4 and 15.4 %, respectively). *Deschampsia cespitosa* and *D. rhenana* formed distinct groups in the PCoA, although three individuals overlapped between the two groups (Fig. 3). Specimens of *D. littoralis* appeared as intermediate between *D. cespitosa* and *D. rhenana*, but were more closely related to the former than to the latter.

Congruent but less clear results were obtained using fuzzy c-means clustering, where the optimal number of groups ranged between 2 and 4 (Fig. S1). Overall, *D. littoralis*, *D. rhenana* and *D. cespitosa* showed unclear genetic differentiation. In fact, 28, 100 and 6 % of the *D. littoralis*, *D. rhenana* and *D. cespitosa* specimens were assigned to a genetic group differing from taxonomic expectations with at least 50 % probability. Considering two groups ($K = 2$), *D. rhenana* was discriminated from the other two species (except for three *D. cespitosa* outliers that were clustered in the *D. rhenana* pool). Adding one group ($K = 3$) revealed a

geographic gradient within *D. rhenana*. Finally, considering four groups ($K = 4$) showed an additional geographic structure within the *D. cespitosa*–*D. littoralis* specimens, with *D. littoralis* appearing genetically related to its geographically closest *D. cespitosa* population (Combe de la Valouse) and to specimens from a more distant population (Tägerst). Finally, it was only when considering five groups ($K = 5$) that *D. littoralis* appeared as an independent lineage (data not shown).

Discussion

The present study using AFLP fingerprints found the following three major results: (1) *Deschampsia littoralis* (Vallée de Joux), *D. rhenana* (Lake Constance) and *D. cespitosa* are closely related species. (2) *D. rhenana* is more distinct from *D. cespitosa* than is *D. littoralis*. (3) The amount of genetic variation within populations was high, even for the mainly asexually reproducing *D. rhenana* from Lake Constance.

Using ITS and chloroplast *trnK-rps16* sequences, Chiapella et al. (2011) showed that the taxa of the *D. cespitosa* complex are genetically only weakly differentiated in North America. As a consequence, these authors recognized only a single species, namely *D. cespitosa*, with four infraspecific units (subsp. *cespitosa*, subsp. *alpina*, subsp. *beringensis* and “*D. brevifolia*”). However, the genetic markers that Chiapella et al. (2011) used are more conservative than the AFLPs we used in the present study. Chiapella et al. (2011) also investigated the morphology of the North American

Fig. 3 **a** Results of the first two axes (axis 1: 33 %; axis 2: 16.4 %) of a principal coordinate analysis of pairwise genetic distances among 102 individuals belonging to *Deschampsia rhenana* (Lake Constance: black symbols), *D. littoralis* (Vallée de Joux: gray symbols) and

D. cespitosa (white symbols). **b** C-means fuzzy clustering of individuals, considering $K = 2$ –4 genetic groups. The ploidy level of each species is indicated (2×—diploid, 4×—tetraploid)

Deschampsia taxa, but the leaf morphology characters studied were mostly related to plant height and thus potentially affected by the environment.

Our results suggested that at least the *D. rhenana* specimens from Lake Constance should be considered as a separate species from *D. cespitosa* (Fig. 3). Indeed, both species differ in leaf morphology, ploidy level and showed the largest genetic differentiation in our data set. Furthermore, *D. rhenana* is the only pseudoviviparous species of *Deschampsia* in Central Europe. Still, the modest amount of genetic differentiation between *D. rhenana* from Lake Constance and the widespread *D. cespitosa* suggested that their differentiation occurred relatively recently. This was in line with the assumption that the pre-Alpine endemics of Lake Constance such as *D. littoralis*, *Myosotis rehsteineri* or *Armeria maritima* subsp. *purpurea* probably evolved in isolated periglacial refugia during the last glacial period (Lang 1967). Using subfossil pollen records, Lang (1967) demonstrated a shift in the distribution of *A. maritima* subsp. *purpurea* since the Würm glacial period, which corresponds with a scenario where this taxa was widely distributed during the late glacial period, but subsequently only survived in two small distribution areas. A similar glacial and postglacial history might apply to *D. rhenana*.

Our results further showed that *D. littoralis* and *D. rhenana* were genetically distinct, with the former being more closely related to *D. cespitosa*. Two possible scenarios could explain this result. First, both tetraploid species could share a common ancestor (i.e., being probably *D. cespitosa*), but have independent polyploid origins at Lake Constance and at Lake Geneva/Vallée de Joux. Indeed, recurrent polyploidy is a common phenomenon in polyploid species complexes (Soltis and Soltis 2009) and has already been supposed for the *D. cespitosa* group (Johnson and Packer 1968; Bush and Barrett 1993; Purdy and Bayer 1995), leading, for example, Kawano (1962) to include tetraploid Canadian populations of *Deschampsia* ($2n = 49$) within *D. littoralis*. The second scenario considers *D. littoralis* and *D. rhenana* as part of a monophyletic entity, but with admixture having occurred between *D. cespitosa* and *D. littoralis* in the Vallée de Joux. This hypothesis is corroborated by morphological (leaf surface) and phenological (flowering time) evidence which also reveals *D. littoralis* from the Vallée de Joux as being intermediate between *D. rhenana* and *D. cespitosa* or even more closely related to *D. cespitosa* (M. Peintinger, unpubl. data). Accordingly, Delarze et al. (2004) proposed a hybrid origin for *D. littoralis*. Although our results cannot prove one hypothesis or the other, they nevertheless outline *D. littoralis* and *D. rhenana* as distinct lineages. We thus recommend considering these two taxa as distinct taxonomic units.

The genetic variation we detected within *Deschampsia* populations was high (81 % of the total genetic variation).

High genetic variation within populations of *D. cespitosa* was also reported in previous studies based on isozymes (Gehring and Linhart 1992; Purdy and Bayer 1995; Nkongolo et al. 2001). A high variability at isozyme loci was also found for *D. rhenana* by Ziltener (1998), even though the sampling of this study was limited. Although pseudoviviparous plants are dominating at Lake Constance, vegetative reproduction does not seem to be dominant. We sampled plants at a minimum distance of 2 m; vegetative reproduction may thus still be important at a smaller scale. The reason for the low degree of clonality detected in *D. rhenana* from Lake Constance could reflect a mixed reproductive strategy. Indeed, several pseudoviviparous plant species can develop sexual flowers at the base of inflorescences (Münzing 1980; Pierce et al. 2003), a reproductive strategy that has also been observed at Lake Constance (M. Peintinger, unpubl. data). Furthermore, Ziltener (1998) even detected complete sexual populations of *D. rhenana* without any pseudoviviparous plants. The above results contrast with low genetic variation reported for highly selfing species such as in *D. mackenziana* Raup., an endemic tetraploid of sand dunes (Purdy and Bayer 1995) or *D. antarctica* from Antarctica (Holderegger et al. 2003; van de Wouw et al. 2008).

From a conservation perspective, it is important to emphasize that the tetraploid populations from Lake Constance and the Vallée de Joux are genetically not identical. They may represent independent polyploidy events, although the status of the *D. littoralis* plants from the Vallée de Joux remains unclear and could reflect hybridization from a phenotypic perspective. We thus suggest that *D. rhenana* from Lake Constance and *D. littoralis* from the Lac de Joux should be treated as independent evolutionary units in conservation management strategies.

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