# The role of facultatively apomictic mothers in the generation of ploidy variation in two model populations of hawkweeds (*Hieracium* subgen. *Pilosella*, Asteraceae)


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## Aims and rationale of the study

**The aim of the study was to compare the capacity to generate variation in ploidy between facultatively apomictic and sexual maternal biotypes, co-occurring in two polyploid hybrid swarms.** Two investigated localities are situated in the towns of Prague (locality no. 1) and Brno (locality no. 2), Czech Republic. The sites differ in abundance of established hybrids and in the complexity of population structure, characterized by co-occurring morphotypes, cytotypes and their mode of reproduction.

**Parental species and the model system**

*Hieracium pilosella* L. (usually sexual, less commonly apomictic), *H. bauhini* Besser (facultatively apomictic) and their homoploid and heteroploid hybrids (sexual, apomictic or sterile).

The two parental taxa, distinct in morphology, are members of the polyploid agamic complex of *Hieracium* subgen. *Pilosella*. This group is characterized by diverse reproduction mode: sexual or apomictic reproduction by seed (autonomous apospory), and the vegetative spread by stolons. The facultatively apomictic and sexual biotypes often coexist and hybridize under suitable conditions (e.g., Fehrer et al. 2007). Generally, the polyploid facultative apomicts of this subgenus produced in experiments following types of progeny (e.g., Bicknell et al. 2003, Krahulcová et al. 2004, Krahulcová et al., unpubl. results): the autonomously derived 2n + 0 and n + 0 progeny, and the hybrids n + n, 2n + n, n + 2n, and rarely 2n + 2n.

**Methodical approach**

Classification of plants based on morphology.

Determination of their ploidy/chromosome numbers (chromosome counts, flow cytometry) and reproduction mode (emasculation and crossing experiments) – Krahulcová et al. 2004.

Pattern of distinct i) genotypes (isozyme analysis, nuclear DNA fingerprinting) and ii) haplotypes (cp-DNA analysis) were studied only in the more complex model population (locality no. 1).

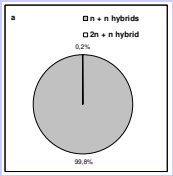
Detection of the origin of seed progeny spontaneously arisen in the field.The maternal – seed progeny relationships were concluded for sexual and apomictic mothers: either comparing the morphology, cytotype and breeding system between cultivated seedlings and their mothers or using the flow cytometric screening of seeds of the respective mothers (FCSS method – Matzk et al. 2000).

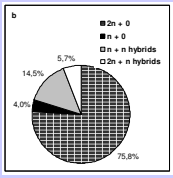
## Results

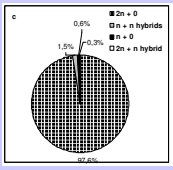
1. Population structure was intricate in the studied hybrid swarms, especially at the locality no. 1. The maternal apomictic ancestor was detected in some of the hybrids established here, both euploid and aneuploid (Table).
2. While the sexual mothers predominantly retained a rather narrow range of ploidy levels/chromosome numbers in their progeny, the facultatively apomictic mothers produced at both localities much more diverse progeny in this respect (Fig. 1, Figs. 2a, b, c).
3. The versatility in reproductive modes detected in the field was also confirmed experimentally in selected open pollinated/crossed apomictic mothers.
4. The maternal breeding system was conserved in the majority of the respective offspring plants. The fraction of sexual progeny formed by apomictic mothers yet prevailed over that of apomictic progeny formed by sexual mothers.
5. Heptaploid and octoploid hybrids originated via fertilization of unreduced egg cells of apomicts (Table). The resulting high-ploid hybrids were able to produce viable seed via parthenogenesis (2n + 0) as did true apomicts, but when emasculated, most of their progeny were polyhaploids (n + 0). The same hybrid maternal plants often hybridized (n + n progeny) after open pollination.



General view of the locality no. 1




Population structure in two model hybrid swarms

| | Locality 1: 79 accessions | | Locality 2: 57 accessions |
|---|---|---|---|
| Plants assigned to | Ploidy/RS | No. of genotypes (no. of analysed plants) | Ploidy/RS (no. of analysed plants) |
| H. pilosella | 4x/sexual | 14 (17) | |
| | 5x/sexual | 2 (3) | |
| | | | 6x/sexual (15) |
| | | | 6x/apomictic (7) |
| | | | 6x/sterile (5) |
| H. bauhini | 4x/apomictic | 2 (3) | |
| | 5x/apomictic | 4 (7) | 5x/apomictic (15) |
| | 6x/? | 3 plants perished | 6x/apomictic (4) |
| | 7x/apomictic* | 1 (1) | |
| Hybrids | Ploidy | No. of genotypes with RS (no. of analysed plants) | |
| | 4x | 3 sexual (4) + 2 apomictic (2) | 4x/sexual (1) |
| | 5x | 1 sexual (1) + 2 apomictic (5) | 5x/sterile (5) |
| | 6x | 1 sexual (1) | 6x/apomictic (1) |
| | | | 6x/sterile (1) |
| | 7x | 9 apomictic* (13) | |
| | 8x | 1 apomictic* (3) | 8x/apomictic* (3) |
| | aneuploids | 9 sexual (9) + 1 apomictic | |
| | | Total no. of genotypes: 52 | |

Explanatory notes:
RS = reproduction system;
* = prominent residual sexuality, i.e., the plants producing plenty of the polyhaploid progeny after emasculation and/or of the polyhaploid and n + n hybrid progeny after open pollination. Some of the genotypes have originated from apomictic maternal ancestor (detected by means of cp-DNA haplotypes).

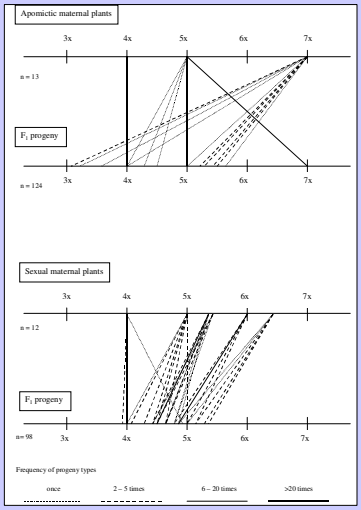



Fig. 1. Chromosome number/ploidy variation in selected maternal plants and their $F_1$ seed progeny, arisen at locality 1. The mother-progeny relationship was independently evaluated for 13 apomictic and 12 sexual maternal plants to demonstrate the range of variation of the progeny of a particular plant.

Fig. 2. Frequencies of reproductive pathways operating in sexual (a) and apomictic (b, c) maternal plants in the field. The source data are combined irrespective of maternal ploidy level/chromosome number. a: progeny origin from sexual maternal plants evaluated for both localities together (12 maternal accessions, 99 progeny individuals/locality 1; 9 maternal accessions, 317 progeny individuals/locality 2); b: 13 maternal apomictic accessions, 124 progeny individuals/locality 1; c: 12 maternal accessions, 336 progeny individuals/locality 2.

## Conclusion

This population study demonstrates **the versatility of reproductive pathways operating in polyploid facultative apomicts in the field**, namely the importance of their residual sexuality. With respect to ploidy, the apomictic mothers in the both model populations contribute more to population variation, than do the sexual mothers. The high-polyploid hybrids generated by apomictic mothers seem to have an unstable genome, decreasing the ploidy in the next generation. Despite this unstability, such genotypes can push forward new hybridizations. Thus, the apomictic biotypes can increase population diversity much more than has been supposed.

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