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PHYTOGEOGRAPHICAL RELATIONS IN THE NORTH WEST EUROPEAN HEATH

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1. Introduction

The water economy, the mineral content of the soil, and human influence are the principal ecological factors governing the variation of the heath vegetation of a limited region. Sloping of the surface is also an important factor. In hilly country it is of a twofold nature: on the one hand the difference between high and low altitudes, based on the water economy, on the other hand differences in (micro-) climate. If the hills are higher, this results in greater climatic differences. In extremely oceanic and in boreal regions a rise in altitude of 100 m is sufficient for creating a noticeable decrease in temperature and an increase in precipitation, aerial moisture, and wind force. This results in the occurrence on the hills of heath communities that have their main distribution more to the North. The same observation was made by Gimingham (1961). On Slieve League on the Donegal coast (Ireland) *Salix herbacea* and *Lycopodium selago* occur in the heath at an altitude of 600 m, near Tongue on the Scottish north coast *Dryas octopetala*, *Saxifraga oppositifolia*, *Alchemilla alpina* and *Thalictrum alpinum* at an altitude of 60 m. West of Apeldoorn in the Netherlands are found extensive stretches of heath with abundant *Vaccinium myrtillus* and *V. vitis-idaea* at an elevation of 60–80 m, even on south-facing slopes. This is an area with high precipitation due to ascending air west of the hill ridge of the Eastern-Veluwe. Here the *Vacciniums*, elsewhere requiring the protection of the forest, can tolerate the habitat of the open heath (Stoutjesdijk, 1959; De Smidt, 1966). Higher elevation combined with north-facing slopes creates extreme conditions e.g. on Roc Trévézel (300–360 m) in Brittany, with *Vaccinium myrtillus*, *Melampyrum pratense*, *Hymenophyllum wilsonii* and *Rhytidiadelphus loreus*. These species are virtually lacking in the surrounding plains where the heath consists of such South Atlantic species as *Erica cinerea*, *E. ciliaris*, *Ulex gallii*, *Lobelia urens*, *Lithospermum prostratum* and *Symethis planifolia*.

Conversely, in protected valleys and on richer soil we find more southerly communities to the North of their main area. In the Maas valley between Maaseik and Maastricht a type of löss, rich in minerals and with a mild local climate supports a type of *Calluna* vegetation 1.50 m high with as co-dominant species *Sarothamnus scoparius*. This is a subatlantic community with Southern and Central European tendencies, mainly developed in low mountains: Eifel, Black Forest,

and in a modified composition on the Plateau Central (DE SMIDT, 1966). Often it is the interaction between local climate and soil conditions that provides a suitable habitat for such "extra-zonal" communities, as is the case with this *Calluna-Sarothamnus* heath. On Roc Trévézel the local climate is the main factor. An "extra-zonal" heath due to soil conditions is the poor *Calluna* heath with *Hypnum cupressiforme var. ericetorum, Festuca ovina, Carex pilulifera* on deep sandy deposits at Revingehed, East of Lund (South Sweden). This type is common in Northern Belgium, the Netherlands, and Northwest Germany with its northern border in South Jutland. A striking phenomenon is the absence of boreal species that are common in the heath of the region: *Vaccinium myrtillus, V. vitis-idaea, Cornus suecica, Trientalis europaea, Lycopodium clavatum.*

This paper chiefly deals with the phytogeographical characteristics of the "zonal" heaths. This term is employed for the main types in the Western European heath vegetation that can be distinguished on the basis of phytogeographical spectra. The criterium for delimiting geographically these main vegetation types is the presence of a group of species with a similar distribution. Since the distribution of the species is chiefly due to climatic factors, the area of the main vegetation types, too, depends chiefly on the macro-climate.

BÖCHER (1943) was the first to employ spectra of distribution types for classifying the European heathvegetations. SCHUBERT (1960) also suggested a classification mainly based upon phytogeographic characters. GIMINGHAM (1961), too, made some phytogeographical conclusions in his study on the variation of floristic composition and quantitative estimates of cover in the North European heath communities.

2. THE DISTRIBUTION OF THE SPECIES IN THE NORTH WEST EUROPEAN HEATHS

In Tables 1–4 are listed the total number of 384 species which have been recorded by the author in the North West European heath. In each separate column all those species are enumerated which were recorded in a certain part of Western Europe. Initially smaller areas had been listed separately, but several could be combined because of their great similarity. This was the case with Scotland and Wales, and with the Northern Netherlands, Northwest Germany, and Southern Jutland.

The following distribution types are distinguished in the tables.

a. widely distributed
b. subatlantic
c. atlantic
d. mediterranean atl.
e. eu-atlantic
f. boreal-atlantic
g. boreal-montane
h. arctic-alpine
i. central-meridional
j. continental

The overall species list can be subdivided into four groups.

TABLE 1. Species widely distributed in the North-West European heath

Distribution type	Region no. *)	1	2	3	4	5	6	7	8	9	10
a.	Calluna vulgaris	x	x	x	x	x	x	x	x	x	x
	Festuca ovina	x	x	x	x	x	x	x	x	x	x
	Molinia caerulea	x	x	x	x	x	x	x	x	x	x
	Hypnum cupr. v. ericetorum	x	x	x	x	x	x	x	x	x	x
	Pleurozium schreberi	x	x	x	x	x	x	x	x	x	x
	Dicranum scoparium	x	x	x	x	x	x	x	x	x	x
	Polytrichum commune	x	x	x	x	x	x	x	x	x	x
	Aulacomnium palustre	x	x	x	x	x	x	x	x	x	x
	Cladonia uncialis	x	x	x	x	x	x	x	x	x	x
	– gracilis	x	x	x	x	x	x	x	x	x	x
	– pyx. v. chlorophaea	x	x	x	x	x	x	x	x	x	x
	– sylvatica	x		x	x	x		x	x	x	x
	– crispata	x	x	x	x	x	x	x	x	x	
	– furcata	x	x	x	x	x	x	x	x	x	
	– squamosa	x			x	x	x	x	x	x	x
	– cocc. v. pleurota	x	x		x		x	x	x	x	x
	– floerkeana	x	x	x	x	x	x	x	x	x	
	– verticillata	x	x		x	x	x	x			x
	– cornutoradiata	x			x		x	x	x	x	x
	– rangiformis	x		x	x			x	x	x	x
	– macilenta	x			x		x	x		x	
	– pityrea		x		x		x	x	x	x	
	Parmelia physodes	x	x		x	x	x	x	x	x	x
	Cornicularia aculeata	x	x		x	x	x	x	x	x	x
	Peltigera canina			x	x	x		x	x	x	
	Leucobryum glaucum	x	x	x	x	x	x	x		x	x
	Polytrichum piliferum	x	x		x	x	x	x	x		x
	Polytrichum juniperinum	x			x			x	x		x
	Scleropodium purum	x	x	x	x	x		x	x	x	
	Sphagnum molluscum	x	x	x	x	x	x	x	x	x	
	– compactum	x	x	x	x	x	x	x		x	x
	– papillosum	x	x	x	x	x	x			x	x
	– plumulosum	x		x	x			x		x	
	Lophocolea bidentata	x		x	x	x		x	x	x	
	Ptilidium ciliare		x	x	x	x	x	x	x	x	x
	Cephaloziella sp.		x	x	x		x	x		x	
	Orchis mac. ssp. ericetorium	x	x	x	x	x	x	x	x	x	
	Succisa pratensis	x	x	x	x	x		x	x	x	
	Viola riviniana	x	x		x	x		x	x	x	
	Carex nigra		x	x	x	x		x	x	x	
	Salix repens	x	x		x	x	x	x	x	x	x
	Agrostis tenuis	x	x	x	x	x		x	x	x	x
	– canina		x	x	x	x	x	x	x	x	x
	– stolonifera	x	x	x	x	x		x		x	
	Solidago virgaurea	x	x	x	x	x		x		x	x
	Thymus serpyllum		x	x	x			x	x	x	x
	Lotus corniculatus	x	x	x	x	x			x	x	
	Juniperus communis	x			x	x		x	x	x	x
	Rumex acetosella	x	x		x			x		x	x
	Scapania nemorosa	x		x	x	x		x		x	
	Plantago lanceolata	x	x	x	x	x			x	x	x
	Rumex acetosa	x			x				x	x	x
	Prunella vulgaris		x	x	x	x			x	x	

*) For explanation of region no's see Table 5, p. 643.

TABLE 1 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
	Linum catharticum	x		x	x					x	
	Sphagnum acutifolium		x	x	x	x			x	x	x
	Rhytidiadelphus squarrosus		x	x	x					x	x
	Polytrichum strictum			x	x	x				x	
	Hieracium pilosella			x	x	x	x	x	x	x	x
	Campanula rotundifolia			x	x	x		x	x	x	x
	Luzula multiflora		x	x	x	x		x	x	x	
	Sorbus aucuparia			x	x	x		x		x	
	Gymnocolea inflata		x		x	x	x	x	x	x	
	Cladonia destricta	x						x	x	x	
	Festuca rubra	x	x	x	x		x	x	x	x	x
	Holcus lanatus	x		x	x			x	x	x	
	Achillea millefolium	x				x			x	x	x
	Frangula alnus	x	x			x		x		x	
	Quercus robur	x	x				x	x	x	x	
	Anthoxanthum odoratum		x	x	x	x		x	x	x	
	Mnium hornum			x	x	x		x			
	Antennaria dioica		x		x	x		x	x	x	
	Poa pratensis		x		x				x		
	Genista tinctoria	x						x	x		
	Cetraria glauca	x		x	x	x		x	x	x	
	Cladonia glauca	x	x		x		x	x		x	x
	Barbilophozia barbata				x	x		x	x	x	
	Hylocomium splendens	x	x	x	x	x		x	x	x	x
	Veronica officinalis		x		x	x			x	x	x
	Platanthera bifolia	x		x				x	x	x	x
	Hieracium umbellatum	x				x	x	x	x	x	x
b.	Galium saxatile	x	x	x	x	x	x	x	x	x	x
	Potentilla erecta	x	x	x	x	x	x	x	x	x	x
	Carex pilulifera	x	x	x	x	x	x	x	x	x	x
	Carex panicea	x	x	x	x	x	x	x	x	x	x
	Nardus stricta	x	x	x	x	x	x	x	x	x	x
	Sieglingia decumbens	x	x	x	x	x	x	x	x	x	x
	Cladonia impexa	x	x	x	x	x	x	x	x	x	x
	Drosera intermedia	x	x	x				x	x	x	
	Pedicularis sylvatica	x	x	x	x	x	x	x	x	x	
	Hypochoeris radicata	x	x	x	x		x	x	x	x	x
	Euphrasia micrantha		x	x	x				x	x	
	Carex echinata			x	x	x			x	x	
	Viola canina	x	x			x		x	x	x	
	Luzula campestris		x	x	x	x		x	x	x	x
	Oxalis acetosella	x		x	x	x			x	x	
	Anthyllis vulneraria	x	x						x		
	Deschampsia flexuosa			x	x	x	x	x	x	x	x
	Polygala serpyllifolia	x	x	x	x	x	x	x	x		
	Gentiana pneumonanthe	x	x				x	x	x		
	Cuscuta epithymum	x	x				x	x			
	Lonicera periclymenum	x	x	x	x			x	x	x	
	Diplophyllum albicans	x		x	x	x		x	x	x	
	Frullania tamarisci	x		x	x	x			x	x	
	Sarothamnus scoparius	x			x		x	x	x		
	Carex pulicaris	x	x		x	x		x	x		
	Lophozia ventricosa	x		x	x	x	x	x	x		
	Calypogeia trichomanes		x	x	x		x	x	x		

TABLE 1 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
	Odontoschisma sphagni	x	x	x	x	x	x	x			
	Orthocaulis attenuatus	x		x		x		x			
c.	Narthecium ossifragum	x	x	x	x	x	x	x	x	x	
	Juncus squarrosus		x	x	x	x	x	x	x	x	
	Erica tetralix	x	x	x	x	x	x	x	x	x	
	Myrica gale	x		x	x	x	x	x	x	x	
	Silene maritima	x				x				x	
	Rosa pimpinellifolia	x			x	x		x	x		
	Genista anglica	x	x		x		x	x	x		
	Campylopus flexuosus	x	x	x			x	x			
f.	Scirpus caespitosus	x	x	x	x	x	x	x	x	x	
g.	Vaccinium myrtillus	x		x	x	x	x	x	x	x	x
	,, vitis-idaea			x	x	x		x	x	x	x
	,, oxycoccus			x	x		x	x	x	x	
	Arctostaphylos uva-ursi			x	x	x		x	x	x	
	Empetrum nigrum	x		x	x	x		x	x	x	x
	Pinus sylvestris		x		x	x	x	x		x	
	Betula pubescens				x	x	x	x		x	
	,, verrucosa		x		x	x	x	x		x	
	Populus tremula		x			x			x	x	
	Rhynchospora alba	x	x	x				x			
	Eriophorum angustifolium	x	x	x	x		x	x	x	x	
	,, vaginatum		x	x	x		x	x	x		
	Drosera rotundifolia	x	x	x	x	x	x	x	x	x	
	Melampyrum pratense	x		x	x	x	x	x	x	x	
i.	Jasione montana	x		x	x			x	x		x
	Armeria maritima	x			x	x			x	x	x
	Filipendula hexapetala	x	x							x	
	Rhacomitrium canescens	x								x	

2.1. *Species widely distributed in the heath* Table 1

These species occur in all ten areas or, if in less, then without clear preference for certain ones among them. To this group belong 138 species, more than one third of the total number recorded in the heath. Nearly 60 % of them are not only widely distributed in the North West European heath, but also in the rest of Europe and Asia, and often as well in North America. More than 20% have a subatlantic area; this is much more than in the three other groups. This shows that the widely distributed type and the subatlantic type form the connecting element in the heath formation of the North West European plains. Besides there are smaller numbers of the boreal-montane (10%) and the atlantic (6%) distribution type. It is clear that in this group we do not find any species with pronouncedly mediterranean, arctic- alpine, continental or extremely atlantic distribution, the area under consideration being situated in

the atlantic and subatlantic region from Southern Scandinavia to Central France and from Ireland to North Germany. Less obvious is the scarcity of species with Central or South European tendencies. Among the four species placed in this category two, viz. *Jasione montana* and *Armeria maritima*, are polymorphic and comprise oceanic forms: *Jasione montana ssp. maritima* in the coastel heath of Ireland and Brittany and the coastal form of *Armeria maritima* in Brittany, Scotland, and Southern Scandinavia.

A striking phenomenon is the rather high percentage of the boreal-montane element (10%). It consists partly of trees of the boreal-montane woods, *Pinus*, *Betula* and *Populus tremula*, that reach rather far South in Central and Western Europe on poor soils in the plains. A few species that form part of these woods in the undergrowth, *Vaccinium myrtillus*, and *V. vitis-idaea*, and *Melampyrum pratense*, also occur in the heath. As they penetrate more southerly regions, they are more strictly confined to the cool and moist microclimate of the woods. In Scandinavia and Scotland the macroclimate permits their frequent occurrence in the open heath, outside the protecting woods. In the heath of Northern Germany and southward they are confined to north-facing slopes and to hilly country with a cool moist micro- resp. local climate. The rest of the boreal-montane species of this group are plants of peat bogs except *Arctostaphylos uva-ursi*. In the oligotrophic peat bogs and boggy heaths of the Dutch and German lowland, of Brittany and the British Isles they find a suitable habitat far to the South of their main area. BÖCHER (1943) calls the distribution of *Arctostaphylos uva-ursi* very problematic, as it is frequent both in extremely oceanic regions (Western Norway, Scotland, Northern Ireland) and in rather continental areas in the northern part of Central Europe. As a possible explanation Böcher suggests the existence of different biotypes originating from populations that survived the glaciation under different climatic conditions.

2.2. *Species with preference for northern heaths* Table 2. Scotland, Western Norway, Southern Sweden, Northern Jutland.

Widely distributed, atlantic and subatlantic species are reduced to half the percentage in the preceding group. In the other hand the portion of boreal-montane species is more than twice as high. The boreal-atlantic element is also strong: 12 out of 15 species with this type of distribution occurring in the North West European heath belong to this group. The arctic-alpine element is, however, lacking as it is confined to group C, Table 3: species with a more westerly distribution in the heath. Apart from the boreal flora element it is the continental element (17%) that particularly characterises this group; it is virtually absent from the others. Within the group of northern heathland species a shift in the flora elements may be observed as one moves eastward.

In Scotland the boreal-montane element (Table 3, g) comprises

TABLE 2. Species with preference for northern heaths

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
a.	Epilobium angustifolium				x			x	x		
	Rhytidiadelphus triquetrus				x			x	x	x	
	Bazzania trilobata					x		x		x	
	Lophozia bicrenata						x	x			
	Ranunculus acer				x	x				x	
	Dicranum polysetum			x	x	x	x	x	x	x	x
	– spurium				x	x	x	x	x	x	x
	Pohlia nutans		x		x		x	x	x	x	x
	Galium verum								x	x	x
	Polygala vulgaris		x				x		x	x	x
	Fragaria vesca				x				x	x	x
	Lophocolea heterophylla						x	x		x	x
	Hieracium laevigatum							x		x	x
	Vicia cracca								x	x	
	Stellaria graminea								x	x	x
	Trifolium repens								x	x	x
	Silene cucubalus								x		x
	Hypericum perforatum									x	x
	Plagiothecium denticulatum								x	x	x
	Orthocaulis lycopodioides							x			x
	Hypericum maculatum									x	
	Silene nutans									x	
	Briza media									x	
	Trifolium arvense										x
	Knautia arvensis										x
	Erigeron acris										x
	Centaurea scabiosa										x
	Medicago falcata										x
b.	Veronica chamaedrys								x	x	x
	Genista pilosa						x	x	x	x	
	Juncus balticus								x		
	Lycopodium inundatum							x	x		
	Rosa tomentosa									x	
	Sedum telephium									x	
	Scleranthus perennis										x
	Ononis spinosa										x
	Ornithopus perpusillus										x
c.	Potentilla anglica									x	
	Carex trinervis									x	
	– arenaria			x	x			x	x	x	x
f.	Pinguicula vulgaris				x	x			x	x	
	Anemone nemorosa				x	x			x	x	
	Luzula pilosa				x	x			x	x	
	Cornus suecica					x			x	x	
	Convallaria majalis					x				x	
	Ajuga pyramidalis					x				x	
	Rhynchospora fusca						x	x		x	
	Sorbus hybrida					x					x
	Lathyrus montanus			x	x				x	x	x
	Leucorchis albida								x	x	
	Ligusticum scoticum								x		

TABLE 2 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
g.	Lycopodium clavatum				x	x		x	x	x	x
	Cetraria islandica				x			x	x	x	x
	Majanthemum bifolium					x	x	x	x	x	
	Polypodium vulgare	x			x			x	x	x	x
	Trientalis europaea				x	x		x	x	x	
	Vaccinium uliginosum					x		x	x	x	x
	Cladonia rangiferina			x	x	x			x	x	x
	Dryopteris spinulosa				x			x	x	x	
	– linnaeana				x	x				x	
	– phegopteris					x				x	
	Galium boreale				x					x	
	Lycopodium annotinum					x				x	
	Equisetum sylvaticum					x				x	
	Sphaerophorus globosus				x				x		
	Evernia prunastri							x	x		
	Andromeda polifolia						x	x	x		
	Cladonia bellidiflora					x					
	Orthocaulis kunzeanus							x			
	Cladonia alpestris									x	
	Cetraria juniperina									x	
	Splachnum ampullaceum									x	
i.	Leontodon autumnalis				x	x			x	x	
	Carex montana								x	x	
	Rosa dumetorum									x	
	Saxifraga tridactylites									x	
	Melica nutans									x	
	Polygonatum odoratum									x	
	Dianthus deltoides										x
j.	Scorzonera humilis	x						x	x	x	
	Arnica montana							x	x	x	
	Hypochoeris maculata							x	x	x	
	Trifolium medium									x	
	Carex ericetorum								x	x	
	Pimpinella saxifraga								x	x	x
	Anemone pulsatilla								x	x	x
	Vicia cassubica									x	x
	Viscaria vulgaris									x	x
	Helictotrichon pratensis									x	x
	Prunus spinosa	x								x	x
	Cladonia mitis								x	x	x
	Genista germanica								x		
	Carex caryophyllea									x	
	Artemisia campestris										x
	Helichrysum arenarium										x

approximately as many species as in most parts of Scandinavia. The representation of the other flora elements is, however, much weaker, as calculated from the species that have a northern distribution in the heath. Instead, Scotland possesses some arctic-alpine, eu-atlantic, and a few mediterranean-atlantic species (see Table 3).

Western Norway has more boreal-atlantic species in the heath than Scotland, but in terms of the other elements it has more in common with the last named country than with the rest of Scandinavia. Floristically speaking too, the Western Norwegian heath is closer to the British than to the Scandinavian type. See especially Table 3 which lists some typically western species from Western Norway: *Erica cinerea, Hypericum pulchrum, Carex binervis, Juniperus nana, Blechnum spicant, Mylia taylori, Bazzania tricrenata, Anastrepta orcadensis, Breutelia chrysocoma, Campylopus atrovirens.*

Eastward the continental element is first encountered in the Dutch-German plain. It increases in North Jutland and reaches its peak in the region under study in South East Sweden (9%). The same is true for the central-southern European species. BÖCHER (1943) lists the same species from the Eastern Danish heaths and SCHUBERT (1960) from the Central European heaths. The most widespread continental species are: *Pimpinella saxifraga, Scorzonera humilis, Arnica montana, Hypochoeris maculata, Carex ericetorum, Anemone pulsatilla* and *Cladonia mitis.* The presence of *Scorzonera humilis* in the Breton heath is a phytogeographical and ecological enigma. This species is common in Central Europe where it shows a predilection for mineral rich, dry, and often warm habitats. It decreases in general toward the atlantic side, except in Brittany where it reaches a second optimum. Contrary to what may be expected it does not occur in the driest habitats, but in very boggy heath. Probably it belongs to a different ecotype than the Central European plant.

2.3. *Species with preference for western heaths* Table 3

As far as heath is concerned these species have their optimum in Northern Ireland, Wales, Scotland and Western Norway. Characteristic is the optimal representation in the heath of the eu-atlantic and the arctic-alpine flora element. Of the 27 recorded eu-atlantic heathland species 23 belong to the present group. The four other species show preference for the south-atlantic heath of Southern Ireland and Brittany. The western heath shares a relatively high percentage of boreal-montane species (20%) with the northern heath (22%).

The arctic-alpine species are confined to this group. It mainly comprises species descending to sea-level on the North coast of Scotland (*Saxifraga oppositifolia, Thalictrum alpinum, Dryas octopetala, Alchemilla alpina*), or at least to low altitudes (*Empetrum hermaphroditum, Lycopodium alpinum*). *Salix herbacea* was met with in the heath of the Irish North West coast and *Juncus trifidus* on the West coast of Norway. The habitats are always exposed to strong wind and face the sea directly. The strong, almost continuously blowing wind is probably the most important factor governing the presence of these species. In combination with the mostly high atmospheric humidity and the low summer temperatures an environment is created that shows certain similarities to mountain conditions.

TABLE 3. Species with preference for western heaths

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
a.	Cladonia strepsilis	x				x		x			
•	Telaranea setacea	x	x	x	x		x	x			
	Cephalozia bicuspidata			x				x			
	Mylia anomala	x	x		x		x	x			
	Lepidozia reptans	x		x	x	x					
	Thuidium tamariscinum	x		x	x	x					
	Brachypodium pinnatum	x			x						
	Pteridium aquilinum ssp. aq.	x	x	x	x	x	x				
	Rhinanthus minor					x					
	Sphagnum rubellum	x		x	x						
	– recurvum		x	x	x						
	– cuspidatum			x		x					
b.	Schoenus nigricans	x	x	x	x						
	Cladonia papillaria	x			x						
	– degenerans	x			x						
	Juncus acutiflorus	x	x	x	x		x				
	Hedera helix				x						
	Lysimachia nemorum				x						
	Aquilegia vulgaris					x					
c.	Cirsium dissectum	x	x	x	x						
	Scapania gracilis	x		x	x						
	Digitalis purpurea	x			x						
	Ilex aquifolia			x	x						
	Blechnum spicant	x	x	x	x	x					
	Rhytidiadelphus loreus	x	x	x	x	x					
	Dicranum majus	x		x	x	x					
	Plagiothecium undulatum	x		x	x	x					
	Rhacomitrium lanuginosum	x		x	x	x					
	Campylopus brevipilus	x	x	x	x	x					
	Plantago maritima	x	x	x	x	x					
d.	Ulex galli	x	x	x	x						
	Pinguicula lusitanica	x		x	x						
	Teucrium scorodonia	x		x	x						
	Luzula maxima	x		x	x						
	Endymion nutans	x			x						
	Lejeunea cavifolia			x	x						
e.	Hymenophyllum wilsonii	x		x	x						
	Thymus drucei	x			x						
	Plagiochila spinulosa	x		x	x						
	Pleurozia purpurea			x	x						
	Herberta hutchinsiae			x	x						
	Mylia taylori			x	x	x					
	Bazzania tricrenata			x	x	x					
	Anastrepta orcadensis			x	x	x					
	Breutelia chrysocoma			x	x	x					
	Lophozia quinquedentata			x	x	x					
	Carex binervis	x	x	x	x	x					
	Hypericum pulchrum	x		x	x	x					
	Campylopus atrovirens			x	x	x					
	Erica cinerea	x	x	x	x	x					

TABLE 3 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
	Cladonia tenuis	x	x	x	x			x			
	Nowellia curvifolia			x							•
	Lepidozia pearsonii				x						
	Hieracium schmidtii				x						
	– styctophyllum				x						
	Scapania compacta				x						
	– irrigua				x						
	Plagiochila denticulata				x						
	Mastigophora woodsii				x						
f.	Juniperus nana			x	x	x					
	Festuca vivipara			x	x	x					
g.	Gentianella campestris		x		x						
	Listera cordata			x	x	x					
	Lycopodium selago			x	x	x					
	Selaginella selaginoides			x	x	x					
	Ptilium crista castrensis				x	x					
	Sanguisorba officinalis		x			x					
	Rubus chamaemorus				x						
	Pyrola rotundifolia				x						
	– minor					x					
	Trollius europaeus				x						
	Dryopteris filix-mas				x						
	Sphagnum robustum				x						
	Dicranum bonjeani				x						
	Cladonia flabelliformis				x						
	– subcervicornis				x						
	Stereocaulon paschale				x						
	Linnaea borealis					x					
h.	Alchemilla alpina				x	x					
	Salix herbacea			x							
	Empetrum hermaphroditum				x						
	Saxifraga oppositifolia				x						
	Thalictrum alpinum				x						
	Dryas octopetala				x						
	Lycopodium alpinum				x						
	Juncus trifidus					x					

The overall percentage of atlantic species in this group is 57, that of the northern species 29; continental species are lacking. The difference with the preceding group with percentages for these elements of 25, 22, 24, respectively, is evident. The western heath is of a much more extreme nature than the northern heath. The percentages for the northern heath show it to be a meeting-ground of atlantic, boreal, and continental species. The percentages of widely distributed species in the northern and western heath are 29 and 14, respectively. This again reflects the extreme nature of the lastnamed vegetation.

2.4. *Species with preference for South-Atlantic heaths* Table 4

The optimal development of these species, as far as their occurrence in the heath is concerned, is in Southern Ireland, Cornwall, Brittany and outside of the region studied till the present, more to the South in the coastal regions of the Bay of Biscay. The low percentage of the widely distributed species (6%) shows that this group, too, shows a strong preponderance of a certain element with a specialised character, in this case the mediterranean-atlantic element which comprises 65% of the species. The species with an atlantic tendency in their distribution type make up together 93%of the group. The total is 64, much less than in the preceding groups, where it is 96 and 86, respectively. Future studies in the heath South of Brittany will probably show this number to be much higher.

TABLE 4

Species with preference for south-atlantic heaths

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
a.	Leontodon hispidus	x	x								
	Chrysanthemum leucanthemum	x	x								
	Stachys betonica	x	x								
	Ranunculus flammula		x	x							
b.	Radiola linoides	x									
	Hypericum humifusum	x									
	Sorbus torminalis	x									
	Serratula tinctoria	x	x								
	Carex flacca		x								
c.	Scilla verna	x	x								
	Cladonia imp. v. leucophaea	x		x							
	Corydalis claviculata	x									
	Hypericum helodes		x								
	Dryopteris borreri			x							
	– aemula			x							
	Saccogyna viticulosa			x							
	Adelanthus decipiens			x							
d.	Erica vagans	x	x								
	– ciliaris	x	x								
	– x watsoni	x	x								
	Agrostis setacea	x	x								
	Scilla autumnalis	x	x								
	Salix atrocinerea	x	x								
	Ulex minor	x	x								
	– europaeus	x	x								
	Anagallis tenella	x	x	x							
	Scutellaria minor	x	x	x							
	Parmelia trichotera	x		x							
	Lotus corniculatus ssp. maritimus	x									
	Daucus gummifer	x									
	Euphorbia portlandica	x									
	– paralias	x									

TABLE 4 (*continued*)

Distribution type	Region no.	1	2	3	4	5	6	7	8	9	10
	Senecio cineraria	x									
	Rubia peregrina	x									
	Asparagus off. ssp. prostratus	x									
	Dactylus glom. ssp. hispanica	x									
	Cirsium filipendulum	x									
	Symethis planifolia	x									
	Ruscus aculeatus	x									
	Lithospermum prostratum	x									
	Hypericum linarifolium	x									
	Helianthemum umbellatum	x									
	Tuberaria guttata	x									
	Astrocarpus purpurascens	x									
	Lobelia urens	x									
	Carum verticillatum	x									
	Sphagnum pylaiei	x									
	Asphodelus arrondeaui	x									
	– sphaerocarpus	x									
	Orobanche cruenta	x									
	Potentilla splendens	x									
	Erica scoparia	x									
	Cladonia endiviaefolia	x									
	Sedum anglicum	x									
	Pyrus cordata	x									
	Erica mediterranea			x							
	– mackai			x							
	Daboecia polifolia			x							
	Koeleria albescens			x							
e.	Cochlearia officinalis	x									
	Erica x praegeri			x							
	Saxifraga umbrosa			x							
	– spathularis			x							
j.	Allium schoenoprasum		x								

3. THE SPECTRA OF DISTRIBUTION TYPES

In the groups 1 through 10 in Table 5 all plant species have been compiled that were found in the heath of the regions under consideration. Ten different distribution types were distinguished. In most of the regions the widely distributed species form ca. 50% of the total set of species; the subatlantic element is also rather evenly represented (13–19%). The boreal-montane element, too, is always present, but shows much wider variation (4–17%). To these three flora elements belong 227 species (= 59%) of the total number of 384 recorded by the author in the North West European heath vegetations. This clearly demonstrates the affinity among the heath regions studied. The other flora elements are absent from one or more regions or have a representation of 1% only. On the basis of the distribution of the last named flora elements, five regions may be distinguished.

TABLE 5

Spectra of distribution types of the heathland species recorded in 10 North-West European regions

Region no.	(%)										(number of species)									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
widely distributed	37	52	41	41	47	57	54	49	51	63	70	65	64	90	70	47	83	76	94	64
subatlantic	17	18	16	13	13	18	16	19	13	14	32	23	25	29	20	15	25	30	24	14
atlantic	**11**	**9**	**14**	8	8	7	7	5	4	1	**20**	**11**	**21**	18	12	6	10	8	8	1
mediterranean atl.	**23**	**10**	5	3	—	—	—	—	—	—	**42**	**12**	8	6	—	—	—	—	—	—
eu-atlantic	**6**	2	**11**	**10**	**6**	1	1	1	—	—	**11**	3	**18**	**22**	**9**	1	1	1	—	—
boreal-atlantic	1	1	3	3	**7**	2	3	5	5	3	1	1	4	7	**10**	2	5	8	9	3
boreal-montane	4	7	9	**16**	**17**	**13**	**15**	**13**	**16**	8	7	9	14	**35**	**25**	**11**	**23**	**21**	**29**	8
arctic-alpine	—	—	1	**3**	1	—	—	—	—	—	—	—	1	**6**	2	—	—	—	—	—
central-meridional	2	1	1	1	1	—	1	3	**5**	3	4	1	1	3	2	—	1	4	**9**	3
continental	1	1	—	—	—	—	4	5	**7**	**9**	1	1	—	1	—	—	6	8	**13**	**9**
										Total	188	126	156	217	150	82	154	156	186	102

1. Brittany
2. Southern-England } South-atlantic
3. Ireland

4. Scotland and Wales
5. Western-Norway } boreal-atlantic
6. Southern-Netherlands and Belgium
7. Northern-Netherlands, N. Germany } subatlantic
8. Northern-Jutland
9. Southwest-Sweden } boreal-subatlantic
10. Southeast-Sweden boreal-subcontinental.

TABLE 6

Spectra of distribution types of the North-West European heathland species, according to their geographic preference devided in four separate groups

Group no.	(%)					(number of species)				
	1	2	3	4	5	1	2	3	4	5
a. widely distributed	6	14	29	**59**	32	4	12	28	**81**	125
b. subatlantic	8	8	9	**21**	13	5	7	9	**29**	50
c. atlantic	**13**	**13**	3	6	8	**8**	**11**	3	9	32
d. mediterranean-atlantic	**65**	7	—	—	13	**42**	6	—	—	48
e. eu-atlantic	6	**27**	—	—	7	4	**23**	—	—	27
f. boreal-atlantic	—	2	**13**	1	4	—	2	**12**	1	15
g. boreal-montane	—	**20**	**22**	10	14	—	**17**	**21**	14	52
h. arctic-alpine	—	**9**	—	—	2	—	**8**	—	—	8
i. central-meridional	—	—	**7**	3	3	—	—	**7**	4	11
j. continental	2	—	**17**	—	4	1	—	**16**	—	17
Total number						64	86	96	138	384

Group 1. Species with preference for south-atlantic heaths.
2. Species with preference for western heaths.
3. Species with preference for northern heaths.
4. Species widely distributed in the North-West European heath.
5. The total number of species (384) listed in the North-West European heath.

3.1. *The south-atlantic region*

Table 5a, no. 1, 2, 3. Brittany, Southern England, and Ireland.

Here the atlantic and the mediterranean-atlantic element have their optimum; the eu-atlantic element is also well represented. The flora elements with boreal or continental areas are much weaker represented than in other regions. The South Atlantic character is most pronounced in Brittany with 23 % of mediterranean-atlantic species. The overall percentage of species with atlantic affinities in Brittany is 58 % (106 species); consequently the percentage of widely distributed species (37 %) is much lower than elsewhere, but the absolute number of species of this type, 70, is not below the average.

3.2. *The boreal-atlantic region*

Table 5, no 4 and 5. Scotland, Wales and South-Western Norway.

The eu-atlantic element is well represented, as in the south-atlantic region, but there is much less of the less extreme western flora elements, viz. the atlantic and the subatlantic; this is naturally more true for the mediterranean-atlantic. The boreal ties are much stronger: the boreal-atlantic the boreal-montane, and the arctic-alpine flora element together comprise 22–25 % (in the preceding region 5–12 %). The presence of arctic-alpine species in this region has been noted already (§ 2.3).

3.3. *The sub-atlantic region*

Table 5, no 6 and 7. Belgium, Netherlands, North-Western Germany, Southern Jutland.

In this region the heath is notable by the absence of species reaching their optimum. This becomes evident when Tables 5 en 6 are compared. Group 1 (Table 6) has its optimum in the south-atlantic (Table 5, no 1, 2, 3), group 2 in the boreal-atlantic (Table 5, no 4, 5), group 3 in the boreal-subatlantic (Table 5, no 8, 9) and in the boreal-subcontinental region (Table 5, no 10). In Table 6 a group with its optimum in the subatlantic region could not be distinguished. Most constituents of the heath vegetation are widespread in this kind of vegetation in North-Western Europe. Only the 6 continental species in the northern part of the region are aberrant. The overall number of species is strikingly low in the southern part, 82, slightly more than half the number of the northern part. The difference is mainly due to the presence of continental species and of a larger number of species with a northern type of distribution on mineral rich soil, coastal and woodland species; but these are distributed among the flora elements in such a way that the constitution of both parts, relatively speaking, differs but little. The larger number of species with a northern type of distribution is not only due to the more northerly position but also to the Riss glaciation. The glaciers formed push moraines whose north-facing slopes provide favorable habitats for northern species (*Lycopodium clavatum*, *Polypodium vulgare*, *Trientalis europaea*, *Vaccinium vitis-idaea*, *Arctostaphylos uva-ursi*) and woodland

species (*Dryopteris spinulosa*, *Anemone nemorosa*, *Hieracium laevigatum*, *Lonicera periclymenum*, *Hylocomium splendens*). The glaciers also deposited richer soils, boulder clay and consequently the heath contains more species than on the poor coversands to the South. Heathland species of the better northern soils are *Succisa pratensis*, *Campanula rotundifolia*, *Luzula multiflora*, *L. campestris*, *Antennaria dioica*, *Platanthera bifolia*. The presence, in the northern part, of coastal species (*Rosa pimpinellifolia*, *Carex trinervis*, *Carex arenaria*, *Genista tinctoria*) is due to the absence of lime in the sand of the coastal dunes North of Bergen on the Dutch coast. The coastal dune heath is well developed from Bergen to Cape Skagen but is absent from the dunes with a higher lime content to the South of Bergen and on the Belgian and northern French coasts. It does not reappear until Normandy, but here on the cliffs of acid rocks rather than in the dunes which are also rich in lime.

3.4. *The boreal-subatlantic region*

Table 5, no 8, 9. Northern Jutland, South-Western Sweden.

The phytogeographic spectra of this region show a characteristic combination of a rather high percentage (18 and 21 %, respectively) of boreal species with relatively rather many species with a continental or a central-southern European tendency (8 and 12 %, respectively). The percentage of atlantic species is lower than in the preceding regions.

3.5. *The boreal-subcontinental region*

Table 5, no 10. South-Eastern Sweden.

The continental tendency, low in the subatlantic region and slightly stronger in the boreal-montane region, is most noticeable in the North-West European heath in South-East Sweden (DAMMAN, 1957) and in Eastern Denmark (BÖCHER, 1943), an offshoot of the subcontinental heath of Eastern Germany and Poland (SCHUBERT, 1960). The total number of species (102) is the lowest in the regions studied, except in the Southern Netherlands and Belgium. This is partly due to the smaller size and consequently smaller variation. But the main reason is probably the climate. The annual precipitation in South-West Sweden is 600–1000 mm, in the heath areas of South-East Sweden only 500–600 mm (DAMMAN, 1957). The formation of humus and leaching take place so intensively in the south western part that heath may occur even on originally neutral or even basic soils. Such heaths can be recognized by its herb-rich aspect with *Scorzonera humilis*, *Orchis maculata*, *Succisa pratensis*, *Solidago virgaurea*, *Lathyrus montanus*, *Sieglingia decumbens*, *Potentilla erecta*. In South East Sweden, however, such habitats are occupied by grassland of a continental type with *Anthericum ramosum*, *Helichrysum arenarium*, *Anthyllis vulneraria*, *Androsace septentrionalis*, *Satureja acinos*, *Artemisia campestris* and *Medicago falcata*. Here the heath covers the poor soils,

also with continental species (9%): *Vicia cassubica, Viscaria vulgaris, Anemone pulsatilla, Artemisia campestris, Helichrysum arenarium.* The atlantic influence is the lowest of all areas studied (18%). The boreal influence (11%) is weaker than in the Southern Netherlands and Belgium and approaches that of Ireland and Southern England. An arithmetical consequence of this low percentage is the high amount of widely distributed species, 63%. The numerical relations between the flora elements and the low overall number of species show that the heath is here near the border of its distribution. The flora is quantitatively and qualitatively poorer than in the other regions; the only addition is the continental element, mostly consisting of grassland species. This shows a transition to the dry continental grassland vegetation. The same transition was described by SCHUBERT (1960) for Central Germany.

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