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Karyogeography of *Taraxacum* sect. *Taraxacum* and the possible occurrence of facultative agamospermy in Bavaria and north-western Austria

By

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Summary

Jenniskens M.-J. P. J., Nijs H. C. M. den & Huizing B. A. 1984. Karyogeography of *Taraxacum* sect. *Taraxacum* and the possible occurrence of facultative agamospermy in Bavaria and north-western Austria. — Phyton (Austria) 24 (1): 11—34. — English with German summary.

Diploid and sexual individuals of *Taraxacum* sect. *Taraxacum* (= sect. *Vulgaria*) appear to occur farther to the north than was hitherto assumed (viz., in the Odenwald), but through a sharp decline they peter out along a zone ranging from the line Frankfurt—Augsburg—Innsbruck, they reappear behind the line Salzburg—Passau—Bavarian Forest, so that in the greater part of Bavaria they are almost entirely lacking. Most probably there are two areas with an abundance of diploids in Europe, viz., a western-south-western and an eastern (to south-eastern?) one. This distributional pattern is discussed in relation to the major phytogeographical trends in that area centred around the role of former glacial refugia.

In the intervening „triploid" region between the two „diploid" ones relatively high percentages (up to 35%) of (triploid) individuals producing pollen grains of subuniform size may occur, especially in the overlapping ranges between the two ploidy levels. The possible correlation between this phenomenon and the incidence of facultative agamospermy is discussed.

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A comparative study of the rate of seed set in two central Bavarian populations showed that such triploids with a uniform pollen size tend to have lower rates of seed set (the decrease may be as high as 15%) as compared to that in obligatorily agamospermous triploids with a clearly inconstant pollen grain size. Lower seed set percentages were also recorded in a number of plants of a series of samples collected throughout the area studied. This sometimes rather marked decrease in the rates of seed set is ascribed to the incidence of facultative agamospermy.

Zusammenfassung

Jenniskens M.-J. P. J., Nijs H. C. M. den & Huizing B. A. 1984. Karyogeographie von *Taraxacum* sect. *Taraxacum* und das mögliche Vorkommen von fakultativer Agamospermie in Bayern und im nordwestlichen Österreich. — Phyton (Austria) 24 (1): 11—34. — Englisch mit deutscher Zusammenfassung.

Diploide, sexuelle Individuen aus der Sektion *Taraxacum* sect. *Taraxacum* (= sect. *Vulgaria*) kommen offensichtlich weiter nach Norden vor (z. B. Odenwald), als bisher angenommen. Entlang einer ziemlich scharfen Zone, die ungefähr der Linie Frankfurt—Augsburg—Innsbruck folgt, lassen die Diploiden aus um dann nach der Linie Salzburg—Passau—Bayerischer Wald wieder aufzutreten; sie fehlen daher im größten Teil Bayerns. Höchstwahrscheinlich gibt es in Europa zwei Gebiete mit gehäuftem Vorkommen Diploider, nämlich ein westlich-südwestliches und ein östliches (bis südöstliches?). Das Verbreitungsbild dieser Diploiden, die wohl nicht alle als „Relikte“ anzusehen sind, wird im Zusammenhang mit sonstigen phytogeographischen Gegebenheiten, wie der Rolle von Glazialrefugien, diskutiert.

Im Gebiet der Triploiden, das zwischen den beiden Teilarealen der Diploiden liegt, kann unter den Triploiden ein hoher Anteil (bis 35%) von Individuen mit nahezu einheitlicher Pollengröße auftreten; insbesondere in den Übergangsbereichen zwischen den Vorkommen der beiden Ploidiestufen ist dies der Fall. Mögliche Zusammenhänge zwischen einheitlicher Pollengröße und fakultativer Agamospermie werden diskutiert.

Ein Vergleich des Fruchtansatzes in zwei bayerischen Populationen zeigte, daß Triploide mit einheitlicher Pollengröße (gegenüber obligat agamospermen Triploiden mit stark schwankender Pollengröße) zu geringerem Fruchtansatz neigen; die Abnahme kann bis 15% betragen. Verminderter Fruchtansatz wurde auch bei einer Anzahl von Pflanzen aus verschiedenen, über das Untersuchungsgebiet verstreuten Aufsammlungen beobachtet. Der mitunter ziemlich markante Abfall im Fruchtansatz wird dem Auftreten fakultativer Agamospermie zugeschrieben.

1. Introduction

The present study is a sequal to den Nijs & Sterk 1980 in which an overall picture of the karyogeography of the diploid versus the polyploid forms of the *Taraxacum* section *Taraxacum* (= sect. *Vulgaria*) is given. Sexual diploids, up to that time supposed to be of rare and very scattered occurrence, appear to be present abundantly, in particular in the southwestern Federal Republic of Germany (GFR) and the Alpine region of Switzerland and western Austria, and in addition in eastern Austria. In the central Tauern area between the Inn- and Enns valleys) they were not found, which was attributed to the well-known phytogeographical pattern in the Alps. Several authors (*inter alia* MERXMÜLLER 1952, KÜPFER 1972, NIKLFELD 1973 and FAVARGER 1975) gave relevant overviews: as the result of the relatively extended periods of heavy glaciation a substantial number of taxa found in adjacent regions does not occur in the central Alps, while frequently two closely allied taxa may be present on either side of this central phytogeographical „gap". The presence of SW and E Alpine glacial refugia as (secondary) centres of remigration is also relevant in this context.

For more detailed data and a good survey of the karyogeographical records from the literature the reader is referred to DEN NIJS & STERK 1980, in which paper also some attention has been paid to the possible consequences of the presence of the diploid taxa for, among other things, the study of taxonomic and ecological problems and/or (micro-) speciation mechanisms.

The present study was undertaken in order to investigate some questions emanating from the previous study cited above:

— What is the pattern of distribution of the ploidy levels in the unexplored part of central and northern Bavaria — do diploids occur in the area as intimated by DEN NIJS & STERK 1980 or does the phytogeographical „gap" extend farther to the north; in other words, are there indeed two separate areas: an eastern and a western one?

— If located at all in the area under discussion, where does the northern limit of the range of the diploids run — this partly in connection with the recent discovery of diploid dandelions in the Netherlands (Limburg: STERK & al. 1982)?

— To what extent does facultative agamospermy occur?

Facultative agamospermy is said to occur in some triploid individuals: in a number of the florets present in a capitulum such an insufficiently known form of megasporogenesis takes place that somehow haploid egg cells originate. In contrast to the unreduced 3x egg cells as normally formed in triploids, such haploid egg cells require to be fertilised before they can produce a viable embryo: with haploid pollen (produced by diploid or occasionally triploid plants) in this way a diploid progeny may originate, while, to a lesser extent, also triploid individuals may arise after fertilisation by (approximately) diploid pollen grains also produced by (some?) triploids in small numbers (see Richards 1970 a, Müller 1972 and Doll 1977). Another relevant characteristic of facultatively agamospermous triploids is that they are supposed to possess also a rather regular microsporogenesis, thus to produce regular, diploid-like pollen (Richards 1970 a).

The possible break-down of the genetical isolation between the taxa and the arisal of novel taxa and, in addition, of new, and to a lesser or greater extent facultatively agamospermous, triploids, may have far-reaching implications for both the taxonomy and the microevolution of the section *Taraxacum.*

The rate of incidence of facultative agamospermy is still unknown. According to Richards 1970 a in county Durham (U. K.) and Slovakia (Č. S. S. R.) 20% to about 70% of the florets of each capitulum of some agamospermous plants appeared to be sexual. Müller 1972, on the other hand, reported (implicitly) only a small percentage in a limited number of the individuals of a population. As far as can now be ascertained the present authors could experimentally not demonstrate such high percentages either (Jenniskens, unpublished).

In two meadow populations a detailed analysis of the possible occurrence of facultative agamospermy has been carried out; in addition, a rough overall screening has been done.

2. Materials and Methods

2.1. Material

The sampling was carried out in 1980 (TBN- and THH-series) and in 1981 (THPM- and TBR-series). Samples were taken from a wide range of grassland-types (from poor hayfields to heavily dunged and grazed pastures) at set distances throughout the greater part of Bavaria. Some ancillary sample series originate from the „Schwäbische Alb“, the „Odenwald“ and from the northwestern part of Upper Austria (the Salzburg—Linz-area). In all about 60 samples became available (see Table 1). Each sample contained 30 to 50 „young“ capitula (i. e., already in anthesis, with still closed florets in the centre of the capitulum) stored in 70% ethanol. From 22 sample sites (those marked with an asterisk in Table 1) also living plants were collected for karyological and experimental purposes in the form of defoliated taproots.

2.2. Assessment of the ploidy levels

All capitula were primarily screened by means of the pollen method first published by Tschermak-Woess 1949 and later used by several other workers (inter alia, Richards 1968, Morita 1980; for a survey, see den Nijs & Sterk 1980). The method is based on the fact that diploid plants by having a regular male meiosis, produce pollen of a constant,

Table 1

Survey of sampling sites, habitats, species numbers and results of the pollen analyses. The * indicates the use of the sample in the garden screening for facultative agamospermy (Chapter 3.4)

Pop. no	Locality, "Landkreis" Country	Habitat (concise desription)	No sp	No pl	% of ploidy level 2x	3x	2x/3x
TBN 1	Allersberg, Roth, GFR	Extensive management hayfield	27	30	0	100	0
*TBN 2	Eichstätt, Eichstätt, GFR	River meadow, town centre	26	39	3	94	3
TBN 3	Schernfeld, Eichstätt, GFR	Ploughed-up hayfield, *Lol. per.* vegetation	21	28	0	75	25
TBN 4	Weissenburg, Weissenburg, GFR	Hayfield	25	30	0	94	6
*TBN 5	Merkendorf, Ansbach, GFR	Hayfield	18	36	0	81	19
*TBN 6	Ansbach, Ansbach, GFR	Extensive management, wet hayfield	30	39	0	97	3
*TBN 7	Fremdingen, Donauworth, GFR	South facing hayfield	23	33	0	85	15
TBN 8	Unterliezheim, Dillingen, GFR	Hayfield, rich in species	34	26	0	69	31
*TBN 9	Adelsried, Augsburg, GFR	Hayfield, *Tar.*!!	16	43	13	87	0
TBN 10	Oberottmarshausen, Augsburg, GFR	Ploughed-up, ruderal hayfield	19	37	3	86	11
*TBN 11	Oberfinning, Landsberg, GFR	Ploughed-up hayfield	17	36	3	72	25
*TBN 12	Diessen, Weilheim, GFR	Ploughed-up, wet meadow	18	42	5	90	5
TBN 13	Bad Tölz, Bad Tölz, GFR	South facing hayfield	16	32	0	88	12
TBN 14	Brannenburg, Rosenheim, GFR	Extensive management grassland	29	36	0	89	11
*TBN 15	Aising, Rosenheim, GFR	Newly sown grassland	25	43	0	84	16
*TBN 16	Traunstein, Traunstein, GFR	Ploughed-up hayfield	24	33	0	100	0
*TBN 17	Tittmoning, Traunstein, GFR	Undulating hayfield	35	42	0	89	11
TBN 18	Sleedorf, Salzburg, A	Hayfield, rich in herbs	29	39	28	67	5
*TBN 19	Frankenberg, Vöcklabruck, A	Hayfield	23	41	0	80	20

Pop. no	Locality, "Landkreis" Country	Habitat (concise description)	No sp	No pl	% of ploidy level 2x	3x	2x/3x
*TBN 20	Grieskirchen, Grieskirchen, A	Ploughed-up hayfield	26	42	0	95	5
*TBN 21	Schärding, Schärding, A	Hayfield, rich in herbs	43	41	10	85	5
*TBN 22	Eggenfelden, Pfarrkirchen, GFR	Forest clearing	20	42	0	88	12
*TBN 23	Rotham, Straubing, GFR	Grazed hayfield	29	43	0	88	12
*TBN 24	Faustendorf, Cham, GFR	Hayfield	23	34	0	83	17
*TBN 25	Schönsee, Weiden, GFR	Hayfield	—	33	0	83	17
*TBN 26	Waidhaus, Weiden, GFR	Ploughed-up hayfield	13	37	0	100	0
*TBN 27	Kennrath, Bayreuth, GFR	Hayfield	28	36	0	100	0
*TBN 28	Auerbach, Bayreuth, GFR	Hayfield	24	37	0	86	14
TBN 29	Lauterhofen, Neumarkt, GFR	Ploughed-up, ruderal hayfield	12	29	0	97	3
*TBN 30	Neumarkt-Oberpfalz, Neumarkt, GFR	Ploughed-up hayfield	20	34	0	85	5
TBN 31	Neustadt, Neumarkt, GFR	Hayfield	19	32	0	100	0
THH 2	Krumbach, Günzburg, GFR	Hayfield, *Tar.*!!	19	36	94	0	6
THH 5	Mittelberg, Kempten, GFR	"Fettweide"	13	31	100	0	0
THPM 2	Pamten, Kelheim, GFR	Hayfield	20	32	0	94	6
THPM 3	Eggmühl, Rottenburg, GFR	River meadow, extensive management	33	31	0	84	16
THPM 4	Landshut, Landshut, GFR	"Fettwiese"	24	28	0	86	14
TBR 2	Breitenbrunn, Mindelheim, GFR	Rich hayfield, *Tar.*!!	25	50	74	26	0
TBR 4	Osterberg, Illertissen, GFR	Hayfield, intensive management, *Tar.*!!	16	50	98	2	0
TBR 5	Ettlishofen, Neu-Ulm, GFR	Rich in herbs	18	50	84	16	0
TBR 32	Lampertshausen, Biberach a. d. R., GFR	*Tar.*!!, many *Anth. syl.*	23	50	100	0	0

			No	No	% of ploidy level		
Pop. no	Locality, "Landkreis" Country	Habitat (concise description)	sp	pl	2x	3x	2x/3x
TBR 33	Schwendi, Biberach a. d. R., GFR	Hayfield, *Rum. obt.*	20	50	92	4	4
TBR 34	Bussmanshausen, Biberach a. d. R., GBR	Hayfield, rich in herbs	28	50	92	4	4
TBR 36	Ebersbach, Illertissen, GFR	Hayfield, rich in herbs	22	50	56	32	12
TBR 37	Beuren, Illertissen, GFR	Hayfield, ruderal	15	50	72	24	4
TBR 38	Oberholzheim, Biberach a. d. R., GFR	Hayfield, intensive management, *Tar.*!!	15	50	32	56	12
TBR 27	Obersontheim, Schwäb. Hall, GFR	Hayfield, *Lol. per.*	28	50	0	100	0
TBR 28	Heidenheim, Heidenheim, GFR	Hayfield, *Trif.*, *Tar.*!!	13	50	10	84	6
TBR 6	Auerbach, Mosbach, GFR	Hayfield, extensive management	64	50	24	68	8
TBR 7	Mudau, Mosbach, GFR	Hayfield, extensive management	36	50	0	96	4
TBR 8	Amorbach, Miltenberg, GFR	Hayfield, extensive management	50	50	20	60	20
TBR 9	Bremhof, Erbach, GFR	Hayfield, forest clearing	26	50	96	2	2
TBR 10	Kimbach, Erbach, GFR	Pasture	47	50	38	52	10
TBR 11	Michelstadt, Erbach, GFR	Hayfield, *Tar.*!!	20	50	44	54	2
TBR 12	Erlenbach, Erbach, GFR	Hayfield, forest clearing	29	50	34	58	8
TBR 13	Lützelbach, Erbach, GFR	Hayfield, intensive management, *Tar.*!!	21	50	46	48	6

Additional sampling sites, not included in Fig. 1: TBR 1 Krumbach, 2x: 96%; TBR 3 Halden, Mindelheim, 2x: 100%; TBR 29 Winterrieden, Illertissen, 2x: 54%; TBR 30 Waltenhausen, Illertissen, 2x: 84%; TBR 31 Erolzheim, Biberach a. d. R., 2x: 84%; TBR 35 Nattenhausen, Krumbach, 2x: 88%; TBR 39 Halden, Mindelheim, 2x: 86%; *TBN 2a, Eichstätt, Eichstätt, 2x: 0%.

hardly variable diameter, whereas triploid plants, on account of disturbed meiotic processes, produce pollen grains with a highly variable diameter.

In the present study the reliability of this pollen method will be critically assessed in connection with the rather regular pollen production of the putative, facultatively agamospermous triploids. From a number of capitula from plants scattered over the sample area frequency distributions of the grain diameters were obtained. The pollen grains were examined in polyvinyl-lactophenol with trypane blue (0.03 gr. per ml.) as the cytoplasm-staining agent.

In a limited number of plants the chromosome numbers were counted by applying the squash technique to root tips or seedlings previously stained with basic fuchsine (RICHARDS 1968; DEN NIJS & al. 1978).

2.3. Facultative agamospermy

In two selected hayfield populations (about 5 km. apart) near Dillingen/Donau, one from Unterliezheim (UL = TBN 8) and the other one from Lutzingen—Goldbergalm (GB), a comparative study of the possible occurrence of facultative agamospermy was carried out in the spring of 1981. The starting point was the expectation that by the exclusion of animal pollination (by caging-in the capitula) the obligatory agamospermous individuals would show a higher percentage of seed set than would do the facultatively agamospermous ones. The latter are supposed to produce an unknown percentage of meiotically reduced egg cells, which will remain unfertilized and without pollination, therefore, will fail to develop into embryos. The same differences may be anticipated when the seed set percentages of caged-in versus free-pollinated capitula within facultatively agamospermous individuals are compared: in the open-pollinated capitula (a part of) the sexual florets will develop embryos, which results in a higher seed set percentage (RICHARDS 1970 a). In both fields studied an average number of 3 capitula of every selected individual was caged in during the whole anthesis and fruit-setting period. The, cylindrical, cages were made of chicken wire covered with glass—curtain material, and in order to prevent damage by falling rain drops, the cages were covered with plastic petri-dishes. The diameter of a cage was about 10 cm., its height about 10 cm. The cages were mounted on an aluminium rod at variable heights, which enabled us to follow the development of the capitular scape (see Fig. 10.1). Of each plant with caged-in heads another 3 capitula were left exposed to open pollination. During the experimental period (20. IV — 20. V) in both fields the temperature and relative humidity were continuously registered with a thermohygrograph, type Thies.

In the experimental garden a collection of plants hailing from the TBN-series of sampling sites was screened in the same way so as to find indications of the incidence of facultatively agamospermous speciments elsewhere in the area studied.

3. Results

3.1. Karyogeography

The results of the pollen analyses, concise descriptions of the sample habitats and the number of species per site have been tabulated in Table 1. In this table three categories of plants are presented, *viz.*, diploids, triploids and a class of doubtful cases. In the latter category those individuals are listed which exhibited such a variation in pollen grain diameter that they could not possibly be classified on the basis of this character alone (compare chapter 3.2). In some samples a markedly high percentage of the plants exhibited such an intermediate variability of the pollen grain diameters.

In Fig. 1 the geography of the results of the analyses is shown; the category of the intermediate specimens has been incorporated in the (square) symbols representing the relative percentages. For the sake of clarity in this figure the greater part of the sites of a previous study (DEN NIJS & STERK 1980) has also been drawn in (as dots).

The combined data show an interesting distribution pattern of the diploid specimens:

1. — In the greater part of Bavaria diploids are rare or absent. This is in sharp contrast to the south-western part of Bavaria, the Allgäu-region, and the area to the east of it through the Alpine foreland to the Inn-valley, where they are of common occurrence.

2. — In the Odenwald, to the north-west of the area studied a fair amount of diploids occur in the populations. This occurrence extends far more to the north than could be deduced from the progressive decrease of the percentages of diploids in the Stuttgart—Karlsruhe region.

3. — In the region between Salzburg and Linz the diploids reappear in the samples, thus showing a continuity with the previously established distributional pattern in eastern Austria.

4. — The population TBR 28 from the neighbourhood of Bayreuth (with the possible occurrence of diploids) suggests that diploids may extend at least in low percentages, rather far to the north in the eastern part of the sampled area.

It is quite clear that the now well-established diploid area in the south-west of the GFR shows a sharp boundary along a zone extending from the north-west to the south-east (roughly speaking from Frankfurt through Stuttgart and Augsburg to Innsbruck).

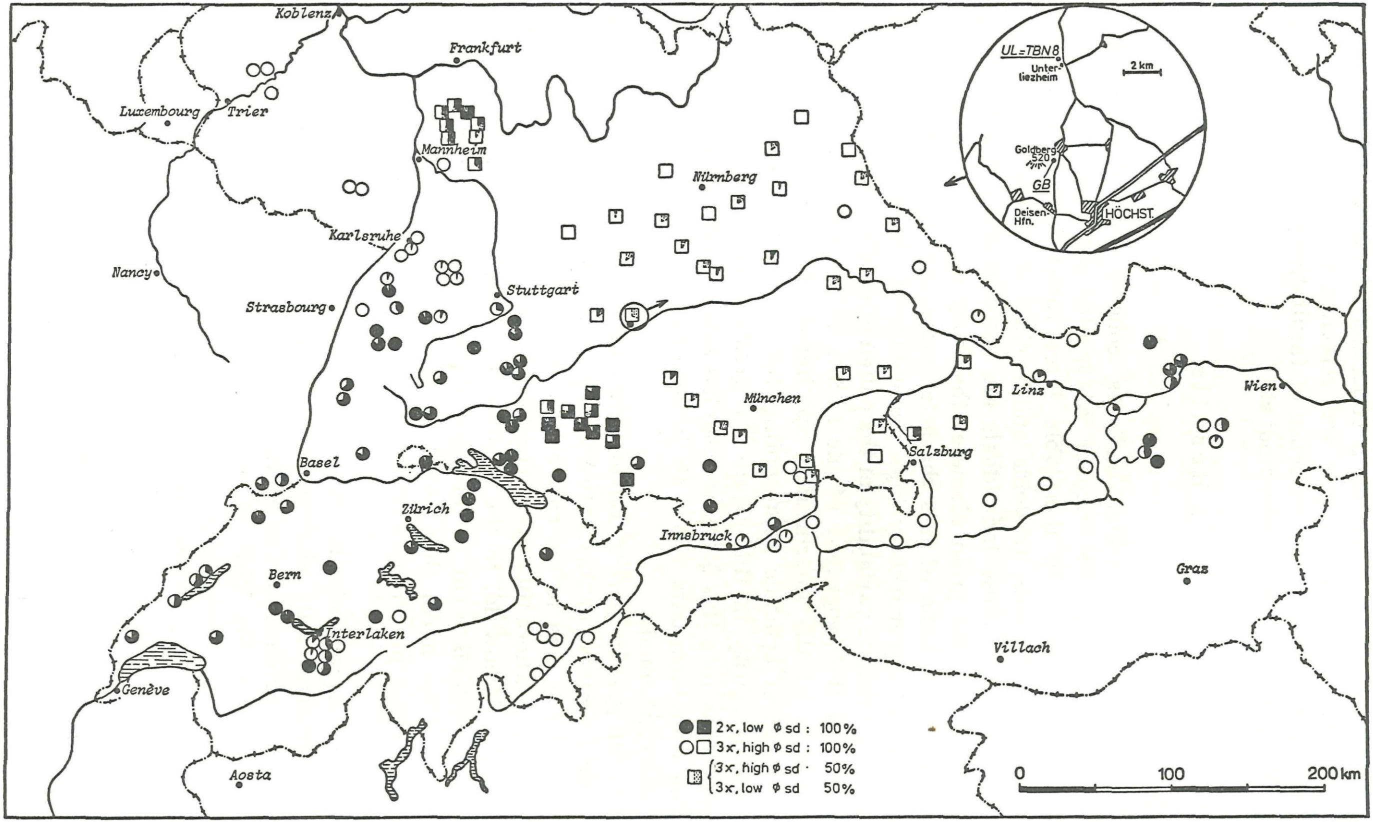


Fig. 1. Distribution of the sampling sites as listed in Table 1 (squares). Circular symbols borrowed from DEN NIJS & STERK 1980. Relative frequencies of the ploidy levels indicated in the symbols

Ecology: As is apparent from Table 1, only rather superficial ecological data were gathered. A detailed comparative ecological study of „diploid“ versus „triploid“ habitats is being undertaken in the Odenwald—Spessart transition zone and will be the subject of a forthcoming publication. An overview of Table 1 shows that samples were taken from a wide range of parcels representing a wide range of ecological situations: undisturbed hayfields (but little dunged or fertilized and hardly grazed, rich in species) and also production meadows, „Fettweiden“ (ploughed up, heavily fertilized, and intensively grazed, with an abundance of *Lolium perenne* and as a consequence only a minor herbal component in it). From the available data no correlation between the occurrence of diploids and triploids and the ecological amplitude of the series of sites could be established.

Yet another point of interest concerns the occurrence of fairly high percentages of doubtful cases. As shown in Fig. 1, the distribution

Table 2

Pollendiagnoses (to assess the ploidy level), pollen diameters and chromosome numbers counted in a selection of 2x, 3x and doubtful specimens

Plant no	Pollen-diagnosis	Pollendiameters $\bar{x}$ (µm)	s (µm)	Chromosome numbers**
*TBN 18—3	2x	32.4	2.8	(16) (16) (16)
*TBN 28—2	2x	28.2	2.0	(16, 16)
TBN 8—21	2x/3x	30.7	3.0	(24, 24)
TBN 8—22	2x/3x	31.2	2.9	(24) (24)
TBN 8—25	2x/3x	30.2	2.9	(24)
*TBN 15—1	2x/3x	32.4	3.5	(24) (24, 24, 24)
TBN 19—10	2x/3x	31.6	3.3	(24) (24, 24, 24)
TBN 26—4	2x/3x	35.1	4.1	(24, 24) (25)
TBN 26—9	2x/3x	32.2	3.5	(24) (24, 24)
TBN 27—2	2x/3x	33.3	4.0	(24) (16, 32, 24, 32) (24, 16) (24) (16) (24) (24) (24, 24)
*TBN 27—7	2x/3x	31.0	2.9	(24, 24) (24) (25, 25)
TBN 15—3	3x	35.3	5.9	(24) (24, 24) (24, 24)
TBN 17—8	3x	37.6	7.6	(24) (24, 24)
*TBN 19—4	3x	33.7	5.7	(24) (24, 24, 24)
*TBN 19—6	3x	40.6	5.5	(24) (24, 24, 24)
TBN 19—8	3x	34.0	4.5	(24) (24) (24)
TBN 19—9	3x	32.9	5.6	(24) (24, 24)
TBN 28—7	3x	30.7	5.0	(24)
TBN 28—8	3x	31.8	5.2	(24) (24, 25)

* For corresponding diameter frequency see Fig. 2—7.

** Chromosome numbers between brackets have been counted in the same root tip.

of such specimens is not at all at random, but appears to be concentrated along the border zones of the diploid area, especially in its western part. The next chapter (3.2) will supply more details concerning this category of plants with subregular pollen grains.

3.2. Pollen diameter, variability and chromosome numbers

Pollen grains of selected specimens were measured so as to attain a firm basis for the establishment of the ploidy levels. Fig. 2—7 give

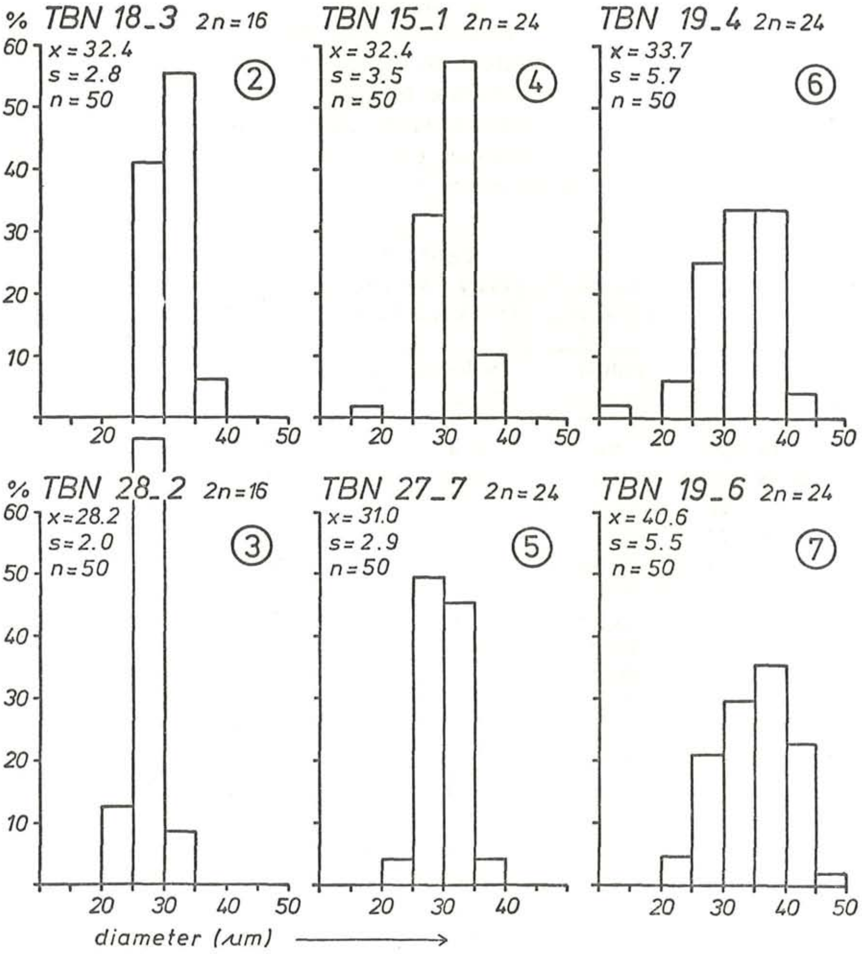


Fig. 2—7. Relative frequency distributions of the pollen grain diameters of some selected specimens (all dimensions in μm):

TBN 18-3, 28-2: diploids

TBN 15-1, 27-7: triploids with subuniform pollen

TBN 19-4, 19-6: triploids with irregular pollen the relative frequency distributions of 6 plants, two of which belonging to the category of doubtful cases mentioned before. Chromosome counts indicated that these two specimens were triploids. As may be deduced from the figures, the frequency distributions and the standard deviations (as a measure for the variability) of the „doubtful“ triploids are very much like those of the diploids. All doubtful specimens which have been studied karyologically turned out to be triploids. Of a number of plants the pollen diameters, standard deviations, pollen diagnoses and chromosome counts are listed in Table 2. This table again very clearly shows that a great many triploid individuals have remarkably uniform pollen grains. In contrast to the common „irregular“ triploids, such „regular“ ones must have a fairly normal male meiosis. According to RICHARDS 1968, 1970 a such plants could be putative facultatively agamospermous individuals.

3.3. A comparison of two populations: does facultative agamospermy occur?

In population sample TBN 8, Unterliezheim (UL), up to 31% of the capitula showed a uniform pollen type, although the plants were triploids. A neighbouring population, Lutzingen—Goldbergalm (GB) contained only „irregular“, normal triploids. Fig. 8.1—2 gives an example of a pollen slide in combination with the frequency distribution of the diameters of an UL-plant. 9.1—2 shows the same data for a specimen of the GB-population. In these two populations a search for facultative agamospermy was carried out (see chapter 2.3).

Description of the fields (for their locations, see the inset in Fig. 1)

Unterliezheim: hayfield, moderately dunged, mown 2 or 3 times a year; heavy, loamy soil; vegetation: dense, productivity high; high *Taraxacum*-density (the chance to encounter a dandelion in a random vegetation sample of 1 dm.^{2} is 100%); total species number in circa 200 m.^{2} : 34; as grass species mainly *Lolium perenne* and *Poa trivialis* were present.

Lutzingen — Goldbergalm: hayfield, ligthly grazed, moderately dunged, mown 2 or 3 times a year; heavy, loamy soil; vegetation: sparser than UL, productivity high; *Taraxacum*-density lower (chance of encounter 75%); total species number in circa 200 m.^{2} : 43; grass species: mainly *Poa trivialis, Alopecurus pratensis* and *Agrostis stolonifera,* sparsely *Anthoxanthum odoratum;* additional herbaceous species: *Centaurea jacea, Heracleum sphondylium, Tragopogon orientalis* and other ones.

The flowering period started on 22. IV and 24. IV in UL and GB, respectively, and ended on 10. V and 12. V respectively, seed set followed from 13. V and 14. V, respectively, onwards. The registration of the relative air humidity and temperatures gave almost identical curves. The weather was rather cold, except on the 25th and the 26th of April, < 10° C; only after the 7th of May the temperature rose above 10° C.

By means of the method described above, the seed set percentages of 52 individual plants from the UL population and of 38 plants from the GB population were determined. Fig. 10.1—2 gives overviews of the UL field showing the experimental situation. Of each plant 2—4 capitula were caged-in and 2—4 remained exposed to pollinators. All fructifications were carefully harvested and in each capitulum the relative frequency of developed versus undeveloped (pale, non-viable) fruits was established.

Table 3 gives a concise survey of the results of the field study. The principal conclusions that can be drawn from this table are:

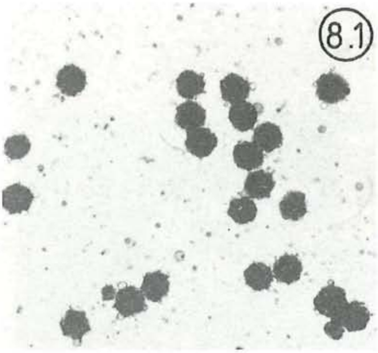
1. — The difference in seed set percentages between UL and GB is remarkable, given the fact that both populations consist of putatively agamospermous triploids. Fig. 11 gives the frequency distributions of the seed set. In this figure the individual capitula form the basic data units, the collection of capitula forming the population sample. This procedure has been preferred among other things because of the amount of intra-individual variation of the seed set. Some examples of the percentages per capitulum per specimen (unpollinated) are presented in Table 4. The GB plants behave like normal, obligately agamospermous individuals, the normal seed set in nature in the main flowering period being 96—98% (Richards 1970 a; Sterk, unpublished data). Clearly the majority of the individuals of the UL population sample deviates in that it has only 85—90% seed set. This sample was, incidentally, not a representative one because during the field study care was taken to include triploids producing uniform pollen in the sample.

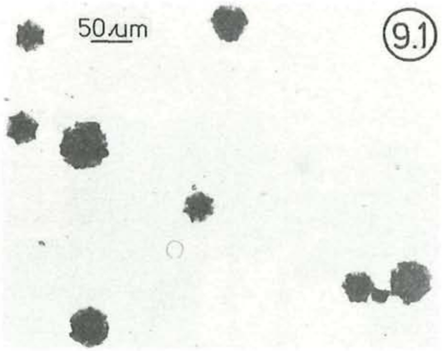
Table 3

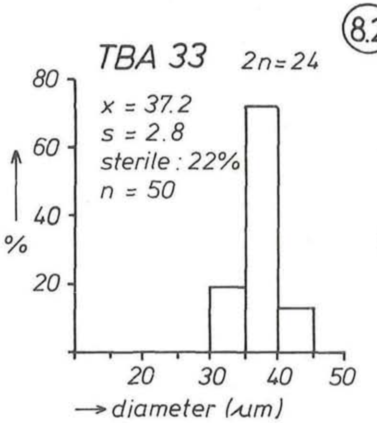
Seed set percentages in Unterliezheim (UL) and Goldbergalm (GB) in non-pollinated and open-pollinated capitula

* significant
— not significant (See text)

		Non-pollinated		Pollinated		
	No of plants	No of capitula	% seed set	No of capitula	% seed set	Pollination effect %
UL	52	132	88.8	146	90.2	+1.4*
GB	38	105	96.5	100	97.1	+0.6⁻







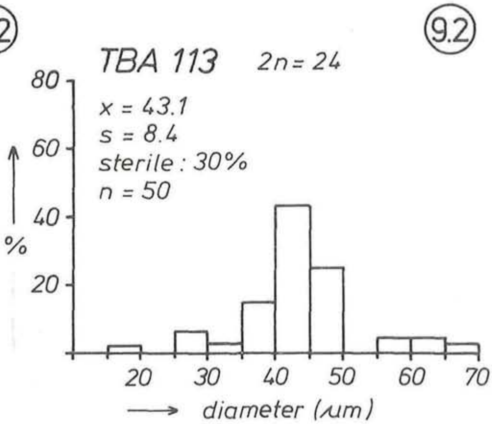


Fig. 8. Unterliezheim, triploid specimens with 'regular' pollen: TBA 33. — 1. Photomicrograph of pollen of subuniform size. — 2. Frequency distribution of the pollen diameters. — All dimensions in µm

Fig. 9. Goldbergalm, triploid specimens with 'irregular' pollen: TBA 113. — 1. Irregular pollen of a variable size. — 2. Frequency distribution of the pollen diameters. — All dimensions in µm

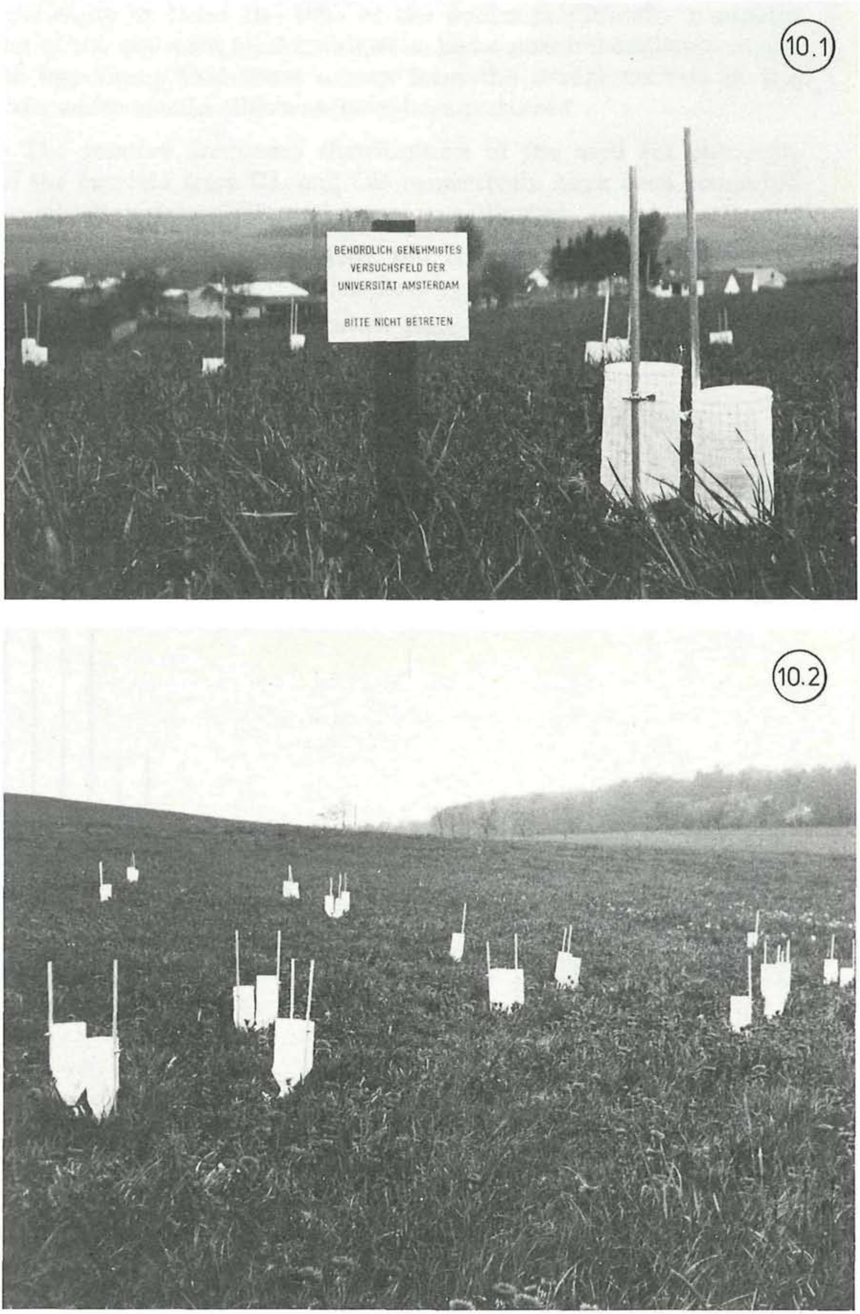


Fig. 10. 1—2. Overviews of the field in Unterliezheim during the experiments in 1981

The perishing of these 10—15% of the ovules is difficult to explain by any of the gathered (ecological) data, but a possible explanation lies in the hypothesis that these ovules form the sexual portion in the capitula, which should otherwise have been fertilized.

2. — The relative frequency distributions of the seed set percentages of the capitula from UL and GB respectively have been compared for the situation: free-pollinated versus unpollinated.

Conform Sokal & Rohlf 1969 the Kolmogorov-Smirnov test for relative frequency distributions has been applied:

UL-field: unpollinated-pollinated: $D_{max.} = 0.146 . D \alpha_{= 0.05} = 0.136$ ($n > 100$), H_0 is to be rejected, so that the distributions of the pollinated

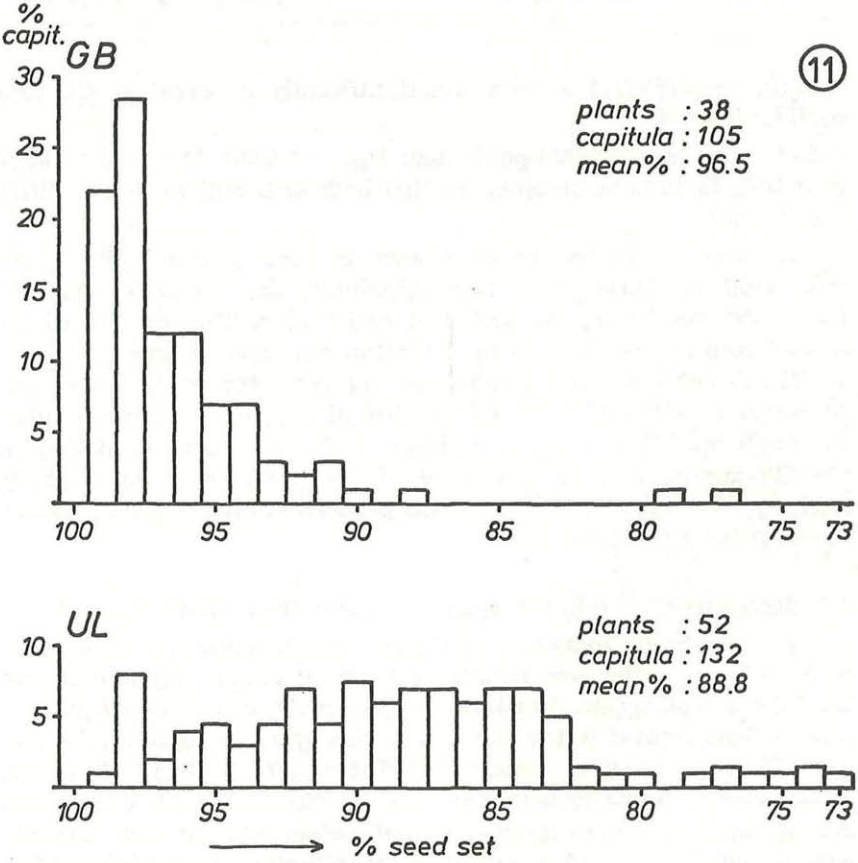


Fig. 11. Percentages of seed-set per capitulum in the Unterliezheim and Goldbergalm fields in non-pollinated, caged-in capitula

Table 4

Seed set percentages without insect pollination. Capitula data per individual, some examples from Unterliezheim (UL) and Goldbergalm (GB)

	Plant code	% seed set per capitulum		Plant code	% seed set per capitulum
UL	TBA 3	82 85 85	GB	TBA 102	96 97 96
	TBA 4	74 75 77		TBA 103	99 99 98
	TBA 5	78 83 85		TBA 104	98 99 98
	TBA 9	96 87 86		TBA 114	98 97 94
	TBA 11	98 97 98		TBA 125	97 98 98
	TBA 24	83 85 84		TBA 129	99 98 99
	TBA 28	98 98 98		TBA 139	98 94 98
	TBA 38	89 91 87 93		TBA 143	93 98 98

and the unpollinated samples are significantly different at the 95% confidence level.

GB-field: unpollinated-pollinated: $D_{max.} = 0.061$. $D\,\alpha_{= 0.05} = 0.136$ ($n > 100$), H_0 is to be accepted, so that both distributions do not differ significantly.

Another conclusion to be drawn is that, provided the above mentioned hypothesis holds true, apparently the pollination was far from complete during the period of registration. The increase of the overall seed set percentages in the pollinated capitula was only 1.4% in UL. Nevertheless one has to bear in mind that these 1.4% may represent 10—15% of the total number of supposedly sexual ovules! Although statistically non-significant, the slight increase (0.6%) in the GB-sample may be indicative of the presence of some partly sexually functioning triploids in this population also. We shall return to this point in the discussion.

3.4. Screening for facultative agamospermy in the sample area

In order to get some idea of the possible occurrence of facultative agamospermy in the area studied, a series of plants originating from the TBN sampling sites has been studied in the experimental garden. The method applied is the same as in the foregoing chapter. Hailing from 22 populations, as indicated in Table 1, 74 triploid individuals, as collected in the fields, have been studied. They produced 305 capitula. All capitula were kept insect-free; pollination experiments were not carried out. The percentage of seed set, therefore, only yields information about the possible incidence of sexual ovules. Table 5 summarises the results in comparison with the UL- and GB-fields.

Table 5

Seed set percentages (mean per capitulum, in classes) by exclusion of potential pollinators of 74 individuals originating from 22 TBN-sample sites (ca 3 specimens per site). The data of UL and GB are added as a reference

		71/75	76/80	81/85	86/90	91/95	96/100
TBN-samples	(n = 74)	1.5	0.3	3.5	8.0	22.0	64.0
Goldbergalm	(n = 38)	0	2.0	0	2.0	20.0	76.0
Unterliezheim	(n = 52)	2.0	4.0	21.0	33.0	23.0	15.0

Apparently there are aberrant individuals in the TBN-series. A survey of the individual results gives some examples of putative, partly sexual specimens:

TBN 2a—3 (Eichstätt, Bav.)	seed set unpoll.: 9 capit., mean 84%
TBN 20 —5 (Grieskirchen, Austr.)	seed set unpoll.: 7 capit., mean 85%
TBN 21 —8 (Schärding, Austr.)	seed set unpoll.: 5 capit., mean 87%
TBN 22 —8 (Eggenfelden, Bav.)	seed set unpoll.: 4 capit., mean 88%

4. Discussion

4.1. Karyogeography

For the assessment of the ploidy levels in the large numbers of samples (or individuals, respectively) the rapid method of pollen uniformity analyses was also used here. Since the numbers of random samples were on the small side and manifestly dubious cases (2x or 3x?) do occur here regularly, the percentages of di- and triploids are only rough approximations and cannot be regarded as sufficiently exact. Also a possible staggering in flowering time between 2x and 3x forms may influence the recorded relative proportions of the ploidy levels if sampling and recording took place only once during the flowering season and not an aselect gathering from living individuals (compare Tschermak-Woess 1949, Fürnkranz 1960, den Nijs & Sterk 1980).

As a supplement to and partly also an emendation of the results of the previous study (den Nijs & Sterk 1980) the following deductions are relevant:

— Diploids occur far more frequently towards the north-west than had hitherto been assumed and extent to the recently studied Odenwald-region and (according to Sterk & al. 1982) also as far as Zuid—Limburg (Netherlands). As a consequence it is an object for further inquiry to elucidate the situation in the zone between Frankfurt and this latter region.

— By extending the assumptions made earlier as regards the existence of a transition zone (2x—3x) between Stuttgart and Passau (den Nijs & Sterk 1980) we had to release the idea that there is a continous west-east boundary zone. There is a sharp decline of diploid percentages along a west-east instead of a south-north gradient: from more than 90% diploids in, for example the surroundings of Krumbach (e. g. THH 2) to less than 5% only about 50 kilometers due east (the Augsburg-region: TBN 10, 11). From this zone onward to the east the diploids are absent or atmost of rare occurrence in the greater part of Bavaria to reappear in the populations farther to the east. The absence of diploids from the intervening area is a continuation of the distribution pattern met within the eastern Alps: roughly speaking, diploids do not occur between the Inn- and the Enns-valleys. By this reasoning the existence of two spatially separated diploid areas is confirmed: a western one (in casu the recently studied area and also including parts of France, den Nijs & Sterk in the press), and an eastern area, the extent of which up to now only includes the eastern Alps, the Vienna region, parts of Slovakia (Fürnkranz 1966, Richards 1970 b) and the Bohemian and to a lesser extent the Bavarian Forest. Sahlin 1972 already discriminates between the nominal, western European forms of the section *Taraxacum* and a pannonic group of forms which, as he stated, is perhaps an eastern subsection of the latter. According to this author specimens of the western centre of distribution (France) have distribution patterns extending through the south-western Germany as far as Bavaria. On the other hand Sahlin 1979 records the occurrence of an 'eastern' species. viz. *Taraxacum leontodontoides* in the surroundings of Munich, so that the two groups need not be fully separated from one another (any longer?). More general data from the literature also render a bipolar (bi-centric) distribution pattern of the diploids probable: Merxmüller 1952, Favarger 1975 and others give many examples of alpine and pre-alpine taxa with an eastern and a western (secundary) centre of distribution. The presence of glacial refugia, in the west located in the south-western Alps (Swiss, French and/or Italian), and in the east in the eastern alpine escarpments, is for the greater part in conformity with this biogeographical pattern. The data pointing towards a pannonic area of diploids are as yet rather scanty; explorations in Czecho-Slovakia and the Balkan countries appear to be required and have been scheduled. Chromosome countings of unindentified specimens of the section *Taraxacum sect. Erythrosperma* hailing from Dürnstein, Wachau, Upper Austria, a well-known xerothermic relict and outpost area, proved them to be diploids (den Nijs, unpublished data). In conjunction with Richards' 1970 b data concerning sect. *Erythrosperma* species from Slovakia, these findings are suggestive of more diploidy involvement in this section also.

The present distributional limits of, apparently two, diploid areas in Bavaria and Austria are presumably of a subordinate level in respect of a putative and still unknown overall northern limit of occurrence of diploids. Such a general limit may exist as a response to as yet undetected (ecological) master factors prevailing in more boreal climatic regions (conceivably in connection with thermophily?). The area between the two 'diploid' area may actually undergo a two-side colonization by the western and by the eastern diploid karyotypes. The frequent incidence of diploidy in such a highly derived section as sect. *Taraxacum* forms a striking parallel with the results of Morita 1976, 1980 obtained from *Taraxacum* sect. *Ceratophora* and sect. *Mongolica* in south-eastern Asia, where also many derived diploids, belonging to an appreciable number of species, occur in anthropogenic habitats.

Obviously these diploids cannot be interpreted as relicts; their relative abundancy and broad ecological amplitude had better be taken for an indication of some selective advantage favouring the diploids at least at the present time and in the 'diploid' areas. The question arises whether in such sections as sect. *Taraxacum*, sect. *Erythrosperma* and sect. *Ceratophora* a process of rediploidisation from a triploid state to the diploid may have taken place (compare de Wet 1980). We shall return to this point in the next paragraphs.

4.2. The pollen grain diameter variability and ploidy level

The correlation between the ploidy level and the variance in the pollen grain diameters as reported previously (den Nijs & Sterk 1980) does not always tally with those established during the present study. The previously recorded results strongly suggested a rather sharp discontinuity between the pollen grains of di- and triploids (attributed to the upon the whole irregular microsporogenesis in triploid individuals resulting in high standard deviation values). Slightly irregular pollen grains may turn out to be of diploid origin. Doubtful cases were concentrated in the wider Vienna region and the Jura (the surroundings of Basel). The present records clearly include many triploids producing pollen of rather uniform size. As stated before, these specimens must have a rather regular microsporogenesis, a character said to be correlated with a regular female meiosis by Richards 1970 a. According to this author such plants are supposed to be facultatively agamospermous.

The distribution of the triploids with subuniform pollen is of appreciable interest: they begin to appear in the border zones of the diploid area (especially in the eastern one: Würzburg—Augsburg—Munich) and to a lesser extent in the concentration area of diploids (Black Forest and Allgäu to Switzerland).

A possible origin of the 'regular' triploids could lie in hybridogenous contacts with the neighbouring diploids resulting in an introgression of 'uniformity' alleles. The relative scantiness of 'regular' triploids elsewhere in the diploid area remain unexplained, however. The singular distribution pattern suggests the question whether this is a case of character displacement within the triploids; if so there must be some selective disadvantage of the 'regular' triploids in an (ofcourse also 'regular') diploid population. These speculations are still to be tested, and also the supposed correlation between the triploids with subuniform pollen size and the incidence of facultative agamospermy.

In some specimens hyperploidy (2n = 25) has been recorded (see Table 2). This may be caused by satellites which may have become separated and have been counted as supernumerary chromosomes (see DEN NIJS & al. 1978). The occurrence of 16, 24 (and 32) chromosomes in the specimen TBN 27-2 may be attributable to irregular mitoses in the root used for the counts, due to a hybridogenous nature resulting from facultative agamospermy (it was presumably an as yet unbalanced, newly originated triploid specimen). Such triploids arisen de novo have been found earlier by RICHARDS 1970 a and by MÜLLER 1972.

4.3. The incidence of facultative agamospermy

There is as yet no clear-cut evidence for the occurrence of facultative agamospermy from the available data. Such evidence may be obtained by the detection of a de novo development of diploids originated from haploid ovules formed in triploid individuals. RICHARDS 1970 a and MÜLLER 1972 found such diploids to a limited extent in the offspring of artificially produced hybrids. Another but in pratice more cumbersome method to demonstrate facultative agamospermy would be to raise from a pollinated triploid mother a F_1-generation in which individuals show paternal characteristics (iso-enzyme analyses).

The decrease in seed set may also be attributable to a reduction of vitality (and, consequently, also of fertility) caused by hybridisation between individuals of 2x and 3x populations in precisely the border zones. In this context two considerations are relevant: such hybridogenous triploids could only have originated from a mass population directly from diploids by fusions of unreduced gametes with haploid ones. Such a process has not yet been encountered to any appreciable extent. The alternative possibility lies in the phenomenon of facultative agamospermy itself: gametes with 2n = 16 produced by triploids do exist (MÜLLER 1972) and may give rise to 'new' triploids by fusion with haploid, or more or less haploid gametes.

RICHARDS 1970 a recorded seed set percentages of only 25 to 70% in emasculated capitula of triploid plants; he, therefore, concluded that from about 30% up to 75% of the florets in a capitulum may function as (female) sexual ones. These high percentages are obviously not present in the populations studied by us.

The conclusion may be drawn that in some Bavarian populations a fair amount of triploid specimens occur with from 10% up to 15% sexual florets per capitulum.

One nevertheless has to reckon with a restriction: so far the data have been gained from only two local populations; experiments elsewhere in the field and, especially, in the experimental garden are required.

In this context it may be seen as a positive point that individuals with lower seed set percentages have been found also in the set of 22 samples from all over the region. These plants showed these percentages when subjected to the uniform conditions of the experimental garden, local influences thus being eliminated.

It appears that the sexuality of the ovules is indeed correlated with the production of sexual male gametes, in other words, with the rate of regularity of the pollen production (Richards 1970 a).

The corollary of the results obtained from 22 samples hailing from all over Bavaria is that putative facultatively agamospermous triploids with 10—15% sexual florets indeed occur. Such specimens are wide-spread in the area although they form a minority in the populations. One has to bear in mind that a small percentage of sexuality per capitulum is difficult to detect and may escape one's attention in the normal seed set variability.

The minor differences in seed set percentages between caged-in and pollinated capitula in the UL-field (+ 1,4%) and the GB-field (+ 0,6%) deserve some more attention. Although partly significant, these differences are too small to yield cogent information, but for all that can be explained:

— The sexual part of the capitula consist of 10—15% of the florets only.

— Diploid sexual plants often produce only 30—50% seed set in the experimental garden (Jenniskens in preparation). Unfortunately both fields studied did not contain any diploids, so that it was not possible to assess this percentage in the field. The garden experiments suggest that a shortage of pollinators may account for the low rate of seed set.

— The populations studied both had high *Taraxacum*-densities: given a mean density of 25 plants per square meter and 5 capitula per plant, each producing about 150 florets, there are ca. 18.500 florets per square meter. Moreover, the fields and the intervening country form an area of several tenths of hectares covered with such dense dandelion populations. The ephemerous but immense size of the flower populations would require the presence of an equal magnitude of pollinators for a complete pollination. It is a question whether the flower population (of other species) which mostly develop later in the season in the region under discussion could possibly provide for the survival of such great populations of pollinators throughout the whole season. According to DROST 1982 one may anticipate that in such anthropogenic, mass-flowering populations the pollination percentages show a tendency to decrease as a consequence of nutritional bottle-necks for the pollinator populations later in the season.

— As mentioned under 'Results' the weather was inclement during the greater part of the flowering period: less than 10° C. Therefore one must assume that of most pollinating species of insects were compelled to remain inactive for most of the time.

These circumstances and the data lead to the conclusion that in the prevailing circumstances the chances of effective pollination of the 10—15% (putative) sexual florets will have been rather low. The rather small but significant positive overall effect in pollinated heads of UL (+ 1.4%) may nevertheless correspond with 10—15% of the sexual portion.

Summarizing the evidence the present authors further more wish to put forward that:

— Given the occurrence of facultative agamospermy in triploids, there is a possibility of an advent of new diploids;

— The wide-spread presence of derived diploids, which in many cases could not be distinguished from their triploid relatives on morphological grounds, is not compatible with their alleged relict status.

These two, admitted partly speculative, conclusions in turn lead to the hypothesis that within the section *Taraxacum* an evolutionary cycle of rediploidisations (DE WET 1980) may well occur. This process of rediploidisation could, in turn further the recolonisation of the triploid 'areas' by diploids.

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