

Hybridisation between diploid and tetraploid taxa of *Centaurea* sect. *Jacea*: morphological variation and role of unreduced gametes

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Centaurea sect. *Jacea* is one of taxonomically difficult groups of European flora. One of the main problems in the section is frequent hybridisation. It seems that its extent depends on ploidy levels of the hybridising taxa. Diploids ($2n = 22$) and tetraploids ($2n = 44$) are known within the section (DOSTÁL 1976). Extensive crossing experiments with taxa of *C. jacea* and *C. nigra* groups in West Europe (GARDOU 1972, HARDY et al. 2001) have demonstrated that taxa sharing chromosome numbers (irrespective whether diploid or tetraploid) hybridise frequently and their hybrids are generally fertile, whereas hybridisation between the different ploidy levels is rare and the hybrids are usually sterile. The inter-ploidy hybrids found within the experiments were usually triploid, i.e. formed by union of reduced gametes, but very rare occurrence of unreduced gametes of diploids was also detected. Some asymmetry between reciprocal crosses was found: diploid individuals pollinated by tetraploids yielded less hybrids than opposite. Existence of the strong reproductive isolation of taxa differing in a ploidy level was also confirmed by a field study, in which no triploid individuals (i.e. hybrids) were found by flow cytometric screening in three mixed populations (HARDY et al. 2000).

From the field experience it seems that similar rules also hold true for Central European taxa. Hybrids between taxa of different ploidy level are rather rare. In opposite, hybrids between taxa of the same ploidy level are frequent (in areas where parental taxa occur together) and they are often fertile and capable of backcrossing, which results in formation of extensive hybrid swarms, introgression and even hybridisation with other taxa (i.e. formation of triple or multiple hybrids) (ŠTĚPÁNEK & KOUTECKÝ 2004).

Surprisingly, one mixed populations of diploid *C. elatior* (GAUD.) HAYEK (= *C. pseudophrygia* auct.) and tetraploid *C. jacea* L. containing numerous hybrids (*C. ×similata* HAUSSKN.) was found in the Krušné hory Mts., Czechia. The hybrids in the population are highly fertile and it also seems that they back-cross with *C. jacea*, which should not be possible, theoretically. DNA ploidy level of

both parental species and the hybrid was therefore analysed by flow cytometry. The DNA ploidy levels of parental taxa agreed with expectation, however, all hybrids were tetraploid instead of triploid. It means that unreduced gametes from diploid were probably involved in their formation. The fact that hybrids are tetraploid could explain observed fertility of hybrids and possible back-crossing with tetraploid *C. jacea*. It might also explain negative results of the West-European studies cited above – also in Czech population no hybrid would have been found if only flow cytometric screening had been used and only triploids had been searched for.

Table 1. Seed set and DNA ploidy levels of offspring in hybridisation experiment with *C. elatior* (“elat”) and *C. jacea* (“jac”). Average seed set for each type of cross (“autog.” stands for autogamy) is in per cent of average seed set of spontaneous pollination by insects of respective species used as mother. For For each DNA ploidy level, portion of all offspring of respective cross and number of analysed individuals are given. Autogamy of *C. elatior* and both crosses within the species yielded large progeny, from which only 20 randomly selected individuals were analysed for DNA ploidy level.

Cross	Seed set	DNA ploidy levels of offspring		
		Diploid	Triploid	Tetraploid
elat autog.	1.1%	100% (20)	–	–
elat ♀ × elat ♂	58.5%	100% (20)	–	–
elat ♀ × jac ♂	8.8%	78.7% (37)	4.3% (2)	17% (8)
jac ♀ × elat ♂	10.1%	–	17.8% (8)	82.2% (37)
jac ♀ × jac ♂	42.8%	–	–	100% (20)
jac. autog.	0.4%	–	–	100% (3)

Pilot hybridisation experiment with the same taxa (*C. elatior* and *C. jacea*) was carried out to get supplementary data comparable with the field study. Three types of crosses were involved: (i) within the ploidy level (taxon), (ii) between the ploidy levels (taxa) and (iii) autogamy as a control. The experiment revealed very low level of autogamy. The seed set in the inter-ploidy crosses was about 4- or 5-times reduced in comparison to the within-ploidy crosses and germination rate was somewhat lower, too. Flow cytometric analysis of progeny of the inter-ploidy crosses has shown that (a) autogamy was enhanced in these crosses (probably a result of so called ‘mentor effect’) and (b) hybrids were

formed both by fusion of two reduced gametes (triploid hybrids) or by fusion of an unreduced gamete of diploid and a reduced gamete of tetraploid (tetraploid hybrids) (see table 1 for details) Tetraploid hybrids were about 4-times more common than triploid hybrids. No higher ploidy levels were detected, i.e. unreduced gametes of tetraploid were not involved. There was some asymmetry between the reciprocal crosses. In crosses that involved diploid mother and tetraploid father fewer hybrid progeny appeared than in reciprocal crosses that involved tetraploid mother plant and diploid father plant. Diploid mother plant yielded 21% of hybrid progeny (4% triploids, 17% tetraploids; the rest of progeny were autogamic diploids), whereas tetraploid mother yielded the majority of hybrid progeny (18% were triploids and 82% tetraploids, which includes both hybrids and autogamic tetraploids; cultivation of a part of the progeny has shown that autogamic individuals are maximally one quarter of the tetraploids).

Hybridisation experiment confirmed that *C. elatior* and *C. jacea* can cross and can produce tetraploid hybrid similar to those found in the population in the Krušné hory Mts. The main difference between the natural population and the experiment is absence of triploids in the former. It can be caused by lower viability of triploids compared to tetraploid hybrids (observed, though not exactly measured, during cultivation of the progeny from the experiment) or by some selection on ploidy level of pollen (pollen of the "correct" ploidy level is preferred for pollination; in the natural mixed population probably mixture of different pollen is delivered by insects, which allows to "choose" pollen of "correct" ploidy level).

Cultivation of a part of the progeny from the experiment brought one unexpected but important result. It seems that morphology of the progeny depends on a mother plant and it is shifted towards it instead of being intermediate, as expected. *Centaurea jacea* and *C. elatior* much differ in shape of appendages of involucre bracts and width of leaves. In *C. jacea* the appendages are rounded, straight, ca 4–6 mm wide and more or less entire, whereas in *C. elatior* they are narrowly lanceolate, recurved, ca 0.6–1.2 mm wide and regularly fimbriate on margin. Leaves of *C. jacea* are lanceolate to linear (ca 4–15× longer than wide) and lower leaves usually has 1–2 pair of lobes, whereas in *C. elatior* leaves are ovate to elongate (ca 2–4× longer than wide), denticulate. Their hybrids that had *C. jacea* as the mother plant had the appendages rounded ca 3–4 mm wide, and almost entire to irregularly fimbriate. Their leaves were usually wider than by *C. jacea* and shallowly lobed. The hybrids that had *C. elatior* as the mother plant had the appendages widely to narrowly triangular, often less than 2 mm wide, slightly recurved, and irregularly to almost regularly fimbriate. Their leaves were usually similar to *C. elatior*, sometimes narrower.

It is probable that the huge variation of the first filial generation discovered in *C. elatior* × *C. jacea* occur also in other hybrids with similar morphology of parental taxa (i.e. one taxon from *C. jacea* group with entire appendages, the

other some other taxon of the section with fimbriate appendages – e.g. *C. jacea* × *C. phrygia* or *C. jacea* × *C. stenolepis*). This variation should be taken into account when determining hybrids. Usually the hybrids are described in literature as (more or less) intermediate between parents and shift of variation towards one of the parents is considered as a sign of back-crossing. However, the results of experimental hybridisation of *C. elatior* × *C. jacea* show that this “shifted” morphology can develop even within first filial generation and it alone is not a reliable marker of back-crossing.

The hybrids *C. elatior* ♀ × *C. jacea* ♂ are of particular interest. They are usually tetraploid and they have triangular to narrowly triangular and recurved appendages, which can be almost regularly fimbriate. Such morphotype is very similar to other taxa of the section, namely *C. macroptilon* BORBÁS [= *C. jacea* subsp. *macroptilon* (BORBÁS) HAYEK] and *C. oxylepis* (WIMM. & GRAB.) HAYEK [= *C. jacea* subsp. *oxylepis* (WIMM. & GRAB.) HAYEK]. These two taxa are both tetraploid (DOSTÁL 1976, KOUTECKÝ 2007) as well and morphologically they are “intermediate” between *C. jacea* group and *C. phrygia* group. Their hybridogenous origin can therefore be hypothesized. The results of crossing experiment with *C. elatior* and *C. jacea* suggests that a tetraploid hybrid of very similar morphology can be formed by hybridisation of diploid (from *C. phrygia* group) and already established tetraploid (from *C. jacea* group). However, the problem requires further study and hybridogenous origin of these two taxa should be tested by a molecular study.

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