SELF-COMPATIBILITY IN DIPLOID PLANTS OF TARAXACUM SECTION TARAXACUM

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SUMMARY

Self-compatibility has been found to occur in a diploid, sexual plant of *Taraxacum* section *Taraxacum* after natural and artifical self-pollination of caged-in capitula. Only one out of 72 plants investigated proved to be self-compatible. This is the first record within the section *Taraxacum* of potential autogamy in a plant collected from the field. It was shown that self-compatibility is heriditary. No relation could be found between the point of time within the flowering season and the self-compatibility of the plants tested.

1. INTRODUCTION

Taraxacum forms a polyploid complex with the basic chromosome number 8. According to DOLL's estimation in 1982, about 10 per cent. of the species is diploid (2n = 16), 78 per cent. polyploid (range: 3x–10x, but mostly triploid) and a rather large number, *viz.*, about 11 per cent., aneuploid.

So far all diploid plants have been found to be sexual and the polyploids nominally agamospermous (RICHARDS 1970, 1973), the latter reproducing by diplosporic parthenogenesis. This obligatory form of agamospermy was first described by OSTENFELD (1899), RAUNKIAER (1903), and MURBECK (1904).

Apart from the long-established obligatory form of agamospermy, however, a facultative type was later recorded by several authors, who showed that in some of the agamospermous, triploid populations occasionally sexual reproduction, *i.e.*, exchange of genetical material, takes place (RICHARDS 1970; MÜLLER 1972; JENNISKENS et al. 1983).

All the primitive, diploid and sexual taxa and the advanced, polyploid and agamospermous ones are known to form an agamic complex in the sense of GRANT (1971). It was demonstrated in the American representatives of the genus *Crepis* that hybridization, introgression and polyploidization have taken place, so that from an original seven, diploid and sexual, taxa an agamic complex and a polyploid superstructure has developed (BABCOCK & STEBBINS 1938; STEBBINS & BABCOCK 1939). This mode of origin may also be present in the agamic complex of the genus *Taraxacum*.

In sexual dandelions protandry (KNUTH 1898; FAEGRI & VAN DER PIJL 1979)

and self-incompatibility (OKABE 1956; DOLL 1982) prohibit self-fertilization. Despite habitual selfing, very few florets produce fruits in absence of cross-pollination (RICHARDS 1973). Investigations among representatives of *Taraxacum* section *Mongolica* have shown that four multiple S-alleles control the self-incompatibility system (OKABE 1956).

However, as reported by RICHARDS (1968, 1973) and DOLL (1982), self-compatibility seems of general occurrence in the sexual taxa of the *Taraxacum* sections *Leptocephala: T. bessarabicum* (Hornem.) Hand.-Mazz. and *Serotina: T. serotinum* Poiret and *T. hausknechtii* Hand.-Mazz.. These three self-fertile taxa, belonging to the rather primitive diploids, contain but a few species and form, within the genus *Taraxacum*, separate, not very successful evolutionary lines in which agamospermy did not originate (DOLL 1982). In subsection *Macrocornuta*, which is according to DOLL (1982) normally agamospermous, sexual plants of *T. kok-saghyz* Rodin seem to have a so-called "end-of-season fertility" (WARMKE 1944). This latter form of self-fertility, *i.e.*, the production after artificial self-pollination of an increasingly higher number of viable achenes as the flowering season has progressed, is of common incidence in *Nicotiana* and in other self-sterile species (EAST & PARK 1917).

SØRENSEN (1958) found self-compatibility in a diploid offspring plant resulting from hybridization between *T. cordatum* aberrant *tenuis* and *T. polyodon* aberrant *tenuis*. RICHARDS (1968) has doubts about the phylogenetic importance of this return to sexuality.

2. MATERIAL AND METHODS

The 72 plants of *Taraxacum*, mainly section *Taraxacum* included in the investigations originated from 15 locations in the two principal areas of distribution of diploids in Europe, as reported by JENNISKENS et al. (1983). A detailed description will be given elsewhere. All plants tested were given a code number, because most of them were unidentified taxa.

Although no self-compatibility had ever been recorded in specimens outside the sections *Serotina* and *Leptocephala,* self-fertility was tested as a routine procedure in hybridization experiments. Of the plants investigated, in total 224 flower heads were caged-in, just before male anthesis of the first florets had commenced, to permit natural self-pollinations (JENNISKENS *et al.* 1983) and in some of these plants, after artificial self-pollination (34 capitula in all tested). These artificial self-pollinations were either carried out by carefully rubbing two capitula of the same plant, in the same phase of anthesis, against one another, or by touching the pistils with the cotton-wool covered tip of "ear cleaners". During the flowering of the capitula, the artificial self-pollinations were repeated about three times. Artificial cross-pollinations were made by removing pollen from the pollen donor with an "ear cleaner" and applying it to the stigmatic branches of the mother plant. This was also repeated three times during the flowering period of both capitula of both plants. "Ear cleaners" were used, so that, after artificial cross-pollination, both capitula remained on the plants and

Table 1. Percentage viable achenes of caged-in capitula of two representative diploid plants after natural and artificial self-pollination.

Plant	n	Percentage viable achenes per capitulum											
		after natural self-polination								after artificial self-pollination			
THM 110-3	71	0	0	0	0	0	0	0	0	0	0	0	0
THM 110-2	1	0	0	5	5	7	9	26		25	41	45	50

also reciprocal crossings could be made on the spot with the same heads.

In order to prevent natural selfings, the stigmas were removed from the florets of di- and triploid plants by snipping off the stigmatic branches with scissors (RAUNKIAER 1903). This treatment had to be repeated several times a day because stigmas keep emerging from the connate anthers throughout the day.

Achenes were sown on 03/07/1981 in sterilized, sieved humic soil and kept in a greenhouse at a temperature ranging from 15°C to 25°C and with a natural light regime. After germination the plants were transferred to earthenware pots (diameter 10 cm), filled with humic soil and dug in in the experimental garden.

The offspring of hybridization experiments was tested for self-incompatibility by caging in capitula under natural, self-pollination permitting conditions and in some plants also after artificial self-pollination. The vitality of the offspring was scored by counting the number of leaves and by measuring the length of the five longest on 12/10/1982. Their fertility was tested by counting the number of capitula per plant during one flowering period and the number of fruits produced per flower head (as the average of five capitula per plant). The significance of the values found was tested using the U-test, in which H_o: $\mu_A = \mu_B$ if $U < 1.96$ ($\alpha = 0.05$). Hybrid indices were made according to ANDERSON (1936).

During the winter of 1982–1983, experiments were carried out in a greenhouse (temperature about 15°C, 12 h light) to test the "end-of-season fertility" as described by WARMKE (1944). In 12 self-compatible plants of the offspring of the self-fertilizing plant, all capitula were artificially self-pollinated. The occurrence of viable achenes was scored in the first, the middle and the last capitulum to flower in one flowering season. As a control, 12 self-incompatible plants out of the same offspring were treated in the same way.

3. RESULTS

3.1. The parent plants
As part of a hybridization scheme between diploid plants, capitula were caged-in after natural and artificial self-pollination. In *table 1* the percentages of viable achenes are presented:
a. THM 110-3 is a representative of normal self-incompatible, sexual plants. No viable achenes were formed under the two experimental conditions. Of all

72 sexual plants examined, 71 (with 217 capitula) reacted in the same way as did THM 110-3. There are some exceptions: in four of these flower heads, of different plants, some ripe achenes were present after natural self-pollination, in number up to five per cent.. Of these plants artificially self-pollinated capitula, permitting autogamy, had not formed any fruits, however.

In one capitulum of the 30 artificially self-pollinated ones of the 71 self-incompatible diploids tested, 10 per cent. of viable achenes had set. Another capitulum of the same plant was artificially self-pollinated, which did not yield viable achenes. The ripe fruits formed in the one flower head after artificial self-pollination may be due to cross-pollination by small insects, such as *Thysanoptera* or aphids, which are difficult to exclude when capitula are caged-in. The viable achenes developing after artificial self-pollinations may also result from pollinations with pollen present as a contamination on the cotton-wool tip used for artificial pollinations, although for every crossing made, a "clean" tip was used. b. In THM 110-2 (*table 1*) five out of seven flower heads, after natural self-pollination, yielded some ripe fruits in percentages ranging from 5 up to 26 per cent. After artificial self-pollination the percentages of viable achenes increased up to 50 per cent.. Especially the high percentages of fruit-set after artificial self-pollination clearly indicate that THM 110-2 is a self-compatible plant. Although agamospermy has not been recorded in sexual dandelions, and THM 110-2 is a diploid (*fig. 2*), the results of my experiments theoretically do not preclude the incidence of agamospermy in this case.

Stigmas were removed from seven capitula of two self-incompatible diploids and from six capitula of two agamospermous triploids, as a control, and from four capitula of THM 110-2. As a result of this treatment no viable achenes developed in the seven capitula of the diploid plants, nor did the four flower heads of THM 110-2 produce any ripe achenes. In the six capitula of the triploids, viable achenes were produced in the same amounts as if the heads had not been tampered with. Agamospermous plants are clearly capable of producing ripe fruits after removal of the stigmas. Diploids, on the contrary, can not produce any viable achenes after such treatment. The results show that agamospermy of THM 110-2 is most unlikely.

3.2. The self-compatible plant THM 110-2

THM 110-2, belonging to population THM 110, was collected in a meadow, alongside the national road (D306) between Laval and la-Flèche, in north-western France in the spring of 1980. According to the opinion of the Dutch taraxacologists HAGENDIJK and ZEVENBERGEN (pers. comm.) the herbarium material of THM 110-2 (AMD no: M 000067, see *fig. 1*) does not exhibit any distinct characteristics of the microspecies *T. cordatum* or *T. polyodon* and is, therefore, certainly not referable to either of these two taxa as was the self-compatible individual produced experimentally by SØRENSEN (1958). It does however belong to the section *Taraxacum* (SAHLIN, pers. comm.). The pollen frequency distribution of THM 110-2 (*fig. 2*) indicates that the plant is a diploid. This was confirmed by chromosome counts (*fig. 3*) of metaphase plates in root tips.
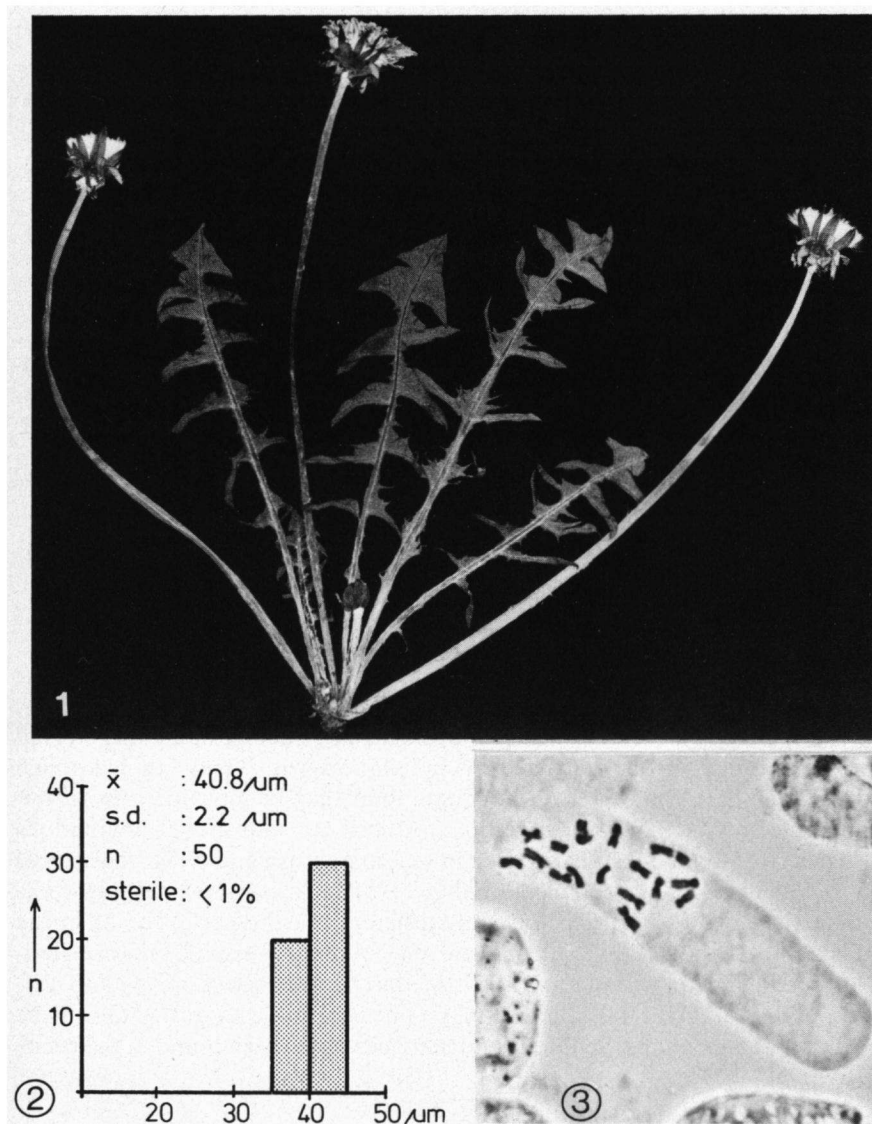
Figs. 1–3. Herbarium specimen of THM 110-2 (ADM no: M 000067), the frequency distribution of its pollen grains and a root tip metaphase plate with $2n = 2x = 16$ chromosomes of THM 110-2.

3.3. Some notes on the genetics of self-compatibility

Since no data are available in literature concerning the genetics of self-compatibility in the genus *Taraxacum*, some artificial cross-pollinations were made between self-compatible and self-incompatible biotypes (*table 2*). It is to be expected that some of these cross-pollinations with THM110-2 as pollen receptor

Table 2. The occurrence of viable achenes in caged-in capitula in the F_1-progenies of
- artificial cross-pollinations between the self-compatible (sc) THM 110-2 and the self-incompatible (si) THM 110-3.
- artificial and natural self-pollinations in THM 110-2.

Parents	Compatibility	Number of F_1-plants after artificial self-pollination	
		without viable achenes produced	with viable achenes produced
THM 110-2 (♀) * THM 110-3 (♂)	sc (♀) * si (♂)	3	6
THM 110-3 (♀) * THM 110-2 (♂)	si (♀) * sc (♂)	5	3
THM 110-2 artificially self-pollinated	sc (♀) * sc (♂)	35	10
THM 110-2 after natural self-pollination	sc (♀) * sc (♂)	19	10

may be successful, because natural self-pollination can only come about during the last phase of flowering. From the results in *table 2* it appears that self-compatibility, as expected, is genetically controlled. The number of alleles involved remains unknown. From artificial cross-pollinations with THM 110-2 as pollen donor, it can be concluded that self-compatibility can be introduced in self-incompatible biotypes. In the progenies of artificial and natural self-pollinations of THM 110-2, a manifest segregation in self-compatible and self-incompatible genotypes has taken place, indicating that THM 110-2 is heterozygous for this characteristic. The appearance of many different phenotypes in the offspring of THM 110-2, after artificial and natural self-pollination, excludes the possibility of pseudogamy in this plant. The distinction between pseudogamy and self-compatibility in THM 110-2 is virtually impossible, due to difficulties in the castration of dandelions. So far pseudogamy has never been found in the genus *Taraxacum*.

3.4. Vitality and fertility of the offspring of the self-compatible plant THM 110-2

Vitality and fertility of the offspring of THM 110-2, after natural and artificial self-pollination, was scored and compared with the same characteristics of a control series of F_1-plants, originating from diploid hybridization experiments and all of the same age (*table 3*). These F_1-plants belonged to 16 groups resulting from different hybridization combinations between seven parent plants, originating from four different locations in France, Switzerland and the German Federal Republic. Of each group four aselectively chosen plants were tested. No

Table 3. Vitality and fertility of the F_1-offspring of the self-pollinated, self-compatible plant THM 110-2, compared with the offspring of crossings between self-incompatible plants. All plants were of the same age.

		F_1 of THM 110-2	F_1 of self-incompatible plants	U-value
Vitality	average total number of leaves per plant	28.54	49.03	
	n	69	64	4.99
	standard deviation	14.28	29.82	
	average length of five longest leaves (cm)	16.13	21.81	
	n	69	64	7.54
	standard deviation	4.25	4.42	
Fertility	average number of capitula per plant	5.40	6.70	
	n	72	64	2.52
	standard deviation	2.67	3.27	
	average number of fruits per capitulum	189.83	216.34	
	n	69	64	5.12
	standard deviation	27.58	31.78	

comparison could be made between THM 110-2 and its offspring, because THM 110-2 was collected in the field at an unknown age. In order to examine the significance of the differences between the two groups, the U-test was applied, although the groups were not completely homogeneous. *Table 3* shows that the four characteristics, *viz.,* the total number of leaves per plant, the length of the longest leaves (together forming a measure for vitality), and the number of capitula per plant in one flowering season and the average number of fruits per capitulum (a norm for fertility) of the two groups tested, proved to be significantly different from one another in all four cases, because all U-values exceed 1.96 ($\alpha = 0.05$). This means that the offspring of THM 110-2 originating from inbreeding is significantly less vital and less fertile than the one resulted from outbreeding between diploid plants. An average of 5.40 flower heads per plant in the F_1 of THM 110-2, with 189.83 fruits per capitulum, yielded a maximum production of 1025 viable achenes in one flowering season, as compared with the control of 6.70 flower heads with an average of 216.34 fruits per capitulum resulting in 1450 viable achenes per flowering season. This is a difference of about 425 fruits (30–40 per cent.) per plant per flowering season between the

Table 4. Production of viable achenes in artificially self-pollinated capitula of 12 self-compatible descendants of THM 110-2, in the first, the middle and the last capitulum coming into flower.

Capitulum	Number of capitula	
	without viable achenes	with viable achenes
First	1	11
Middle	0	12
Last	0	12

progenies of the two groups.

Three F₂-progenies of THM 110-2 were reared from fruits obtained from artificial self-pollinations of three F₁-plants. In these families again, in 18 of the 32 plants examined, self-compatibility occurs. The average number of capitula per plant did not exceed three in one flowering season. No detailed study has been undertaken to test the vitality, but the F₂-plants seemed to be weak, because they had but a few, small leaves, ranging from two to seven in number.

The final conclusion is that the tested self-compatible plants are less vital and fertile than the self-incompatible ones investigated. This can have very important consequences for the population dynamics as will be discussed later on.

3.5. The relation between self-compatibility and the flowering season

WARMKE (1944) described "end-of-season fertility". In order to test this phenomenon in the offspring of THM 110-2, capitula of 12 self-compatible plants were artificially self-pollinated. Of the first, the middle and the last capitulum to come into flower in one flowering period, the fruit-set was recorded (*table 4*). As a control 12 self-incompatible plants of THM 110-2 were treated in the same way. The results (*table 4*) show that in 11 out of these 12 heads tested some viable achenes had formed in the first capitula. In the middle- and last-flowering heads all capitula produced fruits. These results do not suggest a strong relation between the occurrence of viable achenes and the progression of the flowering season. The absence of mature achenes in one capitulum is probably attributable to an inadequacy of the artificial self-pollination. The efficiency of the mode of artificial pollination will be discussed elsewhere. In the self-incompatible control plants none of the capitula produced viable achenes after artificial self-pollination.

4. CONCLUSIONS

The experiments clearly show that self-compatibility occurs in a representative of the section *Taraxacum* in France, but upon the whole self-compatibility proves to be a very rare phenomenon in the plants examined: only one out of 72 plants tested was self-compatible (see *table 1*). The allele combination which

controls self-compatibility is apparently very rare in the gene-pools of sexual populations of this section in Europe. As regards the genetics of the phenomenon studied, but little could be deduced. By artificial cross-pollinations with a self-compatible pollen donor, an offspring was reared which is partially self-compatible (*table 2*). Accordingly, self-compatibility can be crossed in.

A comparison of the vitality and fertility in the experimental garden provides arguments to suppose that the self-compatible strain has a lower fitness than the self-incompatible ones (*table 3*). Differences in leaf-production and leaf-size are indicative of a lower competitive power of self-compatible plants than self-incompatible ones, which means that the survival value of self-compatible plants in natural populations is lower than that of self-incompatible ones. These findings contribute to the explanation of the rarity of self-compatibility in sexual populations.

The origin of the self-compatibility is unknown. The genes which control this phenomenon are apparently present in very low frequencies in natural populations of the section *Taraxacum*. Self-compatibility can arise in plants descended from triploids, as was shown by SØRENSEN (1958). Since THM 110-2 shows no distinct characteristics of *T. cordatum* or *T. polyodon* (*fig. 1*), the self-compatibility in THM 110-2 may well have arisen from hypotriploids of the *tenuis*-type of other microspecies. HAGENDIJK et al. (1982) have recorded that aberrants of the triploid microspecies *T. dahlstedtii* and *T. polyodon* may occur in the field in The Netherlands.

Self-compatibility in THM 110-2 is distinguishable from agamospermy by means of the following criteria:
a) after removal of the stigmas no viable achenes are formed in THM 110-2, in contrast to agamospermous representatives of the section *Taraxacum*, which produce fruits after this treatment
b) chromosome counts have proved (*fig. 3*) that THM 110-2 has $2n = 2x = 16$ and therefore is diploid. In the pertaining literature agamospermy has only been recorded in polyploids (RICHARDS 1970, 1973) and never in diploids.
c) the phenotypical variation in the offspring of THM 110-2 indicates that segregation has taken place in heterozygous gene material. In case of agamospermy all F_1-plants would have shown maternal inheritance.

The "end-of-season fertility" which WARMKE (1944) described in *T. kok-saghyz*, could not be found in the self-compatible F_1-plants of THM 110-2 (*table 4*).

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