

Comparison of breeding behaviour of *Taraxacum* sect. *Ruderalia* and *Taraxacum* sect. *Erythrosperma* (*Asteraceae*)

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Abstract: All three basic breeding systems – allogamy, autogamy and apomixis are found in the genus *Taraxacum*. Most *Taraxacum* sections combine both sexual and asexual way of reproduction. Two of these sections have wide distribution across Europe – the sections *Ruderalia* and *Erythrosperma*. Different life strategies in these sections lead to differences in their breeding systems: In the section *Erythrosperma*, when compared with *Ruderalia*, stronger tendency to autogamy in diploids, lower pollen production by triploids and their lower crossability with diploid sexuals is found. This reflects lower population density and the existence of dandelions from the sect. *Erythrosperma* in stable communities. In the section *Ruderalia* wide range of habitats with frequently changing conditions implies permanent necessity to generate new variability and to spread it through new triploid genotypes. It is assured by high crossability and possible gene flow to higher ploidy levels.

In the paper, diploid individuals of *Taraxacum* sect. *Erythrosperma* with pollen grains with different sizes in diameter are reported, too. This phenomenon is rather unusual in diploid sexuals.

Keywords: apomixis, autogamy, pollen, B_{III} hybrids, life strategy

Distribution and taxonomy

Taraxacum WIGG. is a very large genus. It is widespread in temperate regions of both northern and southern hemispheres (VAŠUT & TRÁVNÍČEK 2004). Members of the genus grow in wide range of habitats and display a considerable

diversification in morphological features (RICHARDS 1970). Basic chromosome number in the genus is $x = 8$. Species in the genus *Taraxacum* represent a polyploid series of diploid sexual species and polyploids. The most common polyploid is triploid (DE KOVEL & DE JONG 2000).

The taxonomy of this genus is a very complicated one. The genus comprises some 2000 species grouped into over 40 sections (KIRSCHNER & ŠTĚPÁNEK 1996) and new ones are still being described (KIRSCHNER & ŠTĚPÁNEK 2004, UHLEMANN et al. 2004).

The sections in the genus *Taraxacum* can be classified as primitive, precursor and advanced ones. The primitive sections are bound to evolutionary centre of the genus in west and central Asia and Mediterranean region (RICHARDS 1973). In some primitive sections – *Dioszegia* and *Piesis*, only sexual (diploid and tetraploid taxa) are known (KIRSCHNER & ŠTĚPÁNEK 1996). However, in most of the sections, diploid sexuals coexist with polyploid apomicts, in some sections only polyploid apomicts are known (KIRSCHNER & ŠTĚPÁNEK 1996, 1997). Sexuals and apomicts have usually different geographical distributions. Apomicts have usually larger areas and tend to range to higher latitudes and altitudes (BIERZYCHUDEK 1985). Sexuals often have distributions centred within much larger ranges of apomictic complexes. This phenomenon is called geographical parthenogenesis and is caused by complex of factors (HÖRANDL 2006). The genus *Taraxacum* provides clear examples of differing distribution areas of sexuals and apomicts in many sections (VERDUJN et al. 2004). Although a total of approximately 29 sections occur in Europe, only two of them comprise both sexuals and apomicts with wide distributions across Europe - section *Ruderalia* and section *Erythrosperma* (VAŠUT et al. 2004).

Taraxacum* sect. *Ruderalia

Taraxacum sect. *Ruderalia* Kirschner, H. Øllg. et Štěpánek is one of the largest and phylogenetically youngest ones (DOLL 1982). Species in *Taraxacum* sect. *Ruderalia* occur in a greater diversity of habitats than most other *Taraxacum* sections do (ØLGAARD 2003). They prefer ruderal and further anthropogenous habitats, meadows, gardens, always the places with soils rich in nutrients and restrained competition (KIRSCHNER et al. 2002). Like other *Taraxacum* sections, the section *Ruderalia* represents a polyploid series with the basic chromosome number $x = 8$. Diploids in the section *Ruderalia* are classified as *Taraxacum linearisquameum* in Pannonian region (MIKOLÁŠ et MIHOKOVÁ 1995). In this region, diploids and polyploids grow usually together in mixed populations. Wide distribution range, ability to grow in different habitats, abundance, synanthropic occurrence and availability of mixed populations, together with possibility of easy growing in culture make this section for a long time a model group for biosystematic research of dandelions.

Taraxacum* sect. *Erythrosperma

Taraxacum sect. *Erythrosperma* is a derived one. It is far less common than *Taraxacum* sect. *Ruderalia* – it is restricted to calcareous xerothermophilous

grasslands, open sand grasslands or thermophilous open forests, less common in mesophilous grazed meadows and pastures, sometimes it occurs also in disturbed dry ruderal places or near abandoned stone pits. The populations are far less abundant than in *Taraxacum* sect. *Ruderalia*, often limited to several plants. The present concept of the section is based on the existence of one sexual diploid (very variable taxon *Taraxacum erythrospermum* Andr.) and about 150 apomictic polyploid microspecies (VAŠUT 2003).

Breeding systems in *Taraxacum*

All three basic breeding systems – allogamy, autogamy and apomixis are known in the genus *Taraxacum*.

Allogamy occurs in diploids, which are obligate sexuals. It is ensured by sporophytic self-incompatibility (OKABE 1956) there.

Autogamy is known in primitive sections *Taraxacum* sect. *Dioszegia* (Heuffel) Heuffel and *Taraxacum* sect. *Piesis* (DC.) A. J. Rich. In these sections, self-compatible species are reported, which are predominantly autogamous (KIRSCHNER et al. 1994).

Apomixis is bound to polyploids. The apomixis in *Taraxacum* consists of three elements – diplospory, parthenogenetic embryo development and autonomous endosperm formation (VAN DIJK et al. 2003).

Despite the fact that diplosporous plants are usually obligatory apomicts (RICHARDS 1997), in apomictic polyploids in *Taraxacum* some elements of sexuality are reported in both female and male functions.

In the female function (i. e. the formation of egg cells), facultative apomixis and B_{III} hybrid formation are reported as elements of sexuality.

Facultative apomixis in the sense of formation of both unreduced and reduced egg cells and following production of mixed progeny of maternal and reduced ploidy by one capitulum was reported several times. RICHARDS (1970) found a triploid plant from the section *Erythrosperma* that produced mixed diploid and triploid progeny. MAŁECKA (1973) reported both reduced and unreduced ovules in one capitulum in *Taraxacum* sect. *Palustria*. Similar finding was presented by van BAARLEN et al. (2002) – tetrades of (probably reduced) megaspores were found besides dyads, which arose as a result of restitution. However, fertility of reduced egg cells is supposed to be very low. This is supported by the fact that after cross-pollination no diploid progenies in these triploid apomictic maternal plants were formed. At the same time, large number of analyses of both cross-pollinated and open pollinated capitula, reported in our previous studies (MÁRTONFIOVÁ 2006, MÁRTONFIOVÁ et al. 2007, 2010) revealed no facultative apomicts in the progeny. This makes the facultative apomixis in *Taraxacum* rather questionable.

On the other hand, B_{III} hybrid formation (i.e. fertilization of some unreduced ovules of apomicts) was reported by MAŁECKA (1973), VAN BAARLEN et al. (2002) and our previous studies (MÁRTONFIOVÁ 2006, MÁRTONFIOVÁ et al. 2007, 2010) reported B_{III} hybrids both in the progeny of experimental crosses and insect-pollinated samples collected in natural localities.

The male function (i.e. production of pollen by apomicts) is often reduced in apomicts. However, in *Taraxacum* it is preserved and can play an important role in fertilization of diploid sexual plants. Pollen of diploids in *Taraxacum* is regular, the pollen grains are well developed and of approximately the same size, while in apomictic triploids the pollen is irregular – it is composed of pollen grains of different sizes and some of them are aborted. However, some of these pollen grains are fertile, especially the pollen grains with diploid chromosome number can produce viable progeny with diploid sexual maternal plants (MÁRTONFIOVÁ, 2006).

The three basic breeding systems – alogamy, autogamy and apomixis can be present in different proportion in different sections. The aim of this work is to compare two of them – sections *Ruderalia* and *Erythrosperma* and to find relation of these differences with their populational characteristics and environment.

Methods of determination of breeding behaviour

Breeding behaviour of particular plants was determined on the basis of data from karyological analyses, experimental isolations and hybridizations with selected plants and flow cytometric analyses of seed samples of different provenience. A method of flow-cytometric seed screening (FCSS, MATZK et al. 2000) allows to determine the ratio of ploidies of embryo and endosperm in a sample of seed progeny of the studied plant and detect (provided the cytoembryology of the genus studied is known) breeding behaviour. Examples of determination of breeding behaviour are given in Fig. 1a-c.

Comparison of breeding behaviour of *Taraxacum* sect. *Ruderalia* and *Taraxacum* sect. *Erythrosperma*

Alogamy: Diploids in both sections are alogamous with the possibility of experimental breakdown of autoincompatibility, the selfing can be induced by mentor effect of incompatible pollen of triploids (MORITA et al 1990).

Autogamy: Without the presence of incompatible pollen, diploids in the section *Ruderalia* produce progeny by autogamy very rarely – only one such plant was recorded. Diploids in *Taraxacum* sect. *Erythrosperma* are sporadically autogamous in the absence of pollen - autogamy was recorded in 28% of capitula.

Apomixis – female function: Facultative apomixis was detected neither in the section *Ruderalia*, nor in the section *Erythrosperma*. B_{III} hybrid formation was, however, recorded in both sections, approximately in the same amount, in about 12% of analysed capitula. B_{III} hybrids were found both in the progeny of crosses of triploid maternal plants with diploid pollen donors and in the samples collected in natural localities which were the result of insect pollination.

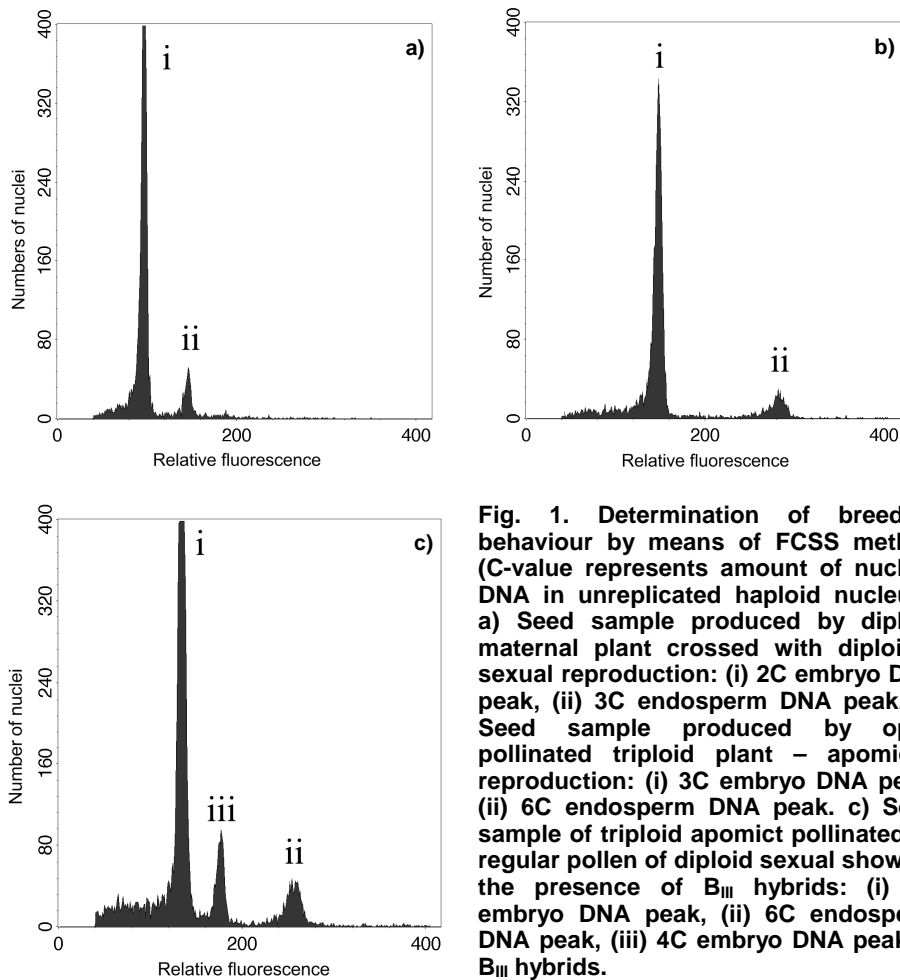


Fig. 1. Determination of breeding behaviour by means of FCSS method (C-value represents amount of nuclear DNA in unreplicated haploid nucleus). a) Seed sample produced by diploid maternal plant crossed with diploid - sexual reproduction: (i) 2C embryo DNA peak, (ii) 3C endosperm DNA peak. b) Seed sample produced by open pollinated triploid plant – apomictic reproduction: (i) 3C embryo DNA peak, (ii) 6C endosperm DNA peak. c) Seed sample of triploid apomict pollinated by regular pollen of diploid sexual showing the presence of B_{III} hybrids: (i) 3C embryo DNA peak, (ii) 6C endosperm DNA peak, (iii) 4C embryo DNA peak of B_{III} hybrids.

Apomixis – male function: Male sterility (lack of pollen) is quite rare in the section *Ruderalia*. Triploids in this section usually produce plenty of pollen, while in the section *Erythrosperma*, 62% of studied plants produced no pollen (In the localities of sect. *Erythrosperma*, this percentage can, however, vary. It is dependent on the presence of the microspecies *T. parnassicum* and *T. proximum* which produce no pollen, SUVADA et al., 2011). Participation of apomicts as pollen donors in the production of progeny with diploid sexual maternal plants was 79% in experimental conditions in the section *Ruderalia*, while in the section *Erythrosperma* only 17%. However, in natural localities with both diploid and triploid plants, or in experiments when diploid maternal plant received mixture of pollen of diploid sexuals and triploid apomicts, no progeny of this type was found.

Pollen in the sections *Ruderalia* and *Erythrosperma*

Diploids in *Taraxacum* are known for regular pollen, the pollen of triploids is irregular (Fig.2a,b) . This is valid also for the section *Ruderalia*. However, in *Taraxacum* sect. *Erythrosperma*, about 25% of diploids studied produced pollen grains not uniform in size. These diploids with irregular pollen exhibited also reduced fertility. The method of assessment of ploidy level on the basis of regularity of pollen (Tschermak-Woess, 1949) thus fails in *Taraxacum* sect. *Erythrosperma*.

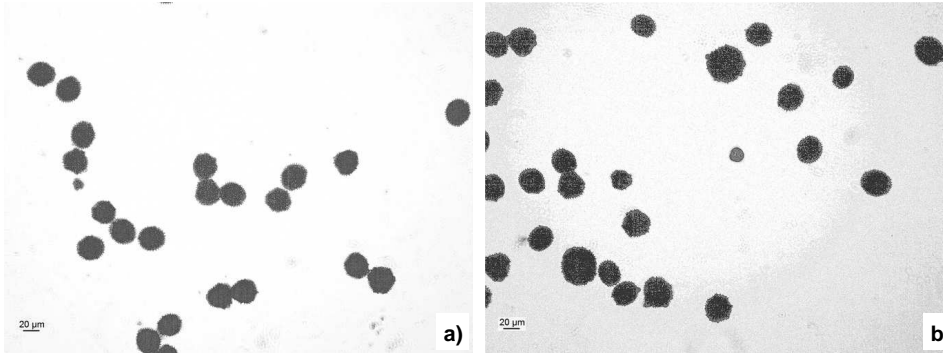


Fig.2: Pollen in *Taraxacum*: a) pollen of diploid *Taraxacum* sect. *Ruderalia*, b) pollen of triploid *Taraxacum* sect. *Ruderalia*.

Conclusions

Breeding behaviour in different sections reflects life strategies in particular sections. Lower assertion of male function - pollen production and its participation in fertilization of diploids, as well as much stronger tendency to autogamy in the section *Erythrosperma* reflects lower populational density and existence in stable communities without permanent necessity to generate new variability. On the other hand, extensive gene flow would suite life strategy of *Taraxacum* sect. *Ruderalia*. Mixed populations of this section are very dense, inhabiting wide range of different communities, they adapt to different changing conditions of disturbed ruderal habitats and other places influenced by human activities. Therefore the possibility of generating of new variability in sexual way, its flow to gene pool of asexuals and quick spread of a part of new genotypes that suit well to new conditions is inevitable.

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