ON THE VARIATION IN THE FLOWER HEADS OF ASTER TRIPOLIUM L. IN THE NETHERLANDS

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SUMMARY

In the Netherlands *Aster tripolium L.* exhibits a considerable variation in the number of ray florets per capitulum. There is a gradual transition from plants producing inflorescences with ray florets to plants producing exclusively flower heads without a single ray floret (so-called discoid plants).

Discoid plants are particularly frequent in the south-western parts of the Netherlands, the populations occurring along the western Scheldt estuary (Westerschelde) showing the highest percentages of discoid specimens, but in the northern part of the country they are far less common. Discoid forms are chiefly found outside of the dikes. The number of ray florets per capitulum is not correlated with the number of disk florets. Accordingly, the recognition in the area of the Low Countries of varieties based on the number of ray florets does not seem to be recommendable.

1. INTRODUCTION

The Sea Aster is a very variable species, showing a great deal of variation mainly in height, in the mode of branching, in the leaf shape, in the structure of the compound inflorescence, in the composition of the capitula, in the time of flowering, and in average life span.

The principal infraspecific taxa distinguished in the relevant literature of western Europe are:

Aster tripolium L. var. *discoideus* Rchb.: capitula without ray florets (REICHENBACH 1854).

A. tripolium var. *solstitialis* Focke: with low growth habit, branched from the base, and flowering in June (FOCKE 1906).

A. tripolium var. *autumnalis* Focke: a tall form branching upwards and flowering in late summer and in the autumn (FOCKE 1906).

A. tripolium subsp. *pannonicus* (Jacq.) Soó: lowermost leaves lanceolate, narrowed towards the base, with narrow petioles, ciliate-serrate; stem ascending to erect, profusely branched, involucre coloured. This infraspecific taxon from the Pannonian Region is usually sharply distinguished from the populations of the western coasts of Europe, but WAGENITZ in HEGI (1964) reports that the characters of the subsp. *pannonicus* are extremely variable and have also been found in plants from the coastal area of northern Germany and WIJNANDS (1969a) agrees with this statement for the Netherlands.

A. tripolium var. *discoideus* has been recorded from the Netherlands by several authors, sometimes as "forma *discoideus*", sometimes without assigning it

taxonomic status: HOEK & REDEKE (1901), Prodr. Fl. Bat. (1902), GARJEANNE (1902), HEUKELS (1910), HEIMANS, HEINSIUS & THIJSSE (1965), HEUKELS-VAN OOSTSTROOM (1968). The other varieties mentioned have not been reported in the Dutch floristic literature.

The species *Aster tripolium* occurs in a number of environments. BEEFTINK (1965) considers the Sea Aster to be a characteristic species of the Class *Asteretea tripolium* Westhoff & Beeftink 1962, which includes all types of halophilous vegetation of the European mud flats and shallows and other ecologically similar sites in the interior.

FEEKES (1936) studied the variation of *A. tripolium* in the then newly reclaimed Wieringermeer-polder (province of Noord-Holland). He found a great deal of variation, which is feasible, considering the special character of the newly created habitat on bare "virgin" soil. Feekes distinguished a brackish and a sea-water convivium of the Sea Aster, the salt-water convivium being supposed to contain a considerable amount of discoid individuals. Other Dutch authors also seem to suppose that the discoid form of *A. tripolium* possesses an ecological tolerance and habitat preference different from that of plants with ligulate heads (WEEVERS 1936). The variability of the population complex of *A. tripolium* in the Netherlands is insufficiently known, and the same applies to the population complexes of the shores of western Europe and the Pannonian Region. This is the reason why we started a biotaxonomic study of this species, whose natural habitats in the Netherlands and elsewhere are in danger of being destroyed and are already decreasing in size at an alarming rate.

In this paper the variation in the composition of the flower heads is dealt with, with emphasis on the absence or presence of ligulate florets in a number of Dutch populations studied.

2. VARIATION IN THE NUMBER OF LIGULATE FLORETS

2.1. Variation in individual plants

The number of ray florets per head has been counted in a large number of plants (details in WIJNANDS 1969a). The variation in seven representative individuals is shown in *table 1*.

It appears that even in a single plant there is a considerable variation in the number of ray florets per head. This study of individual specimens suggested the distinction of three categories of plants, *viz.*,

a. plants bearing only discoid heads: discoid plants *(e.g.* pl. 1);
b. plants producing both discoid heads and heads bearing tubular and ray florets: partly-discoid plants *(e.g.* pl. 2, pl. 3 and pl. 4);
c. plants devoid of discoid heads: "non-discoid" plants (*e.g.* pl. 5, p.. 6 and pl. 7).

Within the groups (b) and (c) the variation in the number of ligulate florets is rather excessive: compare pl. 2 with pl. 4, and pl. 5 with pl. 7.

Table 1 also demonstrates quite clearly that there is a *gradual* transition

Table 1. *A. tripolium.* Variation in the number of ray florets in the heads of 7 representative specimens. (pl. = plant).

Number of ray florets per head	Number of flower heads per plant						
	pl. 1	pl. 2	pl. 3	pl. 4	pl. 5	pl. 6	pl. 7
0	15	27	14	1			
1–4		15	51	20	1		
5– 8			12	40	8		
9–12				32	4		
13–16				7	8	2	
17–20				3	4	6	
21–24						1	5
25–28							17
29–32							17
33–36							2

Table 2. *A. tripolium.* Relative frequency distributions of dis-coid, partly-discoid, and non-discoid specimens of the sampled local populations. For the locality number the reader is referred to the map shown in *fig. 1.* (i.d. = inside of the dikes, o.d. = outside of the dikes, T = the island of Terschelling).

Locality	Situation of locality	No. of locality	Percentage of plants			Number of plants in the sample
			non-discoid	partly-discoid	discoid	
De Kaloot	o.d.	1	10	15	75	100
Ellewoutsdijk	o.d.	2	10	21	69	100
Waarde	o.d.	3	12	27	61	100
Ossendrecht	o.d.	4	8	39	53	100
Kreekrak	o.d.	5	23	34	43	100
De Heene	o.d.	6	23	29	48	100
De Kwade Hoek	o.d.	7	81	13	6	100
Oostvoorne	i.d.	8	80	12	8	100
Veerse Meer	i.d.	9	92	6	2	50
Ellewoutsdijk („inlage")	i.d.	10	100			50
Petten	i.d.	11	100			100
Holwerd	o.d.	12	98	1	1	100
Zoutkamp	o.d.	13	75	15	10	100
Dollard	o.d.	14	100			100
Boschplaat (T)	o.d.	15	100			50
idem	o.d.	16	100			50
idem	o.d.	17	100			50
De Grie (T)	o.d.	18	100			50
Zurich	i.d.	19	100			100

from completely discoid plants to plants bearing heads with a large number of ray florets.

2.2. Variation within populations

In the Netherlands we studied the variation in local populations from:

a. all principal parts of the total range of the Sea Aster so as to be able to detect possible geographic variation, and
b. the principal environments so as to be able to recognise any possible correlation between the morphological variability and habitat.

These populations were studied by representative sampling, the size of the samples being either 50 or 100 specimens (WIJNANDS 1969a). The plants constituting such a sample were placed in one of the three categories (discoid, partly-discoid and non-discoid individuals) mentioned previously, and the relative frequency distributions of the samples were compiled in *table 2.*

It appears from the results tabulated in *table 2* that:

1. discoid individuals are of common occurrence in the SW. Netherlands but relatively scarce in the N. Netherlands, which agrees with HEUKELS-VAN OOSTSTROOM (1968);
2. the variation within a local population may be appreciable; the majority of the southern populations studied (9 out of 10) containing discoid, partly-discoid and non-discoid plants (but only 2 out of the 9 northern populations);
3. the highest percentages of discoid plants occur in the outlying localities (on the seawardside of the dikes) of the western Scheldt estuary (Westerschelde) (populations 1, 2, 3 and 4);
4. the populations outside the dikes of the Westerschelde show a gradual decrease of the percentage of fully discoid plants going upstream and an increase of the percentage of partly-discoid individuals; and
5. at the sites lying in the landward side of the dikes in the SW. Netherlands no discoid plants occur at all (as in 10), or their representation is low (9), which also agrees with the statements in Heukels-van Ooststroom. (It should be borne in mind that the Veerse Meer (9) and Oostvoorne (10) are localities in parts of estuaries recently cut off from the sea which may for that reason still exhibit some ecological characters of the sites lying on the seaward side of the dikes, which may account for the presence of discoid specimens).

The distribution of the various discoid, partly-discoid and non-discoid forms of *Aster tripolium* has some interesting historical aspects. The oldest record of the discoid form in the Netherlands dates from 1878 (the Fort Rammekens on the island of Walcheren: Prodr. Fl. Bat. 1902). Discoid specimens had been found at an earlier date by DU MORTIER (1868), and DE L'OBEL reported the occurrence of discoid Sea Asters along the Belgian coast as early as 1581. There are few reports of the occurrence of the discoid forms in the Dutch floristic literature between the turn of the century and about 1920, but later on they get more numerous and after about 1950 the form has become common in the SW. Netherlands. According to Dr. W. G. Beeftink of the

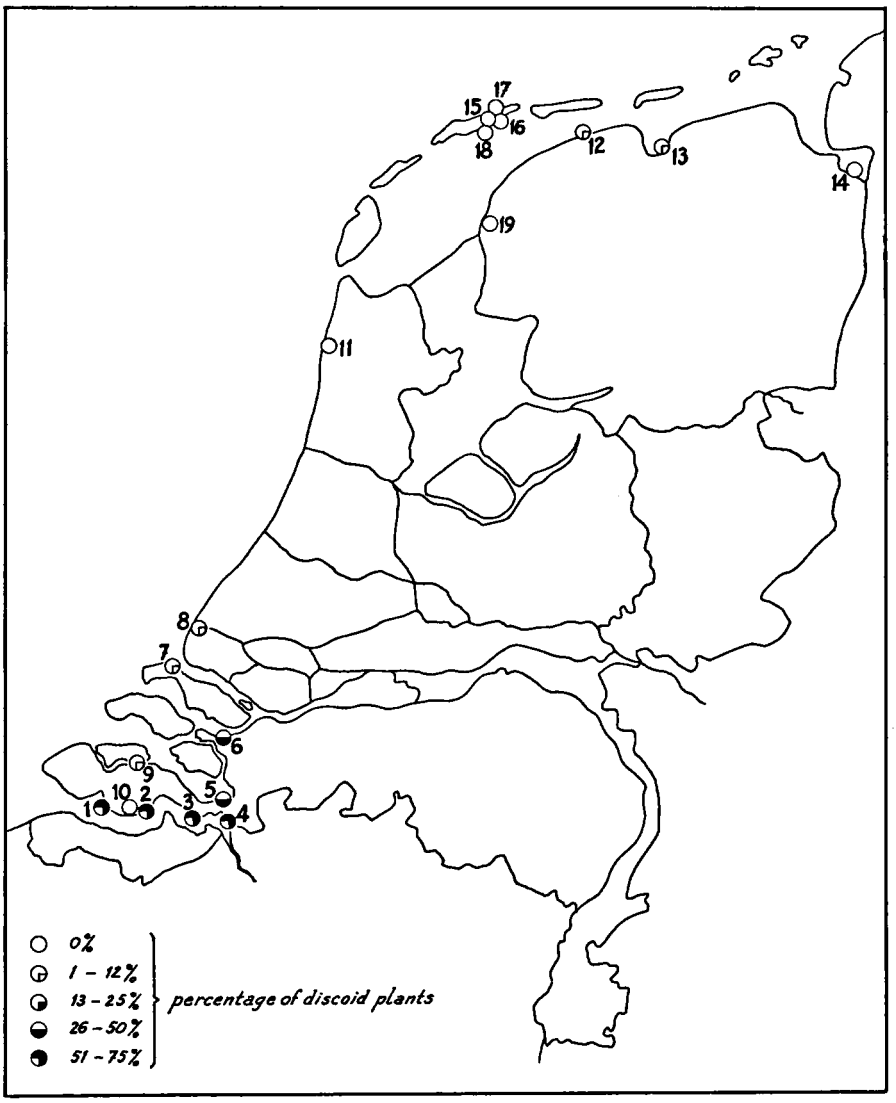

Fig. 1. Map of the Netherlands showing the localities of the investigated populations and the percentages of the discoid plants of the samples.

Delta Insitute for Hydrobiological Research, Yerseke (priv. comm.), the relative frequency of the discoid specimens in the population near Ossendrecht (4) (*fig. 1*) has increased appreciably since 1950, whereas their relative frequency on De Kaloot (1) has remained more or less constant. In N. Germany, according to BUCHENAU (1894), the discoid form occurred as a few scattered specimens among the nominal form by the end of the 19th century. FOCKE (1906) stated

that at the time of writing (1906) the qualification 'a few scattered specimens' was not applicable any more and that he had gained the impression that the discoid form had increased in the last 30 years, at first at a very slow rate, but later gradually faster. Focke anticipated an ultimate dominance of the discoid form if its increase would continue, and apparently in 1906 this was already the case at a site near Jadebusen in the Weser estuary.

In Great Britain the discoid form has also replaced the nominal type of plant more and more (Gray, priv. comm.). A distribution map of "var. *discoideus*" in the British Isles was published in FERRING (1968).

The corollary of these reports is that although the discoid form already occurred in the 16th century along the W. European coast, it only increased at the expense of the nominal form since the turn of the century.

3. VARIATION OF THE NUMBER OF RAY FLORETS IN RESPECT OF THE NUMBER OF TUBULAR FLOWERS

The results of our analyses of the samples of the local populations indicate a considerable variability in the number of ligulate florets per capitulum. The obvious question arises whether there is any relation between the number of ray florets per head and the number of tubular florets per head. This possible connection was studied in a number of population samples showing considerable differences in the percentages of discoid plants, *viz.*, the samples from De Kaloot (1), Ossendrecht (4), Ellewoutsdijk (10) "inlage" (small brackish water area inside of the dike) and the Dollard (14). The results of this study are shown in *fig. 2* (WIJNANDS 1969a).

A comparison of the series of histograms A and B clearly shows that the variation in the number of tubular florets per head is not correlated with the number of ray florets per head. The population of De Kaloot (1), for instance, with 75% of discoid specimens, has a relative frequency distribution which does not significantly differ from that of the Dollard where no discoid specimens occur. The population from Ellewoutsdijk (10) has a frequency distribution which is significantly different from that of all other populations studied. An explanation of this phenomenon can not be given at this stage of our investigations.

A reduction of the number of ray florets concomitant with a constant number of tubular florets presumably causes a decrease in reproductive capacity. That such a decrease may be an appreciable one is apparent from a comparison of the average number of tubular florets and ray florets in the Dollard population (22.7 and 15.1, respectively), which indicates that about 30% of the florets are ligulate and account for about 30% of the potential number of seeds produced per head; the average number of tubular florets in the population from De Kaloot is 24.1, but the average number of ray florets only 1.3, *i.e.*, the mean percentage of ray florets is about 5%. The absolute contribution of the ray flowers towards the total production of seed is probably also much lower in the latter population than it is in the first.

Considering that the ray florets are female, the reduction of the number of

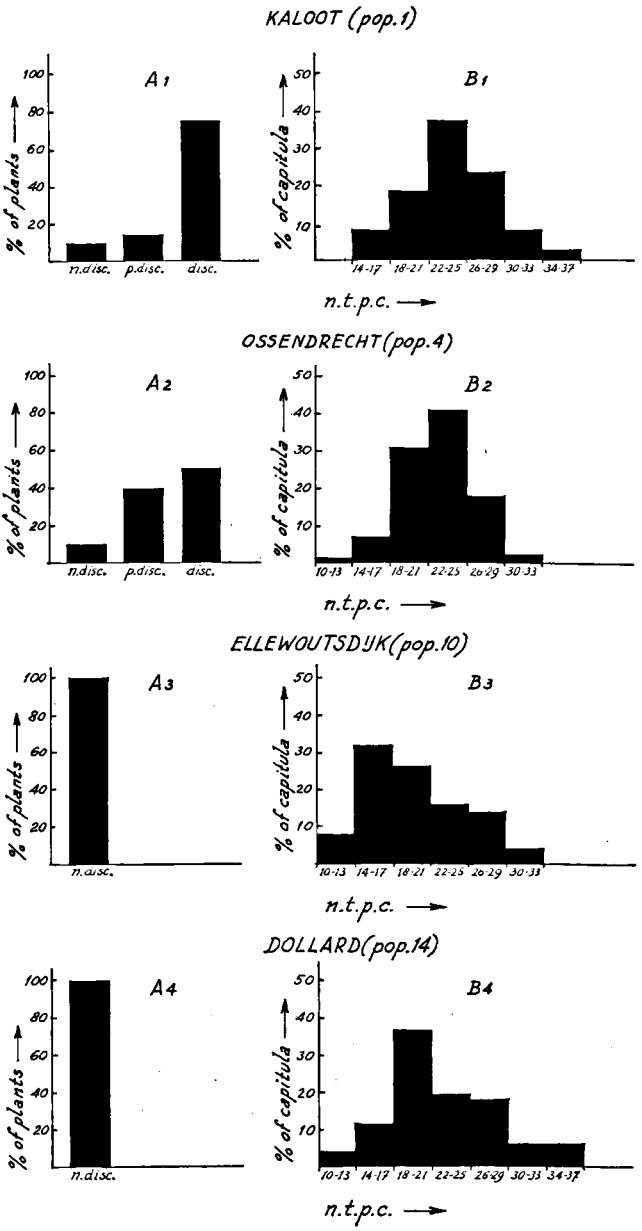

Fig. 2. In the histograms marked "A" the relative frequency distributions are shown of the discoid, partly-discoid and non-discoid plants, respectively, of four representative samples of a population; in the histograms marked "B" the relative frequency distributions of the number of tubular florets per head of the same 4 samples are shown.

n.disc. = non-discoid
p.disc. = part of the heads discoid
disc. = all heads discoid
n.t.p.c. = number of tubular florets per capitulum

these female ligulate florets in certain populations might be taken as an indication of an insignificant role of allogamy in the process of reproduction. If this were the case, the luring function of the female ray florets could be dispensed with. The exact mode of reproduction and the role of the ray florets in this process are virtually unknown, however, and a detailed study of these points is indicated.

4. DISCUSSION

An inquiry into the variation of the number of ray florets per head has demonstrated that in 11 out of 19 populations studied discoid, partly-discoid, and non-discoid forms occur. Since the three categories of specimens may occur in one single site the obvious supposition can be made that the plants differ genetically as far as their tendencies towards discoidy are concerned. Experiments in our experimental garden have confirmed this assumption (*cf.* WIJNANDS 1969b).

The geographical distribution in the Netherlands suggests that the discoid, partly-discoid and non-discoid forms have a somewhat different ecological tolerance and preference, but at the present stage of our studies we can not confirm that this is indeed the case. WEEVERS (1936) ascribes the occurrence of discoid plants along the S. coast of the island of Goeree en Overflakkee and their absence on the N. side to a difference in salinity, the water on the S. side of the island having a higher salt content than that on the N. side. FEEKES (1936) distinguishes a 'discoid' salt-flat type and a more typical brackish type, and the correlation between the decreasing percentage of discoid plants in the Westerschelde in an upstream direction and the decreasing salt content of the water at high tide seems to point in the same direction. In the Scheldt estuary there are also other gradients, however: in the upstream direction, *e.g.*, the phosphate and nitrogen content increases and also the finer (clayey) fractions in the soil (BEEFTINK 1965). The very complex factor of water pollution may also be important in this connection (a progressive increase in numbers of the discoid form in certain areas after 1900 was noticed).

Striking is the ecologically important fact that populations containing a high percentage of discoid plants are always found on the seaward side of the dikes, whereas on the landward side discoid specimens occur only in low frequencies or not at all (discoid forms apparently occurring only in recently reclaimed areas); see also HEUKELS-VAN OOSTSTROOM (1968). It is quite remarkable in this connection that there are no discoid forms among the inland population near Ellewoutsdijk (10), although this population is found at only a relatively small distance (2 km) from a population outside of the dike in which a high frequency of discoid plants was noted. This is rather curious, *Aster tripolium* being anemochorous by having achenes with a pappus, so its dispersal across great distances in this windy region may be expected.

In the present paper the incidence of discoidy is treated, but this is only a single feature of the intricate complex of characters of the Sea Aster (WIJ-

NANDS 1969a). A detailed analysis of the correlations between several morphological characters and of their relation to the environmental conditions seems indicated. Subsequently, apart from the ecological and geographical facets of the variability, certain genetic aspects need to be studied, including hybridizing experiments between the different forms and the number and morphology of their chromosomes.

In anticipation of future work on the subject we can already draw the conclusion that the recognition of a distinct variety *discoideus* is rather futile, at least in the Netherlands. This so-called variety is not separated from the non-discoid form by a tangible discontinuity, and moreover, there is no correlation of the character of discoidy with the other characters mentioned in the introductory paragraphs of this paper.

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