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NOTE ON SOME POPULATIONS OF ARMERIA MARITIMA (MILL.) WILLD. FROM THE SOUTH AND THE NORTH OF THE NETHERLANDS

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SUMMARY

Populations of *Armeria maritima* (Mill.) Willd. collected in the South and in the North of the Netherlands are very different from each other. The Southern (Zeeland and Noord-Brabant) populations typically belong to ssp. *maritima*. The populations from the North (Noord-Holland and Friesland) must be referred to ssp. *intermedia* in which atypical forms intermediate between the atlantic ssp. *maritima* and the north-continental ssp. *elongata* are put together. The occurrence of ssp. *intermedia* is not related to particular ecological conditions. The ratio between "maritima" and "elongata" characters does not show a gradual trend from ssp. *maritima* to ssp. *elongata* along the coasts from the island of Texel to Denmark.

1. INTRODUCTION

The morphological variation of populations of *Armeria maritima* (Mill.) Willd. has been studied by one of us (LEFÈBVRE 1974) in coastal and inland situations in western and central Europe. Seaside material had been collected along the european coasts from Northern Spain to Southern Sweden and Poland but with a gap in the Netherlands. In 1975 and 1976 the opportunity occurred to collect some plant populations from the dutch seaside.

The most complete taxonomic treatment of the group studied here is CHRISTIANSEN's (1931). Populations occurring along the coasts of north-western Europe are classified by him as the atlantic taxon *A. maritima* ssp. *maritima* which is characterized by a short habit (5–20 cm), narrow leaves (< 1 mm), hairy flowerstalks and short, blunt outer involucral bracts. To the east, *A. maritima* ssp. *maritima* is replaced around the Baltic Sea by the north continental *A. maritima* ssp. *elongata* (Hoffm.) Soo which is taller (up to 40 cm) with broader leaves (1,5–2,0 mm), glabrous flower-stalks and has outer involucral bracts elongated with a pointed end. Ssp. *elongata* is mainly a continental taxon growing on well-drained sandy soils in central and northern Europe (Germany, Poland, Baltic States). The taxonomic rank to be attributed to these two groups of populations is controversial. In the Netherlands they have been described as varieties by VAN OOSTSTROOM & REICHGELT (1961). The most appropriate rank appears to be the subspecies, because the two

groups of populations are geographically isolated and morphologically clearly different.

The major trends of variation in *Armeria* populations from maritime areas are, as we have shown in previous work, the following: There is no morphological range of variation in maritime populations from south to north: for instance populations growing in salt marshes in the cantabric Coast (Spain) are very similar to salt marsh populations from Ireland. From the coast of western Denmark to the baltic coast of East Germany a gradual transition from the atlantic taxon *A. maritima* ssp. *maritima* to the continental *A. maritima* ssp. *elongata* has been observed. In this area the populations are composed of individuals in which the characteristics of ssp. *maritima* and ssp. *elongata* are intermingled in various combinations (TURESSON 1922; LEFEBVRE 1969; PHILIPP 1975), which in the taxonomic literature are referred to the ssp. *intermedia* (Marss.). Nordh. The taxonomic status of such atypical populations will be discussed in some details in a following chapter.

Some genetic differences between populations can be related to environmental factors: populations exposed to strong winds or submitted to sheep grazing are dwarfed; populations from saltmarshes have glabrous leaves whereas populations from less saline situations (cliffs, rocks) show a mixture of hairy and glabrous leaves in various proportions. For some characters, like hairiness of the calyx, the variation is apparently random.

The purpose of this note is to examine the populations of *Armeria* from the Netherlands in relation to the material previously collected in other parts of the european coast.

2. MATERIAL AND METHODS

In each locality visited, 30 plants, or some more, were collected and dried. The different populations are listed in *table 1*. Six quantitative and eight qualitative characters were scored for each individual.

In *table 2*, the mean value with its standard error is reported for each population.

The variation of the eight qualitative characters studied is given in two opposite series so that one series (A) corresponds to typical characteristics of ssp. *elongata*. The characters are listed as follow:

A characters ('elongata')	*non-A characters*
1. Flower-stalk glabrous at the base	1. Flower-stalk hairy at the base only
2. Leaves ciliate	2. Leaves glabrous
3. Calyx hairy on the midrib only (pleurotrichous)	3. Calyx hairy all over (holotrichous)
4. Flower-stalk glabrous	4. Flower-stalk hairy all along
5. Leaves 3-nerved	5. Leaves 1-nerved
6. Outer involucral bract long, narrowly pointed	6. Outer involucral bract short, blunt

7. Leaves broad (> 1.5 mm)	7. Leaves narrow (< 1 mm)
8. Flower-stalk smooth	8. Flower-stalk rugous

In each population the frequencies of the alternatives A and non-A are scored for each character. These frequencies are then simultaneously expressed in an octagonal graph where each of the 8 rays corresponds to one specified character, the characters beeing numbered from 1 to 8 as in the previous list (*fig. 1*).

Table 1. List of populations of *Armeria maritima* sampled in the Netherlands.

Zeeland–Noord-Brabant	
Bergen op Zoom 1	Saline meadows
Bergen op Zoom 2	Salt marshes
Zijpe	Salt marshes
Wissenkerke	Dike
Noord-Holland–Friesland	
Texel. De Slufter 1	Salt marshes
Texel. De Slufter 2	Fixed sands at the foot of the dunes
Texel. Den Hoorn	Salt marshes
Texel. De Waal	Walls surrounding the polders
Terschelling – Bosplaat 1-2	Meadows without halophytes
Moddergat	Bricks dike

The ray has a value of 100%, the center of the octagon is 0% for frequency of A and the tops of the octagon are 100% for frequency of A.

The frequencies of A characters are indicated on the 8 corresponding rays. The indication marks are then connected, resulting in an irregular polygon which is blackened inside the octagon. This black polygon represents the distribution of the 8 characters in the populations. Typical "*elongata*" populations would have been pictorialized by a completely black octagon.

3. RESULTS: VARIATION IN THE NETHERLANDS POPULATIONS OF ARMERIA MARITIMA

3.1. Quantitative characters

There is a great deal of variation in quantitative characters between individuals in the same population and between population means (*table 1*). In the population of the tallest plants measured, De Waal, the height of the individuals varies from 12.5 cm to 38.5 cm. In that of the shortest plants (De Slufter 2) the range is from 4.5 cm to 17.5 cm. A similar variation is found in leaf length, sheath length, bract length and capitulum diameter.

The leaf width is less variable. In spite of this great intrapopulational variation population means can differ statistically in nature and the most striking differences can be maintained in transplant experiments, but to a lesser extent

Table 2. Mean values of six quantitative characters with their standard error in populations of *Armeria maritma* from the Netherlands. L = length, W = width, D = diameter, N = number of plants measured.

Populations	Characters L. Stalk (cm)	L. Leaf (cm)	W. Leaf (mm)	L. Sheath (mm)	D. Capitulum (mm)	L. Bract (mm)	N
Texel, De Slufter 1	12.8 ± 0.6	3.9 ± 0.2	1.10 ± 0.05	11.3 ± 0.5	17.4 ± 0.3	5.6 ± 0.2	33
Texel, De Slufter 2	8.1 ± 0.6	2.1 ± 0.1	0.90 ± 0.05	7.2 ± 0.4	14.9 ± 0.4	4.6 ± 0.2	33
Texel, De Waal	22.5 ± 0.8	9.4 ± 0.5	0.95 ± 0.05	15.8 ± 0.5	17.9 ± 0.2	7.9 ± 0.4	45
Terschelling 1	9.8 ± 0.7	3.6 ± 0.2	0.95 ± 0.05	9.6 ± 0.5	16.1 ± 0.3	4.7 ± 0.2	33
Terschelling 2	20.7 ± 0.9	8.2 ± 0.4	1.30 ± 0.10	15.1 ± 0.5	18.9 ± 0.4	7.5 ± 0.4	20
Moddergat	12.3 ± 0.6	3.9 ± 0.2	1.30 ± 0.10	12.9 ± 0.4	17.7 ± 0.2	6.2 ± 0.3	33
Zijpe	12.0 ± 0.5	4.1 ± 0.2	1.20 ± 0.05	12.9 ± 0.4	15.6 ± 0.5	6.8 ± 0.2	30
Bergen op Zoom 1	20.5 ± 0.8	7.0 ± 0.4	1.20 ± 0.05	14.1 ± 0.4	16.4 ± 0.3	6.7 ± 0.3	30
Bergen op Zoom 2	13.7 ± 0.8	4.9 ± 0.3	1.25 ± 0.05	12.7 ± 0.5	14.3 ± 0.6	6.0 ± 0.2	30
Wissenkerke	15.1 ± 0.9	3.6 ± 0.2	0.85 ± 0.05	12.7 ± 0.5	16.2 ± 0.4	5.9 ± 0.3	30

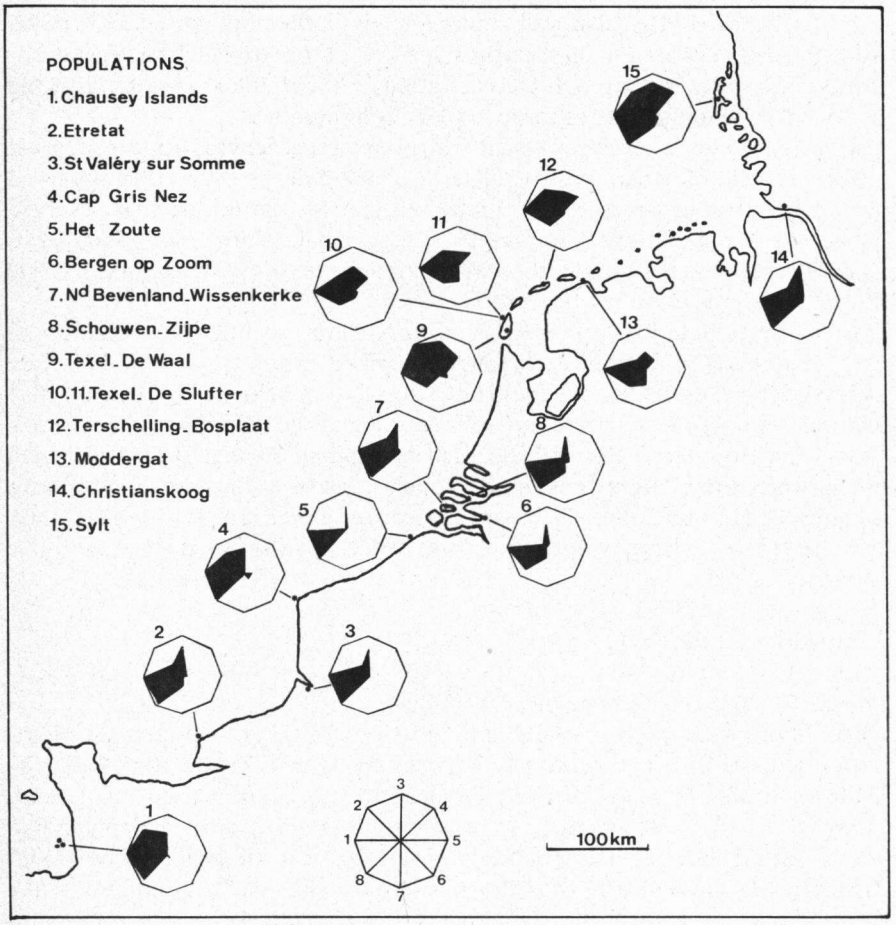


Fig. 1. Polygonal graphs showing the distribution of eight characters in populations of *Armeria maritima* collected in seaside situations from Normandy to Denmark. Legend of the polygonal graphs: frequencies (in %) with the centre as 0% for the following characters (alternative in brackets). 1. scapes glabrous at the base (hairy at the base only); 2. leaves hairy (glabrous); 3. calyx hairy on the rib only (hairy all over); 4. scapes glabrous (hairy all along); 5. leaves 3-nerved (1-nerved); 6. outer involucral bracts long and narrow with a sharp tip (bracts blunt); 7. leaves broad (narrow, less than 1 mm or equal); 8. scapes smooth (rugous).

(LEFÈBVRE 1971). As two years of transplantation are needed for a stabilized response of the plants in their experimental plots, results on transplanted populations are not yet available. But as shown in other populations tested a few years ago (LEFÈBVRE 1971) differences of the magnitude found in mean plant height between, for instance, the population from De Waal (22,5 cm) and the populations from De Slufter 1 (12,8 cm) and De Slufter 2 (8.1 cm) must be maintained in transplantation, being thus genotypically determined

in part. The differences observed in plant height in the populations of *Armeria* studied here are related to the competitive effect of the surrounding vegetation: *Armeria* growing among a high vegetation is taller than *Armeria* growing surrounded by low plants or in open plant communities.

Two quantitative characters, leaf width and bract length, appear as good genotypical characteristics of populations as most of the differences observed in nature are maintained after transplantation. So the differences observed between the populations with broad leaves (1.2–1.3 mm) like Moddergat, Zijpe, Bergen and the populations with narrower leaves (0.8–0.9 mm) like De Slufter, Wissenkerke must be genotypical.

In many populations of *Armeria maritima* the quantitative variation of characters exceeds the variation range described in the taxonomic literature as being typical of the taxon to which the population belongs. The quantitative features supposed to separate the different taxa in the complex *Armeria maritima* in north-western Europe are often misleading so that they do not tell much about the relationships of the populations from the Netherlands with other european populations belonging to ssp. *maritima*, ssp. *elongata* and their hybrids stands. These relationships are better demonstrated by qualitative characters.

3.2 Qualitative characters

Populations from Zeeland and Noord-Brabant

During our collecting trip in Zeeland and Noord-Brabant we used the distribution map of *Armeria maritima* composed by Mr. W. G. Beeftink from the Delta Institute. Ten sites were visited where *Armeria* had been mentioned. However, extensive populations were only found on four sites. The polygonal graphs established from populations occurring near Bergen op Zoom and Zijpe (*fig. 1*) show clearly that they are typical salt marsh populations like those which are growing in other coasts of western Europe, for instance in Belgium and France. The most typical feature of populations from salt marshes, which has been first reported by BAKER (1953) in the British Islands, is that nearly all individuals (90%) have glabrous leaves. The high number of plants with broad leaves (> 1.5 mm) found in the two populations from Bergen op Zoom is rather unusual in maritime populations but may occur in even higher frequency in some populations like the one from Arcachon (France) where 60% of the individuals has leaves 2 mm broad. In Zijpe and Bergen over ninety percent of the plants show hairy flower-stalks, 1-nerved leaves, and blunt bracts which are smaller than the flowerhead.

In Wissenkerke, where *Armeria* was collected on a dike, the populations are very similar to those found on cliffs or rocks along the French coast. Plants from Wissenkerke are of the same type as for instance those from Etretat. The differences observed in the shape of the polygon between Wissenkerke and populations from Cap Gris Nez and Chausey Islands are mainly due to variation in the frequency of hairy leaves. However, such variation has

always been observed in populations from maritime rocks and cliffs. The populations in such situations have typically hairy flower stalks and 1-nerved leaves, with a low frequency of rugous flower stalks, long bracts and broad leaves. Thus the populations from Zeeland and Noord-Brabant are not aberrant and can be readily included in the variation found in populations of ssp. *maritima* from western european coasts.

Populations from Friesland and Texel

From *fig. 1* it can be seen that populations from Texel and Friesland are quite different from classical populations of *A. maritima* ssp. *maritima* found in France, Belgium and the south of the Netherlands. This discrepancy is due to the high frequency of glabrous and rugous flower-stalks viz. hairy and smooth stalks, the other characters being within the normal variation of ssp. *maritima* (*fig. 2*). Populations showing a mixture of hairy and glabrous flower-stalks have been found further to the east along the danish and swedish coasts (LEFÈBVRE 1969). The population from Sylt Island (*fig. 1*) is an example of populations where some characters of ssp. *maritima* and ssp. *elongata* are intermingled; in the taxonomic literature they are referred to ssp. *intermedia* (Marss.) Nordh.

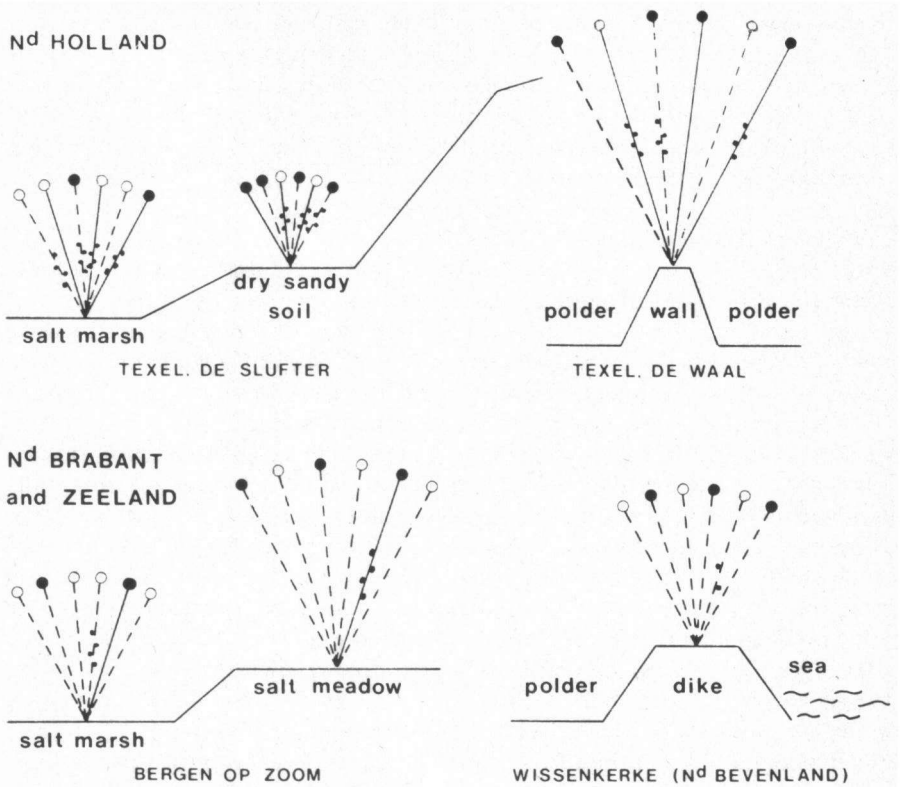
The high percentage of rugous flower-stalks in these populations has never been found in other seaside populations; till now, it was considered a typical feature of metallicolous populations from old zinc-lead mines in the north-east of Belgium (LEFÈBVRE 1974). A X^2 test for six different large population samples (*table 3*) scored for hairiness of stalk shows that the percentage of glabrous stalks is the same in Texel and Terschelling. From *fig. 2* it can be concluded that this constant frequency occurs in different ecological situations: saltmarshes, sand dunes and turf walls ("Texelse tuinwalletjes"), and is thus independent from the ecological situation.

The hairiness of flower-stalks is a stable character of ssp. *maritima* and ssp. *elongata* in most of their ecogeographical range: populations of ssp. *maritima* are exclusively constituted of individuals with densely hairy flower-stalks all

Table 3. Number of glabrous and hairy stalks in six populations of *Armeria maritima* from Texel and Terschelling (Friesland).

	Glabrous	Hairy	% Hairy
Texel			
De Waal	69	76	52.4
De Slufter 1	77	67	46.5
De Slufter 2	89	86	49.2
Den Hoorn	33	42	56.0
Terschelling			
Bosplaat	52	42	43.5
Bosplaat 2	72	66	47.8

$X^2_5 = 4.00$ N.S.



Variation in populations of Armeria maritima from Nd Holland, Nd Brabant and Zeeland in different ecological situations. Mode of representation: Each plant summarizes a population: If 50 % of the plants in the population are hairy stalked, half of the stalks (3 from 6) are indicated as hairy – – – hairy stalk (leaf); ——— glabrous stalk (leaf); ⌒⌒ rugous stalk; o calyx hairy on the ribs only; ● calyx hairy all around; ⌀ long bract (elongate type).

along the western coast of Europe from north-Spain to Belgium and in Great Britain and Ireland; in north Central Europe all inland populations collected from sandy heaths in East Germany and Poland were all glabrous. If we thus assume that percentages of glabrous flower-stalks do reflect the influence of ssp. *elongata* in the population constitution, it appears that there is no general trend toward increasing importance of ssp. *elongata* from Friesland to Denmark as populations collected more to the north-east like Moddergat (Friesland) and Christianskoog (Elbe estuary) have less individuals with glabrous

stalks, 30% and 16% respectively. The population from De Waal is rather exceptional in having more "*elongata*" characteristics: 15% of long bracts and nearly all the leaves hairy.

As argued in the introduction the rank of subspecies appears to be the most reasonable for maritime populations from western Europe (ssp. *maritima*) and for continental and baltic populations from center-north of Europe (ssp. *elongata*).

With the populations from Texel, Terschelling and Moddrgat we have to deal with the taxonomy of intermediate populations resulting probably from hybridization between ssp. *maritima* and ssp. *elongata*.

These populations from the north of the Netherlands studied here show a mixture of characteristics of ssp. *maritima* and ssp. *elongata*, the characters of ssp. *maritima* being more strongly represented. Morphologically they are not very different from populations growing in the south of the Netherlands, the main difference being in the frequency of glabrous flower-stalks; however, since this characteristic is very important for the infraspecific classification of *Armeria maritima*, the differences found in Noord-Holland and Friesland should be reflected in the taxonomic treatment.

VAN OOSTSTROOM & REICHGELT (1961) have pointed out the continuous variation of the hairiness of flower-stalk in the dutch coastal material but without indicating that this polymorphism occurs mainly in the northern part of the Netherlands.

Such intermediate forms were first described as a variety called "*intermedia*" by MARSSON (1869) for specimens collected in Pomerania. For eastern Friesland FOCKE (1902) included the atypical forms in the species *A. ambifaria* Focke intermediate between *A. elongata* and *A. maritima*. NORDHAGEN (1940) referred such specimens to the sub-specific rank which has been conserved in the Flora Europaea by PINTO DA SILVA (1972) as ssp. *intermedia* (Marsson) Nordh.

The infraspecific rank to be attributed to such an intermediary group seems somewhat speculative as more material is needed, especially along the former Zuiderzee, to have an accurate idea about the variation of intermediate forms in the North of the Netherlands. Provisionaly, we propose the rank of subspecies, as it is the more recent one to have been used (PINTO DA SILVA 1972) and as the hybrid swarm occurs in an extensive area from Noord-Holland to east Denmark and Sweden.

4. CONCLUSIONS

Populations of *Armeria maritima* from Zeeland and Noord-Brabant are different from those from Texel and Friesland in respect to the frequency of some morphological characters. In Zeeland and Noord-Brabant populations are typical for ssp. *maritima*. In Texel and Friesland more polymorphic populations occur which belong to ssp. *intermedia* which is, according to the literature,

a mixture of atypical forms, intermediate between ssp. *elongata* and ssp. *maritima*.

The polymorphism of hairiness of flower-stalk is stable in the islands of Texel and Terschelling in different environments (salt marshes, dunes, e.c.) and thus not related to ecological factors. Moreover, the importance of "elongata" characters is the same in Texel and in Friesland as in some parts of the coast of Denmark and Sweden so that no gradual geographical transition occurs in that area, from the atlantic ssp. *maritima*, which is very near to the east-continental ssp. *elongata*. The percentage of glabrous stalks, if seen as an indicator of the importance of "elongata" characters in the population, is surprisingly high in these western populations from Texel and Friesland islands.

Population samplings are needed in the coastal zone from Zeeland to North of Noord-Holland as well as along the former Zuiderzee to investigate a possible replacement process from one country to the other, But the variation could be abrupt as well. This will be the subject of further investigations.

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