



## Allopolyploid origin of highly invasive *Centaurea stoebe* s.l. (Asteraceae)

Patrik Mráz<sup>a,\*</sup>, Núria Garcia-Jacas<sup>b</sup>, Emilie Gex-Fabry<sup>a</sup>, Alfonso Susanna<sup>b</sup>, Laia Barres<sup>b</sup>, Heinz Müller-Schärer<sup>a</sup>

<sup>a</sup> Department of Biology, Unit of Ecology & Evolution, University of Fribourg, Chemin du Musée 10, CH-1700 Fribourg, Switzerland

<sup>b</sup> Botanic Institute of Barcelona (IBB-CSIC-ICUB), Passeig del Migdia, s.n., E-08038 Barcelona, Spain

### ARTICLE INFO

#### Article history:

Received 25 June 2011

Revised 26 September 2011

Accepted 4 November 2011

Available online 20 November 2011

#### Keywords:

Allopolyploidy  
*Centaurea maculosa*  
 cpDNA  
 Flow cytometry  
 Invasion  
 ITS  
 Hybridization  
 Life history traits  
 nrDNA  
 Polyploidy

### ABSTRACT

Spotted knapweed (*Centaurea stoebe*) occurs from Western Asia to Western Europe both as diploid and tetraploid cytotypes, predominantly in single-cytotype populations with higher frequency of diploid populations. Interestingly, only tetraploids have been recorded so far from its introduced range in North America where they became highly invasive.

We performed phylogenetic and network analyses of more than 40 accessions of the *C. stoebe* and *C. paniculata* groups and other related taxa using cloned internal transcribed spacer (ITS) and sequences of the chloroplast *trnT-trnL* and *atpBrbcL* regions to (i) assess the evolutionary origin of tetraploid *C. stoebe* s.l., and (ii) uncover the phylogeny of the *C. stoebe* group. Both issues have not been studied so far and thus remained controversial.

Cloned ITS sequences showed the presence of two slightly divergent ribotypes occurring in tetraploid cytotype, while only one major ribotype was present in diploid *C. stoebe* s.str. This pattern suggests an allopolyploid origin of tetraploids with contribution of the diploid *C. stoebe* s.str. genome. Although we were not able to detect the second parental taxon, we hypothesize that hybridization might have triggered important changes in morphology and life history traits, which in turn may explain the colonization success of the tetraploid taxon. Bayesian relaxed clock estimations indicate a relatively recent – Pleistocene origin of the tetraploid *C. stoebe* s.l. Furthermore, our analyses showed a deep split between the *C. paniculata* and *C. stoebe* groups, and a young diversification of the taxa within the *C. stoebe* group. In contrast to nrDNA analyses, the observed pattern based on two cpDNA regions was inconclusive with respect to the origin and phylogeny of the studied taxa, most likely due to shared ancient polymorphism and frequent homoplasies.

© 2011 Elsevier Inc. All rights reserved.

### 1. Introduction

Successful biological invasions are generally based on both ecological and evolutionary processes, but the latter ones have been studied to a lesser extent (Vanderhoeven et al., 2010). Ellstrand and Schierenbeck (2000) stressed the importance of hybridization as an evolutionary stimulus of invasiveness. In fact, hybridization between species or between divergent populations within the same species leads to the formations of new genotypic and phenotypic combinations, which may allow the colonization of new ecological niches (Stebbins, 1950; Anderson and Stebbins, 1954). Newly formed plant hybrids are often stabilized by polyploidization (genome doubling) alleviating the problems of chromosome pairing during meiosis and thus sterility (Burke and Arnold, 2001; Abbott et al., 2010). Besides the reproductive assurance of otherwise sterile hybrids, polyploidization leads to fixation of heterotic genotypes and increases genetic variation through a higher

number of allelic variants per locus (Comai, 2005). Thus, hybridization and polyploidization either alone, or in concert, may considerably increase the adaptive potential as compared to their ancestors. Many polyploids are successful colonizers of naturally or artificially disturbed habitats (Stebbins, 1985; Ehrendorfer, 1980; Thompson, 1991; Brochmann et al., 2004) and thus polyploidy has been listed in several comprehensive studies focusing on putative determinants of invasiveness in plants. (e.g. Verlaque et al., 2002; Küster et al., 2008; Pyšek et al., 2009). However, these meta-analyses have not distinguished autopolyploids, arising within populations of single species, from allopolyploids, in which interspecific hybridization was involved, most likely because of lack of this information. Nevertheless, knowledge of the evolutionary history of invasive species is crucial for understanding underlying mechanisms of their invasion success.

Several invasive polyploids have recently been found to be of hybridogeneous origin due to progress in molecular biology (Gray et al., 1990; Baumel et al., 2002; Ainouche et al., 2004; Vilatersana et al., 2007; Kim et al., 2008; Jacob and Blattner, 2010). Interspecific hybridization is usually inferred by biparentally inherited

\* Corresponding author.

E-mail address: [patrik.mraz@unifr.ch](mailto:patrik.mraz@unifr.ch) (P. Mráz).

nuclear DNA markers, most often using the internal transcribed spacer (ITS). Wide-spread use of ITS1–5.8S–ITS2 stems from their easy amplification with universal primers and relatively high level of interspecific polymorphism (Baldwin et al., 1995). On the other hand, some constraints might hamper its application for phylogenetic reconstructions. More specifically, ITS nrDNA shows higher level of homoplasmy than other nuclear markers, the nucleotide position is not independent due to conservative secondary structure, paralogues/orthologues can be frequent and they can be subject to various level of intra- or inter-array homogenization (Álvarez and Wendel, 2003). However, in the case of suppression of the last mentioned mechanism, and thus retention of two (or more) divergent ITS copies within one genome, this marker may prove to be highly informative with respect to the hybridization history. Indeed, many case-studies documented a hybridogeneous origin of polyploid taxa using multicopy ITS or ETS (external transcribed spacer) nrDNA markers (Soltis and Soltis, 1991; Sang et al., 1995; Campbell et al., 1997; Andreasen and Baldwin, 2003; Fehrer et al., 2009). In addition to biparentally inherited polymorphism assessed by nuclear markers, incongruencies between nuclear and plastid phylogenies may indicate reticulation event(s) (Rieseberg and Soltis, 1991; Soltis and Kuzoff, 1995).

Frequent hybridization and polyploidization considerably shaped the evolutionary pattern in the species-rich genus *Centaurea* L. (Hellwig, 2004). Interspecific homoploid hybridization is frequent and single hybrids or hybrid populations are often easily recognized due to their intermediate morphology (e.g. Kummer, 1977; Fernández Casas and Susanna, 1986; Garcia-Jacas and Susanna, 1994; Ochsmann, 2000; Koutecký, 2007; Blair and Huffbauer, 2010; Pisanu et al., 2011). The situation is however more complicated in widespread polyploid taxa. Given their high frequency, surprisingly little is known about their auto- or allopolyploid origin. Based on polysomic segregation at two allozymic loci, an autopolyploid origin has been suggested for the tetraploid cytotype of *C. phrygia* L. (Hardy et al., 2000). On the contrary, a quite complex scenario involving several diploid and tetraploid species in several steps has been proposed for the west Mediterranean tetraploid and hexaploid *C. toletana* Boiss. cytotypes (Garcia-Jacas et al., 2009). Similarly, the presence of different ITS paralogues in *C. boissieri* subsp. *atlantica* (Font Quer) Blanca and *C. debdouensis* Breitw. and Podlech has been explained by recent hybridization (Suárez-Santiago et al., 2007).

The *Centaurea stoebe* group (*Centaurea* sect. *Centaurea*, formerly sect. *Acrolophus*) is represented by diploid ( $2n = 2 \times = 18$ ) and tetraploid ( $2n = 4 \times = 36$ ) populations occurring sympatrically in the native European range (Ochsmann, 2000; Španiel et al., 2008; Treier et al., 2009). The taxonomic position of both cytotypes is still debated. While Ochsmann (2000) proposed to distinguish diploid (*C. stoebe* subsp. *stoebe*; *C. stoebe* s.str. thereafter) from tetraploid cytotype at the subspecies level [*C. stoebe* subsp. *micranthos* (Gugler) Hayek; *C. stoebe* s.l. thereafter], Španiel et al. (2008) suggested a single species concept with no recognition of intraspecific units. In addition to diploid and tetraploid *C. stoebe* L. several other morphologically similar species to *C. stoebe* have been described [e.g. *C. corymbosa* Pourr., *C. reichenbachii* DC., *C. triniifolia* Heuff., *C. vallesiaca* (DC.) Jord.], but their phylogenetic relationship to *C. stoebe* remains obscure (Ochsmann, 2000).

*Centaurea stoebe* has been introduced to North America at the end of 20th century and since that became highly invasive (Sheley et al., 1998). More importantly, only the tetraploid cytotype has been recorded so far in the introduced range (Treier et al., 2009; Mráz et al., 2011). This pronounced shift in cytotype composition between the native and introduced range could either be the result of the stochastic introduction of only the tetraploid cytotype, or tetraploids might have a demographic advantage over the diploids, in the case if the diploids had been also introduced (Treier et al.,

2009). Both cytotypes differ in their life cycle and this trait could tentatively explain the invasion success of the polyploid cytotype. In fact, tetraploids are short-lived perennials and polycarpic, while diploids are predominantly annual or biennial monocarpic plants (Boggs and Story, 1987; Müller, 1989; Ochsmann, 2000; Story et al., 2001; Henery et al., 2010; Mráz et al., 2011). In addition to the different life cycle, recent multivariate morphometric study based on plants grown under uniform conditions from more than 60 populations from both the native and introduced range showed that the cytotypes also differ in other morphological traits, thus supporting the distinct taxonomic status of both cytotypes (Mráz et al., 2011). Differences in phenotypic and life-cycle traits between cytotypes could be the results of direct polyploidization (autopolyploidization), as whole genome duplication might induce morphological and physiological changes (Müntzing, 1936; Blakeslee, 1941; Maherali et al., 2009), or alternatively, hybridization associated with polyploidization (allo-polyploidization). In the latter case, greater phenotypic and genetic differences between diploid progenitors and their polyploid derivatives might be expected than under autopolyploidy, although the extent of differentiation depends on the divergence between the parental taxa (Stelkens et al., 2009).

The aim of the present study was (i) to determine the origin (auto- vs. allopolyploid) of the tetraploid cytotype of *C. stoebe* using biparentally inherited nrDNA ITS marker and two cpDNA loci and (ii) to infer their relationship with closely related taxa belonging to the *C. stoebe* group.

## 2. Material and methods

### 2.1. Plant material and ploidy level determination

Forty-two accessions of *Centaurea stoebe* s.l. originating from 38 populations sampled across the native European and introduced North American range and representing all known cytotypes (i.e.  $2 \times$  and  $4 \times$  as major cytotypes, and  $3 \times$  and  $6 \times$  as rare ones; cf. Mráz et al., 2011) were included in the present study (Table 1). Within *C. stoebe* s.l. we included also the accessions recognized by Ochsmann as separate taxa (e.g. *C. reichenbachii*, *C. tauscherii* A. Kern., *C. triniifolia*, *C. vallesiaca*) to cover variation as large as possible within the group (Ochsmann, 2000). In addition, nine other species were added: *C. cuneifolia* Sm., a species morphologically similar to *C. stoebe* from the Balkans; three species from the *C. paniculata* group, namely *C. aplolepa* Moretti, *C. leucophaea* Jord., and *C. paniculata* L.; and three species showing similar ITS sequences based on a previous study (*C. donetzica* Klokov, *C. sarandinakiae* N.B. Illar., and *C. vankovii* Klokov; see Garcia-Jacas et al., 2006). All taxa belong to the sect. *Centaurea*, except of *C. donetzica*, *C. sarandinakiae* and *C. vankovii* which are members of sect. *Phalolepis* (Cass.) DC. (Wagenitz and Hellwig, 1996). Leaf material for DNA extraction was collected either from the plants in the field or from seed-derived plants cultivated in the greenhouse, dried in silica-gel and stored at room temperature. Rarely, herbarium specimens were used. Details on vouchers, population codes and GenBank accession numbers are given in Table 1.

Ploidy level estimations and chromosome counts were determined on seed-derived plants cultivated in the greenhouse, or in rare cases on silica-gel dried material. Details for sample preparation and analyses using flow cytometry and chromosome counting are given in Mráz et al. (2011). Most of the ploidy estimations presented here are new (see Table 1), although some are from our previous publications (Treier et al., 2009; Mráz et al., 2011). For some taxa for which we used already published ITS sequences, ploidy level information were taken from Ochsmann (2000).

Download English Version:

<https://daneshyari.com/en/article/5920498>

Download Persian Version:

<https://daneshyari.com/article/5920498>

[Daneshyari.com](https://daneshyari.com)