

THE ORIGIN AND DISTRIBUTION OF DIPLOID AND TETRAPLOID *TRIPLEUROSPERMUM INODORUM* (L.) SCHULTZ BIP.

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ABSTRACT

The diploid cytotype of *Tripleurospermum inodorum* (Compositae-Anthemideae), previously known only from the Baltic region and eastern Canada, has an Atlantic distribution in Europe and is common in the British Isles and northern France. The tetraploid cytotype, previously known from Scandinavia and western Canada, occurs at a number of sites in central and eastern Europe and probably has a Continental distribution in Europe. Diploid and tetraploid may have mutually exclusive distributions. Diploid *T. inodorum*, now restricted to man-made habitats, may have diverged from the closely related *T. maritimum* before the Weichsel glaciation and tetraploid *T. inodorum* may have arisen from diploid *T. inodorum* by chromosome doubling and catastrophic selection. Chromosome counts for *Tripleurospermum tenuifolium* ($2n = 18$), *T. disciforme* ($2n = 18$) and *T. tchichatchevii* ($2n = 36$) are reported for the first time.

INTRODUCTION

The genus *Tripleurospermum* (Compositae-Anthemideae) consists of some 25 to 35 herbaceous species. The genus is centred in the Caucasus and Western Asia, and although a wide range of taxa occur in this area, from desert annuals to alpine perennials, they are taxonomically little-known and poorly understood. Herbarium material is scanty and often unsatisfactory, lacking the ripe achenes that are essential for the determination of many species. Pobedimova (1961), in the introduction to her treatment of the genus in *Flora URSS.*, pointed out that the delimitation of species is often very difficult, and Fedorov (1949) wrote 'One can often see completely unsuccessful determinations made not only by novices but also by prominent specialists, who obviously make the same fundamental mistakes in the identification of species of this genus (*Tripleurospermum*).'

However, *T. inodorum* (L.) Schultz Bip., a widespread and often abundant annual weed of arable land and waste places in Europe and most other temperate areas of the world, and the related *T. maritimum* (L.) Koch, a perennial or biennial maritime species found on the coasts of western and northern Europe, are well-known to European botanists and have been the subjects of a number of biosystematic and cytotoxic studies. These studies have usually been restricted to a relatively small area; for instance, Turesson (1922) restricted his investigations to the province of Skåne in Sweden, Vaarama (1953) worked mainly within Fennoscandia, Nehou (1954) in Brittany, Rottgardt (1956) in Schleswig-Holstein, and Hämet-Ahti (1967) in Northern Fennoscandia. The ecology of the two species and their morphological differences are now reasonably well understood, but their nomenclature is confused and varies from author to author. Nehou (1954), Lökvist (1963), Kay (1965) and Hämet-Ahti (1967) concluded from biosystematic studies of the two taxa that they merited separation as distinct species, and this is the view taken in the present paper. *T. inodorum* and *T. maritimum* are mutually interfertile at the diploid level, as are several other morphologically well-differentiated species of *Tripleurospermum*, and extensive hybridization may occasionally take place when the ecological isolation which normally separates the two species breaks down.

PREVIOUS CYTOTAXONOMIC WORK ON *T. INODORUM*

The earliest published chromosome count for a plant which may have belonged to this species was made by Tahara (1921); $n = 9$ for a *Tripleurospermum* from northern

Japan. Hüser (1930) determined haploid chromosome numbers of $n = 9$ for three 'forms of *Matricaria inodora*' found in the southern Baltic region; a cliff-form from Bornholm and a beach-form from near Rostock (both probably *T. maritimum*), and an arable-field form also from near Rostock (probably *T. inodorum*). Vaarama (1953) investigated the cytology of *Tripleurospermum* in Fennoscandia. He regarded the Fennoscandian taxa as three subspecies of the species *T. maritimum*: subsp. *inodorum* (L.) Hyl. ($2n = 36$), subsp. *salinum* ($2n = 18$) and subsp. *ambiguum* ($2n = 18$). The chromosome morphology of the tetraploid subsp. *inodorum* indicated that it was of amphiploid origin. Vaarama (personal communication) has told me that the count of $2n = 54$ that he reported in this paper for var. *villosum* of subsp. *ambiguum* was an error, and that this variety is probably also diploid ($2n = 18$). Subsp. *salinum* is a seashore plant occurring only occasionally in ruderal habitats in Fennoscandia, and subsp. *ambiguum* is a highly variable circumpolar group including among a number of maritime and weedy types the ruderal variety *boreale* which has been displaced as a weed in most of Fennoscandia by the aggressive tetraploid subsp. *inodorum* in the past century. Unfortunately Vaarama's work has not been published in detail. Vaarama's subsp. *salinum* probably corresponds to *T. maritimum* in the restricted sense of the present paper, and his subsp. *inodorum* and subsp. *ambiguum* var. *boreale* to tetraploid and northern diploid *T. inodorum* respectively. In Britain, I have found that northern Scottish forms of *T. inodorum* morphologically resembling the northern 'ambiguum' (or, more correctly, 'phaeocephalum' (Pobedimova 1961, Hämet-Ahti 1967)) type are connected by a continuous cline of variation to southern English diploids of the typical *inodorum* type, the latter being morphologically very similar to tetraploid *T. inodorum* (Kay 1965).

Rottgardt (1956) studied *T. inodorum* and *T. maritimum* in Schleswig-Holstein, regarding them as *Matricaria maritima* subsp. *inodora* and subsp. *maritima*. She investigated two populations of diploid and two populations of tetraploid *T. inodorum*, as well as one population of *T. maritimum*, and she found that the cytotypes of *T. inodorum* are morphologically similar to one another but physiologically and ecologically slightly different. Mulligan (1958) reported that there are two similar forms of the introduced weed '*Matricaria maritima* var. *agrestis*' (presumably *T. inodorum*) with separate distributions in Canada—one in the Prairie Provinces, a tetraploid ($2n = 36$) cornfield weed (four sites in Saskatchewan), and the other in the eastern Maritime Provinces, a ruderal rather than a cornfield weed, diploid ($2n = 18$), with pollen grains half the volume of those of the prairie tetraploids. He recorded diploids from seven sites, in Quebec, New Brunswick, Nova Scotia and Prince Edward Island. All plants from both sites in Prince Edward Island had supernumerary chromosomes; one plant had two ($2n = 18 + 2B$) and the rest one ($2n = 18 + 1B$). This is the first record of supernumerary chromosomes in *Tripleurospermum*. I have found that supernumerary chromosomes are widespread both in diploid *T. inodorum* and in *T. maritimum*, occurring in about 10 per cent. of all plants counted.

Lövkvist (1963), in a preliminary account of a re-investigation of Turesson's work on '*Matricaria maritima*' (Turesson 1922), concluded that *T. inodorum* and *T. maritimum* should be regarded as separate species 'at least as far as the situation in Scandinavia is considered'. Unfortunately Lövkvist's chromosome counts, some of which should clearly be assigned to *T. inodorum*, are all allocated to *T. maritimum*: $2n = 18$ from West Skåne, Lancashire (near sea), Cheshire (Wirral), Ireland (coast, near Dublin) and Brittany, and $2n = 36$ from Prague, Skåne (two ruderal sites) and Stockholm (one ruderal site).

THE DISTRIBUTION OF THE CYTOTYPES IN EUROPE

The chromosome counts made by previous workers that are well documented and clearly apply to *T. inodorum* are those of $2n = 18$ for plants from northern Germany (Hüser, Rottgardt), $2n = 18, 18 + 1B, 18 + 2B$ for plants from eastern Canada (Mulligan) and $2n = 36$ for plants from Fennoscandia (Vaarama), northern Germany (Rottgardt) and western Canada (Mulligan). When the work described in the present paper began, the cytological status of British and western European *T. inodorum* was unknown, and it seemed possible that the situation in Britain and western Europe might be similar to that

described for Fennoscandia by Vaarama, with aggressive tetraploids invading and displacing the diploids.

Plants and achenes were collected from wild populations of *T. inodorum*, by the author and by friends and colleagues, from as many sites in the British Isles as possible, and also from a few sites in western Europe. The central and eastern European material was collected in the field by local botanic gardens and research stations. The identity of all material of *T. inodorum* was checked by examination of the morphology of the achenes. *T. maritimum*, the species most likely to be confused with *T. inodorum*, has achenes with broad, inflated, often contiguous ribs and elongated oil-glands, contrasting with the well-separated, dense ribs and rounded oil-glands of *T. inodorum* (Nehou 1954).

Chromosome counts were made from root-tip Feulgen squash preparations in most cases; a few counts were made from pollen mother cell squashes. The most effective technique for root-tip squashes was found to be pre-treatment in colchicine solution for three hours (0.1 per cent. for seedlings, 0.2 per cent. for root-tips from established plants) followed by overnight fixation in acetic alcohol (1:3) at room temperature, maceration in 1N HCl for eight minutes at 60° C, staining in Feulgen's solution for $\frac{1}{2}$ to 2 hours, and squashing in acetocarmine.

The chromosome numbers of 287 plants from 119 naturally occurring British and European populations of *T. inodorum* were counted. The results are summarized in Figs. 1 and 2 and Table 1. A number of plants originating from populations cultivated in Botanic Gardens were also counted but are not shown in the maps and table; those from Lyons, Nancy, Turin, Hamburg, Kassel, Leipzig, Munich, Aarhus, Lund, Cluj (Rumania), Riga, Athens, Ashkhabad and Vladivostok were tetraploid ($2n = 36$) and only the plants grown in Rouen Botanic Garden 'de la flore Normande' were diploid ($2n = 18$).

Although no material could be obtained from most of western Germany and the Low Countries, the general picture of the distribution of the cytotypes is clear, taking into account the counts made previously by German and Scandinavian workers. Tetraploid *T. inodorum* has a continental distribution, occurring mainly in eastern, north-eastern and central Europe; diploid *T. inodorum* has an Atlantic distribution, occurring in northern and western Europe. British *T. inodorum* is nearly all diploid, with a single isolated record of a tetraploid. Tetraploids and diploids meet in northern and eastern Germany, and tetraploids extend to northern and eastern France (Nancy and Strasbourg districts). The tetraploid plant found in Paris was collected in Montparnasse Cemetery, an unusual habitat for *T. inodorum*, and may, like the single British record of a tetraploid discussed below, have been a sporadic and temporary introduction.

The single record of tetraploid *T. inodorum* in Britain is extremely interesting. $2n = 36$ was found for the two plants that were counted in a morphologically uniform group of ten plants grown from achenes collected from a single isolated plant of *T. inodorum* found in barley stubble near Ardley in northern Oxfordshire in August 1962. The achenes of this plant resembled those of typical continental European plants in their rapid germination, and its offspring also resembled typical tetraploid plants in their habit and leaf-morphology. The self-fertility of the isolated Ardley plant was unusual, because strong self-incompatibility is normal in *T. inodorum*, a species which normally grows in populations, not as isolated individuals. The occurrence of a plant of *T. inodorum* in the Ardley area was also unusual in itself, because *Anthemis cotula* is the normal mayweed in the Ardley area; *Anthemis cotula* and *Tripleurospermum inodorum* have mutually exclusive distributions in the whole Oxford area (Kay 1965). The area in which the Ardley plant was found in 1962 was searched thoroughly two years later, in 1964, but no plants of *T. inodorum* were found, although *Anthemis cotula* was still abundant. It therefore seems likely that the tetraploid plant of *T. inodorum* found at Ardley was a temporary and isolated introduction, perhaps originating from grass-seed imported from Scandinavia; *T. inodorum* achenes are a common and abundant contaminant of Scandinavian grass-seed (Kolk 1962) and Scandinavian *T. inodorum* is normally tetraploid (Vaarama 1953). It is probable that tetraploid *T. inodorum* has been repeatedly introduced into Britain as a contaminant of crop-seed, and

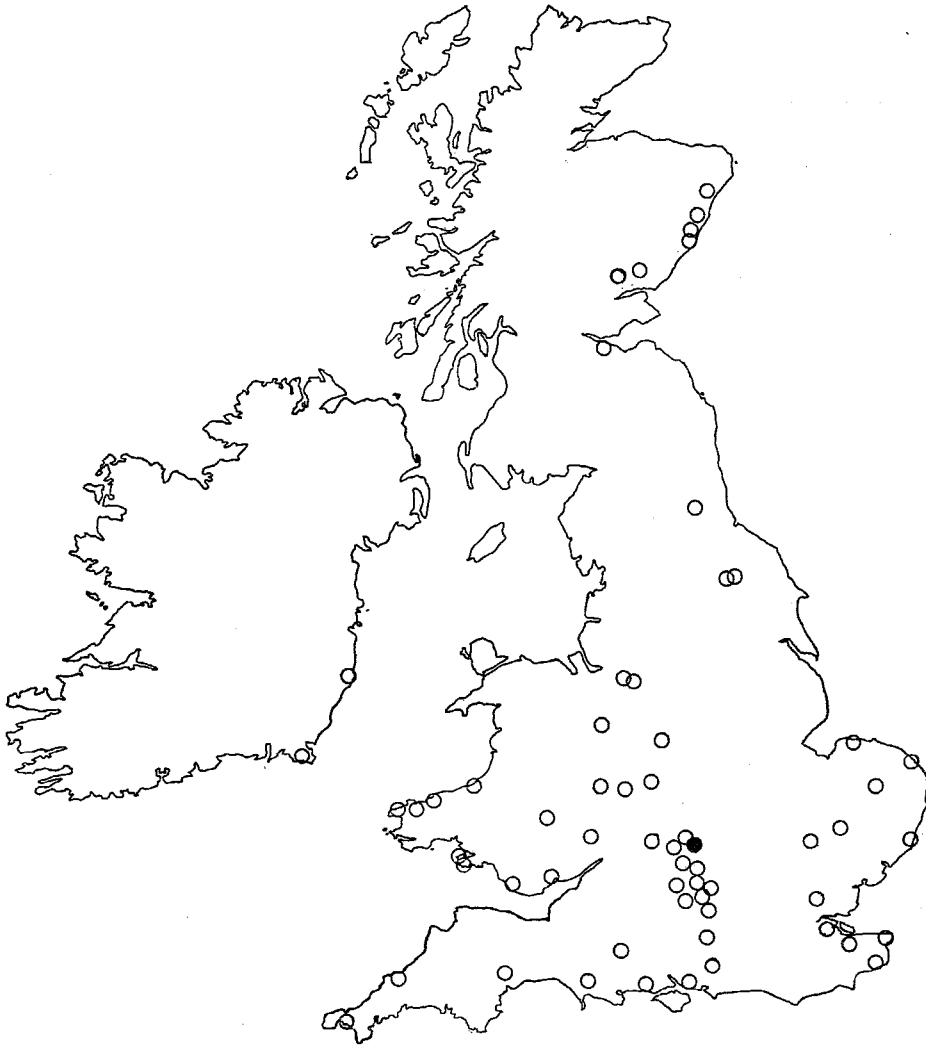


Fig. 1. Distribution of the cytotypes of *T. inodorum* in the British Isles. ○— $2n=18$; ●— $2n=36$.

its failure to establish itself here may have been due partly to poor adaptation to local ecological conditions and partly to inbreeding depression in small isolated pioneer populations (as perhaps at Ardley), but the major factor involved in its exclusion has possibly been reproductive interaction with the well-established and numerically superior diploids (see below).

Diploid and tetraploid *T. inodorum* are morphologically and ecologically very similar to one another. Several populations of each cytype have been compared by Rottgardt (1956) and Kay (1965) with similar results. When grown side by side under identical conditions, tetraploid plants usually grow faster, to a larger size, and have a more erect habit than diploid plants; but some populations of diploids are indistinguishable from tetraploids in these characters even in comparative cultivation, and diploids are usually indistinguishable from tetraploids in the field. Tetraploids nearly, but not quite, always have pollen

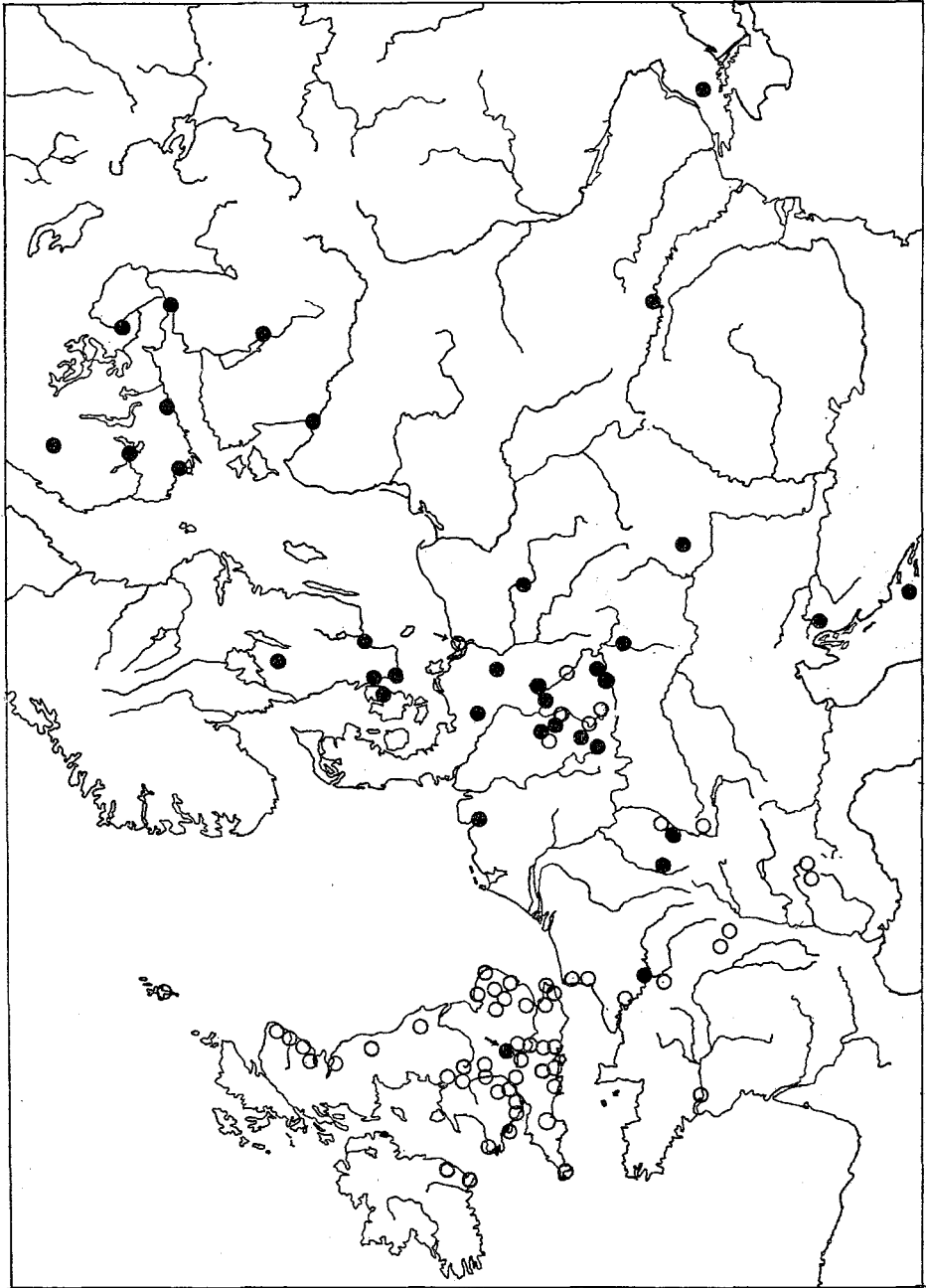


Fig. 2. Distribution of the cytotypes of *T. inodorum* in Europe. O— $2n=18$; ●— $2n=36$.

TABLE 1. Location, habitat, year of collection, number of individuals counted and chromosome numbers found for sampled populations of *T. inodorum*.

Abbreviations used: Ar, cultivated land; Rs, roadside; R, waste place; W, spontaneous but precise habitat not known; a, achene; pl, plant.

Location		Habitat	Year of collection	Number of individuals counted	Chromosome numbers (2n)
<i>British Isles</i>					
Perranuthno.	SW 541 293	Ar	1963	3a	18
Polzeath	SW 957 753	Rs	1962	1a	18
Exeter	SX 976 930	Ar	1963	3a	18
Dorchester	SY 680 904	Rs	1963	3a	18
Salisbury	SU 046 209	Ar	1963	2a	18
Bransgore	SZ 190 970	Ar	1963	3a	18
Fareham	SU 591 061	Ar	1962	3a	18
Harting	SU 774 200	Ar	1962	2a	18
Odiham	SU 728 484	Ar	1962	2a	18
Reading	SU 714 688	Ar	1962	3a	18
Cuxton	TR 717 673	Ar	1963	4a	18
M2	TQ 903 593	Rs	1963	2a	18
Dover	TR 336 442	Ar	1963	3a	18
Manston	TR 340 654	Ar	1963	2a	18
Ross-on-Wye	SO 644 260	Rs	1966	2a	18
Stow-on-the-Wold	SP 154 274	R	1966	3a	18
13 sites in Oxfordshire and Berkshire		Rs, Ar	1962	15pl, 3a	18
Ardley, Oxon.	SP 549 287	Ar	1962	2a	36
Heyford	SP 497 266	Ar	1962	2pl	18, 18 + 1B
Ipsden	SU 634 840	Rs	1962	2pl	18, 18 + 1B
Brentwood	TQ 634 897	Rs	1963	1a	18
Aldeburgh	TM 463 558	R	1963	2a	18, 18 + 1B
Bury St. Edmunds	TL 797 639	Ar	1962	3a	18
Eltisley	TL 267 588	Ar	1962	2pl	18
Wymondham	TM 091 993	Ar	1963	3a	18
Happisburgh	TG 379 314	Ar	1963	4a	18
Brancaster	TF 795 443	W	1962	2pl	18, 18 + 1B
Cleobury Mortimer	SO 659 766	Ar	1967	2a	18
Kidderminster	SO 893 791	Rs	1967	3a	18
Birmingham	SP 047 838	R	1967	2a	18
Burton-on-Trent	SK 149 257	Ar	1962	2a	18
Whitchurch	SJ 562 368	Ar	1967	3a	18
Dunhamtown	SJ 734 882	Ar	1962	2a	18, 18 + 1B
Dunhamtown	SJ 713 905	Ar	1962	3a	18
Stillington	SE 577 664	Ar	1962	2a	18
Stillington	SE 582 673	Rs	1962	2a	18
Piercebridge	NZ 208 217	Ar	1962	3a	18
Llanrhian	SM 814 308	Ar	1967	3a	18
Fishguard	SM 969 358	Ar	1963	3a	18
Cardigan	SN 125 382	Ar	1963	2a	18
Aberaeron	SN 459 623	R	1964	3a	18
Llangennydd	SS 437 916	Ar	1964	3a	18, 18 + 1B (once)
Paviland	SS 447 867	Ar	1967	2a	18
St. Brides Major	SS 909 727	Ar	1967	1a	18
Coedkernew	ST 262 841	Rs	1966	2a	18
Hay-on-Wye	SO 194 399	Ar	1967	3a	18, 18 + 1B, 18 + 2B
Queensferry	NT 155 770	Ar	1962	3a	18
Coupar Angus	NO 213 391	Ar	1962	2a	18
Tannadice	NO 505 577	Ar	1962	1a	18

<i>Location</i>	<i>Habitat</i>	<i>Year of collection</i>	<i>Number of individuals counted</i>	<i>Chromosome numbers (2n)</i>
<i>British Isles—(cont.)</i>				
Stonehaven NO 894 900	Ar	1962	2pl	18
Reinchall NO 853 935	Ar	1962	3a	18, 18 + 1B (once)
Bucksburn NJ 884 106	Ar	1962	2a	18
Newburgh NJ 937 269	Ar	1962	2a	18
Scalloway, Shetland	W	1962	1a	18
Lady's Island, Wexford	Ar	1966	3pl	18
Kilbride, Wicklow	Ar	1964	2pl	18
<i>France</i>				
Nantes	W	1965	3a	18
Grand-Quevilly (Rouen)	W	1964	1a	18
Palaiseau 48·43N, 2·14E	Ar	1963	3a	18
Paris—Montparnasse	R	1963	2a	36
24 km N of Abbeville	Rs	1963	3a	18
9 km S of Le Touquet	Rs	1963	3a	18 + 1B (twice), 18 + 2B
Marigny l'Eglise 47·21N, 3·56E	W	1967	4a	18
Dompierre-en-Morvan 47·15N, 4·15E	Ar	1966	2a	18
Bonneval-sur-Arc 45·22N, 7·03E	Ar	1966	2a	18
Lanslevillard (Savoie)	W	1966?	2a	18
Nancy	W	1967	3a	36
Strasbourg	Ar	1962?	2a	36
Bas-Rhin	Ar	1962?	1a	18
<i>Germany</i>				
Freiburg im Breisgau	Ar	1967	4a	18
Ems estuary	W	1966?	3a	36
Rohrsen (Weser)	W	1967	3a	36
Rudolstadt 50·44N, 11·20E	W	1967	2a	18
Ballenstedt (Harz)	W	1966	3a	18
Roblingen-See (22 km W of Halle)	W	1966	3a	18
Hornburg 52·02N, 10·38E	W	1965	3a	36
Grabsleben, Gotha	W	1965	3a	36
Halberstadt 51·54N, 11·04E	W	1966	3a	36, 37 (once)
Lengenfeld (Vorgtland)	W	1965	3a	18
Lommatzsch 51·12N, 13·19E	W	1967	3a	18
Dessau 51·51N, 12·15E	W	1967	3a	36
Elster 51·50N, 12·49E	W	1966	3a	36
Parchim 53·26N, 11·51E	W	1966	3a	36
Gransee 53·00N, 13·10E	W	1963	2a	36
<i>Poland</i>				
Wolin 53·51N, 14·38E	W	1960	3a	18
Szczepankowo (Poznan)	W	1962	3a	36
Pokrzywno, nr. Poznan	W	1967?	2a	36
<i>Czechoslovakia</i>				
Kadaň 50·23N, 13·15E	Rs	1961	2a	36
Most 50·31N, 13·39E	W	1961	1a	36
Prague (3 sites)	Ar	1961	5a	36
Ivanka 48·14N, 18·07E	W	1967?	3a	36
<i>Yugoslavia</i>				
Viš 43·03N, 16·11E	W	1965	3a	36, 37 (once)
Ogulin 45·16N, 15·14E	W	1967?	3a	36

Location	Habitat	Year of collection	Number of individuals counted	Chromosome numbers (2n)
<i>Denmark</i>				
Tastrup 55·29N, 10·19E	Ar	1962	3a	36
<i>Sweden</i>				
Landskrona 55·53N, 12·50E	W	1964	2a	36
Bunkeflo 55·34N, 12·59E	W	1967	3a	36
Bäckaskog 56·05N, 14·20E	W	1967	3a	36
Vartofta-Åsak 58·06N, 13·40E	W	1967	3a	36
<i>Finland</i>				
Sauvo 60·22N, 22·44E	W	1967?	3a	36
Porvoo 60·24N, 25·40E	W	1966?	3a	36
Nokia 61·29N, 23·31E	W	1967?	3a	36
Kinnula 63·24N, 25·00E	W	1966?	3a	36
<i>U.S.S.R.</i>				
Salaspils (Riga)	W	1962?	4a	36, 35 (once)
Pskov	W	1962?	3a	36
Leningrad	W	1962?	2a	36
Prislersk 61·01N, 30·08E	W	1962?	3a	36
Kamenets-Podolski	W	1962	3a	36
Askaniya Nova 46·27N, 33·53E	W	1966	3a	36

grains twice the volume of those from diploids. Tetraploid achenes usually germinate more rapidly and completely than diploid achenes; high dormancy is especially marked in British diploids, but achenes from north German diploids closely resemble achenes from tetraploids growing in the same area in their germination behaviour. Only one morphological character has been found to differentiate diploids from tetraploid consistently in comparative cultivation—the shape of the terminal lobes of the first true leaves of the seedling, which are relatively broad and blunt in tetraploids but narrow and acute in diploids (Kay 1965).

Ecologically, the cytotypes are phytosociologically indistinguishable; diploid and tetraploid fill the same niche in the weed community. The overall distributions of the cytotypes suggest differing climatic adaptations, with the diploids adapted to wetter and more maritime climates, and the few observations that have been made of their ecological preferences in the zone of overlap tend to confirm this. Rottgardt (1956) noted that, in Schleswig-Holstein, the diploids occurred on the uplands and on poorer sandy soils, the tetraploids in the lowlands; in East Germany, diploids are found in upland areas and near the Baltic coast, tetraploids elsewhere.

Neither mixed populations of diploid and tetraploid *T. inodorum* nor naturally occurring triploids have yet been reported. It is interesting to consider the possible course of events in a natural mixed population, such as may often be formed when crop-seed containing achenes of one cytotype as a contaminant is sown in a field already containing the other cytotype. *T. inodorum* is a strongly self-incompatible annual plant, cross-pollinated mainly by flies, and triploid seed can readily be formed in high yield by crossing diploids and tetraploids (Kay 1965). The triploid plants resulting from crossing are, although vigorous, of extremely low fertility, and triploid seed is, from the reproductive point of view, wasted. The cytotype producing the smaller number of flowers in a mixed population will lose a higher proportion of its progeny in the production of triploids, and should be eliminated in a few generations. Thus mixed populations of diploids and tetraploids are likely to be unstable and transitory and, in the absence of marked ecological differences between the cytotypes, the first cytotype to establish a sufficiently large population in a

hitherto unoccupied area (a frequent event for an aggressive weed of arable land) is likely to quickly eliminate pioneer plants of the other cytotype and to remain in possession. The boundary between an area occupied by diploids and an area occupied by tetraploids is likely to be sharp and may coincide with a field border; the areas could be inter-digitated with enclaves of one cytotype lying well within the area of the other. This kind of situation, 'obligate allopatry', hypothetical for the cytotypes of *T. inodorum*, has been shown to exist between *Clarkia biloba* and *C. lingulata* (Lewis 1962).

THE ORIGIN OF DIPLOID AND TETRAPLOID *T. INODORUM*

T. inodorum is a weed of man-made habitats, arable land and waste places, and appears to have no natural habitat in the greater part of its range. It is most abundant and widespread in western, northern, central and eastern Europe; it is absent from the Mediterranean region and it is local in south-central Europe (the Alps), south-eastern Europe, Asia Minor, the Caucasus and central Asia. The only natural habitats in which apparently native populations of *T. inodorum* maintain themselves at the present day are *solonchak* regions on the Lower Volga and mountain slopes in the Caucasus. These populations are morphologically rather different from typical *T. inodorum*, with the ray-florets often short or absent, but fall within the extreme limits of variation found in other populations of the species (Pobedimova 1961).

(a) *Diploid T. inodorum*

Diploid *T. inodorum*, which appears to have no natural habitat at present (if, as seems probable, the Volga and Caucasus populations are tetraploid), has three likely modes of origin:

1. From *T. maritimum*
2. From the common ancestor of *T. maritimum* and *T. inodorum*
3. From a Caucasian or central Asian species unrelated to *T. maritimum*.

T. maritimum is diploid and almost completely inter-fertile with diploid *T. inodorum* (Kay 1965), with which it is sympatric in a large part of the native range of *T. maritimum* on the coasts of western and northern Europe. It is easy to suppose that *T. inodorum* might have originated from *T. maritimum* since the spread of agriculture to the Atlantic coasts in about 3,000 B.C. There are, however, considerable ecological, morphological and physiological differences between *T. maritimum* and *T. inodorum*, and the discovery of achenes which appear to belong to *T. inodorum* in a Late Pleistocene deposit at Upton Warren in Worcestershire (Coope, Shotton & Strachan 1961) dating from the beginning of the Gottweig Interglacial, about 42,000 years ago, suggests that a recent origin from *T. maritimum* is unlikely. The third possible mode of origin of diploid *T. inodorum*, from a Caucasian or central Asian species unrelated to *T. maritimum*, seems ecologically, geographically, and genetically unlikely. The second possible mode of origin, divergence from a common ancestor, is supported by the interfertility and similarity in geographical range but sharp ecological separation of diploid *T. inodorum* and *T. maritimum*. The initial separation of the two species may have taken place in the early Pleistocene. Diploid *T. inodorum* may have originally occupied a natural habitat that no longer exists as such. One possible habitat is in the vicinity of drinking-places used seasonally by wild herbivores, especially in lowland areas, where the soil may have been heavily trampled in winter and spring but relatively undisturbed in summer. This kind of habitat may have been rather similar to the farmyards in which *T. inodorum* now flourishes, and the Upton Warren site, where *T. inodorum* was associated with a number of other weeds including *Polygonum aviculare* and *Potentilla anserina*, may have been of this type. *T. inodorum* achenes survive burial in soil well (Kay 1965), and retain 30 per cent. of their initial germinating capacity after passage through the bovine digestive tract (Dorph-Petersen 1925).

(b) *Tetraploid T. inodorum*

Although tetraploid *T. inodorum* is morphologically very close to diploid *T. inodorum*, it is not necessarily an autotetraploid derived from diploid *T. inodorum* by chromosome doubling. Vaarama (1953) considered it to be an allotetraploid derived from '*T. maritimum* ssp. *maritimum*' (*T. maritimum*) and '*T. maritimum* ssp. *ambiguum* var. *boreale*' (northern diploid *T. inodorum*), but this apparent allotetraploidy could be secondary, the consequence of chromosomal rearrangements in an autotetraploid. Allotetraploidy resulting from doubling of the chromosome number in a sterile diploid interspecific hybrid is most unlikely in this case; all the F_1 hybrids between species of *Tripleurospermum* that I have obtained (*T. inodorum* \times *T. maritimum*, *T. inodorum* \times *T. tchichatchevii*, *T. inodorum* \times *T. disciforme*, *T. inodorum* \times *T. decipiens*, *T. disciforme* \times *T. decipiens*, *T. inodorum* \times *T. tenuifolium*) have proved to be fertile (see below) and even if a sterile interspecific hybrid were formed it would be unlikely to persist vegetatively until chromosome doubling took place, because *T. inodorum* and many other species of *Tripleurospermum* are annual or biennial. Rottgardt (1956) observed that the chromosomes of tetraploid *T. inodorum* are half the size of those of diploid *T. inodorum*, indicating that the doubling of the chromosome number took place some time ago.

Triploid hybrids between diploid and tetraploid *T. inodorum* can be produced very easily by ordinary cross-pollination. The triploid plants are vigorous. Trivalents predominate in pollen mother cell meiosis, averaging 4.85 per cell in 20 cells analysed; the plants are pollen sterile but, under favourable conditions, will set about 10 per cent. of the normal number of achenes when used as the female parent in crosses with diploids or tetraploids. The functional female gametes produced by the triploids can be either 'reduced' ($n = 12$ or 13) or unreduced (in the one example observed, $n = 26$). The aneuploid offspring of the triploids are less vigorous than their parents, but also, in some cases, have some degree of fertility (3–5 per cent.) on the female side; in principle, the diploid or tetraploid level might eventually be regained and gene-flow in both directions between diploid and tetraploid is theoretically possible (Kay 1965). Chromosome homology and hybrid fertility does not necessarily indicate an especially close relationship between taxa in *Tripleurospermum*. I have found that diploid F_1 hybrids between diploid *T. inodorum* and *T. disciforme* (C. A. Mey.) Schultz Bip. ($2n = 18$) and between diploid *T. inodorum* and *T. tenuifolium* (Kit.) Freyn ($2n = 18$) and tetraploid F_1 hybrids between tetraploid *T. inodorum* and *T. tchichatchevii* (Boiss.) Bornm. ($2n = 36$) are more than 50 per cent. seed fertile, with regular pollen mother cell meiosis, although *T. disciforme*, *T. tenuifolium* and *T. tchichatchevii* are morphologically and ecologically very different from one another and from *T. inodorum*.

Artificial autotetraploids have not yet been synthesized from diploid *T. inodorum* but I have synthesized artificial autotetraploid *T. maritimum* and it is moderately fertile (c. 25 per cent. as ovule parent, 50 per cent. as pollen parent) with relatively normal pollen mother cell meiosis (63 per cent. bivalent formation) producing a majority of normally reduced diploid ($n = 18$) gametes (Kay 1965). Thus low fertility resulting from meiotic irregularities is unlikely to have been a barrier to the establishment of newly-formed autotetraploid *T. inodorum*. However, *T. inodorum* is normally strongly self-incompatible; the self-incompatibility is sporophytic and tetraploids are as self-incompatible as diploids (Kay 1965), so a single autotetraploid plant would normally be unable to set seed by self-fertilization. Even if a small group of self-incompatible autotetraploids were to establish themselves in a numerically superior diploid population, they would eventually be eliminated because they would produce a greater proportion of triploid seed than the diploids. The best prospects for the establishment of autotetraploids appear to exist in small marginal and pioneer populations, growing in habitats where individual plants are often isolated from one another and the number of plants in the population may vary greatly from year to year. Roadside and botanic garden populations meet some of these criteria. One would expect self-fertility to be advantageous in this type of habitat, and self-fertility has in fact been found in a number of such populations of *T. inodorum* (Table 2). In the one case that I have analysed, self-incompatibility was recessive to self-fertility (Kay 1965). A single

original autotetraploid plant arising in a marginal habitat of this type in nature might be both self-fertile and isolated from other (diploid) *T. inodorum* plants, and could then establish a new tetraploid population; self-fertility in itself would, of course, confer a degree of isolation at first, but would presumably be selected against as the density of the tetraploid population increased. The whole process would resemble the mechanism of 'catastrophic selection' involved in the origin of new species of *Clarkia*, as described by Lewis (1962).

TABLE 2. Self-incompatibility and self-fertility in *T. inodorum* plants isolated in a greenhouse.

Origin	Total number tested		Self-fertile (at least 3 per cent. achene-set)		Self-incompatible	
	Plants	Popns.	Plants	Popns.	Plants	Popns.
British Isles $2n = 18$	75	24	9	2	66 (37)	24 (19)
$2n = 36$	3	1	2	1	1	1
Europe $2n = 18$	9	4	2	1	7 (2)	4 (2)
$2n = 36$	37	10	12	6	25 (10)	8 (5)

The figures in brackets show the number of cases in which unsuccessful selfings were checked by simultaneous successful crosses on the same plant.

The populations in which self-fertility was found were as follows: small roadside populations at Ipsden, Oxfordshire and Stillington, Yorkshire; a single isolated tetraploid plant at Ardley, Oxfordshire; Botanic Garden populations at Kassel (Germany), Turin (Italy), Cluj (Rumania) and Ashkhabad (Turkmenistan); cornfield populations (self-fertility low) at Tastrup, Denmark and Prague, Czechoslovakia; and a population of unknown status in Wolin Island, Poland. Some self-incompatible plants were also found in most of these populations.

The most likely mode of origin of tetraploid *T. inodorum* therefore appears to be by chromosome doubling from diploid *T. inodorum*, probably in marginal populations on the eastern boundary of the range of the species, preceded or followed by some hybridization with Caucasian or central Asian species of *Tripleurospermum*. Climatic changes may then have separated the diploids and tetraploids, with the diploids surviving in refugia in northern and western Europe (trampled places near water?) and the tetraploids surviving in refugia in south-eastern Europe or the Caucasus (solonchak areas?). Both tetraploids and diploids may have started their association with man as habitation-weeds, spreading into cultivated crops as agriculture developed and extending their ranges until they met again in central and northern Europe. Obligate allopatry may then have stabilized their ranges. The distribution of the cytotypes in Canada resembles their distribution in Europe, with diploids in the eastern Maritime Provinces and tetraploids in the more continental climate of the Prairies; this could be due in part to the differing climatic adaptations of the cytotypes, but an alternative and perhaps more likely explanation is that most of the *T. inodorum* introduced to eastern Canada came with French, Scottish and English settlers from western Europe, where diploids predominate, whereas most of the *T. inodorum* introduced to the Prairies came with crop-seed from northern and eastern Europe, where tetraploids predominate.

Much work remains to be done on the problem of the origin and inter-relationships of diploid and tetraploid *T. inodorum*, especially in the field in central Europe, on the status of the Volga solonchak populations, and on the relationships between *Tripleurospermum* spp. and *T. inodorum* in the Caucasus and the Middle East.

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