

Distribution and habitat range of diploid, sexual dandelions (*Taraxacum* section *Vulgaria*), a Central European flora element in The Netherlands

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SUMMARY

The cytogeography of *Taraxacum* section *Vulgaria* in The Netherlands has been analysed on the basis of 190 population samples, a literature dataset of several hundreds of herbarium specimens and some samples from the upstream Meuse valley near Liège, Belgium. Diploid, sexual specimens have been found to be restricted to some phytogeographical districts: the Fluviatile and the Chalk; the diploids constitute a Central (South) European flora element in The Netherlands. Outside the Fluviatile district, diploids are absent even in grasslands with low agricultural stress; they were studied in official nature reserves. The taxon must be considered 'very rare', but may be overlooked. The possible relictual state of the populations, including some consequent, promising, genetic research items is discussed. Vegetation recordings and ecological data showed a positive correlation between the occurrence of the diploids and the degree of xerothermy of the habitat (relatively dry and warm microclimate, main components of the Fluviatile habitat). It is expected that taxonomic difficulties concerning the microsystematics will be a consequence of the genetic exchange (1) between the diploids *inter se* and (2) between the cytotypes.

Key-words: cytogeography, *Taraxacum* section *Vulgaria*, habitat range.

INTRODUCTION

From previous studies on the cytogeography of *Taraxacum* section *Taraxacum* it became obvious that diploid sexual individuals have a vast and remarkably disjunct distribution pattern in West versus Central–Southeast Europe (den Nijs & Sterk 1980, 1984a,b; Jenniskens, den Nijs & Sterk 1985). Roughly speaking there are two disjunct 'diploid areas', namely a western European, Atlantic, one, including France, Belgium, the western and southwestern parts of Western Germany and the western alpine range from the Tyrole westwards. The Central European area, of continental character, stretches through the southeast of Western Germany, the eastern half of Austria, including the Alps, and (the greater?) part of Southeastern Europe, including Czechoslovakia (den Nijs, *et al.* in preparation). Within these regions diploid sexual and triploid asexual specimens

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occur in mixed stands, the relative proportion in the populations varying from a few to nearly 100%. The mechanisms permitting the coexistence of the two synoecic (?) components have not been unravelled yet. Detailed data on the extension of the distribution area to the North are also lacking. Data from Belgium (den Nijs & Sterk 1984b), and more recently from the southern part of the province of Limburg, The Netherlands (Elzinga *et al.* 1985, Elzinga *et al.* 1987), show the occurrence of diploids throughout these regions, albeit in some populations in only minor quantities. In Belgium the diploids seem to be restricted in their northern extension to the edaphically defined Loess-zone, which runs from south-west to north-east through the central part of the country. In the southern part of the adjoining Dutch province of Limburg this Loess-zone is also present.

Elzinga *et al.* (1985) studied in some detail ecological data from a series of stands and it appeared that the diploids show a preference for pastures and meadows alongside the brooks. Within these kind of habitats they slightly prefer the more or less south-exposed banks, indicating a thermophilic tendency.

In a number of heavily stressed agricultural pastures from a series of localities situated elsewhere in the country no diploid specimens of *Taraxacum* have been found (Fengler 1978, Bosch 1979, Hagendijk *et al.* 1982, den Nijs & Sterk 1982). The current study must be seen as an ultimate search for diploids and presents the data of a cytogeographic study, in which the above mentioned data have been compiled and new materials have been collected, especially from the main river valleys and a series of nature reserves from throughout The Netherlands. It, therefore, forms an elaboration of the preliminary results published earlier by Sterk *et al.* (1982). This study was mainly based on data from herbarium material and revealed the rare occurrence of diploid specimens not only in the southernmost part of South Limburg but also in two localities in the down-stream valleys of the rivers Rhine and Overijsselse Vecht.

MATERIALS AND METHODS

Population samples

During the successive years 1981–1984, about 190 population samples were collected, each sample consisting of 30–40 flowerheads, which were preserved in 70% ethanol. A part of the samples was collected as whole-plant specimens and dried and handled as herbarium material. From some populations living tap roots were also taken to perform chromosome counts.

The geographical distribution of the sampling sites is shown in Fig. 1. There are several series (the numerical code in the river valley series corresponds to the down-stream direction):

1. Valley of the river Meuse, including the down-stream delta region in the province of Zeeland: TM 1-54. In these series some samples from the adjoining part of Belgium are incorporated: from alongside the Meuse from Liège down-stream and from some of its tributaries in the Ardennes foothills.
2. Valley of the river Rhine, including the rivers Lek, Lower Rhine and Waal; TR 1–28.
3. Valley of the river IJssel: TY 1-26.
4. Valley of the river Vecht, province of Overijssel: TV 1-20.
5. Samples from nature reserves from throughout the country: TN 1-63. These samples are listed according to the Dutch departmental division in provinces from the North to the South. Samples from the river valleys were taken from pastures and meadows alongside the streams at set distances of 5–10 km.



Fig. 1. Distribution of the sampling localities representing formerly studied herbarium specimens from the National Herbarium, Leiden (Stern *et al.* 1982). In adjacent Belgium some of the earlier published records by den Nijs & Stern (1984a) are drawn in. For an explanation of the code numbers see the text. C=samples from which individuals were selected to study the chromosome number (see Table 1).

Three main types of habitat can be distinguished:

1. Riverforelands, so-called *uiterwaarden*; these are the low lying grounds between the dikes and the summer embankments, which may be flooded for some time, at least in the winter. *Uiterwaarden* generally form flat grounds with soil ranging from sandy to rich in clay, they are fertilized and grazed with a variable intensity.
2. River dunes and levee deposits; these are mostly narrow sandy banks, forming the summer embankments or situated alongside the stream; they normally have an

elevation of 1–3 m above the adjoining foreland. They are mostly managed as pastures in the same way as the forelands. The relatively well-drained sandy soil and the microrelief produces a particular microclimate in this habitat: warm and dry compared with the foreland situation.

3. Dikes; these man-made embankments mostly consist of clay and are covered by a vegetation of grasses which is normally fertilized, mown and extensively grazed. Although dikes rarely reach a height of more than 5 m above the surrounding ground, there exist great differences in microclimate between their different facing slopes and the flat grounds around.

According to the reports by Neijenhuis (1971), de Soet (1976) and Becht (1977), special attention has been given to botanically outstanding and species-rich riverforelands, dunes and dikes.

To obtain information on the possible occurrence of diploid *Taraxaca* in slightly manured biotopes elsewhere in the country, a series of nature reserves was selected in which pastures, meadows and other types of habitat with relatively low agriculture stress are present. These terrains are situated throughout the country, as with earlier recordings, as mentioned in the introduction.

Concise habitat descriptions of all the newly studied fields are given in appendices 1 and 2.

In general the sampling localities were chosen on a selective basis. Samples were taken systematically by collecting the flower heads per population at set distances along an imaginary network of lines regularly spread over the sampling field. Usually the sampled area of a field comprises 150–300 m². As a routine procedure the ploidy levels of the plants were assessed by analysis of the pollen, especially the rate of variation of the pollen diameters (Tschermak-Woess 1949, Richards, 1968, Morita 1976, den Nijs & Sterk 1980). From a selected series of localities the chromosome numbers of some plants were counted by means of the squash technique using basic fuchsin and Ph-microscopy (den Nijs *et al.* 1978).

Ecological data

In each sampling locality short descriptions of some ecological factors were recorded: soil type, moisture, exposition and inclination; the agricultural stress was also estimated. In a selected series of the stands a detailed registration of the vegetation was recorded. To this end the following agricultural technique was used: per field 30 samples of vegetation of about 25 cm² each were collected by complete cutting of the standing crop. These vegetation samples were carried out systematically throughout the sampling area. The crop samples were analysed integrally with respect to the relative presence of all the grass and herb species. With each set of 30 samples an overall vegetation description per population was composed. For references concerning this method see Mooi (1960) and Kruyne *et al.* (1967). In the present text this method of vegetation description is referred to as CABO.

Sampling for the vegetation analysis was done in summer or autumn, not during the dandelion flowering time in early spring.

The selected set of CABO vegetation data was subjected to a cluster analysis: Ward's Method with the Euclidian distance as dissimilarity value (Wishart 1982). We used the Clustan 2.0 program package at the Cyber 170–175 computer at Sara-Amsterdam.

Table 1. Chromosome counts in some samples from diploid–triploid mixed populations

Code number	Location	Chromosome number (2n)	Number of individuals
TM 2	Dolhain, Belgium	16	1
TM 6	Eisden, Belgium	16	4
TM 14	Asselt, L.	16	2
TM 3	Poederoyen, G.	16	2
TM 2	Ooyse Polder, G.	16	1
		24	3

RESULTS

Cytogeography

The results of the pollen analysis are listed in appendix 1 and 2. The enumeration is according to the transects recorded before. The percentage of diploid specimens per sample is given; when no percentages are indicated all capitula proved to be triploid. A very concise description of the habitat is given per sampling locality. Stands from which a CABO vegetation analysis was made are indicated as such.

For each locality the magisterial province is indicated; the abbreviations used are: L(imburg), G(elderland), N(orth) B(rabant), U(trecht), S(outh Holland), Z(ealand) and O(verijssel). The Dutch sites where diploids were found are also indicated by their coordinates according to the national Dutch kilometre–grid system (Anonymous, 1981).

Figure 1 shows the sampling localities and the data from earlier studies concerning the Dutch dandelion cytogeography. To indicate the locality of each of the transects the first and last locality show its listed code number. Data are also incorporated in the figure from the following studies: den Nijs & Sterk (1982) and Sterk *et al.* (1982). These studies mainly present analyses of herbarium material collected throughout the country. Some data from den Nijs & Sterk (1984b), concerning Belgium, are also drawn in. The chromosome countings are presented in Table 1.

Some conclusions can be drawn from the data presented:

Diploids rarely occur in The Netherlands and seem restricted to a large extent in their distribution to the valley of the river Meuse. There, however, they can become the dominant component of some of the *Taraxacum* populations, even when they are surrounded by triploid populations. Samples TM 37 and TM 39, for instance, contain 94% and 67% diploid individuals, respectively.

No diploids occurred in the series of samples from the nature reserves. In spite of the much lower level of agricultural stress in these terrains only triploids are present.

For The Netherlands, as a whole, the distribution pattern of the diploids does not seem to be influenced primarily by the rate of agricultural management of the plots. Whether this is also the case within the diploid distribution area, i.e. the river valleys concerned, remains to be studied.

In Fig. 2 all the known diploid localities are drawn in a formal distribution map as used in the *Atlas van de Nederlandse flora* (Mennema *et al.* 1980). On this map the



Fig. 2. Grid map showing the distribution of the diploid records and the phytogeographical districts of The Netherlands. Data in the South of Limburg borrowed from Elzinga *et al.* (1987). Legends for the numbers of the districts: (1) Chalk district; (2) Loess district; (3) Subcentroeupean district; (4) Campinian district; (5 and 6) Guelanders and Drenthian district respectively; (7) Haf or Polder district; (8 and 9) Wadden and Dune district respectively; (10) Fluviatile district, district of river valley bound taxa.

phytogeographical districts of The Netherlands are also shown (van der Meyden *et al.* 1983). It is quite obvious that the distribution of the diploids is almost exclusively restricted to the Fluviatile and (in the south-east) to the Chalk District (code 10 and 1 in the map). So far, the causes for the rarity in these districts are not clear. Comparing the vegetation data from the stands in this valley region will probably produce more information on the ecology of the diploids versus the triploids.

Ecological data

The clustering method was applied to a group of 46 samples, hailing from the Fluviatile district and the Vecht series (TV), which is located in the transition zone to the Guelders and the Drenthian district (numbers 5 and 6 in Fig. 2); the sites concerned are indicated with CABO in appendix 1. Species input data were weighed values. Initially it was decided to incorporate the *Taraxacum* records themselves in the species lists. The main reason for this is based upon the fact that the differences in densities of the dandelion stands are so great that they may influence the surrounding vegetation to an appreciable extent. Furthermore, it is well known that the agricultural management may cause enormous differences in dandelion densities (Sterk, *et al.* 1983) and, apart from that, one has to reckon with a possible structural difference in density between full triploid populations on the one hand and the di-triploid mixed ones on the other. In this way the presence of diploid (or triploid) specimens, as such, may influence the relative composition of the vegetation. To avoid an important bias in the procedure, only the abundances of the dandelion stands were on the list and not the ploidy levels. In this way a precocious separation (on the basis of the discriminating factor) was prevented.

Figure 3 shows the cluster dendrogram. Populations with a diploid component are indicated by asterisks, the code numbers referring to appendix 1 are also given. The figure leads to the following conclusions: The majority of the TV samples was set apart at about the 1-240 level of the dissimilarity index. Apparently the floristically and ecologically distant relationship of this set of vegetation data to the Fluviatile set is responsible for this. The absence of diploids from this region is consistent with this outcome. It is remarkable that the TV series was split up into two main groups which obviously differ more than these series do with any of the other subgroups calculated. The differentiation of the series in a part from sandy, nutritionally poor places (river dune areas), versus sites from heavily fertilized pastures from clay holding soils, is responsible for this.

The upper part of the dendrogram, in which all the diploids containing samples are situated, only shows minor dissimilarity steps, indicating the mutual resemblances of the vegetation stands concerned. As far as they originate from the Meuse valley, there are obviously only minor differences between the vegetation stands containing diploids or triploids.

A second run of the program under exclusion of the *Taraxaca* produced a dendrogram which hardly differs from the first one.

There is a slight indication of a similarity between the stands containing diploids, according to the ecological factors not included in the cluster procedure: most of these sites are situated in relatively dry terrains or in southern expositions on the dikes or river dune reliefs.

From the List of Fluviatile Plants according to Neijenhuijs (1971), and some species more generally typical of dry grassland habitats, the following series of species were found in the habitats studied:

Agrimonia eupatoria, *Allium vineale*, *Campanula rotundifolia*, *Carduus nutans*, *Cichorium intybus*, *Cynodon dactylon*, *Eryngium campestre*, *Galium mollugo* ssp. *mollugo*, *G. verum* ssp. *verum*, *Melilotus altissimus*, *Ononis spinosa*, *Ornithogalum umbellatum*, *Pimpinella saxifraga*, *Primula veris*, *Plantago media*, *Sanguisorba minor*, *Senecio erucifolius*, *Thymus pulegioides*.

A closer analysis of the 'diploid' species lists revealed an additional differentiation pattern: in the diploid sites, as a rule, species are more often present from this list of Fluviatile species. It is not surprising that this is not reflected in the cluster dendrogram

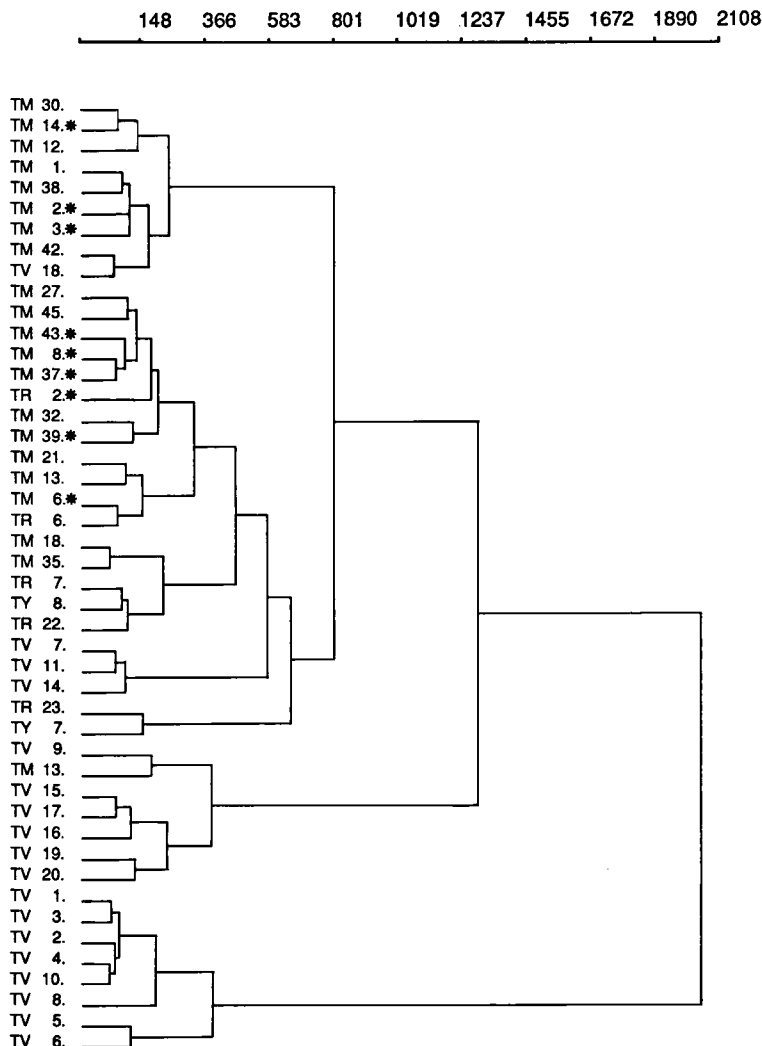


Fig. 3. Cluster dendrogram of the 46 vegetation analyses, based on the CABO data as calculated from the standing crop samples (see text for an explanation of this method). The items are numbered according to the lists in appendix 1. Sites containing diploids are marked with asterisks.

because it concerns a group of species, which, as such, has not been incorporated in the calculations, since each of them only occurs a few times. Table 2 shows the numbers of Fluviatile species in the populations in which diploids have been found.

In particular, the sites from down-stream have relatively many Fluviatile species, while such species are missing in sites from the Chalk and the Loess district. From the majority of the sampling sites without diploids, the Fluviatile species are absent or represented only by a single one. Further down-stream the diploids apparently are restricted to the habitats with a relatively pronounced Fluviatile character, i.e. relatively continental.

DISCUSSION

Diploid, sexual individuals of *Taraxacum* section *Vulgaria* occur in The Netherlands; phytogeographically, their distribution is restricted to the Chalk district (in the south-

Table 2. List of sites with diploid *Taraxacum* specimens, their percentages, the number of Fluviatile species and the total number of species recorded

Code number	Locality	Percentage diploids	n Fluviatile species	Total number species
TM 2	Dolhain	13	—	13
TM 3	Hergenrath	3	—	13
TM 6	Eisden (Belgium)	36	4	16
TM 8	Obbicht	6	8	22
TM 14	Asselt	3	—	13
TM 37	Empel	94	7	35
TM 39	Hedel	67	8	38
TM 43	Poederoyen	33	8	44
TR 2	Nijmegen	27	3	37

eastern part of the country: South Limburg, see Elzinga *et al.*, 1987) and to the Fluviatile district. In this district they mainly occur in the valley of the river Meuse and in the most south-western extension of this district, the Zeeland-Flanders delta region. In the region concerned, the diploids are restricted to habitats that show a relatively strong Fluviatile character, i.e. sandy banks (levee deposits, riverdunes) and more or less southern exposed dike sites. A strong agricultural management stress seems to be disadvantageous; it is likely that in such circumstances the diploids cannot compete with the triploid biotypes, some of which are well adapted to very high levels of nutrients and have higher relative growth rates, for example *T. sellandi*, than a Dutch diploid taxon, e.g. *T. limburgense* (Roetman & Sterk 1986 and Sterk unpublished data). No pure diploid populations were found, in all stands diploid and triploid plants grow together, the relative amount of the diploids may, nevertheless, reach high percentages.

It is likely that in the Loess district the diploids are also present (or were present, as this district has been subjected to an extremely heavy anthropogenous stress). A more detailed search for the regular pollen will give the answer.

The absence of the diploid plants from the heavily agriculturally stressed pastures, as reported earlier by a.o. Hagendijk *et al.* (1982) and the present data from a series of low-stressed grasslands in nature reserves, leads to the conclusion that the present distribution pattern shows the most northerly extension of the diploid area. The very common occurrence of diploids in the greater part of France, Western Germany, Switzerland and even Belgium ends in The Netherlands. The pattern recorded demonstrates the kind of responses typical for a marginal situation: the taxon concerned virtually shows a narrowing of its ecological amplitude and occupies—due to the fact that suitable conditions are becoming rare—a small range of habitats compared with the more centrally situated populations.

The diploid *Vulgaria* specimens must be considered as a Central (South) European element in the flora of The Netherlands. According to the 'Standaardlijst van de Nederlandse Flora' (van der Maarel 1971) the taxon must be given the status of very rare, since until now it was found in less than 10 areas of the national 5 × 5 km-grid. A more detailed screening of the suitable habitats may, however, show the presence in many additional squares. Such a study could easily be performed by means of the pollen method.

The taxonomy of the taxon is not well known; *T. limburgense*, a species described from South Limburg, turned out to be diploid in its type locality. Given the doubtful taxonomic status of diploid *Vulgaria* microspecies in general, this problem has to be studied in more detail. A recent study of the *Taraxacum* flora of Belgium and Northern France (den Nijs & Sterk, 1984b) revealed that about 75 of the microspecies studied are represented by diploid as well as triploid specimens.

Beyond the ecological circumstances of the river valleys the diploids are obviously not able to produce viable seeds, this is apparent from a field study by Sterk (1987), who transplanted a group of diploids to a triploid stand near Abcoude, situated in the Haf district. These plants developed well vegetatively, but they produced only a small amount of seed. The necessity of cross pollination in the self-incompatible diploids is obviously a limiting factor under the climatic circumstances during the flowering time of *Taraxacum* in the more northern sites.

Although the diploids generally rarely occur in The Netherlands, possible hybrid-ogoneous contacts *inter se* and, especially with the co-occurring triploids, throw considerable doubt on the validity of the microspecies taxonomy which is based on the assumption of exclusive agamosperous reproduction of the triploids (Jenniskens *et al.* 1985 and den Nijs & Menken unpublished data). Given the fact that the suitable Fluvatile habitat has been strongly reduced in extent over the past 50 years—mainly due to the intensive agricultural practice—one would speculate that the diploids of the *Vulgaria* section could have been much more common in the past and that the existing populations only represent relict stands. We suggest that the diploid taxon is to be regarded as a threatened one in the Dutch flora and, in this respect, has to be given the same status as the representatives of the sections *Palustria* and *Celtica* (formerly called *Spectabilia*): this conforms to the proposals by Sterk *et al.* (1987).

The diploids may constitute small island populations of sexuality in between a mass of asexual triploids. Such populations could be very useful to study the genetic consequences of small isolated populations.

A contrasting point of interest is the putative gene flow between diploids and triploids in mixed populations (Richards 1970a,b; Müller 1972, Jenniskens *et al.* 1985). Most of these studies are based on experiments in the greenhouse. There are few comparable data from the actual field populations. When this gene flow effectively occurs in nature, the above hypothesis on the island status of the small diploid populations should be abandoned.

Analysing the genetic constitution of both components of the populations by isozyme techniques will produce information on the relation and the rate of gene exchange between the cytotypes. Studies of this kind are in progress.

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APPENDIX 1

Sampling localities and results of the analyses: if no percentage of diploids is given, all the plants in the sample are triploids. A note to the habitat descriptions: a pasture is always grazed, some special situations are indicated; hayfields, in the same way, are always ungrazed.

Transect series river Meuse: TM1-54

TM 1 Clermont-s-Berw., Liège, B.: fertilized pasture, poor in species; CABO; TM 2 Dolhain, Liège, B.: **13% dipl.**; heavily fert. pasture, valley floor, very poor in species; CABO; TM 3 Hergenthath, Liège, B.: **3% dipl.**; brook meadow, per. flooded, grazed, fert., poor in spec.; CABO; TM 4 Plombières, Liège, B.: moderately fert. pasture; TM 5 Eijsden, L.: intensively fert. pasture; TM 6 Eisdien, Limburg, B.: **36% dipl.**; slightly fert., hayfield; grid: 59.48.55; CABO; TM 7 Stokkem, Limburg, B.: mod. fert. pasture; TM 8 Obbicht, L.: **6% dipl.**; foreland & spec. rich dike, exp. W; grid: 60.31.33; CABO; TM 9 Elen, Limburg, B.: mod. fert. pasture; TM 10 Vissersweerd, L.; spec. rich dike, exp. S.; TM 11 Echt, L.: per. flooded pasture, mod. fert.; TM 12 Merum L.: spec. rich dike, exp. S.; TM 13 Lerop-Melick, L.: heav. fert., ext. grazed foreland; CABO; TM 14 Asselt, L.: **3% dipl.**; mod. fert., ext. grazed pasture; grid: 58.44.14; CABO; TM 15 Donderberg, L.: spec. rich dike, exp. S.; TM 16 Donderberg, L.: dike, exp. S.; TM 17 Rijkkel, L.: mod. fert. pasture; TM 18 Kessel, L.: mod. fert., ext. grazed foreland & river dunes; CABO; TM 19 Blerick, L.: int. fert. hayfield (foreland); TM 20 Lorum, L.: river side pasture, mod. fert.; TM 21 Arcen, L.: mod. fert. ungrazed foreland on silt; CABO; TM 22 Well, L.: orchard pasture; TM 23 Ayen, L.: riverside pasture, ext. grazed, mod. fert.; TM 24 Groeningen, N.B.: meagre pasture, ext. grazed; TM 25 Afferden, L.: pasture, mod. fert.; TM 26 Oeffelt, N.B.: dike, exp. W., int. grazed; TM 27 Oeffelt, N.B.: foreland, mod. fert., ext. grazed, sandy; CABO; TM 28 Oeffelt, N.B.: spec. rich river dunes, mod. fert. ext. grazed, sandy; TM 29 Middelaar, L.: foreland, mod. fert. grazed; TM 30 Plasmolten, L.: pasture, ext. grazed; CABO; TM 31 Overasselt, G.: int. fert. & grazed, foreland; TM 32 Reek-Overlangel, N.B.: mod. fert., ext. grazed dike, exp. SW.; CABO; TM 33 Demen, N.B.: int. fert. & grazed foreland; TM 34 Oijen, N.B.: mod. fert. & grazed foreland; TM 35 Heerewaarden, G.: mod. fert., ext. grazed pasture; CABO; TM 36 Alem, G.: mod. fert. & grazed dike, exp. S.; TM 37 Empel, N.B.: **94% dipl.**; mod. fert. & ext. grazed levee deposits, exp. N.; grid: 45.22.45; CABO; TM 38 Hedel G: transition zone pasture-dike, int. grazed, mod. fert.; exp. S.; CABO; TM 39 Hedel, Mussenwaard, G.: **67% dipl.**; ext. grazed S-facing levee deposits, spec. rich; Nature reserve; grid 45.22.41; CABO; TM 40 Slijkwell, G.: ungrazed river dunes; TM 41 Heusden-Aalburg, G.: ext. fert., ungrazed, S-facing dike; TM 42 Poederoyen, G.: ext. fert. & grazed, wet foreland; CABO; TM 43 Poederoyen, G.: **33% dipl.**; ext. grazed, spec. rich levee deposits, exp. S.; grid: 44.17.44; CABO; TM 44 Drongelen, N.B.: int. fert., ext. grazed, S-facing dike; TM 45 Waspik, N.B.: int. fert. & grazed pasture; CABO; TM 46 Dussen-Biesbosch, N.B.: ext. fert. & grazed dike, exp. E.; TM 47 Zonnemaire, Z.: dry, sandy, species rich dike, exp. E.; TM 48 Noord-Gouwe, Z.: ext. grazed, species rich dike, exp. S.; TM 49 Ankevere, Z.: dry dike; TM 50 Heinkenszand, Z.: grazed dike; TM 51 Ovezande, Z.: ruderal dike vegetation; TM 52 Hulst, Groot Eiland, Z.: pasture; TM 53 Zaamslag, Z.: **3% dipl.**; pasture near to the "Sasdijk"; grid: 54.28.11; TM 54 Cadzand, Z.: relatively meagre & locally dry grassland, incl. *Erythrosperma* & *Palustria* specimens.

Transect series River Rhine, including the rivers Waal, Lek and Lower Rhine: TR 1-28

TR 1 Lobith, G.: not fert., not grazed, species rich, dike; nature reserve; TR 2 Ooyse Polder, G.: **27% dipl.**; S-facing dike, species rich; grid: 40.52.25; CABO; TR 3 Oosterhout, G.: ext. fert. & grazed dike, exp. S.; TR 4 Ewijk, G.: dike, exp. S.; TR 5 Doornenburg, G.: foreland; TR 6 Huissen, G.: ext. fert. & grazed, S-facing summer dike & foreland; CABO; TR 7 Arnhem, G.: mod. fert. & ext. grazed foreland; CABO; TR 8 Driel, G.: foreland, pasture; TR 9 Heteren-Randwijk, G.: foreland, pasture; TR 10 Opheusden, G.: foreland, pasture; TR 11 Elst, G.: foreland, pasture; TR 12 Elst, G.: summer dike & foreland; TR 13 Elst, G.: foreland, pasture; TR 14 Amerongen, U.: foreland, pasture; TR 15 Amerongen, U.: fert. & grazed dike, exp. S.; TR 16 Wijk bij Duurstede, U.: S-facing dike & foreland; TR 17 Beusichem, G.: S-facing dike & foreland; TR 18 Culemborg, G.: S-facing winter dike & foreland; TR 19 Culemborg, G.: wet foreland, pasture; TR 20 Vianen, Z.H.: foreland; TR 21 Lopikerkapel, U.: S-facing dike & foreland; TR 22 Lexmond, Z.H.: foreland & river dunes, mod. fert. ext. grazed; CABO; TR 23 Luistenbuul, Z.H.: hardly fert., ext. grazed, river dunes; nature reserve; CABO; TR 24 Tienhoven, Z.H.: river dunes, many *Erythrosperma* specimens; nature reserve; TR 25 Tienhoven, Z.H.: as TR 24; TR 26 Langerak, Z.H.: very wet foreland; TR 27 Schoonhoven, Z.H.: ungrazed foreland & dike, exp. S.; TR 28 Bergambacht, Z.H.: summer dike.

Transect series River IJssel: TY1-26

TY 1 Velp, G.: dike & sandy foreland; TY 2 De Steeg, G.: foreland, pasture; TY 3 Leuvenheim, G.: gravel pit in foreland; TY 4 Zutphen, G.: road margin in foreland; TY 5 Ravenswaarden-Gorssel, G.: river dunes, SW exp.; TY 6 Ravenswaarden-Gorssel, G.: river dune, exp. W.; TY 7 Voorst, G.: mod. fert. ext. grazed dry dike, exp. S.; CABO; TY 8 Wilp, G.: mod. fert., ext. grazed, dry dike, exp. SE; CABO; TY 9 Terwolde, G.: foreland, pasture; TY 10 Randerwaarden, Deventer, G.: SW-facing, species rich dike; TY 11 Wijhe, O.: SW-facing, species rich dike; TY 12 Welsum, O.: foreland, pasture; TY 13 Oenedijk, G.: species rich dike, nature reserve; TY 14 Veessen, G.: SE-facing, species rich dike; TY 15 Marle, O.: species rich dike; TY 16 Hattem, G.: dike & foreland;

TY 17 Zwolle, O.: SW-facing, species rich dike; TY 18 Zwolle, O.: dike and foreland; TY 19 Vreugderijkerwaard, O.: hardly fert., ext. grazed, species rich river dunes, nature reserve, many *Erythrosperma* specimens; TY 20 Zalk, O.: species rich, wet foreland, pasture; TY 21 Zalk, O.: mod. fert. ext. grazed, species rich dike, exp. SW; TY 22 Zalk, O.: sandy foreland; TY 23 De Zande, O.: S-facing, species, rich dike; TY 24 De Zande, O.: species rich wet foreland, pasture; TY 25 De Zande, O.: hardly fert., species rich foreland, pasture; TY 26 Kampen, O.: species rich, sandy foreland, pasture.

Transect series River Vecht: TV1-20

TV 1 Ommen, O.: dry. fert. pasture, rich in species; CABO; TV 2 near Vilsteren, O.: dry. fert. pasture; CABO; TV 3 near Vilsteren, O.: dry. fert. pasture; CABO; TV 4 near Vilsteren, O.: dry, only scarcely fert. pasture; CABO; TV 5 near Vilsteren, O.: dry, fert. pasture; CABO; TV 6 near Vilsteren, O.: dry. fert. pasture; CABO; TV 7 Ommen, O.: grazed, intensively fert. pasture; CABO; TV 8 Junner Koeland, O.: river dune, dry. ext. fert. grassland; CABO; TV 9 Rheezer Belten, O.: river dune: dry. ext. fert. grassland; CABO; TV 10 Rheezer Belten, O.: river dune: dry, ext. fert. grassland; CABO; TV 11 Ommen, near Arrien, O.: int. grazed and fert. pasture; CABO; TV 12 Ommen, near Arrien, O.: fert. and int. grazed pasture; CABO; TV 13 Ommen, near Arrien, O.: rather dry, intermediately fert. pasture; CABO; TV 14 Ommen, O.: int. fert. and grazed pasture; CABO; TV 15 Rheezermaten, O.: hardly fert. grassland; CABO; TV 16 Hardenberg, O.: nature reserve: wet, ungrazed, not fert. grassl.; CABO; TV 17 Rheezermaten, O.: but slightly fert., rather moist pasture; CABO; TV 18 near Beerze, O.: int. grazed and fert. pasture; CABO; TV 19 near Beerze, O.: grazed and fert. pasture; CABO; TV 20 near Beerze, O.: grazed and fert. pasture; CABO.

APPENDIX 2

Sampling localities in a series of Nature Reserves (TN 1-63), scattered throughout the country and grouped according to the administrative division into provinces. All the samples analysed contain only triploid plants.

Province of Groningen. TN 1 Slochter en Scharmer Ae's, Hoogezand: pasture; TN 2 Punt van Reide, Dollard wadden area; TN 3 Metbroek, Vlagtwedde: wet pasture; TN 4 Dwarsdiep, Marum: moist pasture.

Province of Friesland. TN 5 Klaarkampermeer, Dokkum: wet pasture on clay; TN 6 Workumerwaard, Workum: wet pasture; TN 7 Jan Durkspolder, Eernewoude, Grouw: wet pasture; TN 8 Wijnjeterper Schar, Drachten: "blue grassland"; *Molinion*; TN 9 Delleburen, Ooststellingwerf: pasture; TN 10 Sondeler Leyen, Gaasterland: wet pasture; TN 11 Oude Mirdumerklif, Gaasterland: dike, ext. grazed, exp. S.

Province of Drenthe. TN 12 Mensinge Hazematén, Roden: wet pasture, slightly fert., ext. grazed; TN 13 Stroomdallandschap Drentsche A, Eelde: wet pasture, slightly fert., ext. grazed; TN 14 Stroomdallandschap Drentsche A, Anderen: pasture, slightly fert., ext. grazed; TN 15 Stroomdallandschap Drentsche A, Anderen: dry pasture, sheep grazing; TN 16 Reitma Westerborn: wet pasture, *Molinion*.

Province of Overijssel. TN 17 Meppelerdiep, Olde Staphorst: moist, meagre, *Carex*-rich hayfield, not fert.; TN 18 Junner Koeland, Ommen: river dune, slightly fert., ext. grazed, dry S-SW-facing slopes; TN 19 Rossumermenden, Rossum: wet hayfields, not fert.; TN 20 De Brommert, Hasselt: S-facing dike and foreland, ext. grazed; TN 21 Kromme Kolk, Zwolle: ext. grazed foreland and dike, exp. S.; TN 22 Marienberg, Ommen: river dune, pod damaged; TN 23 Rheezermaten: ungrazed, moist hayfield.

Province of Gelderland. TN 24 Hoophuizen, Hierden: former bank of the lake IJsselmeer; TN 25 Polder Arkemheen, Nijkerk: hayfield, until recently fert.; TN 26 Bennekomsse Meent, Ede: poor, wet, *Carex*-rich hayfield, not fert.; TN 27 Ossekampen, Wageningen: meagre hayfield; TN 28 De Bloemkampen and Grote Weiland, Nunspeet: ext. grazed pasture; TN 29 Oosterwolde, Elburg: poldergrassland with *Phragmites*-aspect; TN 30 Lochemse Berg, Lochem: orchard pasture.

Province of Utrecht. TN 31 Meeuwenkampje, Renswoude: poor, wet, *Carex*-rich hayfield; TN 32 Bovenpolder, Amerongen: dike; TN 33 Broekhuizen Manor, Leersum: int. grazed pasture, not fert.; TN 34 Broekhuizen Manor, Leersum: hayfield, not fert.; TN 35 Zegveld: meagre meadow alongside the river Meije, rich in *Carex* species.

Province of North Holland. TN 36 Wieringermeer Forestry, Robbenoord: underneath mixed deciduous forest, not grazed, not fert.; TN 37 Zwanewater, Callantsoog: unfert. dune grassland; TN 38 Hoge Berg, Texel: pasture; TN 39 De Waal-Den Burg, Texel: pasture; TN 40 Dijkmanshuizen, Texel: sandy sheep grazed pasture in dune area.

Province of South Holland. TN 41 Nieuw Leeuwenhorst, Noordwijk: wet pasture; TN 42 Westduinen, Ouddorp: ext. grazed river dune; TN 43 Voorne's Duin, Oostvoome: dune grassland; TN 44 Ibidem; TN 45 Smoutjesvlietlanden, Goudriaan: wet reservoir hayfield of a polder; TN 46 Streefkerk: poor, wet, *Carex*-rich hayfield, not fert.; TN 47 Kwade Hoek, Ouddorp: outdike wadden and dune pastures; TN 48 Voorne's Duin, Rockanje: ext. grazed dune grassland.

Province of Limburg. TN 49 Schuitwater, Homberg: mod. fert. pasture; TN 50 Griendtsveen, Mariapeel: dry, grassy heath; TN 51 Meynweg, Herkenbosch: dry, hilly heath vegetation with *Quercus* and *Pinus*.

Province of North Brabant. TN 52 Kornse Boezem, Almkerk: hayfield; TN 53 Bergen op Zoom: ext. grazed wadden pasture; TN 54 Oisterwijkse Bossen en Vennen, Moergestel: hayfield cuttings in woodland; TN 55 Helmond: brook valley, pasture with *Primula* species; TN 56 Helmond: ext. sheep grazed (heath) pasture; TN 57 as TN 53; TN 58 De Leemkuilen, Udenhout: meagre sandy road verge.

Province of Zeeland.; TN 59 Zouten-en Zoeten Haard, Renesse: wet pasture; TN 60 Dijkwater, Sirjansland: S-facing dike; TN 61 Zwin en Kievitte Polder, Cadzand: pasture; TN 62 Muyepolder, St. Maartensdijk: S-facing dike; TN 63 Groot Eiland, Hulst: pasture.