Flora 207 (2012) 530–540

Contents lists available at SciVerse ScienceDirect

Flora

journal homepage: www.elsevier.de/flora

Is hybridization involved in the evolution of the *Chenopodium album* aggregate? An analysis based on chromosome counts and genome size estimation

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ARTICLE INFO

Article history:
Received 28 November 2011
Accepted 10 March 2012

Keywords:
Chenopodium
Chenopodiaceae
Flow cytometry
Hybridization
Polyploidization
Unreduced gametes

ABSTRACT

For our study of the *Chenopodium album* aggregate, we selected those species of Euroasiatic origin that represent the diploid–polyploid complex in Central Europe: *C. album* (6*x*), *C. ficifolium* (2*x*), *C. opulifolium* (6*x*), *C. striatiforme* (4*x*), *C. strictum* (4*x*) and *C. suecicum* (2*x*). We especially focused on (a) the origin of polyploid species and (b) the frequency of hybridization between species with different ploidy levels. We did not find any direct evidence of the existence of hybrids between two species with different ploidy levels within the *C. album* group. The sample/standard ratio of tetraploid and hexaploid species does not equal multiples of that of diploid species, which suggests that (i) tetraploids are not diploid autopolyploids and that (ii) hexaploids have not evolved from diploid species alone. Moreover, we have not found any hybrid plant either in the field or even in the offspring resulting from our experimental crosses. In view of these results, we adhere to the opinion that *Chenopodium* species do not hybridize freely across ploidy levels. Our analysis of DNA amounts, however, suggests that *C. album* is an allopolyploid that has arisen by hybridization between a diploid and a tetraploid species the identity of which is unknown.
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Introduction

Polyploidy, the state of having more than two sets of chromosomes, is widespread among a diverse array of plant taxa, although it also infrequently occurs in animals (Soltis, 2005). Polyploidization has been recognized as one of the major speciation mechanisms in plant evolution. It produces evolutionary novelty from generation to generation through chromosome doubling, which, in fact, represents a kind of reproductive isolation mechanism (Ramsey and Schemske, 1998). The persistence of a new polyploid is hindered by minority cytotype exclusion (Levin, 1975), which causes the extinction of many newly formed polyploid cytotypes. Many polyploids are hybrids in origin and occupy different ecological niches than their parents. Polyploids are often perennial plants that can survive for a long time, awaiting repeated formation of the same cytotype, which allows the new cytotype to establish a population (Levin, 1983; Ramsey and Schemske, 1998). Recent research has been focused on the immediate genetic consequences of polyploidy. Studies are finding evidence of epigenetic effects, gene silencing and rapid changes in phenotype (Buggs et al., 2009; Flagel and Wendel, 2009; Gaeta et al., 2007; Shaked et al., 2001). From the perspective of plant taxonomy, however, there are still many groups that form putative polyploid series which have not yet been studied systematically even though polyploidy has evidently played an important role in their evolution.

The genus *Chenopodium* L. (including *Dysphania* R. Brown) has a worldwide distribution with the highest species diversity in temperate areas; it includes more than 170 species (Chu et al., 2003). Many of the species have some economic importance. Some for example, serve as grain crops in the Andean region of South America [*C. quinoa* Wild., *C. berlandieri* subsp. *nuttalliae* (Safford) H.D. Wilson et Heiser] or the Himalayan region of India (*C. giganteum* D. Don, *C. album* L.: Risi and Galwey, 1984), while others have various medicinal uses (*C. ambrosioides* L., *C. botrys* L., *C. murale* L.: Aellen, 1960). Others are among the worst weeds and are some of the most widespread synantropic plants on Earth. This is the case of the *C. album* complex. Rohring and Stutzel (2001), for example, estimate that the decrease in total dry matter production of agricultural products caused by weed infestation, especially by *C. album*, is about 20–30%. Wahl (1954) points out that few plant species outside the genus *Chenopodium* with such wide distributions exhibit so much variability, and this latter is currently still not understood. This is especially true for members of the section *Chenopodium*.

The confusing taxonomy of the cosmopolitan *Chenopodium album* group has been attributed to (a) frequent hybridization and introgression, (b) a high level of autogamy, (c) the presence of different ploidy levels and (d) high phenotypic plasticity. It is

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0367-2530/$ – see front matter © 2012 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.flora.2012.03.010

basically a loosely arranged aggregate of poorly understood races. Hundreds of segregate microspecies and infraspecific entities have been described or recognized by various authors within the *C. album* group. Some authors have recognized numerous segregates as species or hybrids (e.g. Dvořák, 1990, 1992a,b, 1993, 1994), while others have developed elaborate intraspecific hierarchies comprising numerous subspecies, varieties, forms and even subforms (e.g. Jüttersonke and Arlt, 1989). Most authors, however, have recognized a certain number of basic species delimited by morphology and ploidy level (Aellen, 1929, 1960; Aellen and Just, 1943; Clemants and Mosyakin, 2003; Uotila, 1972, 1973, 1978, 1997, 2001). In addition, many transitional forms among species have been reported (Jüttersonke and Arlt, 1989) and are probably the main source of common misidentification within *C. album* agg. These enigmatic and deviant forms of the *Chenopodium album* group have also been recognized as hybrids with other (occasionally several) species or infraspecific entities (see Aellen, 1960; Clemants and Mosyakin, 2003; Uotila, 2001). Still, neither approach has resolved the problems concerning the degree of hybridization, ploidy level variation and phenotypic plasticity (Bassett and Crompton, 1982; Cole, 1961; Mosyakin, 1993; Scott, 1978; Uotila, 2001; Wahl, 1954).

Different ploidy levels exist in the *C. album* aggregate (Table 1; Dostálek et al., 1990; Uotila, 1972, 1973). *Chenopodium suecicum* J. Murr and *C. ficifolium* Sm. with $2n = 2x = 18$ are diploid (Uotila, 1978). *Chenopodium strictum* Roth, *C. striatiforme* J. Murr and *C. novopokrovskyanum* (Aellen) Uotila (an Asiatic species which does not occur in Europe) have mostly been reported as tetraploids with $2n = 4x = 36$ (Uotila, 1973, 1977). *Chenopodium album* L. s. str. has generally been reported to be hexaploid ($2n = 6x = 54$; Rahiminejad and Gornall, 2004; Uotila, 1973), although there are some reports of it being diploid as well as tetraploid (Table 1). Cole (1962) points out that *C. album* is a hexaploid species. Uotila (1972, 1973) who studied chromosome numbers in the *C. album* aggregate in Europe and SW Asia supports Cole's view. Uotila (1973) suggests that the hexaploid level is the most common or perhaps even the only level of ploidy within *C. album* s. str. He also reports *C. giganteum* D. Don and *C. opulifolium* Schrader as hexaploid species.

It has been reported that *C. album* hybridizes with *C. suecicum* (to produce *C.* × *fursajevii* Aellen et Iljin), *C. opulifolium* (to produce *C.* × *preissmannii* Murr), *C. strictum* [to produce *C.* × *pseudostriatum* (Zschacke) Murr], *C. ficifolium* (to produce *C.* × *zahnii* Murr), *C. berlandieri* Moq. (to produce *C.* × *variabile* Aellen) and other species (see Aellen, 1960; Clemants and Mosyakin, 2003; Uotila, 2001). Because these taxa are very closely related and overlap morphologically, especially under extreme ecological conditions, some authors recognize the existence of hybrids between nearly all of the species described (Dvořák, 1990, 1992a,b, 1993, 1994). However, the role of hybridization is probably overestimated (Dostálek et al., 1990), and the frequency of hybrids is probably not as high in nature as some authors suggest.

Rahiminejad and Gornall (2004) have recently published a hypothesis concerning the allopolyploid origin of *C. album* s. str. based on an analysis of secondary metabolites. In their view, *C. album* has evolved by hybridization between two diploid taxa, *C. ficifolium* and *C. suecicum* (or taxa very similar to them), followed by polyploidization. The origin of *C. album* remains unclear, nonetheless, because there are several other possible pathways through which *C. album* could have originated from various *Chenopodium* species. Considering that *C. album* is hexaploid, we propose several possible evolutionary pathways (Fig. 1): (a) fusion of unreduced and reduced gametes of diploid species and subsequent triploid polyploidization (Fig. 1A), (b) hybridization with other tetraploid species and subsequent triploid polyploidization (Fig. 1B), (c) fusion of two unreduced gametes from diploid and tetraploid species (Fig. 1C) or (d) fusion of unreduced and reduced gametes from two tetraploids (Fig. 1D). The origins of the tetraploid species (i.e. *C. strictum* and *C. striatiforme*) remain similarly unresolved. Again, there are several possibilities including autopolyploidization of a diploid progenitor, polyploidization of a diploid hybrid progenitor or evolution by the coincidence of unreduced gametes from diploid species.

For our study of the *Chenopodium album* aggregate, we have selected those species of Eurasian origin that represent the diploid–polyploid complex in Central Europe, i.e. *C. album*, *C. ficifolium*, *C. opulifolium*, *C. striatiforme*, *C. strictum* and *C. suecicum*. This study is aimed at improving our understanding of the cytological variability of taxa from the *C. album* group and is especially focused on (a) the origin of species with higher ploidy levels and (b) the frequency of hybridization between species with different ploidy levels; in other words, how frequent is hybrid formation under both natural and experimental conditions.

Materials and methods

Material collection

Plant collection was focused on the Czech Republic; especially the warmest areas of Bohemia and Moravia were sampled intensely, where taxa of the *C. album* group are very abundant (Appendix I). We collected 482 individuals from 53 populations and 6 species: *C. album* – 18 populations (160 plants), *C. strictum* – 9 populations (88 plants), *C. striatiforme* – 5 populations (46 plants), *C. suecicum* – 8 populations (71 plants), *C. ficifolium* – 8 populations (72 plants), *C. opulifolium* – 5 populations (45 plants), see Appendix I. From each population, we collected (1) samples of leaves from 1 to 10 individuals, all of which were analyzed by flow cytometry, and (2) fruits from five plants for further experiments. The minimum distance between each individual sampled was 5 m. Samples were collected from July to November 2007, transported to the laboratory in plastic bags and analyzed within 24 h. Voucher specimens are deposited in the first author's own herbarium at the Institute of Botany, Academy of Sciences of the Czech Republic in Průhonice.

Chromosome counting

A modified method of Bailey and Stace (1992) was used to prepare slides for chromosome counting. Actively growing roots were pretreated in 0.002 M 8-hydroxyquinoline for 22–24 h at 4 °C, fixed overnight in 3:1 ethanol:ice-cold acetic acid and stored at 4 °C in 70% ethanol until used. The root-tips were hydrolyzed in 2N HCl for 10 min at 60 °C, rinsed in water, and the meristematic tissue was cut off and squashed in a drop of lacto-propionic orcein. The chromosomes were counted using a phase-contrast microscope. We visually counted chromosomes from five plants of each of six *Chenopodium* species.

Experimental crosses

We carried out experimental crosses in spring 2008 using plants grown in the Experimental garden of the Institute of Botany, Academy of Sciences, Průhonice, Czech Republic (49°59′30″N, 14°34′00″E, ca. 320 m above sea level). Given the relatively dense inflorescence and small flower size, it is impossible to emasculate individual flowers. We therefore simply dusted approximately 10 cm of the inflorescence with appropriate pollen grains from another species. Specifically, we brought together two branches with inflorescences of different species before flowering and isolated them in pollen-free bags. Branches with inflorescences were bagged with two layers of nylon net bag with a 0.5 mm × 0.5 mm weave. Every day, the inflorescences in each bag were carefully wiped to increase the chances of pollen transfer to the stigmas.

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