

## ASPECTS OF THE ECOLOGY OF SOME MICROSPECIES OF TARAXACUM IN THE NETHERLANDS

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### SUMMARY

The present report deals with the dandelion flora of 78 lots of grassland from the coastal area and from the interior. It appeared that grassland types under the same agricultural management and with a similar phytosociological character also exhibit a similarity in their *Taraxacum* flora; when they differ in these respects they also have a different dandelion flora, which differences tend to increase as the vegetational and agricultural differences become greater.

Several microspecies of the section *Taraxacum* may occur sympatrically in the same type of pasture, the stronger the manuring and grazing the greater the number of co-existing taxa (up to 19 per 125 m<sup>2</sup> have been recorded).

In near-natural dune habitats representatives of the sections *Erythrosperma* and *Obliqua* are the most common, in grazed ones the number of taxa belonging to these two sections tends to be lower. Representatives of the sections *Palustria* and *Spectabilia* have exclusively been found in unfertilized or but lightly fertilized grasslands and are now of rare occurrence. Those of sect. *Taraxacum* are very common and are frequently encountered in agricultural pasture land, the number of microspecies represented increasing as the agricultural pressure increases.

It proved to be possible to distinguish within these sections microspecies with a broad ecological range and other ones with a much narrower amplitude, the latter apparently being more specialized ecologically. Among the *Taraxacum* microspecies those with a broad ecological tolerance find their optimum in the not strongly fertilized and grazed pastures and they may, therefore, be regarded as the older microspecies among the Dutch *Taraxacum* aggregate. The microspecies from heavily fertilized and grazed pastures must be considered to be specialized and apparently constitute the youngest among the complex.

### 1. INTRODUCTION

Dandelions belong to the most common species of the Dutch flora. The genus *Taraxacum* is represented in The Netherlands by five sections, viz., *Erythrosperma* (with 23 microspecies), *Obliqua* (with 1 microspecies), *Palustria* (with 10 microspecies), *Spectabilia* (with 9 microspecies) and sect. *Taraxacum* (= sect. *Vulgaria*, with 153 microspecies). All sections have recently been taxonomically treated by HAGENDIJK et al. (1975, 1982).

ØLLGAARD (1983) has segregated a group of microspecies from sect. *Taraxacum* to form a new section *Hamata* (see also MOGIE & RICHARDS 1983). This section is also represented in The Netherlands. Since Øllgaard's paper appeared when our manuscript was ready for the press the new section is only mentioned here in passing.

Sect. *Obliqua* is restricted in its occurrence to the coastal region, sect. *Erythrosperma* is found along the coast and also inland (namely in open grassland vegetation on dry and humic, sandy soils), the sections *Palustria* and *Spectabilia* prefer not or hardly fertilized, wet grasslands and have become increasingly rarer, and the by far largest sect. *Taraxacum* is very common throughout the country; it is mostly found at trodden sites, in road-sides and in fertilized and grazed pastures. Since *Taraxacum* was only recently treated monographically, data concerning the ecology and distribution of the Dutch microspecies are scarce and, besides, the ecological records are mainly of a phytosociological nature (BOERBOOM 1957, 1960; DEN NIJS et al. 1978; DOING 1964, 1966; FENGLER 1978; HAGENDIJK et al. 1975, 1982; LOENHOUD & DUYS 1981; LONDO 1978; OOSTERVELD 1978; WESTHOFF & DEN HELD 1975). Representatives of the sect. *Taraxacum* figure frequently in agriculturally oriented literature, but the microspecies are not distinguished. As a rule the authors use the name *Taraxacum officinale* in a collective sense and most probably also microspecies of the sections *Palustria* and *Spectabilia* are included (KRUIJNE et al. 1967).

Investigations into the distribution of the various species have shown that several species may occur sympatrically in the same biotope. Both in natural and in grazed dune grasslands in The Netherlands, four to eight microspecies of sect. *Erythrosperma* may occur at the same site and sometimes even sympatrically with a few microspecies of sect. *Taraxacum* (DEN NIJS et al. 1978). In a small number of pasture types up to 10 microspecies of *Taraxacum* have been recorded per 125 m<sup>2</sup> (FENGLER 1978). According to OOSTERVELD (1978) in pastures under an average kind of management which turn completely yellow in spring from the flowering dandelions, usually from about 20 to about 30 microspecies of sect. *Taraxacum* may be represented. Also elsewhere in Europe microspecies of *Taraxacum* frequently occur sympatrically and synoecially (FORD 1981a; VON HOFSTEN 1954; GADGIL & SOLBRIG 1972; KAPPERT 1954; NILSSON 1947 and RICHARDS 1970).

In order to gain a better insight into the ecology of the Dutch microspecies of *Taraxacum* a study was made of their occurrence in natural and in extensively grazed dune grasslands, in little fertilized and grazed meadows, and in strongly fertilised and in intensively grazed, agricultural pastures. This selection of habitats ensured the inclusion of representatives of all Dutch sections in the inquiry.

The acquisition of data concerning the ecology of the microspecies may not only yield important information about the processes of niche differentiation and micro-evolution, but also contribute towards a better insight in the phenomenon of co-existence of (micro-)species. Speaking in a general sense, one might say that co-existence of related species in the same area has been a moot point ever since Darwin's time (GRANT 1971; GRUBB 1977; BRAAKHEKKE 1980). As far as the genus *Taraxacum* is concerned, recent investigations strongly suggest that microspecies are fine-tuned to their specific environment (FORD 1981a, b; LOENHOUD & DUYS 1981).

## 2. METHODS

The distribution of the microspecies was studied by means of samples taken from selected grasslands; the latter having been chosen on account of the following criteria:

- (a) The presence of a certain kind of *Taraxacum* flora: in the dune region habitats were looked for where representatives of sect. *Erythrosperma* occurred exclusively and such where microspecies of sect. *Erythrosperma* and/of sect. *Taraxacum* occurred sympatrically; in agricultural pastures both sites with microspecies of the sections *Taraxacum*, *Spectabilia* and *Palustria*, and sites with only microspecies of sect. *Taraxacum* were selected, but no special selection for microspecies was intended; the plants gathered were identified later.
- (b) Ecological differentiation: the most important criteria being vegetational composition and management, soil type and water regime.

### 2.1. Vegetation sampling and description

Dune grasslands are usually inhomogeneous and have a mosaic-like vegetation pattern. They have mostly been analysed by means of the methods of the French-Swiss school of phytosociology (BOERBOOM 1957, DOING 1964), and in the present inquiry the same technique was followed. The relevés were made in the usual way of  $3 \times 3 \text{ m}^2$  sample plots in physiognomically homogeneous vegetation differentiants (GROENHART in prep.). The scale of estimation of LONDO (1975) was used. The results are shown as the relevé-groups 1, 2 and 3 in table 1.

The Dutch agricultural grasslands were intensively studied by KRUIJNE et al. (1967), by means of a method previously described by MOOI (1960) and also used in the present investigation (for which 30 stand samples of  $25 \text{ cm}^2$  each were taken from an area of about  $125 \text{ m}^2$ ). The results are tabulated as relevé-groups 4 and 5.

The vegetation samples and the species present were mutually condensed to clusters of scores. The clusters are formed by mutual rearrangements (GROENHART in prep.). The clusters thus obtained were phytosociologically characterized by character species and differentiating species of the phytocoena according to the classification as rendered by WESTHOFF & DEN HELD (1975) and subsequently transformed into phytosociological spectra. These spectra were correlated with the local representation of the microspecies of *Taraxacum*.

The relation between microspecies of *Taraxacum* and the abiotic environment was studied by transforming the relevés into ecological indication values according to ELLENBERG (1974) and KRUIJNE et al. (1967).

In our investigation per relevé the mean indication value was calculated, the percentage cover or the percentage of occurrence of the constituting species in the relevés being taken into account. The factors nitrogen, phosphate and potassium were included in the calculations and as indication values used for a direct ordination to determine the relative ecological position of the microspecies of *Taraxacum*. "Direct" is used here in the sense of an X-Y-ordination of the eco-factors. The relative ecological position was only determined for those micro-

species of *Taraxacum* which were recorded in more than 8 relevés; this was done because in the case of microspecies which have but rarely been found in grasslands chance may play a relatively important role, especially in view of the ample possibilities of dispersal and the high rate of achene production of microspecies of *Taraxacum*. In the case of the relevés from the dunes only the indication values according to ELLENBERG (1974) could be employed because KRUIJNE et al. (1967) do not give any indication values for the majority of the coastal species.

## 2.2. Sampling of the microspecies of *Taraxacum*

The occurrence of the various microspecies of *Taraxacum* was established by gathering 30 flowering individuals from a surface area of about 125 m<sup>2</sup>. The samples were collected systematically. To this end an imaginary meshwork was laid over the plot and on the intersection of the meshwork or as closely as possible to them a flowering specimen was gathered.

The nomenclature of the species is according to HEUKELS-VAN OOSTSTROOM (1977) except for the microspecies of *Taraxacum* which is adopted from HAGENDIJK et al (1975, 1982); for the nomenclature of the syntaxonomical units WESTHOFF & DEN HELD (1975) is followed except for the name *Lolio-Potentillion anserinae* (= *Agropyro-Rumicion crispi*) (SYKORA 1983).

All microspecies of dandelions have been identified or verified by the specialists mr. A. Hagendijk, prof. dr. J. L. van Soest and Mr. H. A. Zevenbergen. When dandelion material was submitted for identification the same phenomenon as previously encountered was noted, viz., that not all flowering specimens of *Taraxacum* could be named. HAGENDIJK et al. (1982) mentioned a number of possible causes of this problem, but this is irrelevant to the present study because it has not essentially affected our results.

## 3. SITES INVESTIGATED

The microspecies of the sections *Erythrosperma* and *Obliqua* were studied in dry dune grasslands of the coastal area. In the Noordhollands Duinreservaat (Province of N.Holland) 16 near-natural stands of grassland (13 near Egmond aan Zee and 3 near Wijk aan Zee) and 7 extensively grazed (or formerly grazed) ones (near the Koningsbos, Bakkum) were sampled (VAN DER HAMMEN 1977; DEN NIJS et al. 1978). In the island of Terschelling (Province of Friesland) the sampling occurred in a single stand of near-natural dune vegetation (near Formerum) and in 5 extensively grazed dune grasslands (4 near Oosterend and 1 near West-Terschelling) (FENGLER 1978). The latter ones are usually situated in the inner dunes.

Microspecies of the sections *Taraxacum*, *Palustris* and *Spectabilia* were studied in wet to moderately moist pastures in Terschelling and in the Krimpenerwaard (Prov. of Zuid-Holland), the Tielerwaard and the Bommelerwaard (Prov. of Gelderland). In Terschelling 17 grassland plots were studied comprising meadows (some subsequently grazed) and in addition extensively grazed and

Table 1. Phytosociological spectra of the stands of dune and grassland communities studied (see text):

Bo = Bommelerwaard, K = Krimpenerwaard, N = Noordhollands Duinreservaat, T = Terschelling, Ti = Tielerwaard, a = absent, cp = clay on peat, e = extensively grazed, he = heavily fertilized, hs = humic sand, i = intensively grazed, li = lightly fertilized, m = meadows, n = nature reserve, pa = pasture, p = peat, rc = river clay, s = sand.

Relevégroup	Mean percentage cover			Mean relative frequency in %	
	1	2	3	4	5
Habitat	Dunes	Dunes	Grassland	Grassland	Grassland
Locality	N	N, T	T	K, Ti, Bo	K, Ti
Use	n	pa, n	pa	pa	pa
Grazing	a	e	a, e	a, e	i
Fertilizing	a	a	a, li	a, li	he
Soil	s	s	hs, s	cp, p, rc	cp, rc
Number of relevés	16	12	17	16	17
<hr/>					
Bidentetea			0,4	0,3	1,4
Chenopodietea	6,8	10,0	4,7	5,4	17,1
Ammophiletea	2,3	0,4	0,6		
Plantaginea	9,2	27,1	48,0	29,2	46,4
Artemisietea	0,8		6,4	7,2	8,4
Phragmitetea			0,7	8,4	1,2
Koelerio-Corynepherea	46,2	51,7	6,4	3,4	1,2
Saginea			10,3		
Asteretea			1,3		
Molinio-Arrhenatheretea	4,7	6,4	20,0	43,6	24,4
Nardo-Callunetea	2,8	1,4			
Rhamno-Prunetea	27,1	2,7			
Alnetea				2,2	0,4

little fertilized pastures; the latter are situated in the dunes on moist to moderately wet sandy soil or on sandy soil in the zone of transition between the dunes and salt-marshes. At some sites there was some saline influence.

In the Krimpener-, Tieler- and Bommelerwaard the distribution of microspecies of *Taraxacum* was investigated in two kinds of grassland, viz.,

(a) In damp to moderately wet, unfertilised or little manured meadows of which 10 were situated in nature reserves in the Krimpenerwaard on a mineral-poor peaty soil or on a soil type of clay on peat and 6 in nature reserves in the Tieler- and Bommelerwaard on heavy and badly drained basin clays.

(b) In moderately moist, well-drained and usually intensively grazed and heavily fertilized grasslands in the Krimpenerwaard on both peaty and clayey soils and on the more raised parts of the Tieler- and Bommelerwaard on fairly heavy river clay.

#### 4. RESULTS

##### 4.1. Microspecies of the sections *Erythrosperma* and *Obliqua*

###### 4.1.1. Their occurrence in the stand

The stands of vegetation in which the dandelions were found appeared to be classifiable into two groups on account of their floristic resemblances and differences, the one group comprising the natural dune grasslands (1) and the other (2) the grazed dune grasslands. The phytosociological spectra of the two groups based on character species and differentiating species according to WESTHOFF & DEN HELD (1975) are shown in *table 1*. It appears that in both groups species of the *Koelerio-Corynephoretea* (*Galio-Koelerion*) predominate. The alliance *Galio-Koelerion* includes the vegetation types of dry and fairly basic to somewhat acid coastal dunes. The stands summarised in the spectra indeed belong to this syntaxon. It appears that a further classification to the association level is not possible because most probably we are dealing here with association complexes.

Some clear-cut differences between the near-natural and the grazed dune plots are:

- (a) the more common occurrence and/or greater percentage cover of species of the *Rhamno-Prunetalia* (dune scrub) in the natural grasslands, and
- (b) the more common occurrence and/or higher percentage cover of *Plantagine-tea* species in the grazed plots, which is indicative of disturbance in the form of treading and cattle grazing.

The microspecies of *Taraxacum* found in the sampling plots studied are shown in *table 2* which clearly indicates that the dandelion flora of the two series of relevés is different. The natural stands are upon the whole richer in microspecies of *Obliqua* and *Erythrosperma* than the grazed ones, which is also evident from the number of microspecies recorded per relevé and per dandelion sample (see *table 3*). The mean number of microspecies recorded is 6 in the first series and 3 in the second. It is also clear that the habitat of the grazed plots is not very suitable for a number of microspecies of *Erythrosperma*, viz., *T. taeniatum*, *T. commixtum*, *T. oxoniense* and also for *T. obliquum* (sect. *Obliqua*), and presumably not for *T. brachyglossum* either. It seems as if *T. scanicum* prefers the grazed habitat. *T. proximum* and *T. silesiacum* are too rare in the area studied to permit pertaining ecological conclusions.

*T. rubicundum*, *T. tortilobum* and *T. lacistophyllum* occur both in the near-natural and in the grazed plots, evidently because they have a wider ecological amplitude than the afore-going groups of microspecies. Also in the phytosociological literature these three species are reported to have a broader eco-amplitude than *T. taeniatum*, *T. commixtum* and *T. obliquum*. *T. tortilobum* is considered to be a character species of the order *Festuco-Sedetalia* (*Koelerio-Corynephoretea*) and *T. rubicundum* and *T. lacistophyllum* are said to be character species of the alliance *Galio-Koelerion* (*Koelerio-Corynephoretea*), as against *T. taeniatum* and *T. obliquum*, which have been recorded as character species at the association level, both of the *Taraxaco-Galietum maritimi* (*Galio-Koelerion*), and *T. commixtum* which is also a character species of an association, the *Anthyllido-Silenetum nutantis* (*Galio-Koelerion*) (WESTHOFF & DEN HELD 1975).

Table 2. The *Taraxacum* flora of the grasslands studied. The presence is given per species according to the following scale code: “-” means represented in < 16%, “+” 16-33%, “++” 33-50% and “+++” in > 55% of the relevés, E = sect. *Erythrosperma*, O = sect. *Obliqua*, P = sect. *Palustris*, S = sect. *Spectabilia*, T = sect. *Taraxacum*.

Bo = Bommelerwaard, K = Krimpenerwaard, N = Noordhollands Duinreservaat, Te = Terschelling, Ti = Tielerwaard.

a = absent, cp = clay on peat, e = extensively grazed, he = heavily fertilized, hs = humic sand, i = intensively grazed, li = lightly dunged, m = meadow, n = nature reserve, pa = pasture, p = peat, rc = river clay, s = sand.

Relevégroup	Representation of individuals					
	1	2	3	4	5	
Habitat	Dunes	Dunes	Grassland	Grassland	Grassland	
Locality	N	N, Te	Te	K, Ti, Bo	K, Ti	
Use	n	pa, n	m, pa	m, pa	pa	
Grazing	a	e	a, e	a, e	i	
Fertilizing	a	a	a, li	a, li	he	
Soil	s	s	hs, s	cp, p, rc	cp, rc	
Number of relevés	16	12	17	16	17	

T. proximum	(E)	-			
T. silesiacum	(E)	-			
T. brachyglossum	(E)	+			
T. obliquum	(O)	++			
T. taeniatum	(E)	+++			
T. oxoniense	(E)	+++			
T. commixtum	(E)	+++			
T. rubicundum	(E)	+++	+++		
T. tortilobum	(E)	+++	+++	-	
T. lacistophyllum	(E)	+++	+++		
T. scanicum	(E)		+		
T. unquifrons	(T)	-			
T. pachymerum	(T)	-			
T. vastisectum	(T)	-			
T. planoides	(T)	-			
T. dahlstedtii	(T)	+			
T. obtusilobum	(T)				
T. haematicum	(T)			+	
T. wijtmaniae	(T)			+	
T. cordatum	(T)			+	
T. friscum	(P)				
T. hamiferum	(T)			+	
T. atactum	(T)			++	
T. raunkiaeri	(T)	-		++	
T. bracteatum	(T)			+++	
T. rubrisquameum	(T)			+++	
T. nordstedtii	(S)			+++	+
T. adamii	(T)			+++	+
T. hollandicum	(P)				++
T. hamatulum	(T)			+++	++
T. hamatum	(T)			+++	++
T. hamatiforme	(T)	-		+++	++
T. quadrans	(T)			+++	++
T. fulgidum	(T)			++	++

Relevégroupp		1	2	3	4	5
T. hamatum group	(T)			-	+++	++
T. infestum	(T)		-	-	+	-
T. armatifrons	(T)			-	+	-
T. olitorium	(T)			-	+	-
T. copidophyllum	(T)			-	-	-
T. lamprophyllum	(T)			-	-	-
T. planum	(T)	-	-	-		+
T. hemicyclum	(T)			-		-
T. oblongatum	(T)			-		-
T. subhamatum	(T)			-		-
T. prionoides	(T)			-		-
T. severum	(T)	-		-		-
T. kernianum	(T)				-	
T. prionum	(T)				-	
T. hygrophilum	(S)				+	
T. johannis-jansenii	(S)				+	
T. lacerifolium	(T)				+	
T. excellens	(T)				+	
T. lucidum	(T)				+	+
T. linguatum	(T)				+	+
T. lancidens	(T)				+	+
T. subditivum	(T)				++	+
T. laeticolor	(T)				+	++
T. ancistrolobum	(T)				+	++
T. sellandii	(T)		-		+	+++
T. eudontum	(T)				-	+++
T. ekmanii	(T)				-	+++
T. atonolobum	(T)				-	++
T. effusum	(T)					++
T. sagittipotens	(T)				-	+
T. falciferum	(T)				-	+
T. pannulatiforme	(T)				-	+
T. atrovirens	(T)				-	-
T. lucidiforme	(T)				-	-
T. brabanticum	(T)				-	-
T. corynodiforme	(T)				-	-
T. undulatiflorum	(T)					+
T. croceiflorum	(T)					+
T. ekmanniiforme	(T)					+
T. pectinatiforme	(T)					+
T. pannulatum	(T)					+
T. multifidum	(T)					+
T. lacinosifrons	(T)					+
T. monochroum	(T)					+
T. sinuatum	(T)					-
T. sublaeticolor	(T)					-
T. subericinum	(T)					-
T. calochroum	(T)					-
T. piceatum	(T)					-
T. pectinatiforme	(T)					-

Table 3. Number of microspecies of *Taraxacum* present in a population sample of 30 dandelion plants.

	No. of samples	Domineering section	No. of species per sample belonging to domineering section		
			Mean	Minimum	Maximum
Dunes (group 1) (ungrazed)	16	Erythrosperma	6	2	8
Dunes (group 2) (grazed)	12	Erythrosperma	3	1	6
Grassland (group 3) (little grazed sand)	17	Taraxacum	7(7.3)	4	11
Grassland (group 4) (little grazed, humid, clay)	16	Taraxacum	8(7.9)	0	15
Grassland (group 5) (intensively grazed, intensively fertilized, clay)	17	Taraxacum	12(11.8)	3	19

4.1.2. Relations with the abiotic environment

In *fig. 1* the ecological relations of different microspecies of *Taraxacum* are shown in diagrams relating to the factors nitrogen (N-number) and moisture (F-number) according to ELLENBERG (1974). The diagrams indicate a clear connection between the N- and F-numbers in the sense that low N-values seem to be correlated with low F-values, and high ones with high ones, respectively. The low values are characteristic of the near-natural dune grasslands, and the high ones of the grazed sites; the higher values are chiefly attributable to the higher humus content of the soil in the inner dunes and to the organic dunging as the result of extensive grazing.

The fact that *T. obliquum* is almost exclusively restricted to the near-natural stands of dune grasslands is clearly associated with the low N- and F-values. *T. rubicundum*, on the other hand, which occurs in both types of dune grasslands, is found within a wider range of N- and F-numbers, whilst *T. commixtum* occupies an intermediate position. As far as the N- and F-values are concerned, *T. rubicundum* agrees rather closely with *T. tortilobum* and *T. lacistophyllum*, and *T. commixtum* with *T. taeniatum* and *T. oxoniense*.

4.2. Microspecies of the sections *Taraxacum*, *Palustria* and *Spectabilia*

4.2.1. Their occurrence in the stand

4.2.1.1. Sect. *Taraxacum*

On the basis of floristic resemblances and differences the relevés in which microspecies of sect. *Taraxacum* occurred can be divided into three groups, viz.,

- (a) those from Terschelling (= group 3),
- (b) those from the little manured and grazed pastures in the Tieler-, Bommeler- and Krimpenerwaard (= group 4), and
- (c) those of the intensively grazed and fertilised grasslands of the Tieler- and

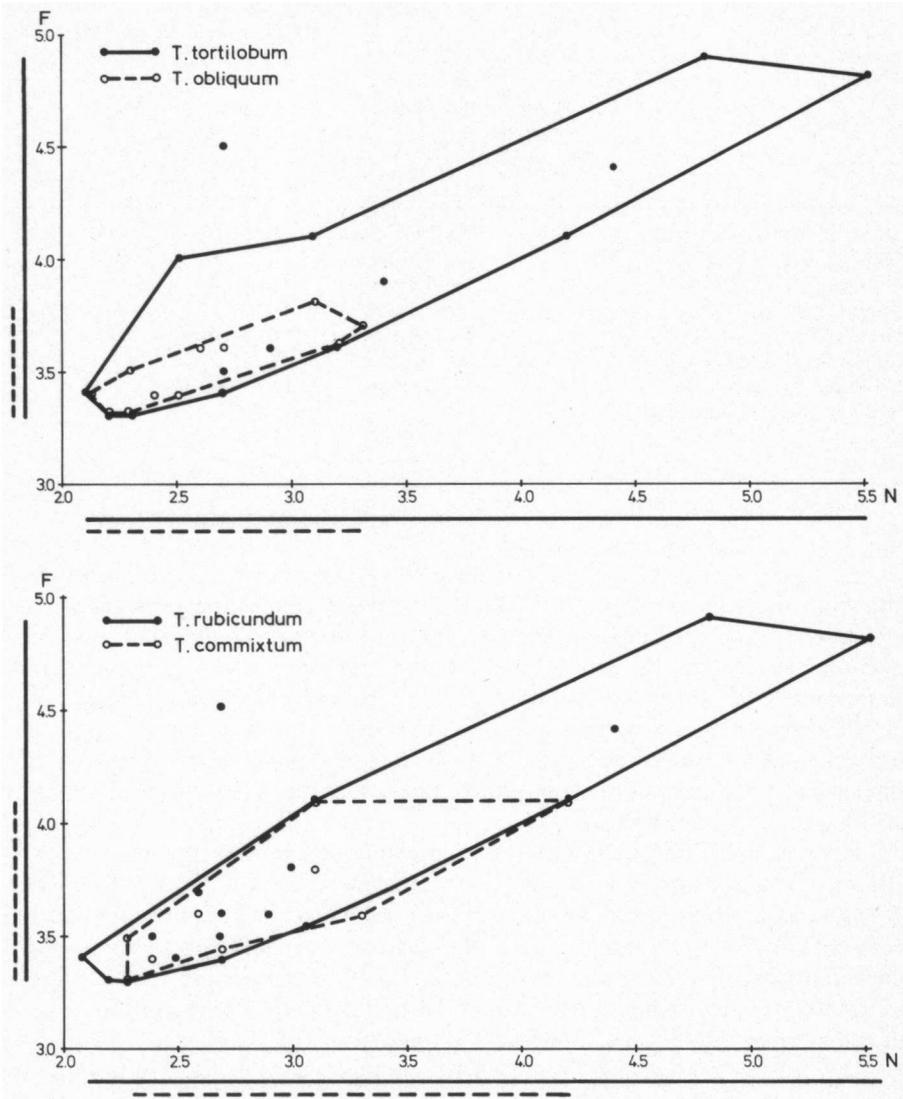


Fig. 1. Ecological amplitudes of some microspecies of sections *Erythrosperma* and *Obliqua* in relation to moisture (F) and nitrogen (N), expressed as mean indication values according to ELLENBERG (1974).

Krimpenerwaard (= group 5).

Table 1 shows the phytosociological spectrum of the relevé groups 3–5. A more precise phytosociological characterisation of the relevés at the association level by means of the system of WESTHOFF & DEN HELD (1975) proved to be impossible; as a rule character species and differentiating species of a syntaxon-

omic class predominate, but often quantitatively important elements of other classes are intermingled. According to WESTHOFF & DEN HELD (1975) this situation is often met with among the *Plantaginetea* (*Lolio-Potentillion anserinae*) which shows numerous transitions towards other syntaxonomic classes.

The *Lolio-Potentillion anserinae* occupies a central position in the phytosociological spectrum of groups 3–5 (see *table 1*). In the Terschelling relevés (group 3) the *Plantaginetea* species predominate. They are indicative of disturbance attributable to grazing on the one side and to the situation of the sampling plots in the transition zone between dunes and salt marshes on the other. The proportion of *Arrhenatheretea* species, which prefer nutrient-rich soils, is, accordingly, high (*table 1*).

Some representatives of the *Saginetea*, indicators of the contact zones between xerosere and halosere are characteristic in some of the relevés recorded. In addition representatives of the *Asteretea* (indicating saline conditions) are present. The *Koelerio-Corynephoretea* species, indicative of xeric conditions, are still relatively numerous.

In the relevés from the moist and little fertilized grasslands of the Krimpener-, Tieler- and Bommelerwaard (group 4) species of the *Arrhenatheretea*, *i.e.*, taxa of grasslands rich in dicotyledonous herbs found on moist and nutrient-rich soils, are most common. The high degree of representation of the *Plantaginetea* indicates disturbance attributable to fertilizing and grazing. The incidence of *Phragmitetea* species, indicating wetness of the habitat, is also relatively high.

In the relevés from the intensively fertilized and grazed pastures of the Krimpener- and Tielerwaard (group 5) the disturbance indicators of the *Plantaginetea* (*Poo-Lolietum*) dominate. This is explained by the intensive agricultural management. *Arrhenatheretea* species still contribute largely to the stand. A characteristic feature is the representation of taxa of the *Chenopodietea*, *i.e.*, of ruderal, nitrogen-rich and trodden plant communities.

*Table 3* shows the number of dandelions found per sample of 30 individual plants in the various pastures of groups 3–5. It appears that:

- (a) the mean number of microspecies is largest in group 5 (12) and smallest in group 3 (7);
- (b) the largest number of species per sample is in group 5 (*viz.*, 19) and the lowest in group 3 (*viz.*, 11), and
- (c) the number of microspecies per sample varied appreciably in all three groups, more particularly in groups 4 and 5, which implies that in some types of pasture only a few species may dominate, whereas in other kinds a much greater variability in the dandelion flora may be encountered.

Summarising the evidence, one may conclude that the largest variation in the number of microspecies of sect. *Taraxacum* is found in the most intensively fertilised and grazed pastures in which the number of microspecies may be as high as 19 per 125 m<sup>2</sup>. In ungrazed and unfertilized and also in extensively grazed but otherwise unfertilized grasslands the number of microspecies of the sect. *Taraxacum* recorded from sample plots with the same surface area is decidedly lower.

The dandelion flora of the grasslands studied is shown in *table 2*. A comparison of the data from this table with the vegetational records in *table 1* reveals that the occurrence of taxa of the sect. *Taraxacum* is, roughly speaking, conformable to the data given by WESTHOFF & DEN HELD (1975). That this agreement is only in broad lines is also attributable to the difficulty that the recorded relevés could not satisfactorily be phytosociologically identified. SISSINGH (1969) reports that species of the sect. *Vulgaria* (= sect. *Taraxacum*) belong to the character species of the *Lolio-Plantaginion* (*Plantaginea*) and to the character-combination of the *Lolio-Plantaginetum* of that alliance which comprises vegetation types of trodden ground. According to WESTHOFF & DEN HELD (1975) sect. *Vulgaria* has a much wider ecological amplitude. In addition the representatives of sect. *Vulgaria pro max. parte* belong to the character-combination of the *Poo-Lolietum* of the *Lolio-Potentillion anserinae* (*Plantaginea*) which comprises communities from the most intensively grazed and most heavily fertilized (and, hence, species-poor) pastures (WESTHOFF & DEN HELD 1975). Finally WESTHOFF & DEN HELD (1975) mention that representatives of the sect. *Vulgaria* belong *pro max. parte* to the character species of the *Arrhenatherion* and the *Arrhenateretalia*. *Table 3* indicates that the character species and differentiating taxa of the *Plantaginea* and the *Arrhenatherion* are best represented in the groups 3, 4 and 5. Most of the relevés are transitional, those of group 5 approaching the *Poo-Lolietum* (*Plantaginea*) the most closely. Those of group 4 are closest to the *Arrhenatherion* (*Arrhenateretalia*), especially to its more hygic variants, and those of group 5 approximate the *Plantaginea* vegetations in the somewhat more xeric variants.

In our investigation microspecies of sect. *Taraxacum* have not only been found in groups 3–5, but also in the groups 1 and 2 which comprise relevés from dry dune grasslands; in these grasslands the microspecies are represented in low frequencies. There are some differences between groups 1 and 2, the mean number of microspecies of sect. *Taraxacum* in the former being 1.0 (0.8), range 0–4, and in the latter 2 (1.8), range 0–5. This means that in the relevés of group 2 the microspecies of sect. *Taraxacum* are of more common occurrence than they are in group 1. The cause is conceivably the higher incidence of disturbance associated with the treading and grazing by cattle.

When the representation of the individual microspecies of sect. *Taraxacum* is considered, they appear to show appreciable differences (*table 2*). Some of these taxa are well represented in groups 3–5 and in addition, albeit in (much) lower frequencies, also in group 1 and 2: *T. hamatum* and *T. hamatiforme*, which two microspecies exhibit the broadest ecological amplitude within the taxa belonging to sect. *Taraxacum* studied. They most probably prefer not very intensively dunged and grazed, moist pastures; from this optimum they extend to drier unfertilized grasslands on the one side and to more strongly fertilized and grazed habitats on the other. Some other species with a broad ecological amplitude and a similar ecological optimum are: *T. hamatum*, *T. quadrans* and *T. fulgidum*.

There are taxa with a marked preference for extensively grazed pastures on

sandy soils (group 3), such as *T. atactum*, *T. raunkiaeri*, *T. bracteatum* and *T. rubrisquamum*. This is not so manifest in the microspecies *T. haematicum*, *T. wijtmaniae*, *T. cordatum* and *T. hamiferum*. The taxa *T. pachymerum*, *T. dahlstedtii*, *T. wijtmaniae*, *T. cordatum*, *T. atactum*, *T. raunkiaeri* and *T. severum* are known to prefer sandy soils (HAGENDIJK et al. 1982), which may explain their occurrence in relevés of group 3 and sometimes (also) in those of groups 1 and 2. These are within the *Taraxacum* aggregate apparently adapted to dry and nutrient-poor, sandy habitats, some of them even penetrating into the very dry, near-natural dune environment which constitutes the domain of sect. *Erythrosperma*.

*T. atactum*, a microspecies preferring sandy soils may, however, penetrate into peaty grassland (HAGENDIJK et al. 1982). This taxon may, therefore, be expected to occur in the peaty pasture land of the Krimpenerwaard, but its absence there is explained by its distribution which, as far as could be ascertained, is restricted to the northern parts of The Netherlands (HAGENDIJK et al. 1982). No published data regarding *T. obtusilobum* are available from this country, but it is at any rate of rare occurrence and is not mentioned in HAGENDIJK et al. (1982).

There are some species with a marked preference to extensively grazed and fertilized, moist pastures, both of sandy soils and on peaty soils and river clays (groups 3 and 4), viz., *T. adamii*, *T. hamatulium*, *T. fulgidum* and possibly *T. hamiferum*. Taxa found in rather similar grasslands but almost exclusively on peaty soils and river clays (and hardly or not on sands) include *T. lacerifolium*, *T. excellens* and possibly also *T. kernianum*. There is also a group of microspecies preferring peat and river clay soils under extensive management, but extending to similar grasslands on sandy soils on the one side, and to intensively managed pastures on the other: *T. infestum*, *T. armatifrons*, *T. olitorium* and probably also *T. copidophyllum* and *T. lamprophyllum*; these taxa apparently have a broad ecological amplitude.

A fairly large group of microspecies prefer intensively grazed and fertilized pastures but to a greater or lesser extent also occur in extensively managed grassland; it comprises the taxa: *T. laeticolor*, *T. ancistrolobum*, *T. sellandii*, *T. eudontum*, *T. ekmanii*, *T. atonolobum*, *T. effusum*, *T. sagittipotens*, *T. falciferum* and *T. pannulatiforme*.

*T. atrovirens*, *T. lucidiforme* and *T. brabanticum* most probably prefer pastures under extensive management, and *T. corynodiforme* more intensively managed ones.

Finally there is a group exclusively encountered in heavily fertilized pastures: *T. calochroum*, *T. croceiflorum*, *T. effusum*, *T. ekmaniiforme*, *T. falciferum*, *T. laciniosifrons*, *T. monochroum*, *T. multifidum*, *T. pannulatum*, *T. pectinatiforme*, *T. piceatum*, *T. sinuatum*, *T. subericinum*, *T. sublaeticolor* and *T. undulatiflorum*.

#### 4.2.1.2. Sections Spectabilia and Palustria

The most important taxon outside sect. *Taraxacum* in our study area is *T. nordstedtii* (*Spectabilia*). Especially in Terschelling it is very wide-spread and occurs

within group 3 in 16 out of the 17 relevés. It is also well represented in group 4 but only in the Krimpenerwaard and not in the Tieler- or Bommelerwaard. Whether this means that *T. nordstedtii* does not occur on heavy clayey soils is not very probable. An explanation of its absence from the relevés in the latter two areas can as yet not be given. It seems to feel at home in moist to rather humid, extensively grazed and little fertilized pastures, in our experience especially in vegetation types between *Arrhenatheretea* and *Lolio-Potentillion* communities. When their distribution is compared with the other Dutch representatives of the *Spectabilia*, *T. nordstedtii* is the one with the broadest ecological amplitude of the section.

Other microspecies of the *Spectabilia* encountered during the present investigation are *T. hygrophilum* and *T. johannis-jansenii*, which have only been found in the Krimpenerwaard in only three relevés which contained but few microspecies of sect. *Taraxacum*. According to HAGENDIJK et al. (1975) these two taxa must have been much more common but became progressively rarer owing to modernised agricultural management. They are apparently rather particular in their habitat preference and ecologically more highly specialised than *T. nordstedtii* which can maintain itself much longer in the generally deteriorating environment. HAGENDIJK et al. (1971, 1975) also report that *T. hygrophilum* and *T. johannis-jansenii* only occur in the central and southern Netherlands and, therefore, are not found in the island of Terschelling. We may add that these two taxa cannot always be distinguished satisfactorily and should be considered to be critical microspecies.

*T. hollandicum* of sect. *Palustria* was found in the Tieler- and the Bommelerwaard in unfertilized meadows and scantily manured meadows with aftermath grazing in nature reserves (viz., Komgrondenreservaat Tielerwaard and Bommelerwaard). *T. hollandicum* occurred here in habitats corresponding to those reported in the literature. According to WESTHOFF & DEN HELD (1975) *T. hollandicum* is a character species of the *Calthion palustris* found on permanently or periodically flooded, mineral-rich and nitrogen-containing clayey or peaty soils in stream- and riverbeds and in meadows which are fertilized and mown once or twice yearly. HAGENDIJK et al. (1975) note that the microspecies is found within the alliance in the somewhat drier situations, just outside the *Caltha* habitat. Also in the Tieler- and Bommelerwaard we encountered it on slightly more elevated ground than the sites where the king's cup finds its optimum. Remarkably the microspecies under discussion was not recorded from the Krimpenerwaard; conceivably it is restricted in its occurrence to truly riverine deposits and, therefore, does not grow on the peaty soil types of the latter Waard. Most probably *T. hollandicum* has, within sect. *Palustria*, the widest ecological amplitude.

*T. friscum*, also of the last-mentioned section, was recorded in very large numbers in a single relevé from Terschelling taken in an extensively managed dune pasture, 100 m to the S of the artificial sand dike near Oosterend on a humic soil type. This taxon was formerly rather common in the province of Friesland in vegetation related to the *Cirsio-Molinietum*, but is on the decline

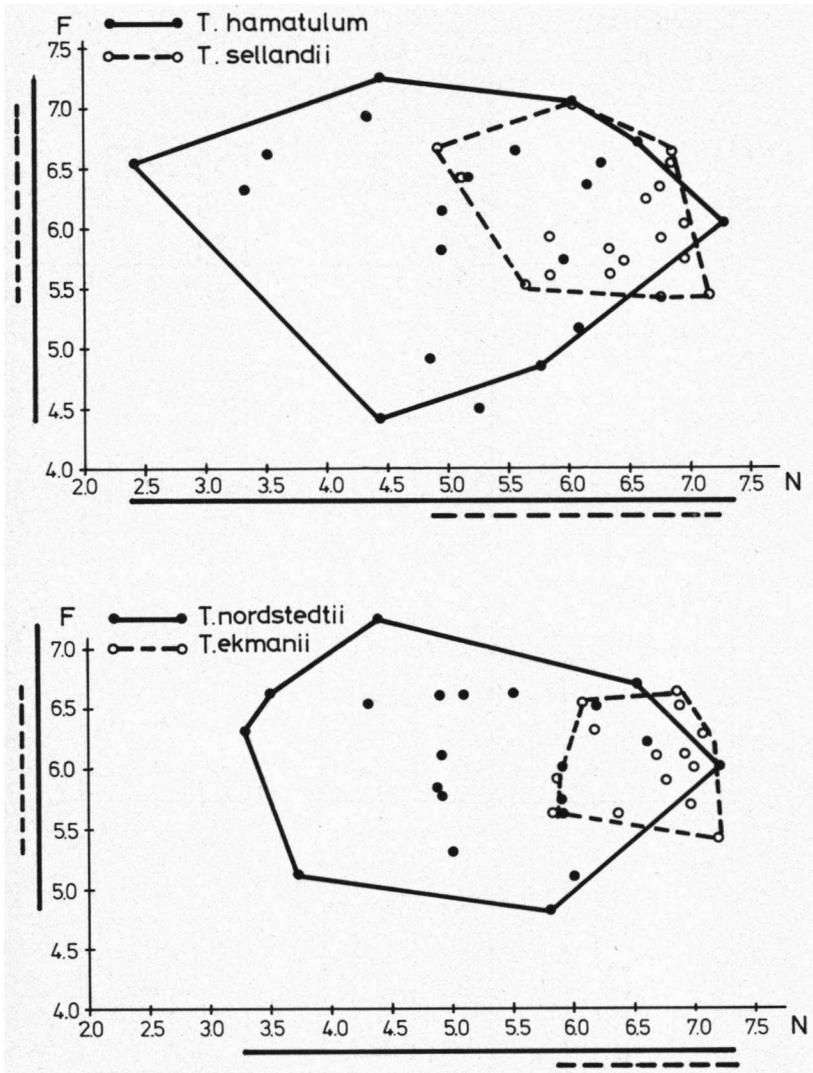


Fig. 2. Ecological amplitudes of some microspecies of sections *Spectabilia* and *Taraxacum* in relation to moisture (F) and nitrogen (N), expressed as mean indication values according to ELLENBERG (1974).

owing to modern agricultural management (HAGENDIJK et al. 1975).

4.2.2. Relations with the abiotic environment

*Fig. 2.* shows the relation between the indication values for moisture (F) and nitrogen (N) according to Ellenberg for the taxa *T. hamatulum* (*Taraxacum*)

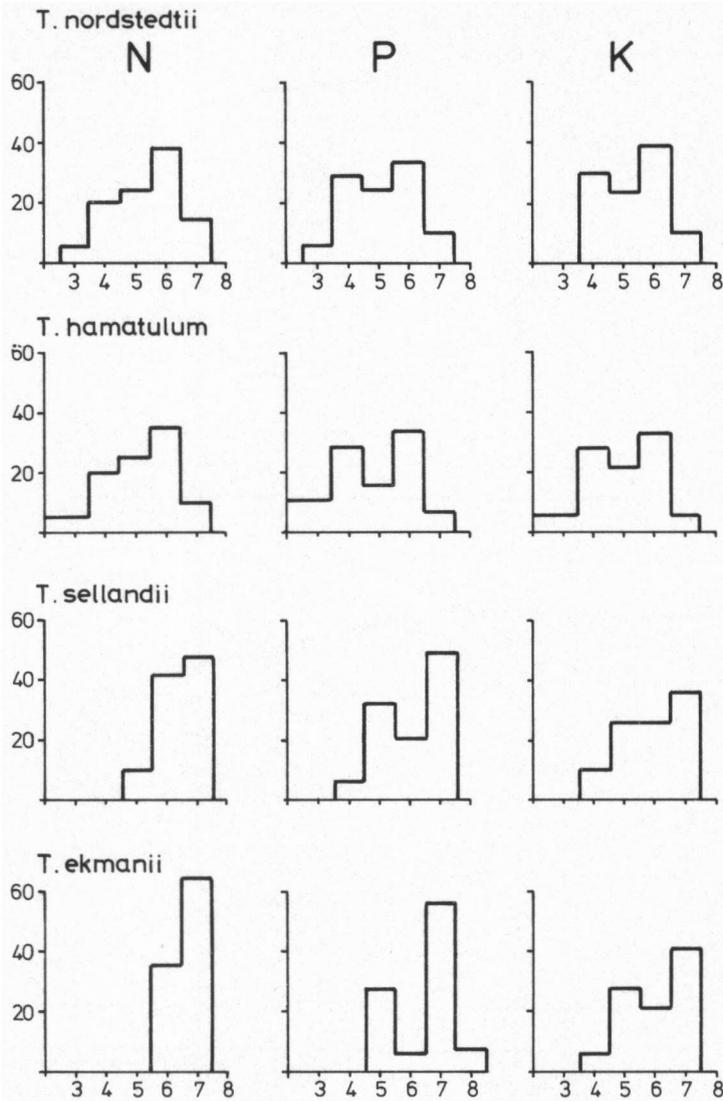


Fig. 3. Ecological amplitudes in relation to nitrogen (N), expressed as mean indication value according to ELLENBERG (1974), and to phosphate (P) and potassium (K) expressed as mean indication values according to KRUIJNE et al. (1967).

and *T. nordstedtii* (*Spectabilia*). It appears that there are clear differences between these taxa. *T. hamatulum* has the widest amplitude in both, and occurs at sites with low N- and F-values (2.0–3.0 and 4.0–4.5, respectively) encountered in relatively dry and nutrient-poor dunes, also at sites with average N- and F-values in humid and moderately nitrogen-rich and little dunged situations, and,

Table 4. Colours of the petiole of microspecies of section *Taraxacum* of groups 3–5 as compared to all Dutch taxa of that section (see text).

	TARAXACUM taxa (section <i>Taraxacum</i> )	Percentages of plants		
		red petioles	coloured	green petioles
All Dutch species	153	38	44	18
Group 3	13	92	8	—
Group 4	20	55	20	25
Group 5	29	34	24	42

Table 5. Position of involucre bracts of microspecies of section *Taraxacum* of groups 3–5 as compared to all Dutch taxa of that section.

	TARAXACUM taxa (section <i>Taraxacum</i> )	Percentages of plants Involucre bracts		
		adpressed	adpressed to patent	patent to reflexed
All Dutch species	153	3	32	64
Group 3	13	23	69	8
Group 4	19	11	42	47
Group 5	27		22	78

finally, at sites with high N- and F-values (5.0–7.5 and 5.5–6.5, respectively) on heavily fertilized and more or less heavily drained grasslands.

*T. ekmanii* exhibits the narrowest amplitude of the two indication values, those of N high, ranging from 6.5 to 7.5, and those of F average, ranging from 5.5–6.5; it is found on heavily fertilized and intensively grazed, well-drained biotopes. *T. hamatum* resembles *T. hamatulum* rather closely in these respects, but it does not penetrate so far into drier biotopes. *T. sellandii* resembles *T. ekmanii* but also occurs on soil types with lower N- and higher F-values, i.e., in not so heavily dunged and moist pastures.

The following corresponding features can be established between:

- (a) *T. hamatiforme* and *T. hamatulum*
- (b) *T. adamii*, *T. fulgidum*, *T. hamatum*, *T. quadrans*, *T. rubrisquamum*, and *T. nordstedtii*
- (c) *T. ancistrolobum*, *T. armatifrons*, *T. eudontum*, *T. laeticolor*, *T. pannulatum*, and *T. sellandii*.

The possible relations with the abiotic environment have also been assessed by means of the indication values of KRUIJNE et al. (1967) for phosphate (P) and potassium (K). These values range from –100 to +100 and have been recalculated to form a scale from 1–10 as follows: (–100) to (–80) = 1; (–80) to (–60) = 2, etc. The results are shown in *fig. 3*; the N-values are according to Ellenberg.

*T. nordstedtii* and *T. hamatulum* exhibit a wide range of tolerance in respect

of N and P, *T. sellandii* and *T. ekmanii* a narrower one, the latter two taxa apparently preferring higher N- and F-values and somewhat higher K-values than the other two.

### 4.3. The colour of the petiole and the position of the involucreal bracts in sect. *Taraxacum*

#### 4.3.1. Colour of the petiole

Table 4 shows the colour of the petiole of the microspecies of sect. *Taraxacum*, of groups 3–5 studied in comparison with all microspecies of sect. *Taraxacum* recorded from The Netherlands. Only those taxa were included which occurred in at least three of our relevés. The analysis is based on the table in HAGENDIJK et al. (1982: 84–85). The following combinations have been made:

- (a) red + red and slightly coloured
- (b) slightly coloured
- (c) green + green and slightly coloured

Table 4 indicates that there is a relation between petiole coloration and environment, the red-petioled forms domineering in grasslands without management or under light, extensive management, the more so on the poorest soil types (sand: group 3), on which the green-petioled taxa do not occur. The green-petioled microspecies of sect. *Taraxacum* are predominant in heavily fertilized and grazed pastures, where the red-petioled ones are clearly scarcer. The microspecies of group 4 occupy an intermediate position.

#### 4.3.2. The position of the involucreal bracts

Table 5 shows the position of the involucreal bracts of those microspecies of sect. *Taraxacum* of groups 3–5 which occurred in at least three of our relevés, again in comparison with all its Dutch representatives. The analysis is based on the above-mentioned table in HAGENDIJK et al. (1982: 84–85). The following combinations were made:

- (a) adpressed
- (b) adpressed-patent to patent
- (c) patent-recurved, recurved or reflexed.

The table indicates that the position of the bracts is indeed related with the environment, the forms from unfarmed or extensively managed grasslands (of group 3) more frequently possessing adpressed or adpressed-patent bracts, and much more rarely patent-recurved ones, whereas in heavily fertilized and grazed pastures the taxa with patent and/or recurved bracts are dominant and those with adpressed bracts are altogether absent, those of group 4 again occupying an intermediate position. OOSTERVELD (1983) was the first to draw attention to the relation between the petiole colour and the position of the involucreal bracts on the one hand, and the environment on the other. On the basis of this correlation he proposed a classification by which dandelions can be used as indicators of environmental conditions.

## 5. DISCUSSION

### 5.1. An overview of the results

- a. Per grassland usually several microspecies of *Taraxacum* are found, which points towards a strong ecological correspondence of the taxa. This will be discussed in greater detail in 5.3.
- b. Grasslands with a phytosociological resemblance which are under similar agricultural management also resemble one another in their *Taraxacum* flora. Different types of grassland also differ in their *Taraxacum* composition which difference is usually of a gradual nature. It increases as the difference in the environmental conditions is greater, the grasslands which differ most having the smallest number of species in common or none at all. It is thus quite clear that the microspecies of *Taraxacum* may exhibit appreciable ecological differences. The assessment of ecological resemblances and differences is quite a problem in view of their close relationship. This problem is under investigation. In 5.2. a preliminary and overall ecological characterisation will be given of the section *Taraxacum*. We assume that the ecological peculiarities of the microspecies are variations of the ecological characteristics of the section as a whole.
- c. It proved to be possible to distinguish within the sections microspecies with a broad ecological amplitude and other ones with a narrower range, the latter presumably being the more specialized ones. In sect. *Taraxacum* the taxa with a broader ecological amplitude most probably find their optimum habitat in not strongly grazed and fertilized pastures; this will again be touched upon under 5.4.
- d. In near-natural dune grasslands dandelions of sections *Obliqua* and *Erythrosperma* are the most frequent, their number decreasing in grazed dune pastures. In the near-natural dune grasslands but a few microspecies of sect. *Taraxacum* are encountered, their number increasing in grazed and fertilized dune pastures but always remaining relatively low. See under 5.5 for a discussion.
- e. Representatives of sections *Palustria* and *Spectabilia* have exclusively been found in unfertilized or lightly fertilized and ungrazed or extensively grazed pastures and meadows, but most of the microspecies are rather rare. For a discussion, see 5.5.
- f. Representatives of the sect. *Taraxacum* are characteristic of pastures under more or less intensive agricultural management, in which the number of microspecies per unit of surface area increases as the agricultural activities are more thorough and, conversely, decreases when the pressure through agricultural practice becomes lower.
- g. The present study is based on samples from 78 lots of grassland and, geographically, only involves a small part of the Netherlands, which implies that the possibility to generalize our results are decidedly limited. On the other hand the frequently encountered biotopes and all sections of *Taraxacum* recorded from the Netherlands were included in the investigation.
- h. The study of the sect. *Taraxacum*, with 153 microspecies the largest in The Netherlands, remained restricted to grassland biotopes; road sides, lawns,

and such remaining sites being left out of consideration. Of the grassland types investigated 17 were intensively fertilized and grazed pastures as against 33 far less intensively exploited grasslands, the latter nowadays mostly remaining restricted in their occurrence to nature reserves, and constituting only an insignificant fraction of the area covered by grassland in The Netherlands. It is clear that as far as their representation is concerned the types under intensive agricultural exploitation were under-represented. On the other hand, the formerly present variation in Dutch grassland types has, owing to the intensification of agricultural procedures such as heavy dunging, intensive grazing, periodical sowing of agriculturally useful grass species, drainage, watering by spraying, etc., become ecologically and phytosociologically much more uniform.

### 5.2. Ecology of sect. *Taraxacum*

It will be tried here briefly to outline the characteristics of the environment of sect. *Taraxacum* as a whole in relation to the adaptive strategy of the group. This characterisation will be an overall one because its ecology is only known in principal respects. Moreover, the stress will be laid here on the ecology of dandelions more or less strongly influenced by agricultural practice. In view of their sometimes very great abundance the microspecies of sect. *Taraxacum* must be well-adapted to the agricultural exploitation of their habitats. During the principal flowering period in spring it is often quite striking that the yellowing of the pastures is often quite different in two adjacent lots. Clearly the form of farm management largely decides the population densities of the microspecies present.

The inclusion of the life cycle of the dandelions in the ecosystem prevailing in the grassland is generally considered to be an important adaptive feature. Dandelions are able to flower early in the spring, presumably because the root system contains an appreciable quantity of storage assimilates. The spring is, accordingly, the principal reproductive period, which falls at a time when most grasses have not yet or hardly started growing. The adaptive significance is most probably the avoidance of competition, which is also evident from the consideration that through the brief period of reproductive activity the fruits are being dispersed before a high stand of grasses becomes a hampering factor. The second and usually by far less important, autumnal flowering period is especially noticeable in the agriculturally more disturbed habitats, in which per population (per plot of pasture) fewer plants come into flower and per flowering individual fewer flower heads are being produced; usually the plants concerned have already had a vernal period of flowering.

In summer, when the stand of grassland attains an optimum, the growth of the dandelions is often strongly retarded, which expresses itself in the number of leaves produced per plant, which is the lowest in this part of the growing season.

Dandelions exhibit many characteristics of colonisers and prefer open or sparsely covered spots in the stand for their settlement. Such open places often appear in pastures on account of agricultural exploitation: opening of the sods, e.g.,

by treading when the grazing density is high (especially when the weather is damp), or when the adjustment of the mowing machines is too low and the grass-mat is damaged (DIRVEN & NEUTEBOOM 1975), or by the excessive use of farmyard manure causing a localized dying off of shoots, etc. Open spaces also originate from natural causes: mole hills, selective frost killing of grasses in severe winters (e.g., *Lolium perenne*) or perishing in dry summers (e.g., *Poa trivialis*) (DIRVEN & WIND 1982). The incidence of openings in the vegetation mat is hardly predictable, but at much trodden sites near fence-gates and dams, and also at the end-zones of the lots where agricultural machines (tractors!) make their turns, open places are subpermanently available. As far as the time of the year is concerned the presence of small open spaces is in so far more predictable that one may accept that, dependent on the intensity of agricultural activities, more or fewer bare spots are available during the season. Such available microhabitats must be occupied rapidly, and dandelions have the capacity to do so on account of their efficient mode of dispersal (achenes with a pappus plume) and their high rate of seed set (about 5000 achenes are normally produced per m<sup>2</sup> in pastures (see also ROMMENS 1980)). The seeds of most microspecies of sect. *Taraxacum* do not have a very specialized germination ecology and for the best part a weakly developed seed dormancy (LOENHOUD & DUYTS 1981). Whenever open spaces appear or the stand of grass becomes locally sparser by mowing, grazing and/or treading, a relatively large number of achenes may germinate, but not all, however, some remaining in the soil as a seed reserve which ensures a spreading of the germination in time (ALTENA & MINDERHOUD 1972). Incidentally, dandelions are not only found in open and sparsely covered spaces, but also occur in more closed patches, presumably because adult individuals can maintain themselves for a considerable length of time in denser stands of pasture.

Dandelions are also ecophysiologicaly adapted to the very high nutrient level of their habitat as found in our unnaturally rich pasture land (HOMMELS et al. 1982), which, among other things, expresses itself as a high growth rate and leaf turnover.

The plants rapidly develop a rosette of leaves adpressed to the soil surface and pull the apical meristem downwards to 1–2 cm below the surface by means of pulling roots (KEULEN 1981). These two strategies protect the plants against predation by grazers, treading and mowing. Also the ripening fruits are protected against mowing and grazing, because after flowering has ceased the scape of the inflorescence performs a downward bending, the capitulum with its ripening achenes thus becoming pushed down against the soil surface to re-erect itself and to resume elongating shortly before seed maturation. Ultimately the head raises a little higher than the grasses and the achenes are subsequently dispersed by air currents.

The plants have an amazing power of regeneration, so that even after heavy damage by treading or otherwise they recover rapidly. In intensively grazed lots treading by cattle may be excessive and represents the most important cause

of mortality of young seedlings and juvenile specimens of *Taraxacum* (KEULEN 1981).

As colonisers, dandelions are susceptible to competition (MØLGAARD 1977). A study by OOMES & MOOI (1981) showed that by leaving the stand alone or by mowing only one or twice yearly in most cases the dandelions will disappear from a grassland after 3–4 years.

Mowing in August favours their survival, however. Apparently the frequency and the time of mowing are critical as far as the competitive relations of the species in a stand of pasture are concerned. They also largely decide the occurrence and taxonomic composition of the local dandelion flora. Lots which are mown frequently, such as lawns, assume the characteristics of open, low pioneer vegetation types in which many dandelions feel quite at home.

A study by OOSTERVELD (1978) has indicated that in impoverishing grassland (when agricultural exploitation decreases) retrogressive succession starts and the taxonomic composition of the *Taraxacum* flora gradually changes, the microspecies which are tolerant of intensive agricultural management disappearing to be replaced by other ones. The dandelions come and go according to a more or less fixed pattern, a "disappearance-appearance series". In the moister habitats an oligotrophiation results in a "shift" towards taxa of sections *Spectabilia* and *Palustria* whereas at drier sites the change proceeds in the direction of *Erythrosperma* microspecies. In sect. *Taraxacum* the extremes of the series before and after oligotrophiation are relatively well-known according to OOSTERVELD (1978) but the intermediate stages are not so clear. An intensification of pasture exploitation also results in a shift in the taxonomic build-up of the local *Taraxacum* population but of course in the direction towards species better adapted to an intensive use. DIRVEN & WIND (1982) report that in their experience an intensification of grassland exploitation did not result in any significant change in the representation of *Taraxacum*, but in our opinion it is very probable that the taxonomic composition did change.

According to SOLBRIG & SIMPSON (1974, 1977) biotypes of *Taraxacum* may occupy a different position in respect of the r- and K-continuum. Dandelions of relatively much disturbed biotopes with principally density-independent mortalities tend to be more r-selective whereas other forms from less disturbed environments with a more density-dependent mortality are more K-selectionistic.

The mode of reproduction is very important in connection with the adaptive strategy of *Taraxacum*. In The Netherlands, agamospermy predominates and sexual forms are decidedly rare (STERK et al. 1982). The adaptive significance of agamospermy varies a great deal (GRANT 1971, DOLL 1982, MAYNARD SMITH 1979). In this connection the genotypical identity of the motherplant and its offspring is of major consequence. In this case the microspecies are built up by one or more clones. A very important advantage of this form of asexual reproduction is the immediate, high degree of "fitness" of the individuals.

### 5.3. The occurrence of microspecies of *Taraxacum* in the same habitat

The co-occurrence of several to many of dandelions in a single habitat (pastures) is a striking phenomenon. In our present study up to 19 microtaxa of sect. *Taraxacum* were recorded per 125 m<sup>2</sup> in heavily grazed grassland. OOSTERVELD (1978) reported that per lot of pasture (covering several hectares as a rule) 30 microspecies may be encountered. This has also been noted elsewhere in Europe. (VON HOFSTEN 1951) and is conceivably the rule in the whole area where agamosperous forms occur. The sympatric occurrence of closely related taxa in a single habitat has repeatedly been the subject of relevant studies (see BRAAKHEKKE 1980 for a survey of the pertaining literature). It is often associated with the Gaussian principle or the principle of competitive exclusion, according to which species cannot co-exist in the same habitat indefinitely unless they occupy different niches. An important pertaining question is whether sympatrically growing microspecies of *Taraxacum* do indeed occur in different niches. It must be borne in mind that next to niche differentiation also other possible explanations of sympatricity of taxa can be given (BRAAKHEKKE 1980). Although no special study was made of the common occurrence of microspecies of dandelions the phenomenon will be briefly dealt with here.

An important element in disquisitions concerning sympatricity in the same habitat is co-existence, *i.e.*, the occurrence at the same site but in different niches. The growth rate of a population is in this case regulated by various ecological factors such as a different nutrient supply or different concentrations of the same nutrient. Furthermore, the sympatrical species may have root systems at different levels or their roots may have a different susceptibility to predators (eel worms, etc.) or pathogens. Most probably niche-differentiation is of great significance in the sympatric occurrence of dandelions in the same habitat. *Taraxacum hamatum*, for instance, is found in heavily fertilized pastures together with *T. ekmannii*. The former has its optimum in not heavily manured meadows whereas the latter microspecies prefers heavily fertilized ones (compare *table 2* and *fig. 2*). Presumably these two taxa have different nutritional requirements or they prefer unequal concentrations of the same nutritional factor and may find different niches even in the heavily fertilized pasture types. Generally speaking one may accept that dandelions, also in view of their colonising abilities, have an appreciable tolerance as regards niche-overlapping.

A second, possible cause of co-existence is the heterogeneity of the environment at a small scale. Grasslands under agricultural management often show small-scale heterogeneity, *e.g.*, between dry ditch- and dike-edges and the flat parts in between, and between the latter and the end sites where tractors are turned round and the stand is subjected to a relatively great deal of mechanical damage, and between places with different treading (near dams, gates, paths, etc.), with or without mole hills, with unequal spreading of farmyard manure, with small differences in the soil profile and the micro-climate and with or without open spaces in the grass-mat with reduced competition. These different micro-habitats may be preferred by different microspecies.

A recent study by OOSTERVELD (1983) is of particular interest in this connection. He examined the concentration of the nutrients N, P and K in the soil in the immediate vicinity of the root system of three ecologically diverse microspecies of *Taraxacum* found growing close together in the same stand of pasture. The mineral contents proved to differ appreciably. The three taxa in question, *T. ancistrolobum*, *T. hamatum* and *T. nordstedtii*, in this sequence constitute a series from a preference for more dynamic environments to less dynamic ones. This series can be associated with the amount of mineral phosphorus in the soil, *T. ancistrolobum* being found in soil with the highest P-values and *T. nordstedtii* in soil with the lowest.

According to OOSTERVELD (1983) these findings support the hypothesis posed by dr. C. G. van Leeuwen (Rijksinstituut voor Natuurbeheer, Leersum) that the great morphological and ecological variation within the genus *Taraxacum* (which is supposed to have developed especially in recent times) may well be connected with the increasing rate of availability of assimilable phosphate in the environment.

A third explanation may be immigration (by means of introduced achenes) followed by the ousting out of some or all of the immigrants. Translocation experiments with dandelions from little dunged habitats which were planted in heavily fertilized ones, and *vice versa*, showed that the taxa which do not belong in the "new" habitat exhibited a greater mortality rate than the endemic ones and consequently were gradually ousted out, although their complete disappearance may take years (details to be discussed in a forthcoming publication). This phenomenon of immigration followed by replacement by the "legitimate" taxa is presumably of common occurrence in view of their excellent mode of dispersal and the always more or less open grassland habitat. Incidentally, as far as achene transportation is concerned, one should not only take an anemochorous displacement into account but certainly also a zoochorous one by cattle and an anthropochorous one through agricultural machinery and transportation of crops. Through the last forms of dispersal there is a greater interaction between the lots of one farmer than between fields of different farmers. This may lead to an appreciable homogenisation of the pattern in pastures under the same management by a single owner and thus to a special spatial structure of the populations within the agricultural landscape. It is noteworthy in this connection that quite a number of studies have shown that the bulk of the achenes produced, land in the immediate vicinity of the parent plant and that long-distance dispersal takes place far less frequently (LEVIN & KERSTER 1974, TER BORG 1979). This means that the number of immigrant seeds is appreciably lower than the number of seeds (especially in the seed bank) of the locally already established taxa. These conclusions indicate that once a certain *Taraxacum* flora has become firmly settled in a pasture or a grassland complex it will not so readily become replaced by a different one.

Whatever the case may be, one must also take various chance happenings leading to dispersal and settling into account, which means that the presence of a number of microspecies found in a given field does not imply that this assem-

Table 6. Some characteristics typical of the generalists and of the S2 specialists of fig. 4 (see text).

	Generalists	Specialists (S2)
1. Ecological amplitude	Euryoecious	Stenoecious
2. Optimum	Lightly dunged fertilized and extensively grazed grasslands	Heavily fertilized and intensively grazed grasslands
3. r- and K-continuum	Relatively K-selectionist	Relatively r-selectionist
4. Genotypical variation	Much clones per microspecies	Few clones per microspecies
5. Age of taxa	Relatively old	Relatively young
6. Colour of petiole	Red	Green
7. Position of involucrel bracts	Adpressed	Recurved
8. Example	<i>T. hamatum</i>	<i>T. ekmanii</i>

bly of dandelions consists solely of taxa living under optimum conditions.

A fourth possible cause of sympatricity of habit is the incidence of environmental fluctuations. Generally speaking the floristic composition of a given piece of pasture land is continually changing and fluctuating around a certain equilibrium. One gets the impression that most pastures are still shifting towards an equilibrium (DIRVEN & WIND 1982). Environmental fluctuation may be the result of, e.g., severe winters, very wet or very dry summers and changes or inconsistencies in the agricultural regime, so that the factors involved in taxon competition are continually changing. The dandelions have their specific tolerances and preferences which means that at one time some taxa have a greater chance of survival than other ones and at some other time different microspecies may be better off.

When the dandelion flora of grassland types is being investigated also the phytogeography and degree of rarity of the taxa present must be taken into account (see STERK 1982).

Some of the microspecies occur only in a part of The Netherlands e.g. *T. atactum* is only found in the northern provinces) and other ones are more or less strictly local (such as *T. flevoense* of SW-Friesland and the northern coast of the Veluwe), whereas some species are always rare (*T. pulchrifolium*). The distribution and the rarity of certain dandelions may well account for their absence in a *Taraxacum* flora of a stand of grassland even if the locally prevailing environmental conditions are favourable.

#### 5.4. Section *Taraxacum*: generalists and specialists

For an evaluation of the results of our inquiry it is of major importance that sect. *Taraxacum* most probably originated very recently (DOLL 1982) and that the latest phase of evolution of the group was strongly influenced by the advent and subsequent "evolution" of large stands of grassland (SCHOLZ 1975). In The Netherlands the grassland biotope containing dandelions originated after the cutting of forests, which took place fewer than about 1500 years ago in the E and SE Pleistocene parts of the country and more recently in the lower NW and W Holocene areas (especially after reclamations started to become impor-

tant since the 12th or 13th century). The agricultural pastures as we know them to-day date from very recent times, mostly from the last three or four decades, as the result of the full-scale mechanisation of agricultural techniques and the progressively intensive application of fertilizers. The present cultural grassland types consist mainly of vegetation poor in species to a large extent comprising cultivars sown on unnaturally enriched soils. Such fields form the preferred biotope of many *Taraxacum* microspecies which appear to be well-adapted to this environment.

Less intensively influenced types of grassland are extant but they have become rare and are now mostly restricted in their occurrence to nature and landscape reserves. Such meadows may be regarded to represent remnants of vegetation types which were formerly quite common. In these "older" biotopes we find the sections *Palustria* and *Spectabilia* and certain microspecies of sect. *Taraxacum*.

Against this historical background and on the basis of the results of published studies and our present inquiries a much simplified and tentative, two-dimensional model has been constructed in the form of an assembly of optimum functions whose mathematical meaning is as yet unknown. This representation is shown in *fig. 4*. The abscisses show the rate of fertilizing which may be considered to represent a complex ecological parameter for the relative richness of soil nutrient, the ordinates the seed production per plant as an estimate of the fitness.

*Table 6* enumerates some important characteristics of generalists and of specialists. On the basis of our inquiries it appears to be possible to subdivide the microspecies of sect. *Taraxacum* into three categories, viz., generalists, specialists, and intermediate forms. The first group comprises taxa with a broad ecological range which find their optimum in lightly fertilized and grazed pastures (the "older" biotope). We may assume that they also constitute the group of "older" species. Of the section *Taraxacum* the microspecies *T. hamatum*, *T. hamatululum*, *T. hamatifforme*, *T. quadrans* and *T. fulgidum* are included among the generalists. Possibly also the taxa *T. infestum*, *T. armatifrons*, *T. olitorium*, *T. lamprophyllum* and *T. raunkiaeri* belong here (see *table 2*). The majority of these generalists have been referred to the section *Hamata* by ØLLGAARD (1983). The specialists have a narrow range and this group presumably includes several types of specialists. *Fig. 4* shows two specialisations, viz., one from oligotrophic habitats (S1) and one from eutrophic one (S2).

S2 forms are conceivably recently originated specialists occurring in "young" biotopes, but perhaps they formerly occurred long before the agricultural revolution at, e.g., localized nutrient-rich sites around farm-yards or still earlier along migratory paths of the larger herbivores now mostly extinct here. In the latter case also S2 specialists might be old. In the representation it is assumed that the generalists are older than the specialists. We include in the specialists group the microspecies:

*T. eudontum*, *T. ekmanii*, *T. atonolobum*, *T. effusum*, *T. sagittipotens*, *T. falciferum*, *T. pannulatifforme*, *T. undulatiflorum*, *T. croceiflorum*, *T. ekmaniiforme*, *T. pectinatiforme*, *T. pannulatum*, *T. multifidum*, *T. lacinosifrons* and *T. monochroum* (compare *table 2*).

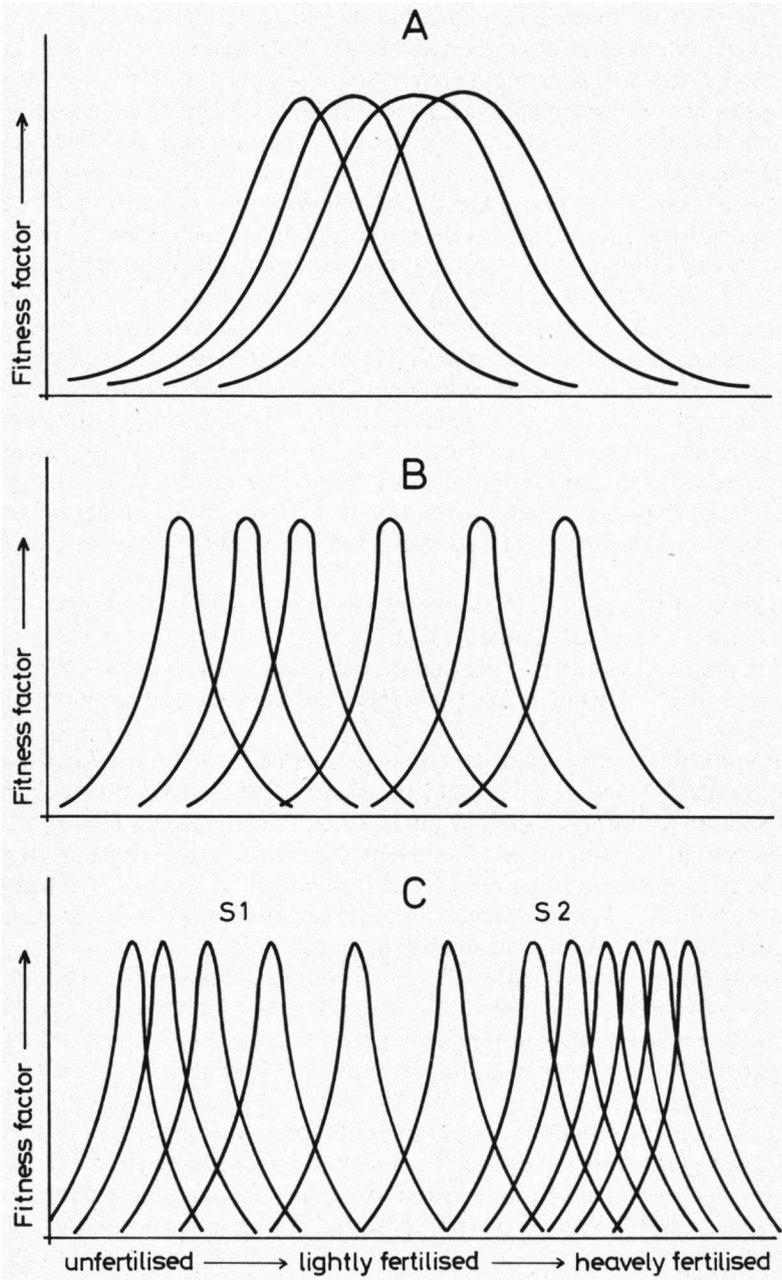


Fig. 4. Ecological relations of microspecies of sect. *Taraxacum*. A: Generalists, B: Intermediates, and C: Specialists.

There are several intermediate cases between the generalists and the specialists here called "intermediates". Intermediates are: *T. lucidum*, *T. linguatum*, *T. lancidens* and *T. subditivum* (compare table 2).

It seems as if the microspecies of sect. *Taraxacum* constitute a continuum of which the generalists and the specialists are the extremes. As stated before, several specialisations occur within sect. *Taraxacum* such as dry versus wet, saline versus non-saline, eutrophic versus oligotrophic., much-trodden versus more undisturbed stands, intensively grazed and defoliated versus less intensively grazed and cropped, and combinations of these (and of other) series. The possible combinations, which cannot be properly expressed in a two-dimensional figure, render the picture within the sect. *Taraxacum* a much varied one.

The enumeration of features in table 6 is intended to be indicative rather than exhaustive. Under point 4, for instance, there are more possible cases, e.g., among the generalists few euryplastic clones against many stenoplastic ones and also combinations of both. Further investigations are required to elaborate on the given scheme, to verify it or to falsify it as the case may be.

The diagram starts from the assumption that a fairly fixed number of classifiable microspecies is present (HAGENDIJK et al. 1975, 1982). These microspecies are supposed:

- (a) to have a discontinuous variation pattern in respect of one another,
- (b) to possess an ecological identity, and
- (c) to be genetically isolated from one another, mainly on account of their mode of reproduction, which implies that they can maintain their taxonomic identity.

The suppositions all require experimental confirmation. Since the discovery of the frequent incidence of sexuality in Central Europe (DEN NIJS & STERK 1980) and the recording of diploids in The Netherlands (STERK et al. 1982) the possibility of hybridisations and the advent of new variants or even microspecies must be reckoned with. Conceivably the system of microtaxa is far less rigid than was hitherto assumed. One cannot expect to be able to design a simple two-dimensional model of such an evolving system.

Possibly there exists in Central Europe a complex of sexual and agamosperous groups within the range of the sexual forms which may be considered to constitute a large and multivariable taxonomic species. Towards the N this aggregate species can, owing to the predominance and ultimately exclusive representation of agamospermy, be split up into agamosperous taxa which are more or less clearly separable and ecologically specialized microspecies separated in time. In The Netherlands the situation may for that reason be more complicated because in this region some sexuality occurs within a predominantly agamospermic area. The rate of incidence of sexual reproduction is under investigation.

### 5.5. The remaining sections

The preceding chapters deal exclusively with sect. *Taraxacum*, but also some representatives of the sections *Palustria* and *Spectabilia* were encountered as

we have seen albeit more incidentally and in lower numbers. The great difference with the section *Taraxacum* is the much lower taxonomic diversity, sect. *Taraxacum* comprising 153 recorded microspecies and the other two "only" 9 and 10, respectively. Relatively little is known of the ecology of the sections *Palustria* and *Spectabilia*. At one time, before the agricultural revolution, these sections are supposed to have been much more numerous in grassland than they are to-day. They became rare and are mainly restricted in their occurrence to nature reserves, i.e. in relatively old biotopes. As is the case among the microspecies of sect. *Taraxacum*, microspecies have been recorded with a broad ecological range: *T. hollandicum* (sect. *Palustria*) and *T. nordstedtii* (sect. *Spectabilia*), and more specialized ones with a narrow ecological amplitude: *T. friscum* (sect. *Palustria*) and *T. johannis-jansenii* and *T. hygrophilum* (both of sect. *Spectabilia*). The species generally do not tolerate excessive dunging nor much grazing and require moist biotopes.

Representatives of sect. *Erythrosperma* occur in altogether different biotopes. The section is, with 23 microspecies relatively small and has hardly been studied ecologically. It prefers near-natural, dry and oligotrophic environments not grazed by cattle. The population densities are usually on the low side. The various microspecies of this section are found in open vegetation types along the coast and locally in the interior. The population density is apparently largely regulated by density-independent factors although predation by smaller herbivores may be of some importance. Human interference is usually badly tolerated. Our studies have revealed that in this section, like in the other ones, also generalists occur: *T. rubicundum*, *T. tortilobum* and *T. lacistophyllum* next to specialists: *T. taeniatum*, *T. oxoniense*, *T. commixtum*, *T. obliquum*, *T. bractyglossum* and *T. scanicum* (see table 2). The generalists may have migrated from the ancient, natural biotopes to the more recent, cattle-grazed dune grasslands at the same time having become adapted to the somewhat different ecological conditions. In The Netherlands, so far no sexual reproduction has been recorded in representatives of sections *Erythrosperma*, *Obliqua*, *Palustria* and *Spectabilia*; this is under investigation.

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