THE NETHERLANDS

AS AN

ENVIRONMENT *for* INSECT LIFE

by

M. F. MÖRZER BRUIJNS

Department for Nature Protection of the State Forest Service, Utrecht

and

V. WESTHOFF

Institute for systematic botany, Agricultural College, Wageningen

PRESENTED TO THE MEMBERS OF THE

IXTH INTERNATIONAL CONGRESS OF ENTOMOLOGY

BY THE

NETHERLANDS ENTOMOLOGICAL SOCIETY

AMSTERDAM, 1951

CONTENTS

A. GENERAL INFORMATION

B. IMPORTANT BIOTIC COMMUNITIES

A. GENERAL INFORMATION

Introduction

When studying insects in their natural surroundings it is of great importance to know something about the historical, geological and botanical peculiarities of the locality.

The entomologist cannot fail to recognize the fact that the environment is a dominating factor in the occurrence of species and the numbers of each species.

The following has been written to assist foreign entomologists when collecting or studying in the Netherlands.

Climate. Apart from historical factors, the climate is primarily responsible for the constitution of the insect populations of a region. This is not only the case in each of the climatic zones, to be distinguished as large belts round the earth. It is obvious that differences in climatic conditions in parts of these regions are of equal and sometimes even greater importance. Even in a small country like the Netherlands the insect-populations of the southern, northern, eastern and western parts show differences according to the different climatic conditions in these parts, as will be pointed out in chapter II. Finally there are the micro-climatical influences, but they will not be treated here.

Soil. Soil conditions too are of great importance to the distribution of living creatures and especially to insects.

Insects living in or in near relation to the soil are evidently directly influenced by soil conditions, such as granular composition, structure, humus-content, water table, mineralogical composition etc.

Almost all plants and plant-communities are confined to special types of soil and by far the majority of insects are dependent on plants for food, dwelling space and shelter. It is evident that the soiltype in this way indirectly influences insect life too.

The same applies also to insect life in ponds, lakes and streams, as the composition of the water and its vegetation are dependent upon the soil through and over which the water runs or stands.

These questions will be treated in chapter III.

Biotic factors. Besides the influences excercised by the complete set of abiotic factors, generally known as "action", we have to recognise those, between the organisms themselves, usually indicated as "coaction".

Animals and plants are without exception constituents of biotic communities of plants and animals and if we want to know something about this the mutual relations must be studied, especially in the field. These relations can also be decisive for the appearance or the absence of a species in certain places. This study, however, is made difficult by the complexity of the relations which are often not easy to analyse, as all factors do not act separately but in combination. Fortunately one of the most important set of factors can be provisionally taken together as "vegetation", and its study may take us a long way towards a better understanding of the problem.

All the different plant communities or phytocoenoses in a country like the Netherlands constitute as many different environments for insect life. For this reason in chapter IV a survey is given of the most important vegetation types of this country.

The vegetation differs from landscape to landscape, due to climate, soil conditions, exposure (microclimate[6], shape of the biotope and anyway in the Netherlands, most of all to human interference. This last factor is treated separately (IV, C).

I. GEOGRAPHICAL DATA

The Netherlands belong to the western border of the North-West European plain. More specifically they are for a large part built up as the estuary of the rivers Schelde, Maas, Rhine, IJssel and a few smaller rivers, all of which flow into the North sea (figure 1).

About 40 % of the Netherlands lies at or below sea-level. Large areas of the western parts of the country would be flooded by sea and rivers permanently or at least periodically, if dikes, sluices and pumps did not keep the water out (fig. 2).

Although the landscape of the reclamation-works, the "polders", with grass- and arable land predominates here, there are still many great marshes, swamps, lakes and along the Northsea several salt marshes. Together with some other landscapes typical for the Netherlands only, such as dunes and heaths, they give "Nederland" a special character, which is not found anywhere else in the world, though similar areas are found in adjoining countries.

The following summary may give some idea of the areas of most importance:

Netherlands	33.320 km²
Arable land	12.000 ,,
Grassland	12.220 ,,
Forests	2.500 ,,
Waste land	2.000 ,,
other areas	6.600 ,,

II. CLIMATIC FACTORS IN THE NETHERLANDS

a. General climatic characteristics

The climate in Western- and Middle-Europe is greatly influenced by the near presence of the Atlantic ocean and the bordering seas (e.g. the Northsea), especially by the proximity of the Gulfstream (fig. 3), which brings relatively warm water to the East and North Atlantic. The Netherlands situated between 50°45'49" and 53°52'21" NL., are well within the sphere of influence of the Gulfstream.

Due to this the climate of the Netherlands has a maritime character and is often called by biologists an "atlantic" one. The summers are rather cool and winters mild, the prevailing western and southwestern winds bringing plenty of rain throughout the year.

The influences of the Gulfstream can well be judged by comparing the climate of the Netherlands with the subarctic one of New Foundland and Labrador lying at the same latitude at the opposite coast of the Atlantic Ocean.

The climate of the Netherlands belongs to the temperate-humid type, the "C.f. type" according to the climate classification by KÖPPEN, to the sub-humid climate according to LANG and to the subhumid and humid climate type according to the classification by THORNETHWAITE.

The following data give some indications about the most important climatological factors for the country as a whole. They are from the publications of The Royal Neth. Meteorological Institute at de Bilt. The differences in the climatical conditions of the different parts of the country will be dealt with in the next paragraph.

Air-Temperature. Measurements taken during the last 200 years show the average summertemperature in July and August, the warmest months, to be 16.5° and 16.7° C.; maxima, however, in July of 26–31° C. and extremes of 33–37°; "coldest summers" have monthly means in July of 13.9–14.1° C.

Lowest temperatures in winter occur in January, the mean value being 1.0° C.; lowest means per month −5° C. to −10° C. and extreme low temperatures −16° C. to −22° C. Highest mean per month for January during these 200 years 6.2° C.

The average annual amplitude is about 15° C.

Precipitation. The average amounts of precipitation calculated from the mean of periods of thirty years during a period of about 200 years vary from 670–740 mm per year. The maximum average rainfall over 30 years, calculated per year was 1083 and the minimum 427.

The western and southwestern winds bring the highest amounts of precipitation, most rain falling in the western part of the country in October, in the eastern parts in July. The heaviest showers fall from June to September, the mildest in March. Snow falls mostly in February. The period from January till May is comparatively dry. The average precipitation for each section of the year amounts to:

winter	163 mm
spring	143 ,,
summer	203 ,,
autumn	204 ,,
total	713 mm

The effective precipitation viz. the precipitation actually sinking down into the soil, after evaporation and natural drainage along the surface, is biologically of great interest. For the Netherlands it may be roughly calculated, for soil covered with vegetation, at about 50 % of the precipitation.

Air pressure and wind. The variations in air-pressure in the Netherlands are relatively large. Numerous, often deep depressions, taking their course over the Northsea, cause strong winds regularly in the coastal areas especially in the first 30 km from the coast.

Air-pressure usually varies between 780 and 730 mm Hg. The depressions often give rise to relative high wind-forces. The average wind velocity corrected to 6 m above groundlevel, taken from measurements during thirty years varies at the coast from 5.0–7.3 meters per second and inland from 2.5–4.8 meters per second. Highest wind forces generally occur with westerly winds, specially during the wintermonths.

The highest mean for hourly periods is 21–29 meters per second (i.e. wind-force 10 and 11 according to the Beaufort-scale). In exceptional cases windgusts attain still higher velocities (12 Beaufort scale).

Humidity and evaporation. Humidity and evaporation are of great importance for all living beings. Therefore it is a pity that only very little is known about these factors. The average relative humidity in the Netherlands is rather high. It varies from 70–90 %. The lowest relative humidity occurs inland at about 15–25 % in the month of May. Diurnal variations are but slight.

Evaporation rate is of importance to the relative humidity and the humidity-deficit. It could be calculated for moist arable land in the polder-area at about 300–500 mm (about 50 %) from 750–800 mm precipitation. On naked sandy soil in the dunes of Terschelling 85 % of the precipitation was effective; in "Ammophila"-dune vegetation 50 %.

The evaporation differs greatly in summer and winter as is illustrated by the following figures giving averages:

winter	16 mm
spring	121 ,,
summer	280 ,,
autumn	64 ,,
total	481 mm

During the summer evaporation exceeds precipitation. Organisms living in high sandy soils and similar localities therefore have to be adapted to life in dry surroundings.

Insolation (Sunshine and cloudiness). The suns greatest daily altitude varies between $\pm 14°$ and $\pm 61°$ in the middle of the country. The length of day between $7^h 7'$ and $16^h 40'$.

The hours of sunshine are of course variable. The yearly average is 29 % which is low, considering that the lowest average in Europe is 26 % (North-Scotland) and the highest 60 % (Madrid).

The months April to September inclusive bring the highest percentages of sunshine.

b. Climatic regions

Variations in climatic conditions. Although, on the whole, the climate of the Netherlands without doubt is a maritime one, considerable variations in climatic conditions are found, especially in the extreme North, i.e. in the regions of the West-Frisian wadden islands, and in the far South of the province Limburg as well as in the middle-eastern parts of the country.

Summers in the southern and southeasterly parts for instance are warmer than those in the northern and northwestern parts (fig. 4).

Winters in the northeastern provinces are colder than those in the Northwest and in the South (fig. 5). The maximum rainfall in the easterly parts occurs during July, which is normal for the region of the summer-rains of the European continent. (fig. 6) The coastal areas on the contrary have their maximum in October (fig. 7) which is characteristic for the eu-atlantic climate-type. In the parts of the Netherlands South of the Rhine moreover rainfall is less at an average compared with the northern parts. For other climate factors such as wind-force, sunshine etc. differences often are striking also. Yet, we are seldom able to distinguish these differences travelling from North to South or from West to East, which may be attributed to the rather important local fluctuations and rapid changes of the weather type.

Classification. Nevertheless these diversities enable us to suggest a climatic classification of the country, though we must keep in mind, that this classification like all others is to a certain extent arbitrary and artifical.

A classification for bio-geographical purposes should be based on the differences in those climatic conditions which are of considerable importance for the distribution of animals and plants. The distribution of those organisms in the Netherlands living on the border of their natural distribution-area is of primary interest for such a classification.

There are quite a lot of these organisms and among them are insects, living only in the colder northern parts of the country. On the other hand there are a fair number of organisms, which live only in the "warm" southern provinces or in the sub-continental eastern parts.

The causes of this unequal distribution are certainly to be found to a large extent in the climatic differences.

The importance of extremes. For a number of living organisms the average values per year or even per month of the climatic factors are usually not of

decisive importance, but the extremes, occurring occasionally in a period from 5–10 years.

It is a well known fact that extremely cold and extremely hot and dry weather-directly or indirectly-make it impossible, or at least very difficult for the less-well adapted organisms to survive.

The division of the Netherlands in climatic areas for biogeographical purposes therefore, should be based on the degree of heat during the summers and the severity of the winters.

It is as yet impossible to suggest a division based on the combined effects of the complete set of climatic factors. To a certain extent, it could be done according to the method of THORNETHWAITE (1933), for the Netherlands worked out by VEEN (1949). The meteorological stations, however, which give adequate data are too few to be able to get sufficiently reliable results for further geographically detailed study.

Summer days and icy-days. For this reason a provisional division of the Netherlands is given based on the average numbers of real "summer days" per year in summer and of "icy-days" per year in winter. For this division we are much indebted to Mr C. G. VAN LEEUWEN, UTRECHT, who made the preliminary studies, necessary for the conclusions mentioned. Summer days in this sense are days, with airtemperature-maxima above 25° C., "icy-days" are days with airtemperature maxima below 0° C.

We separate areas with an average of less than 5, 5–22, 22–30 respectively and more than 30 summer days per year and with less than 8–9, 8/9–11/12 and more than 11/12 icy-days per year (fig. 8) and at the same time take the following facts into consideration:

1. The part of the Netherlands South of the Rhine as a whole has a milder climate, with less rain and more sunshine than the northern parts;

2. The eastern half of South Limburg has a special (i.c. rainy) climate due to the submountainous character of its hills.

Climatic regions. In this way we get 11 "regions" (see fig. 8) for the Netherlands, each of which has its summer- and winter-conditions more or less different from those of the neighbouring regions. The summers vary in order of succession from cool to rather cool, mild, rather warm and warm, the winters from very mild and mild, rather cold to cold.

These distinctions of course are naturally only to be applied to the Netherlands.

A. Region of the Wadden, with cool summers, mild winters and strong winds.

B. Coastal regions of North and South Holland. Rather cool summers, mild winters and high windforces.

C. The Zeeland-region having mild summers and very mild winters.

D. The northern-central region, with the province Friesland, the IJsselmeer coastal areas, the province Utrecht, the Veluwe etc. having rather cool summers and rather cold winters.

E. The southern-central region, with western Brabant and parts of the

valleys of the rivers Rhine, Waal and Maas, has mild summers and rather mild winters.

F. The northeastern region, with large parts of the provinces Groningen, Drenthe and Overijssel, the summers here are rather cool, the winters cold.

G. The Twenthe-region with circumjacent country has rather warm summers and cold winters. The climate of this region is the most continental of the Netherlands.

H. The Lijmers-region with circumjacent parts, has rather warm summers and rather cold winters.

I. The region of eastern Brabant and northern Limburg. These parts having almost warm summers and rather mild winters.

J. The region of the West of South Limburg; this region has warm summers and mild winters.

K. The region of the East of South Limburg; with warm, rainy summers and mild winters.

III. EDAPHIC FACTORS IN THE NETHERLANDS

Apart from the effects of climate, soil conditions largely determine whether plants or animals can live in a certain place or not.

The mineralogical and chemical composition and the granular composition of the soil are of considerable importance as well as structure, humus content, the position of the phreatic level etc.

To appreciate the significance of these environmental factors a short survey of the geological structure and the pedological elements and the history of the Netherlands is necessary.

a. Geological structure

The superficial layers in the Netherlands belong almost entirely to the holocene and plistocene. At the surface older strata occur only in South Limburg (upper-cretaceous), where they form a plateau with vallies, the maximum hight being about 200 m, partially covered with plistocene loess-loam.

In the "Gelderse Achterhoek" near the village Winterswijk in a few localities Trias crops out and in Dutch Flanders the village de Cauter near the Belgian border is built on pliocene sand. Praeplistocene strata are present throughout the country, but more or less deep below the surface, covered by plistocene and holocene deposits.

The depth varies from a few to several hundred meters. The sediments mostly have a marine character, but in the East and the South fluviatic sediments are formed. The material comes both from Scandinavian regions and from the South.

Plistocene. The plistocene layers cover a good deal of the surface of the Netherlands, forming a hilly landscape, especially in the eastern half of the country. A good impression can be got by looking at the white patches in fig. 9,

although it should be realised that the praeplistocene formations in this figure are white also, which however, is only of importance for the East of South Limburg.

The plistocene in general slopes down from about an average of 10–20 m above NAP (NAP being the average sea-level) in the East to about 10–20 m below NAP at the coast. In the western half of the country the plistocene therefore is wholly covered by holocene formations (fig .9). Figure 10 also gives an idea of the geological structure of the country.

During the plistocene period before the great glaciation, usually called the Riss-glaciation, the formations were built up mainly by fluviatile deposits, chiefly sand and gravel, called "prae-glacial" sediments. These sediments sometimes are mentioned as "the base" of the Netherlands.

Great glaciations. The Riss-glaciation has had a considerable influence on the surface-structure of the Netherlands as the ice cap coming from Scandinavia covered the country for a great part (fig. 11).

The moving ice masses in several regions locally pushed up the praeglacial subsoil to a hight of 50–100 m, shaping in this way the sandy hillridges, which still play a dominant part in the landscapes of Overijssel and Gelderland.

The glacier brought large amounts of groundmoraine (boulder clay) and other moraine too, such as the northern erratica, which can be found to-day in a great many localities, especially Drenthe. To the South of the icebarrier erosion took place, while at the same time sedimentation of sand from the air occurred and in South Limburg and elsewhere the loessloam was deposited too as an eolian sediment. The Riss-glaciation was followed by a rising of the sealevel and in consequence by a transgression of the Northsea. In this Eem Sea-period all over the country sedimentation went on forming the Eem Sea layers as a marine facies in the West and the low terrace layers in the East as fluviatic strate. After this period the sea retreated again due to the Würm-glaciation. During this glaciation period the icecap did not reach the Netherlands. The climate, however, became arctic, the vegetation being a tundravegetation. Erosion was important again. Due to snowdrifts, solifluction and eolian forces the cover sand deposits developed which to-day cover a good deal of the plistocene part of the Netherlands.

After the Würm-period the climate became warmer and gave rise to a new transgression of the Nortsea, which still continues. At the beginning of this period, about 20.000 years ago, the holocene in the Netherlands is considered to have begun.

Holocene. The vegetation in the beginning of the holocene, the subarctic period, was a steppe-vegetation on dry soil. Peat formation was rare and only occurring in a few places. In consequence of the steady rising of the sealevel, the groundwater became higher and higher and peatgrowth started, especially in the low-lying western part of the country. The sea level at that time was about 15 m lower, than it is to-day.

About 5000 B C in the "boreal" period, the western parts of the Netherlands

consisted for a great deal of peat. Thousand years later the rising Northsea transgressed into this peat landscape and on the peat sedimentation of sand and clay took place, peatgrowth only continuing in the extreme East of the peat-area.

During periods of temporary regressions in the "midatlantic" period at about 3000 B.C. and afterwards about 1800 B.C. in the "subboreal" period a sandy shorewall with dunes was formed, almost in the same place where the Dutch coast is nowadays. The relics of these formations still exist beneath and behind the contemporary young dunes and are known as ,,old dunes". The sand which formed these old dunes was tossed up by the surf into a shorewall during preceding transgression periods, the material originating from the neighbouring seabottom.

Behind this shorewall the "old blue seaclay" was deposited in two phases. This clay forms the bottom of several of the oldest reclamation works in Holland (fig. 10), which before the reclamation were waters.

The growth of the upper-peat on this seaclay started in a regression period after the second phase of dune formation (about 1800 B. C.). This peat now covers large areas in western Holland and in Friesland, so far as it has not been dug out by men or swept away by the sea or by other causes. On several occasions the sea destroyed large parts of the old dune system both in the South (Zeeland) and in the North (Wadden Islands). "Young seaclay" was deposited in the conquered areas.

The peat in the low lying parts of Holland and Friesland, now often below sealevel, started as groundwater peat in eutrophic conditions, forming a swamp. These fen-formations partially developed to oligotrophic bog-peatcomplexes in those places where the superficial living peatlayers were isolated from the eutrophic groundwater by succession processes.

The holocene in the East of the Netherlands. Comparable bog-peatcomplexes originated in the same period in the high plistocene grounds in the east of the country. This happened in those areas where owing to a high groundwatertable, due to insufficient natural drainage, peatgrowth could start.

On the poor sandy soils only oligotrophic sphagnum-bogs could develop. These formed large raised bogs (fig. 12), which nowadays are dug off and reclaimed as arable land, with the exception of a few remains (fig. 13).

In this part of the Netherlands a large scale sedimentation took place during the holocene in the eroded valleys of the plistocene landscape. Rivers, rivulets and brooks depositing large quantities of their sandy and clayish materials.

At the same time the inland dunes originated on the fine sandy loamless plistocene formations, especially on the "fluvioglacial" sands covering the slopes of the hills pushed up by the glaciers (fig. 10).

b. Pedological elements

Introduction. The soil of the Netherlands developed during centuries out of the superficial layers of the geological formations through the influences of the

slightly podzolizing climate, the often high groundwater table, the vegetation and human interference.

The mineralogical composition and the way the components are deposited determine whether we have to do with a rich or a poor soil, whether it consists of clay, loam or sand or of a combination or mixture of these. The quality of the soil moreover is strongly influenced by the position of the groundwater table. The latter in the Netherlands is often very near the surface and peat-formation occurs therefore in a good many places. Gleyprofiles, with the gleyzone at 0–50 cm below the surface are frequent.

Besides these very wet and wet soils, very moist, moist and dry soils can be distinguished. The natural vegetation, differing from place to place according tot he conditions, formed humus- or vegetationprofiles in the soil characteristic for substrate and vegetation. These profiles still exist, although often influenced by man as by reclamation work, which started over 400 years ago. They are a startingpoint for the classification of the soiltypes. Thus a single geological formation gives rise to many different soiltypes, resulting in even more different biotopes for insects and insect life to develop in different ways.

Classification. The Soil Survey Institute at Wageningen during the last 6 years made intensive studies of the soiltypes of the Netherlands, especially for agricultural purposes. Recently the first "Provisional Soil Map" of the Netherlands was published (scale 1:400.000). In this map the soiltypes (comparable with the soiltypes of American pedology) are united to soil complexes (not identical with American soil-series). The soilcomplexes, however, are parts of soil-associations, which belong to the same (III) category as the soil-associations of American pedology.

In the Netherlands 9 soil-associations are distinguished. (EDELMAN, 1950), viz.:

old sea clay soils
young sea clay soils
river "loam" soils
river clay soils
peat soils
dune and beach bank sandy soils
plistocene sandy soils
loessloam soils
artificial soils

The distribution of the associations is roughly sketched in fig. 13. The Provisional Soil Map of the Soil Survey Institute gives the following data (Edelman, 1950).

Old sea clay soils. The old sea clay soils occur only in the West of the Netherlands, especially in the provinces Noord- en Zuid-Holland, as reclaimed and wholly cultivated lake bottoms. There are differences between "calcareous old sea silt soils", "non calcareous old sea clay soils" and "non-calcareous soap clay soils" according to the conditions under which the silt or clay was deposited during the Atlanticum in a salt-marsh landscape.

Young sea clay soils. These soils too are all reclaimed salt marsh soils, occurring along the coasts of the Northsea and the former Zuiderzee. The soilmap gives 16 complexes. The most important ones are: the young and "older" silt soils, the young sandy silt soils, the clay soils and the sticky clay soils, the silty and clayey "creek ridge and coastal barrier soils," calcareous in the subsoil but poor in lime at the surface, and the "peat soils with clay cover".

The "salty peat soils with clay cover", poor in lime as many other peat soils, originally high but now low lying ("inversion" by shrinking of the peat layers, owing to drainage) occur only in the South of the Netherlands especially on the islands in the provinces Zuid-Holland and Zeeland.

The "estuary silt soils" occur northwards and eastwards of the other young sea clay soils between these and the river clay soils. They started as marine sediments, but developed as tidal fresh water (river-) deposits.

River loam soils. River "loam" is a clayey sediment, pedologically very interesting. Long ago (about 10.000 years backward) it covered the bottom of the valleys of the rivers Rhine and Maas. Now only in the east of the Netherlands the river "loam" is at the surface in the valleys of the Maas and locally in that of the Oude IJssel. Elsewhere it is wholly covered by the younger river clay deposits.

The "loam" is distinctly different from river-clay. Although there is no difference in granular composition, there is however in colour and other qualities. Two complexes are descerned, the low lying (wet) grey river loam soils and the high brown river loam soils.

River clay soils. The river-clay landscape consists mainly of the "high river levée soils" of the "ridges" formed by sedimentation of the coarser materials along streamcourses and the low "river basin clay soils" formed by sedimentation of fine clay in the areas behind these ridges.

(The "river levée soils" are calcareous in the riversystem of the Rhine. Those of the Maas are non-calcareous. The riverbasin clay soils are always poor in lime).

Outside the embankments the "river foreland clay soils" develop, where the coarse and fine material are often deposited homogeneously.

Peat soils. Peat soils occur in considerable areas in the low parts of western Holland and Zeeland and in Friesland and Overijssel. The swamps which formed these soils are nearly all reclaimed nowadays, mostly as grassland, which can be found on the "Phragmites peat soils", the "low wood peat soils" and on the "low Sphagnum and Carex peat soils". In Holland as well as in Friesland and Overijssel the last category in most cases is to be found in the neighbourhood of the still existing swamps and broads.

On the plistocene sands "Sphagnum-raised bogs" still exist only in a few places (eastern Drenthe, N.E. Overijssel and eastern Brabant), as most of them are drained and dug off and the plistocene sandy subsoil reclaimed.

Along rivulets and little streams the "Alnus and Carex peat soils" developed, most reclaimed as grassland.

Dune and beach bank sandy soils. The soils of this complex occur only along the coast of the North sea. The "young dune sand soils" form the natural soils in the dunes rich in lime South of Bergen, poor in lime to the North. The dry and moist "beach bank soils" exist behind the dunes; they are, when not too dry, in use as arable land, the moist ones being of importance for the culture of the famous Dutch flower bulbs.

Plistocene sandy soils. These sandy soils cover about half of the surface of the Netherlands. There are big differences in soil conditions here. On the provisional soil map 16 complexes are discerned. These differences are due to the groundwater table, the content of clay or loam, the influences of the original vegetation etc. Most sandy soils are bad and poor from the point of view of the agriculturist, especially the dry ones. They can only be reclaimed by afforestation or with aid of much artificial and organic manures as arable land.

Grasslands are widely distributed on the low lying "moist sandy soils" and on the "loamy brook soils" along brooks and rivulets. The "high but moist sandy soils" have a character of their own, they occur only there where an impermeabel subsoil prevents the water from sinking down. This happens e.g. where layers of boulder clay are present, especially in Drenthe. The "old arable land soil" has a deep humus profile, owing to the use of organic manure during hundreds of years; there are loamy and sandy ones. Very good arable land was obtained by the farmers on the "brown forest soils". Extremely poor are the "inland sand dune soils". Poor too are the "podzolised heath soils", though for the major part reclaimed. The same can be said of the "podzolised soils on stratified drift".

The podzolised soils occur in the Netherlands both in the northern provinces and in the southern ones, but are only well developed on the poor sandy soils.

The soil beneath the dug off "bogs" is reclaimed as "peat subsoil" when the superficial peat layers are left behind. When no peat is left there remains very poor "sandy peat subsoil".

The soil conditions in the plistocene sandy areas often vary greatly due to topography and subsoil, within very short distances.

Loessloam soils. The loess is deposited in the Netherlands as an eolic sediment in three areas: near Arnhem, near Nijmegen and in the South of Limburg.

The loess counts among the richest soils in the Netherlands. The loess on the hills near Arnhem is non-calcareous and deposited on rather steep slopes. It is mostly therefore covered with forests and heath. The brown loess loam near Nijmegen is for a large part reclaimed forestsoil; it is calcareous and rich arable land, when well above the groundwater table. When too low it forms a bad grey sticky loam (nature-reserve "Het Bruuk").

The South of Limburg is entirely covered with loess. The layers are locally up to 18 m thick. As a whole the loess here forms rich soils too, although it is not rich in lime. The country is almost entirely cultivated, only the hill sides bear forests. In the southern half of South Limburg the geological senonic substrate is at the surface at a good many places. This formation gives rise to

the calcareous "residual limestone soils". These give a special character to this part of the Netherlands, as they are, with the calcareous dune sandy soils along the coast, the only calcareous soils in the country.

The artificial man-made soil, from dumps etc., are for the biologist of little importance.

IV. FLORA AND VEGETATION

a. Flora.

The present higher flora of the Netherlands is relatively poor, because the non arctic plantlife of to-day could only recently settle in the country i.e. after the subarctic period about 8000 years ago.

The majority of the higher plants (about 2500 species with 1100 native ones and 1400 adventives) and of the mosses and liverworts (about 600 species) came from the South, immigrating by the courses of the rivers Schelde, Maas and Rhine and along the coastal area of the North Sea. Only a few species of the retreating nothern flora-elements are still found in the "coldest" northern parts of the country. In general the same is true for the fauna.

Phytogeographical data. The Netherlands belong with Belgium, N.W. Germany, western Denmark and the coast of Norway to the northern sector of the "atlantic province", which together with the British sector forms the N.W. part of the Euro-siberian phytogeographic region. This region borders in the North on the arctic or circumpolar region and in the South on the mediterranean region (fig. 14).

In the flora of the Netherlands a number of phytogeographical elements occurs. First of all a number of holarctic element can be recognized e.g. Ranunculus acer and Cardamine pratensis and in the second place the eurosiberean elements, e.g. Melandrium rubrum and Anemone nemorosa.

The medio-europaean element to which belong Quercus robur and Q. sessiliflora (= petraea), Fagus silvatica and other trees is of importance. Characteristic for the Netherlands however is the northern element with e.g. Parnassia palustris, Vaccinium uliginosum, Juncus balticus, Pirola and Salix-species, whereas a number of atlantic species are characteristic as well e.g. Erica tetralix, Genista anglica, Myrica gale and others. In the South even the mediterranean element occurs such as a number of orchids.

Among the plants which reach their southern boundary on the plane in the Netherlands can be mentioned Arnica montana and Trientalis europaea; other species have not been observed farther to the North e.g. Silene conica, Ulex europaeus, Euphorbia paralias and Glaucium flavum.

Floristic subdistricts. Since about 1900 the distribution of the flora in the Netherlands has been systematically explored. The "Institute for the investigation of the Vegetation in the Netherlands" (I.V.O.N.) organises the inventories since 1930. To-day many maps are published (in "Nederlands Kruidkundig

Archief") showing the distribution of a large number of species in the Netherlands.

These maps demonstrate striking differences in the flora of diverse parts of the country, which are not due to different intensity of the study of different areas. According to this the Dutch botanists discern with VAN SOEST a number of floristic and vegetational subdistricts which correspond pretty well with those distinguished in Germany and Belgium.

These subdistricts are 11 in number, in the Dutch literature usually called "districts" (fig. 15).

Wadden-District: Northsea islands and dunes North of Bergen (N.H.). Flora of beach and dunes poor in lime, atlantic heath with northern elements.

Dune-District: Dunes South of Bergen (N.H.), beach and dune flora with southern elements in the calcareous dunes, many species occurring elsewhere especially along the big rivers. Floristic rich forests behind the dunes.

River-District: Strips along the big rivers and the province Zeeland. Characterized by several hundreds of species, which immigrated along the courses of the big rivers and occur only there (e.g. Euphorbia cyparissias and Inula brittannica).

Haff-District: The low parts of western and northern Holland and Friesland. Characteristic for this district are the fens, broads and swamps (Lathyrus paluster, Euphorbia palustris).

Drenthe-District: The north-eastern "heath-district" with many northern species e.g. Empetrum nigrum, Arnica montana.

Gelderland-District: Transition area from the northern to the southern parts of the country, a heath-district too.

Kempen-District (= Campina-District): The southern heath district without northern elements. Erica cinerea and Carum verticillatum occur only here, both atlantic species.

Flemish District: Sandy-soil district in Zeeland. For the Netherlands of little importance.

Subcentral European District: The mid and south-eastern parts of the Netherlands. The flora of this district is more continental than that of the other districts, e.g. Hieracium sabaudum and Equisetum silvaticum.

Loess-District: The northern part of southern Limburg, characterized by a number of calcicole species.

Cretaceous district: The southern submontaneous parts of southern Limburg, characterized by a number of subcontinental and calcicole plants, which are not found elsewhere in the country.

Although this division is based on the distribution of the flora elements only, it is clear, that climate and soil play a dominant part in it. Thus it is interesting to note that this division of the Netherlands in floristic subdistricts shows much resemblance with the classification of the country resulting from the combination of the climatic regions of chapter II and the distribution of the soilcomplexes described in chapter III.

b. Vegetation

The development of the vegetation as far as it is not influenced by man also demonstrates to what extent climate and soil are responsible for the characteristic composition of the Dutch phytocoenoses and through them of the biotic communities.

These communities are without exception coenoses of the deciduous forest biome of Northwest Europe. During the first centuries A.D. the Netherlands actually were covered mostly by forests of different composition.

Owing to high waterlevels and other causes in the low western parts of the country locally fens, swamps and natural grassland occurred, in between the forests whereas on the high sandy soils apart from woodland, heaths, moors and bogs existed. The dunes too never were covered completely with forests and shrubs.

Natural coenoses. The natural and semi-natural phytocoenoses in the first place are characteristic for the vegetation of the Netherlands. Natural and semi-natural are called those coenoses, where human influence is so slight, that they are composed of native wild plants and animals only, which live in a state of biological equilibrium. These coenoses lodge far more interesting species of plants and animals than those of the cultivated areas.

For this reason the most important vegetationtypes will be mentioned here and partially described in the following chapter (B).

Forests. The climax-vegetation of the Netherlands consists mainly of Quercus robur forests; only where the groundwater table is too high for the oak, other trees take his place.

Almost certainly not a single original forest of the climax-vegetation is left and even natural forests are rare.

About 8 % of the surface of the country is wooded, but this woodland consists almost completely of non-natural, floristic poor conifers: Pinus, Larix and Pseudotsuga. A total area of about 1 % of the surface of the Netherlands is left to the natural foresttypes.

The natural forests develop in different ways according to climate and soil (see B, V). Those growing on dry and moist soils rich in minerals are oak-forests, from a phytocoenological viewpoint associations, variants and forms of the medio-europaean Fraxino-Carpinion[1], in the Netherlands e.g. the Querceto-Carpinetum, to be found along the rivers and rivulets, on clayey and loessloam soils and along the inner side of the calcareous dunes. In the dunes of the "Dunedistrict" the Hippophae-Liguster-vegetation forms associations and sub-associations of the Quercion pubescentis-sessiliflorae, an alliance characteristic for the southern parts of the atlantic province.

The dry and moist plistocene sandy soils poor in minerals bear other forest-types, belonging to the atlantic and sub-atlantic alliance Quercion roboris-

[1] In the Netherlands the foresttypes and other phytocoenoses are chiefly described and characterized using the methods of the French-Swiss Phytosociologists (Dr J. Braun Blanquet, Montpellier, France). The naming and classification of this school is used here.

sessiliflorae with phytocoenoses of the Querceto-Betuletum. The forests of these types during the last century were often used as coppice woods.

When the groundwater table is too high throughout the year for Quercus robur, carrs and other swampforests develop. Alnus glutinosa or Salix species and Betula pubescens being dominant, corresponding with the amount of nutricient salts in the groundwater.

These Alnion glutinosae forests occur chiefly in the low parts of the Haff-district (fig. 15) and along the brooks and rivulets in the other "districts". Populus and Salix-forests, mainly used as coppice-woods (grienden) occur as representations of the Alnion-alliance on the river-basin clay soils in the valleys of the big rivers.

A special type of these riverbank-forests should be mentioned: the "grienden" in the estuaries of the big rivers in the provinces Zuid-Holland and Brabant, well to be studied in the "Biesbosch". The tide is still felt here, high and low tide often differing about 1 m. The seawater however doesn't come up so far, the water is fresh or oligohalinic. These tidal-forests mostly consist of Salix species. They lodge an interesting, characteristic flora and fauna, adapted to the inundations twice a day. Forests of this type are not found elsewhere in N.W.-Europe.

Swamps and bogs. Although since about 1500 A.D. most of the swamps, bogs and waters in the Netherlands are reclaimed, still large swamps and a few remains of bogs exist (fig. 13).

The swamps occur in two complexes, one in the low part of the provinces Zuid-Holland, Utrecht and Noord-Holland (e.g.: Vechtplassen), the other in Friesland and N.W.-Overijssel. In both complexes, numerous communities are discerned according to the depth of the water, the content of nutrient salts, the degree of salinity etc. Phytocoenoses belonging to the Potamion eurosiberium, the Glycerieto-Sparganion, the Phragmition-eurosibericum, the Magnocaricion elatae and the Caricion fuscae (Parvo-caricion) exist here, described more exactly in the next part of this booklet. Many communities are developed in large stretches and in a way only possible in such swamp areas as are characteristic for the Netherlands. They lodge quite a lot of plants and animals in North-Western Europe only living here, and for that and for their scenery are famous far beyond the borders of the Netherlands.

On the plistocene sandy soils in the East of the Netherlands on a good many places the Quercion roboris forests, due to human influence, made place for the semi-natural heath and moorland (c.f.: part B, II). Where the groundwater-level is high, oligotrophic pools and bogs are present. The Littorellion uniflorae vegetations only occurring inthe at lantic province and Sphagnion europaeum-vegetations of the pools and bogs bordering the atlantic Ericion tetralicis phytocoenoses of the moorland and the Calluneto-Genistetum heath vegetations of the atlantic Ulicion alliance.

Grasslands. The grasslands of the Netherlands are almost without exception cultivated grasslands, largely influenced by drainage, egalisation and manuring

with artificial manure, especially during the last decennia. They belong to the Arrhenatherion elatioris with numerous grassland-types according to differences in phreatic level and soil conditions.

Grasslands with a more natural floristic composition are present: 1. in the rivervalleys, 2. in swamp-area's, and along brooks and rivulets and 3. on very high and dry, often sandy soils.

1. In the riverforland drainage, egalisation and manuring often are omitted. The soil of these grasslands is rich in minerals due to the sedimentation of riversilt, which is left by the rivers during the inundation periods nearly every winter and early spring. The grasslands are chiefly in use as hayfields and are of great interest from a floristic as well as from a faunistic viewpoint. The phytocoenoses are associations and other coenoses of the Arrhenatherion elatioris with Arrhenatherum elatius, Chrysanthemum leucanthemum, Tragopogon pratensis and other characteristic species.

2. Wet grasslands in swampy areas and in local depressions for instance along brooks and rivulets become rare even in the Netherlands, owing to better drainage carried out on a large scale during the last decennia. The phreatic level in these grasslands as a rule is too high for manuring, often it is even impossible to graze cattle on them, so they are mainly used as hayfields. The vegetation of these fields is "poor" for the present-day farmer but rich for the botanist and the zoloogist. Orchids are often abundant as well as fine flowers e.g. Filipendula ulmaria, Lysimachia vulgaris, Thalictrum flavum, Cirsium palustre. The vegetations often are slightly blueish in color due to the dominant species Molinia coerulea and Carex panicea. For this reason these fields are called "blauwgrasland" 'bluegrassland") and belong to the Molinion coeruleae. They are excellent biotopes for waders as *Limosa limosa*, *Tringa totanus* and *Philomachus pugnax*.

The natural grasslands of the dry sandy soils belong to two alliances. One of them, the Corynephorion canescentis (with Corynephoretum canescentis) is characteristic for the dry sandy soils poor in lime. These are found in the inland dunes and in the seadunes of the Wadden District. Corynephorus canescens, Hieracium pilosella, Jasione montana and other species form an open vegetation, which is only suitable to feed sheep.

The dry sandy soils rich in lime are covered with the phytocoenoses of the Bromion erecti. Those found in the calcareous dunes of the Dune District are described in part B. IV. They are characterised by Phleum arenarium, Koeleria albescens and the moss Tortula ruralis var. arenicola or by Anthyllus vulneraria.

Interesting are the Bromion vegetations of the dry calcareous soils bordering on the lowlying grounds of the rivervalleys. They are used as meadows or hayfields. Medicago falcata, Avena pubescens, Euphorbia cyparissias and Salvia pratensis are among the most conspicuous elements. These coenoses are for the faunist of interest as well.

In the South of Limburg on calcareous soils still another Bromion vegetation

is present: the Meso-Brometum erecti with Cirsium acaule, Brachypodium pinnatum and others. These "brometa" are the most northern representatives of this association.

The natural grasslands of the saltmarshes along the coasts of Zeeland and the Wadden islands, belonging to the alliances Salicornion herbaceae, Puccinellion maritimae and the Armerion are described in B, V.

c. Human influence

The influence of man on the nature of the Netherlands is very great, as can be concluded from the preceding paragraphs. It is probably much greater than in any other european country. It is for instance very obvious in all parts below sealevel or at about sealevel, about 40 % of the surface of the Netherlands, where natural drainage is impossible and the water table is always kept between fixed levels by artificial means. The "polderland" is cultivated almost completely, natural coenoses, such as reed vegetations, existing only on a few spots.

In prehistoric times already men "cleared" parts of the woodland of the high plistocene soils, giving rise to large heath complexes. Reclamation went on since and nowadays human interference has gone so far that only about 7 % of the surface of the country is uncultivated land, which, however, is influenced as well. The following data give the uncultivated areas in 1932 and 1950:

	1932	1950
fresh waters	65.000 ha	id
tidal flats	39.000 ,,	id
dunes	42.000 ,,	id
swamps	90.000 ,,	50.000 ha
heath	285.000 ,,	100.000 ,,

Reclamation is going on quickly, because with the increase of the population (1830: $2{,}6 \times 10^6$, 1933: $8{,}3 \times 10^6$, 1950: about 10×10^6) the demand for land becomes more and more pressing.

From the preceding facts it is obvious that the heath, the moorland, the pools, fens and swamps, and the dunes, tidal flats and beaches are economically of little importance compared with the cultivated areas. However, as areas for recreation, and for the scientist they are of particular interest because only here the flora and fauna can have a natural development.

The visit and the investigation of these regions is therefore recommended, certainly to entomologists.

B. IMPORTANT BIOTIC COMMUNITIES

I. WATERS ('BROADS'), SWAMPS AND FENS

By far the greater part of the holocene W. and N. region of the Netherlands has been designated, from a plant geographical viewpoint, as the Haff distict. The many different soil types (see chapter IIb) of this district may be grouped into two categories: sea silt and fossilised low peat soils. The latter in general are occupied by intensively cultivated grasslands, but from the early middle ages or perhaps even earlier man has been digging out the peat, mainly in soils belonging to two of the soil types distinguished by EDELMAN (1950): "low sphagnum and carex peat soils" (the bulk of the areas employed for peat-digging) and "peat-soils, deep below sea level". As the phreatic level reached nearly to the surface, open water arose where the peat had been dug out. Generally peat-digging was allowed only by the method of leaving intact numerous long, narrow parallell strips of land ("ribben", "legakkers"), on which the peat was deposed, dried and cut into pieces. When exploited, this mosaic of land and water was left to its own development. The strips of water, varying from a few to several hundred meters in width, became the habitat of a water vegetation, the starting point of an autogenic succession (hydrosere) which lead to bulrush and reed swamp, sedge fen, finally fen wood ("carr") or sphagnum bog. This development can still be pursued and studied, as peat digging has been continued up to the present time. In many cases, however, the distance between the strips of land was made too large, so that the wind destroyed them afterwards – totally or partly – and extensive, although very shallow waters ("plassen": "broads") were formed. Fragments of the "ribben" remained in the form of islands. The depth of the "plassen" varies with the thickness of the peat-cover dug out, but seldom surpasses 4 meters. In the open water vegetations of waterplants developed, different from those in the small water strips; also the zones of swamp plants along the edges differ from the "strip swamp".

Floristic composition and structure of the communities of the hydrosere vary to a great extent, according to the degree of salinity of the water, the condition of the substratum (sand, clay or peat), the degree of contents of soluble mineral salts ($CaCO_3$, phosphate, potash, nitrate) of the water, the influence of wind (largely dependent on the extension of the water, see above) and some other

factors. Interaction of these factors has led to an almost endless number of hydro- and helophytic communities. It is possible, however, to schematize these vegetations to a smalle number of vegetation types. The following survey of them is not intended to be complete.

a. Meso- to oligohalinic waters

Content of chloride 10.000 to 100 mg/l. Such waters are found in the provinces North-Holland and South-Holland, generally on a clayish substratum; waters rich in nutritive salts will only be considered here. In large open water is found a community of Naias marina, Potamogeton pectinatus, Nitellopsis obtusa, Chara species, mainly Chara hispida, and Chlorophyta such as Vaucheria dichotoma and Spirogyra sp. These are all submerged hydrophytes, partly swimming ("elodied plants" sensu Du Rietz), partly covering the bottom ("isoetid plants"). The intolerant Chara species may also occur without any companying phanerogam plants; so it may form large submerged "fields". In mesohalinic water (content of chloride 10.000–1000 mg/l) the steeper edges (0,3–2 m, max. 3 meters deep) are populated by a community of Scirpus maritimus and Schoenoplectus tabernaemontani, halophilous reeds, in the most cases accompanied by Phragmites communis, sometimes by Aster tripolium too. This "Scirpetum maritimi" is poor in other species. It may be replaced by a community of Althaea officinalis and Oenanthe lachenalii, which is more often found on the edges of smaller brackish waters (canals and ditches); however, Scirpetum maritimi in the latter habitat may thrive as well; the ecological difference between the two communities is not yet clear. Abrased edges, rich in nitrates, often bear the tall stems of Sonchus paluster (up to 73 m high). Another interesting species, characteristic of the brackish reed swamp, is Cochlearia officinalis.

In oligohalinic water Althaea officinalis and Oenanthe lachenalii disappear; Scirpus maritimus and Schoenoplectus lacustris still may be found, but no longer growing in masses, their association having a more limited amplitude than the species themselves. They are found, now, in the association of great reed (Schoenoplectus lacustris), reedmace (Typha angustifolia) and common reed, the Scirpeto-Phragmitetum, which however attains its complete specific assemblage only in fresh water. In oligohalinic water more or less rich in lime and rich in dissolved oxygen, the edges may be colonized by large consociations of the stout, brownish, saw-leaved sedge Cladium mariscus, equally dominant on certain fresh water edges. As the submerged soil approaches the surface of the water by the continued accumulation of organic debris, these swamps are succeeded by a reed fen, most remarkable for the rapid entering and dominating of some Sphagnum species (chiefly S. plumulosum, S. palustre, S. fimbriatum and S. acutifolium); in this vegetation the pH falls from $\pm$ 7 (open water) to $\pm$ 4, and the brackish influence is disappearing. At first, this stage contains a number of phanerogams which designate it to the "fen" type: Hydrocotyle vulgaris, Viola palustris, Lychnis flos-cuculi, Cirsium palustre, Orchis praetermissa

etc., and among the taller plants e.g. Juncus subnodulosus. Frequently Phragmites communis dominates: "Phragmites-Sphagnum-consociation". When developing, this fen is succeeded however by a type of vegetation which might be called a Sphagnetum bog: Platanthera bifolia, Erica tetralix, Hammarbya paludosa, and sometimes even Empetrum nigrum, Oxycoccus quadripetalus and Andromeda polifolia appear. The occurrence of these small oligotrophic bog-like vegetations in the midst of a brackish reed swamp is a curious and highly interesting feature of the N.W.-part of the Haff district.

In small open water – ditches and dug gaps – the succession shows a somewhat different starting point. In the mesohalinic habitat Ceratophyllum demersum and Potamogeton pectinatus are the most frequent species; Ruppia rostellata and Zannichellia pedicellata, highly characteristic for the brackish water, are not found so often. Other Potamogeton species are wanting here. In the oligohalinic water the freshwater community of Stratiotes aloides and Hydrocharis morsus-ranae is able to develop; here it is rich in Enteromorpha intestinalis (Chlorophyta).

b. Fresh waters and swamps

Content of chloride less than 100 mg/l. They form the bulk of the swamps of the centre of the Netherlands ("Vechtplassen") and reach their largest extension in the N.W. of the province Overijssel; they are important, too, in the centre of Friesland.

Large open water, more than 1 meter deep, but not too much swept by the wind, is the habitat of the Myriophylleto-Nupharetum, which is characterized by: Nymphaea alba, Potamogeton lucens fo. acuminatus and Myriophyllum spicatum; Nuphar luteum is often a deminant species. The following insects may be found on Nymphaea: *Galerucella nymphaeae* L. (Col.), *Hydromyza livens* Fall. (Dipt.), *Donacia crassipes* F. (Col.). Contrary to the halophilous Naias community this vegetation is rich in plants with floating leaves, which is important for insect life. The taller plants all are rooting and therefore they are protected against a passive transport by wind influence. Generally the bottom of these waters is covered by organic ooze. If the water is too deep or too heavily moved by wind, most of these phanerogams are absent (Potamogeton lucens being very resistant, however); then the water bottom may be covered by a Chara vegetation. In many cases, especially in periodically dredged canals and moved (not streaming) rather small open water, on clay or sand soil (rarely on peat or organic ooze), another community is found, characterized by Potamogeton perfoliatus, P. pectinatus fo. vulgaris and Nymphoides peltata.

Small shallow eutrophic waters, e.g. ditches, peat-gaps and sheltered inlets, frequently are populated by one of the commonest hydrophyte communities of the holocene part of the Netherlands: the Hydrochareto-Stratiotetum. Stratiotes aloides and Hydrocharis morsus-ranae, together or separately, are dominant here; in summer the former may fill up the water totally, so that navigating

and fishing are seriously obstructed; in the autumn it dies and only the winter buds remain in the mud on the bottom. Other rather characteristic species of this community are Utricularia vulgaris, Potamogeton compressus and the alga Hydrodictyon reticulatus; besides, quite a lot of species frequently occur. Hydrocharis forms a "swimming layer" together with Spirodela polyrrhiza, Lemna minor and more rarely the interesting liverwort Ricciocarpus natans. Most of the species of this community do not or but poorly root, and may easily be transported through the water by wind: this vegetation is adapted to a wind-protected habitat. *Bagous binodulus* Hrbst (Col.) may be found here.

Freshwater hydrosere has a different course according to the content of soluble mineral salts of the water. Schematically it may be divided into a sere with an eutrophic starting point and a sere with a mesotrophic one; the oligotrophic succession which is not found in the Haff district, is dealt with in paragraph 2. The two subseres will be dealth with here separately.

1. *Hydrosere starting in eutrophic fresh water.* In the Netherlands as well as in the greater part of Europe the edges of eutrophic fresh water are colonised by bulrush or great reed (Schoenoplectus lacustris), Typha angustifolia, T. latifolia and common reed (Phragmites communis): the wide-spread Scirpeto-Phragmitetum. The former species is able to thrive already in water more than 3 meters deep, so it enters first; the Typha species prefer soft organic mud, but the rhizomes of Phragmites may thrive in hard soil too. According to these conditions, but still more to the luck of first occurrence, the four species are often found in separate stands (consociations). Characteristic plant species of the association are: Sparganium erectum ssp. polyedrum, Acorus calamus, Typha latifolia and Sagittaria sagittifolia (the latter being the first pioneer in sheltered shallow water); among the other frequent species (characteristic species of the alliance and order) may be named Rumex hydrolapathum, Butomus umbellatus, Ranunculus lingua, Alisma plantago-aquatica and Sium latifolium. Characteristic insects are: *Philudoria potatoria occidentalis* Lempke (Lep.), *Donacia* div. spec., *Plateumaris sericea* L., *Dicranthus elegans* F. (Col.). In often dredged ditches in the area of cultivated grasslands the association can only develop fragmentarily, rapid growing plants with a short life-cycle being favoured here: often a vegetation of Oenanthe aquatica, O. fistulosa, Sagittaria and Sium erectum results. In vitiated water, rich in nitrates, as in many ditches, the Scirpeto-Phragmitetum is replaced by the Glycerieto-Sparganietum neglecti, characterized by Sparganium erectum ssp. neglectum, Glyceria fluitans, Veronica anagallis-aquatica, etc.; constant and often dominant species of it are Glyceria maxima and Sium erectum.

It the water is not vitiated (not rich in nitrates), the swamp fern Dryopteris thelypteris may occur in Scirpeto-Phragmitetum; it often tends to dominate, and it has a great dynamo-genetic value for the succession; its amplitude is as large as that of Phragmites, reaching up into the fen wood.

Besides Scirpeto-Phragmitetum another association of the alliance "Phrag-

mition communis" may usher in the eutrophic swamp sere. This "Cicuteto-Caricetum pseudocyperus" characterizes a very special, but rather common habitat, which might be interesting from an entomological point of view: the "drijftillen". This habitat consists of a thick mass of organic matter which in sheltered inlets and corners may adhere to edge and bottom, but which is frequently floating freely on the water, taking its origin: 1. by evolution of gas in the substratum, 2. by the clinging together of Typha rhizomes and similar remnants, 3. by the action of man (digging, boating etc.). The "drijftil" may secundarily adhere to some edge and so it accelerates the process of succession. Its community is characterized by Calla palustris, Cicuta virosa and Carex pseudocyperus. It forms the habitat of the following insects: *Eulalia ornata* F., *Eulalia angulata* Panz., *Parhelophilus versicolor* F., *Eurynomyia lineata* F., *Eurynomyia transfuga* L. (Dipt.), *Lixus paraplecticus* L., *Lixus iridis* Oliv. (Col.).

Reed swamp and "drijftil" vegetation are succeeded by some communities characterized by tall sedges (Carex spp.) and united to the alliance of "Magnocaricion". These sedges have a great dynamo-genetic value; they change the habitat from an inundated swamp to a "trembling swamp", where the phreatic level equals the surface, the latter following the oscillations of the former. It is only possible to tread a trembling swamp by walking (jumping) from one sedge tuft to another. In the eutrophic vegetations of Magnocaricion, Carex vesicaria, C. riparia, C. acutiformis, C. paniculata, C. gracilis and C. disticha are the most important species. Carex inflata may occur too, but its optimum is found in meso- and oligotrophic habitat. The three former species, "Caricetum acutiformo-paniculatae", prefer the most eutrophic environment. The large tussocks of Carex paniculata rapidly turn the swamp into land, especially on the "drijftillen": so it even is a constant species of Cicuteto-Caricetum pseudocyperus, though destructive with regard to the specific assemblage of that association.

In extremely eutrophic environment Magnocaricion is succeeded directly by "carr", i.e. fenwood consisting of alder (Alnus glutinosa), willow (Salix cinerea, S. aurita and cultivated species like S. alba and S. viminalis), Viburnum opulus, Rubus fruticosus, Frangula alnus, Sorbus aucuparia, Lonicera periclymenum and, sometimes, Humulus lupulus. Among the large number of hydrophytes thriving in it, species of the former succession stages still are frequent and often abundant: Phragmites communis, Carex paniculata, Dryopteris thelypteris; among the other species Calystegia sepium, Solanum dulcamara, Lysimachia vulgaris, Peucedanum palustre, Filipendula ulmaria, Iris pseudacorus, Valeriana officinalis, Caltha palustris may be mentioned. This community is closely allied to the "Alnetum glutinosae" of the plistocene region of the country; the latter, however, is characterized by such species as Carex elongata and Ribes nigrum, absent or rare in the Haff district, while Dryopteris thelypteris is wanting in this plistocene alder wood. Recently the holocene Alnetum has been described as "Thelypterideto-Alnetum", forming with the plistocene "Cariceto elongatae-Alnetum" a pair of geographic vicarious associations, together a "coenassociation" or "collective association".

If Alnetum wood is cut down, many of its species reach their optimal vitality: in shadow they rarely flower. These species, then, together with a number of shade-evading ones, form a luxurous community of tall, beautifully flowering plants, a paradise for insects: the Valerianeto-Filipenduletum. Characteristic species of it are Euphorbia palustris, Valeriana officinalis, Stachys palustris, Lathyrus paluster and Crepis paludosa; among the frequent species of the alliance and the order (Filipendulo-Petasition, Molinietalia) the next may be mentioned: Filipendula ulmaria, Angelica silvestris, Thalictrum flavum, Lysimachia vulgaris. Important and still flowering relics of the Phragmition are Epilobium hirsutum and Iris pseudacorus. Among the characteristic insects of this habitat the following species may be mentioned: *Oedemera croceicollis* Gyl., *Hylobius fatuus* Rossi (Col.), *Adelphocoris ticinensis* M.D. (Heteropt.), *Diataraxoa splendens* Hb., *Lycaena dispar batavus* Obert. (Lep.), *Macropis labiata* F., *Epeoloides coecutiens* F. (Hym.). The association can also primarily arise in succession, mainly on spots covered with dredged organic matter by man, and it occurs in the oligohalinic environment too, being connected there with the vegetation of Sonchus paluster.

In less eutrophic environment Magnocaricion is rarely succeeded directly by fen wood. It develops into the "trembling swamp" already mentioned, characterized by minor sedges ("Parvocaricion canescentis-fuscae"). From this point the sere coincides with that of the mesotrophic habitat; there the Parvocaricion will be dealt with.

2. *Hydrosere starting in mesotrophic fresh water.* Mesotrophic fresh water is found above a sand bottom, chiefly there, where the holocene "low Sphagnum and Carex peat soils" adjoin higher situated plistocene sand soils. The soil water of the latter, poor in nutrients, flows down and mingles with the water of the holocene "broad" and swamp. This situation is found in the "Vechtplassen" e.g. in the nature reserve "Het Hol" near Kortenhoef, bounded by the pleistocene "Gooi"; in the swamps of N.W.-Overijssel one can see it in the "Zandbelten", the swamps of Wanneperveen and the "Kierse Wiede", adjoining the plistocene "Land van Vollenhove". Transitional cases between eu- and mesotrophic hydrosere occur, also mosaics of them. Another feature of the mesotrophic habitat is its relative isolation and purety with respect to the more vitated large open waters. So it may be rather rich in calcium, but poor in nitrates and potassium.

In mesotrophic water the Myriophylleto-Nupharetum, if present – it may be replaced e.g. by a vegetation of Hottonia palustris or by Nitella sp., Elisma natans, Juncus bulbosus, Isolepis fluitans – is not bordered by Scirpeto-Phragmitetum, but by a sociation of the tall saw-sedge Cladium mariscus, mentioned already with respect to the oligohalinic habitat. This intolerant sedge supports very few companion species, and these only in a few individuals. Its community has to be designed to Magnocaricion rather than to Phragmition. Succession from a Cladium community to the trembling swamp of a "Parvo-

caricion" rarely takes place by repulsing the saw sedge by other species: the former dies when its habitat is no more suitable (too dry, too poor in oxygen or too acid), and only after its death the small sedges like Carex diandra and C. stolonifera are able to eceze.

In other cases, however, Cladium is locally wanting and the succession in the open water starts immediately with a community of small sedges, Caricetum lasiocarpae. Besides Carex lasiocarpa, C. stolonifera and C. inflata, also Lysimachia thyrsiflora, Juncus subnodulosus, Galium palustre, Menyanthes trifoliata, Comarum palustre, Dryopteris thelypteris etc. may occur in it; a highly characteristic feature is its half submerged swamp moss layer, consisting of Scorpidium scorpioides, Drepenocladus spp. and other Musci, and the phanerogam Utricularia minor. Gradually the submerged soil reaches the surface of the water and the Caricetum lasiocarpae merges into the real "trembling swamp", the Caricetum diandrae, closely related to the former and by some authors joined with it to a single association. Here the rare orchids Liparis loeselii and Hammarbya paludosa are locally frequent and characteristic of it, just like the rare Eriophorum gracile. Pedicularis palustris, Viola palustris, Stellaria palustris, Parnassia palustris, Eriophorum angustifolium and Veronica scutellata are some of the other species of this "florestic jewel" which are worth being mentioned.

When the soil turns more acid, Caricetum diandrae is replaced by the Caricetum canescentis-fuscae: a certain number of species of the former community are still found, but Carex canescens and C. echinata replace C. diandra and C. lasiocarpa, and in the moss layer Sphagnum species tend to dominate. Interesting insect species are: *Mylopsila meditabunda* F., *Hebecnema umbratica* Mg., H. *vespertina* Fall., H. *affinis* Mg. (Dipt.). The subclimax of this trembling swamp is a fen wood, is which the birch (Betula pubescens) is dominant and that otherwise differs from the alder wood in the wanting of "eutrophic" species and in the occurrence of Myrica gale, Polytrichum commune, Molinia coerulea, Sphagnum fimbriatum, S. recurvum, Aulacomnium palustre and Dryopteris cristata. If the wood is prevented from developing, a succession to a Sphagnum bog is possible: pH falls below 4.0; Erica tetralix, Pyrola rotundifolia, Oxycoccus quadripetalus, Microlepidozia setacea etc. may enter.

II. HEATH FORMATION: MOORLAND AND BOGS

a. Heaths and moorlands

The plistocene sandy soils in the East of the Netherlands vary with respect to:

1. Their relief: the hilly parts of the "sandy push moraines complex" (mainly on the Veluwe) as opposed to the flat grounds.

2. Their hydrology and their physical composition, two factors which cannot be separated as to their influence on biotic communities. If reclaimed soils, forest soils and the "loamy brook soils" along the rivulets are left out of con-

sideration, heath-, moorland- and sandy bog soils remain. The most important types of them are, for our purpose:

a. "Podzolised heath soils" and "podzolised soils on stratified drift", occurring on high, dry sand without a considerable amount of loam; they bear the plant community Calluneto-Genistetum typicum, the real dry heath-association where ling (Calluna) is dominating. These soils are scattered throughout the plistocene. According to EDELMAN (1950, pag. 22), the most pronounced heather podzol profiles with a dark-brown iron humus pan (B-layer) are to be found on the coarse, non-loamy cover sands, the fluvioglacial sands without silt and the coarse parts of the pre-glacial river sands with little silt. On the relatively good soils a heather vegetation of long standing does not even develop a clear heather podzol profile.

The dry heaths are maintained in their condition by burning and grazing; where such influences are stopped, they become overgrown with birch and common pine (Pinus silvestris) and develop into woodland (Querceto-Betuletum typicum).

b. "Inland dune sand": shifting or resting dry sand hills, covered with an open vegetation of grass and lichens (Corynephoretum canescentis). In the north of the country, mainly in the province of Drente, Empetrum nigrum may abound here: it is a pioneer to the succession stage, Calluneto-Genistetum typicum (see "a"). This succession however also occurs where Empetrum is wanting.

c. "Medium-high heath soils" and high but moist sandy soils, found on sand not too high above the phreatic level or provided with an impermeable layer in the subsoil: boulderclay or a thick hardpan. According to Edelman (1950, p. 29) the heaths of medium height are more characterized by the occurrence of humiferous hardpans than the high ones. On this soil a moist heather vegetation occurs, which might be called "moorland": Calluneto-Genistetum molinietosum, dominated by Calluna, Erica tetralix and Molinia. The latter may supersede the former completely (Molinia sociation). This soil- and vegetation type is almost limited to the province of Drente, where it has been reclaimed on a large scale in recent times. The moorland heather does not easily develop to wood and might, at least in many cases, be considered an edaphic subclimax.

d. "Moist sandy soils", only slightly above the phreatic level and showing a gley profile. If the soil is sandy and the phreatic water poor in nutrients, Calluneto-Genistetum molinietosum may be found here too, and besides it the Ericetum tetralicis cladonietosum; contrary to the case mentioned under "c" however, this heath is a temporary stage like the dry heath, rapidly developing into woodland (Querceto-Betuletum molinietosum) when human influence is stopped. If the soil is more or less loamy or the phreatic water contains more nutrients, a richer vegetation type may arise: Calluneto-Genistetum orchidetosum, mosaically interchanged by mown or grazed vegetations with purple moor grass (Molinia coerulea), orchids, sedges etc.: Cirsieto-Molinietum orchidetosum and C.-M. juncetosum acutiflori.

e. "Wet sandy soils", where the phreatic level surpasses the surface in winter and equals it – or nearly so – in summer. Here on sandy soils without loam Erica-heather has been abundant (in present time it is reclaimed nearly everywhere): Ericetum tetralicis typicum and Ericetum tetralicis sphagnetosum, the latter on the wettest spots. Both are anthropogenic stages, rapidly succeeded by sweet gale (Myricetum gale) and birch wood (Betuleto-Salicetum), when left to itself. More or less loamy soils bear a richer vegetation (compare with "d"): Ericetum orchidetosum and Schoenetum nigricantis (almost completely reclaimed).

Small pools are often found in the moist and wet heathers. The oligotrophic hydrosere starting in them may be considered under the bog formation (see sub B). They form the habitat of *Dytiscus lapponicus* Gyl.

Some plant communities mentioned above will be dealt with more in detail, considering also the geographical (climatic) variation in them.

Corynephoretum canescentis is the open vegetation of more or less mobile inland sand dunes and of sea dunes poor in lime; the latter are dealt with in § 4. Its most characteristic species are the small winter therophytes Spergula vernalis and Teesdalea nudicaulis, flowering in early spring, and some lichens, e.g. Cladonia verticillata; among the other species we name the dominant, superficially rooting xerophyte grass Corynephorus canescens, the therophytes Aira praecox and Filago minima, the geophyte Carex arenaria, some mosses (Polytrichum piliferum, Racomitrium canescens) and a number of lichens. A striking feature of the habitat is the extreme microclimate with very high daily maxima on the surface (up to more than 50° C. in summer) and in the soil and the air near to it. Together with the dry, loose sand, this factor is important for a relatively optimal insect life, mainly of Hymenoptera and Coleoptera. The differences between the open initial phase on mobile sand (much Carex arenaria, hardly any lichens), the phase on stabilised sand (Corynephoretum agrostidetosum, marked by Agrostis canina var. arida and Hypochoeris radicata) and the terminal phase on resting humus sand (a closed cover of many lichens) must be important for insect life too. *Gryllus campestris* L. (Orthoptera), *Formica glebaria* Nyl., *F. rufibarbis* F. and *Tetramorium caespitum* L. (Formicidae) and the Lepidopteron *Hipparchia statilinus* Hufn. are some examples of insect species preferring this habitat.

The Calluneto-Genistetum, the ling heath, is characterised by the common species Calluna vulgaris (dominant), Genista anglica, G. pilosa, Antennaria dioica, Cuscuta epithymum; less common are Juniperus communis and the club-mosses Lycopodium clavatum and L. complanatum. Common companion species are Deschampsia flexuosa, Carex pilulifera, Festuca ovina and Triodia decumbens. The association presents a well developed moss layer of Musci (p.e. Pleurozium schreberi, Hypnum cupressiforme var. ericetorum and Dicranum scoparium), Hepaticae and lichens. In the Northern part of the country (mainly the province of Drente) Empetrum nigrum and Arnica montana frequently occur; their areas extend to the South roughly as far as the Rhine. In the

cool-continental North-Eastern part of the country (Drente, Salland, Twente) the beautiful lichen Cetraria islandica is a rather frequent heath species, wanting more to the South. The Calluneto-Genistetum in the Central and Southern part of the country presents a poorer floristic composition, but it is distinguished by the occurrence of the gorse, Ulex europaeus, which dies off in the cold winters in the northern provinces. In some localities in the S.E. region of the country, e.g. at Mook near Nijmegen, the atlantic species Erica cinerea is found in the heather association, mostly on dry spots (Calluneto-Genistetum typicum); it does not form, however, a separate community (Ericetum cinereae) as it does in Britain, Eire and W.-France.

Typical insects of the Calluneto-genistetum are: *Poecilus dimidiatus* Ol., *Strophosomus fulvicornis Dyrph., Lochmaea saturalis* Thom., *Micrelis ericae* Gyl. (Col.); *Paragys tibialis* (Dipt.), *Orgyia ericae* Germar., *Malacosoma custrensis* L., *Lycophotia molothina* Esp., *Ortholitha coarcturia* Schiff., *plumbaria* F., *mucronata* Scop., *Pachycnemia Lippocastanaria* Hb., *Procris pruni* Schiff., *Rhyparia purpurata* L. (Lep.), *Acalypta parvula* Fall., *Dictyonota Strichnocera* Fiel., *Dictyonota fuliginosa* Costa., *Nysius helveticus* H.S., *Macrodema micropterum* Curt., *Raglius pini* L., *Raglius phoenicus* Rossi. (Heteropt.).

The subassociation Calluneto-Genistetum typicum is characterized by the absence of all hygrophilous species, even of such wide-spread heath plants as Erica tetralix and Molinia coerulea. Its optimal habitat is resting inland dune. It can often be observed that the Corynephoretum canescentis – the normal vegetation of these dunes – is succeeded by Calluneto-Genistetum typicum establishing itself on the most exposed spots at first, i.e. on the top of the dunes which become covered with a "heath-cap" (Holtinger Zand in Drente, Loonse Duinen in Brabant, etc.) Such "caps" are rapidly succeeded by shrubs. Polypodium vulgare is a special fern of this sere. If many individuals of Quercus robur thrive in the neighbourhood so that enough acorns can be conveyed, this shrub (in this case not a tree) is the first to eceze; it presents the greatest competition power. Ordinarily, however, Betula pendula and Sorbus aucuparia are the first phanerophytes to be established, because their dissemination capacity is much higher. Calluneto-Genistetum typicum in other habitats (more or less podzolised soils, not shifting sands) is frequently succeeded by scattered common pines or by a stage of Sarothamnus scoparius, merging into the Querceto-Betuletum. In these scrubs lives *Ephippigera vitium* Serv. (Southern European fauna element). In all these cases the installation of shrubs is mostly preceded by a strong expansion and a dominance of the grass Deschampsia flexuosa. If the heather has been burnt down, succession often begins with a stage of Epilobium angustifolium; thereafter Deschampsia flexuosa tends to complete dominance. Vegetations of bracken (Pteridium aquilinum), very common on British sand soils, are hardly found in the heather habitat in the Netherlands; here this fern is confined to the wood, Querceto-Betuletum. The same is true for the bilberry (Vaccinium myrtillus); in heather formation in the Netherlands it occurs nearly only in the "heath caps" of the inland dunes mentioned above.

The dry heath is an optimal habitat for many insects; for this reason it is dealt with here in more detail, and for the same reason attention still must be given to the open, trampled heath places, such as walks, foot-tracks and verges of larger roads. Here some common open dry grassland communities may arise, e.g. Festuceto-Thymetum and a community of Agrostis tenuis; species which may be mentioned here are Festuca ovina, Nardus stricta, Thymus serpyllum ssp. angustifolius, Campanula rotundifolia, Hieracium pilosella, Hypericum perforatum, Ornithopus perpusillus, Potentilla argentea, Trifolium arvense, Jasione montana. The more open this vegetation, the more warm the microclimate on summer days, and the more optimal a habitat for many Hymenoptera (*Ammophila*, *Philanthus* etc.).

Moist heath (moorland), Calluneto-Genistetum molinietosum, is distinguished by Molinia coerulea and Erica tetralix; it presents a number of characteristic insects, e.g. the boreal ant species *Formica exsecta* Nyl. nesting in colonies in Molinia tufts. Foot tracks, walks, etc. in it present a special vegetation of therophytes and a distinct insect life. This community, Panico-Illecebretum, closely allied to the Cicendietum (see below) and joining with it in the alliance of "Nanocyperion", as yet is known only from the Netherlands and Belgium. It contains a.o. Illecebrum verticillatum, Digitaria ischaemum, Corrigiola littoralis, Veronica serpyllifolia, Hypericum humifusum and Spergularia rubra. Heath on loamy soil, Calluneto-Genistetum orchidetosum, has been widely spread in the N. and E. regions of the country, but it has been reclaimed on a large scale. It is marked by many differential species, e.g. Orchis maculata, Platanthera bifolia, Polygala serpyllifolia, Pedicularis sylvatica, Gentiana pneumonanthe.

The wet heaths are summarized as the "Ericetum tetralicis". Erica tetralix is hardly a characteristic species for them, being equally constant and often dominant in the moist Calluneto-Genistetum. More selective species of the Ericetum are: Trichophorum caespitosum, Juncus squarrosus, Narthecium ossifragum, Sphagnum compactum and some liverworts, of which Gymnocolea inflata is the most common. A rare but a very characteristic Hymenopteron of this community is *Bombus humilis* Ill. in the N. of the country. Other important insect species are: *Psallus betuleti* Fall., *Lygus contaminatus* Fall., *Elasmucha fieberi* Jak., *grisea* L. (Heteropt.), *Pterostichus aterrimus* Hrbst. (Col.), *Epicnoptera ilicifolia* L. (Lep.). Where sods have been removed in Ericetum, an open community of Rhynchospora alba, R. fusca, Lycopodium inundatum and the alga Zygogonium ericetorum establishes, to be rapidly succeeded by Ericetum again. On loamy soil, Ericetum may present itself in its subassociation "orchidetosum", a community comparable with the Calluneto-Genistetum orchidetosum, but sometimes containing some rare and interesting species: Spiranthes spiralis, Hammarbya paludosa, Carex dioica, Pinguicula vulgaris. Foot tracks in Ericetum may bear a remarkable, yet nearly exterminated atlantic community of very small plants, the Cicendietum filiformis (Cicendia filiformis, Radiola linoides, Centunculus minimus, Isolepis setacea).

b. Bogs (Dutch: "hoogveen")

In wet heath landscape a great number of little pools ("vennen") was found, especially in Drente, Twente and Brabant; nowadays most of them have been reclaimed. Their vegetation development presents a great variance according to the depth of the water, the steepness of the edges, and mainly the contents of nutrients of the water. There are mesotrophic and oligotrophic pools; here only the latter will be considered: they are beautifully developed in the wet heath reserves in S.W.-Drente (Dwingeloo: Geuzingerveld, Schurenberg, Brandeveen). Besides in heath, they are found too in the rare remains of "living" large bogs which still are found in the Netherlands, that is to say not on sandy soil but on "sphagnum and carex peat soil". Here they mostly occur in gaps dug out in the peat, i.e. in a secundary habitat, but their type may be considered the starting of oligotrophic bog succession.

The large bogs of Drente, Overijsel and the "Peel" (borderland between Brabant and Limburg) have been drained or excavated. In so far as the drained peat has not been reclaimed, most of it is overgrown with a moorland poor in species: a consociation of Calluna vulgaris, Erica tetralix and Molinia coerulea in alternating dominance. Some Sphagnetum plants still are able to live here (Eriophorum vaginatum); so do some Sphagnetum animals, e.g. the peat ant *Formica picea* Nyl. This stage may develop to a poor Calluneto-Genistetum molinietosum or it may be succeeded by a birch wood with Myrica gale, Frangula alnus, Vaccinium uliginosum, V. myrtillus and V. vitis-idaea, Galium hercynicum, Molinia coerulea, Polytrichum commune etc. (Betuletum pubescentis).

There are remaining, however, some relics of large "living" bogs, comparable with British "raised bog" and "blanket bog": the bogs of Fochteloo (border Friesland–Drente), Engbertsdijk (Vriezenveen, N.E.-Overijsel) and Postel (the "Moeren", border N.-Brabant-Belgium) are the best known of them. Besides, some large bogs have been partially excavated, so that in the pools between the peat banks and ridges a secondary bog succession may be observed (see above). This is the case e.g. in the bogs near Winterswijk in the extreme East of Gelderland (Korenburgerveen, Vragenderveen, Wooldse Veen). A typical coleopteon of this region is *Blethisa multipunctata* L.

Succession in oligotrophic pools and bog gaps may start by flocks of Juncus bulbosus and Carex inflata (together or separated) with a moss layer of Sphagnum cuspidatum (dominant), S. subsecundum (codominant) and Drepanocladus exannulatus. These two Sphagna are rather characteristic of the habitat. Sociations of Menyanthes trifoliata and more sparsed Eriophorum angustifolium are seldom wanting in this community; Eleocharis palustris and tussocks of Carex elata may occur too. The next stage, in general, is marked by Rhynchospora alba, R. fusca, Agrostis canina (often var. fascicularis), Drosera intermedia; Sphagnum cuspidatum remaining dominant in the moss layer. Sometimes a dominance of Eriophorum angustifolium precedes one of Rhynchospora alba. Molinia coerulea and Hydrocotyle vulgaris may enter early. The communities mentioned are found about the oscillating phreatic

level and may dry up in summer. As soon as the growing Sphagna raise above the water, the "raised bog" starts and the floristic composition changes considerably: four other Sphagna become dominant, viz. S. papillosum, S. recurvum, S. medium and S. rubellum (in varying combinations, seldom all together), and in the herb layer Andromeda polifolia, Oxycoccus quadripetalus and sometimes Orchis maculata ssp. elodes appear, characteristic species of the raised bog (Sphagnion europaeum). Here the optimal habitat of *Formica picea* Nyl. is found. Other characteristic insects are: *Acylophorus glaberrimus* Hrbst. (Col.), *Acylophorus wagenschieberi* Kiesw. (Col.), *Oeryphorus picipes* Payk. (Col.), *Tachyporus transversalis* Grav. (Col.), *Cinxia borealis* (Dipt.), *Cinxia lappona* (Dipt.), *Coenonympha Aullia* Müller (Lep.). Nearly in the same period Erica tetralix and even Calluna vulgaris may eceze already. The Sphagnion is rich in characteristic liverworts, of which Cephaloziella elachista, Cephalozia connivens, Microlepidozia setacea seem to have the narrowest amplitude, whereas Mylia anomala, Odontoschisma sphagni, Calypogeia sphagnicola and Leptoscyphus anomalus are found in the wet Ericetum too. On the contrary, the submerged communities of Sphagnum cuspidatum and the raised Sphagnion seem to have only one species of liverwort in common, Cladopodiella fluitans. It is probable that the evolution of the raised bog involves an abrupt change in insect life too. The tussocks of Sphagnum papillosum and S. medium (etc.), when growing on, become succeeded by Ericetum sphagnetosum; in the degeneration phase of the Sphagnion, Eriophorum vaginatum attains a relative optimum, and also Narthecium ossifragum may abound here.

The living raised bog without open water in dug gaps presents a cyclic succession. The Sphagnum tussocks grow out of the Rhynchosporetum troughs, but at a certain moment (for instance when they reach the height of a foot) they accumulate more and more slowly and degenerate to tufts overgrown with Ericetum; then they dessiccate and subside. Surrounding and still living Sphagnum tufts surpass them in height; by consequence, the included Erica tussock becomes a Rhynchosporetum trough again, but yet on a higher level. By this cycle the whole bog gradually grows, until it is destroyed by draining or excavation.

III. SALT MARSHES

The salt mud flats and salt marshes are marked by two master habitat factors: they are covered by the higher sea tide, and they are found only there, where the sea is quiet enough for the sea silt to rest, so that the soil varies from clayey sand to pure clay. These conditions are extreme, so that salt marshes bear a characteristic halophilous vegetation and a typical insect fauna: mostly Coleoptera, in which practically all the species are peculair to this habitat (*Apion limonii* Kirby, *Polydrosus chrysomela* Olv., *Anisodactylis poeciloides* Steph., *Pogonus luridipennis* Germ., *litoralis* Dft., *chalceus* Mrsh., *Bledius spectabilis* Kr., *tricornis* Hrbst, *furcatus* Oliv., *bicornis* Germ., *unicornis* Germ.,

Cillenus lateralis Sam., *Mecinus collaris* Germ.) and some Diptera. The mud covered by every tide is too mobile for plant colonisation: it is only the stretches which lie above the high neap tides that are ordinarily covered with vegetation.

Thanks to the preponderating habitat factors mentioned, climatic and biotic influences are of minor importance, so the salt vegetation in N.W.-Europe bears a rather uniform character; the same might be true with respect to the fauna. In the Netherlands salt marshes are very beautifully developed, both on the coasts of the "Wadden sea" between Friesland and the "Wadden" islands of Texel, Vlieland, Terschelling, Ameland and Schiermonnikoog, and the estuaries of Rhine, Meuse and Scheldt, surrounding the islands and peninsulae of South-Holland and Zealand and the coasts of Brabant and Zealand Flanders. The habitats of these two regions, separated by the dune coast of Holland, show two marked differences: 1. the tidal range in the South, 3–4 m, is much larger than that in the Wadden Sea (1–1½ m); 2. in the Southern estuaries heavy clayey soils preponderate, whereas most soils of the Wadden coast are sandy.

As the salt marshes of the island of Ameland will be visited by the Congress, the halosere (the total of the succession stages of salt marsh vegetation) will be considered here with respect to the Wadden islands mainly; finally some comparative remarks on other salt marshes will be made.

The master factors determining the different stages of the halosere are the salt content and the humidity of the soil; the former undergoes a regular spatial change in intensity (salt gradient), causing the salt marsh vegetation to be clearly zonated. Broadly these zones correspond with succession stages. Two series of habitat have to be distinguished. Firstly the mud flat, where succession is brought about mainly by settling down of tidal silt and rise of soil level correlated to it, lateron by leaching out of the salt and accumulation of humus ("halosere on mud"). Secondly the silt containing sand flat; here desalinating by precipitation and flowing down of fresh water out of the adjacent dunes, counteracted by ± irregular submersions, must be considered the most effective initial condition; afterwards it becomes coupled with humus accumulation ("halosere on sand"). In the former sere desalinating is a rather continuous process; the latter is marked by strong fluctations of the salt content. Although no sharp line of demarcation can be traced the difference in ecological control has to be stressed. Both seres start with rapidly changing, transient, open therophyte communities; the more hemicryptophytes tend to predominate the slower the changes come about. In mud halosere however the vegetation gets more quickly closed and the allogenic succession is replaces sooner, partly by autogenic development; in the more open sand halosere therophytes play a certain part throughout the stages, and competition is less effective in determining the trend of the process.

On salt marsh (mud halosere) accrescent and abrasive (decrescent) coasts must be distinguished; their alternation depends on the trend of sea currents, the increasing of tidal range, etc. Accrescent coasts show regular succession,

but on abrasive coasts an "inverse" zonation is often observed: the most highly situated and most desalinated stages are adjacent to the unvegetated flat, the more halophilous communities are found behind the former.

The plant communities of the halosere are divided into two alliances: Puccinellio-Salicornion and Armerion maritimae.

The alliance of Puccinellio-Salicornion comprises the most halophilous phanerogam communities of atlantic and baltic coasts, i.e. the salt marsh of the tidal zone in a narrower sense, submerged daily or at least each fortnight (normal spring tide zone). The chloride content of the soil rises periodically above 9 g per l. The characteristic species of the alliance are: Suaeda maritima, Spergularia marginata, S. salina var. media, Spartina maritima ssp. glabra (syn.: S. townsendii) and Salicornia europaea s.l.

The alliance of Armerion maritimae comprises the halophilous communities of atlantic and baltic coasts whose habitats are only submerged by gale flood and at most a short time by spring tide. The chloride content of the soil does not exceed 9 g per l except perhaps for some days in a year. The characteristic species of the alliance are: Juncus gerardi, Glaux maritima and Agrostis stolonifera var. salina.

Halophytes occurring in both alliances are: Triglochin maritima, Plantago maritima, Festuca rubra var. litoralis and Aster tripolium. The other halophyte species present a more or less pronounced optimum in one or two of the associations mentioned below.

The two alliances will be dealt with separately.

a. The lower salt marsh communities: Puccinellio-Salicornion

Salicornia europaea ssp. stricta, the glasswort, is the pioneer on the mud flats. It is only accompanied by one phanerogam species: Spartina maritima ssp. glabra (= S. townsendii). On the Wadden coasts, however, this tall grass occurs rarely and only on very muddy soil. All other phanerogams found in the "Salicornieto-Spartinetum" are strangers or mark the terminal phase of it (Suaeda maritima, pioneer tufts of Puccinellia maritima). If the community is well developed the soil is entirely covered with Microcoleus chthonoplastes, Rhizoclonium sp. and other algae, cutting off the substratum from the air and covering a bluish ferrosulphide horizon. If the soil consists of silty sand, only among the root systems of the regularly spaced Salicornia the sand is white with rustcoloured ferri-spots. The mean submersion period of the community is 10 % of the day. The salt content of the soil may vary from 10 to 18 g Cl per l. It shows the highest minima of all halophilous associations on account of the silt content; but the maxima are low, as the habitat never runs dry enough for salt accumulation. The following insects are characteristic for the Puccinellio-Salicornion: *Machaerium maritimum* Hal., *Lispa litorea* Fall., *Meliera cana* Lw. (Dipt.), *Orthotylus moncreaffi* Dgl. Sc., *Orthotylus rubidus* Put. (Heteropt.).

On accrescent coasts (e.g. Boschplaat on Terschelling) the Salicornieto-Spartinetum is gradually succeeded by the Puccinellietum maritimae, charac-

terized by: Puccinellia maritima (constant, dominant), Obione pedunculata and Bostrychia scorpioides (a Rhodophyte, i.e. a red alga). This association falls into the subassociations Puccinellietum maritimae typicum (mud halosere) and Puccinellietum maritimae pholiuretosum (sand halosere); differential species of the latter are Pholiurus filiformis, Agrostis stolonifera, Salicornia europaea ssp. ramosissima and Triticum junceum. The former subassociation is an entirely closed grassmat, even where grazing regime fails; it is grazed by sheep and cattle almost everywhere, but on the Boschplaat grazed and not grazed samples of the community can be compared. The influence of this difference on the insect fauna has hardly been studied, but might be rather interesting. The second subassociation is an open community, but closed in the actual rhizosphere. – The habitat and the floristic structure of the Puccinellietum maritimae typicum are influenced by fresh water flowing out of the dunes: Plantago maritima, Glaux maritima, Triglochin palustris, here present are almost completely wanting in this community where it extends along polder dikes; here a facies of the very halophilous Obione portulacoides is found, succeeded by Artemisietum maritimae. Elsewhere the subassociation is succeeded by Armerieto-Festucetum.

Both subassociations are mostly daily submerged, but only for a short time ("ducking"). The Puccinellietum maritimae typicum is marked by lower minima of salt content in the soil, compared with Salicornieto-Spartinetum (5–9 g Cl at varying depths). The maxima in the uppermost soil layer are higher, but the normal amount is lower. In the soil of Puccinellietum maritimae pholiuretosum, however, precipitation can throw back the salt content to 0 (quickly percolated sand!), but the daily chloride maximum attains almost to that of the former subassociation. The soil of the P. m. pholiuretosum is far more aerated; FeS is rarely found. This community is succeeded by Junceto-Caricetum extensae (see below).

On foot-tracks, cattle walks, open spaces (e.g. where sods have been cut off) on the saltings, etc. another association establishes: Puccinellietum distantis, of which open community Puccinellia distans, P. retroflexa and Spergularia salina var. genuina are characteristic (in Zealand also Puccinellia fasciculata and P. rupestris). This association is synecologically interesting by the very high chloride content in the uppermost soil zone, attained in the dry months of April and May, the germinating period of most halophytes.

A third association of the low salt marsh is the Artemisietum maritimae, characterized by the combination of the three species Obione portulacoides, Limonium vulgare and Artemisia maritima. It is a rather southern-atlantic Salicornion, only submerged by spring tide and gale flood. It needs a clayey soil; although the salt content of the substratum fluctuates considerably, the fine silt holds NaCl long enough to enable pronounced halophytes to stay and to dominate. The optimal conditions of the community are realised on the heavy clayey salt marshes along the southern estuaries of the country. On the sandy "Wadden" coasts Artemisietum is a transient stage; it is well-developed only

on the most clayey salt-marsh along the dikes in the centre of the "Wadden-coasts" of the islands.

b. The higher salt marsh communities or "saltings": Armerion maritimae

The best known and most common association of Armerion is Armerieto-Festucetum, a very closed and homogeneous grassmat in which the dominants Festuca rubra var. litoralis and Juncus gerardi are closely intermingled; Glaux maritima and (at least on Terschelling) Agrostis stolonifera var. salina have a maximal frequency alike, but dominate rarely. The pink flowers of Armeria maritima are more sparsely spaced; together with Cochlearia anglica this species is characteristic of the association. The community has been pastured nearly everywhere, often for centuries. It avoids a constantly wet soil, in which the roots of Armeria rapidly decay; on such soil (if brackish) it is replaced by Junceto-Caricetum extensae. It most cases the soil is rather sandy and it may already bear a considerable humus turf. According to the less frequent submersions, the chloride content of the soil is much smaller than it is the case in Puccinellietum maritimae. The less extreme habitat allows some salt tolerant glycophytes to thrive (e.g. Potentilla anserina). So the conditions for insect life, too, differ much from those in the previous stages; e.g. in Armerieto-Festucetum nests of ants (*Lasius niger* L. and *L. flavus* de G.) are not uncommon: in Puccinellio-Salicornion they have never been observed. Other insects of interest are: *Nemotelus notatus* Zett., *Nemotelus uliginosus* L., *Syntormon pallipes* F., *Hercostomus nigripennis* Fall., *Dolichopus plumipes* Scop., *Limnophora aerea* Fall. (Dipt.), *Phaedon armoraciae* L. (Col.), *Chiloxanthus pilosus* Fall..

In sand halosere Armerieto-Festucetum is found in a variant with Carex distans, differentiated moreover by Pholiurus filiformis and Euphrasia litoralis.

The most important community of sand halosere is a second association of the Armerion, Junceto-Caricetum extensae, characterized by Carex extensa and locally (in the "Wadden-district") moreover by Blysmus rufus and Euphrasia litoralis. Its optimal development is found on the Boschplaat (Terschelling), where it covers large stretches, mostly in extensive circles (diameter up to several hundred metres) surrounding dune islands or creek systems. The dominant Carex extensa has as large a dynamic power as Schoenus nigricans or Molinia coerulea; the young plants, sparsely spaced in the initial phase (arising out of Puccinellietum maritimae pholiuretosum), close in the course of 3–5 years to an entire dominance, forming tussocks which retain shifting sand and on which salt tolerant glycophytes like Thrincia hirta and Carex serotina can establish themselves, as also may many insects (e.g. ants). Together with codominants like Juncus gerardi and Festuca rubra var. litoralis, Carex extensa builds up a definite humus zone, thus preparing the succession from halosere to hygrosere.

Junceto-Caricetum extensae falls into two subassociations with several distinct phases. The first of them, Junceto-Caricetum extensae pholiuretosum, grows on large flat sands, where the tide can enter and recede freely. In summer

it is only submerged by high tides which are swept by strong wind; in winter it is more often inundated. The habitat is mostly brackish, but the fluctuations are still considerable: chloride content varies from 2 to 9 g per l. The upper soil zone is generally rather moist, sometimes dry. Differential species are: Pholiurus filiformis, Carex distans, Armeria maritima.

The second subassociation, Junceto-Caricetum extensae blysmetosum, is limited to a wetter and more desalinated habitat, mainly in beginning dune valleys on the margin area of submerged silty sand shallows. In these rain water is accumulated; the soil is water-logged except for dry spring. This community is marked by the differential species Blysmus rufus, Eleocharis uniglumis var. pumila, Phragmites communis and Juncus anceps var. atricapillus, moreover by the installation of a number of glycophytes, e.g. Schoenus nigricans and Parnassia palustris.

Where the vegetation is not pastured, the association is mostly succeeded by Schoenetum nigricantis metuonense (see § 4). On brackish silty-sandy pastures, however, Carex extensa is hardly able to thrive and Schoenetum is entirely kept down. Here a rather homogeneous, entirely closed turfy grassmat occurs, staying for decennia and resembling Junceto-Caricetum extensae blysmetosum, but lacking Carex extensa. Agrostis stolonifera var. salina is dominant, Trifolium fragiferum var. pulchellum is codominant; the combination of those species with Blysmus rufus and Eleocharis uniglumis var. pumila is characteristic of this "stage with Trifolium fragiferum var. pulchellum" with its cold, wet, peaty soil.

The halosere of inland saltmarsh (i.e. saltings at the inner side of the sea dikes), which is situated mostly on heavy clay, presents a somewhat different terminal stage: a community of dominant Juncus gerardi with Alopecurus bulbosus (e.g. Waalenburg, island of Texel).

This discussion of halosere may be finished by briefly comparing the communities considered with the vegetation in the S.W. estuary region. In the latter territory the communities of Puccinellio-Salicornion have been overgrown to a considerable amount by the neophyte Spartina maritima ssp. glabra, which has superseded the indigenous ssp. stricta, originally a common characteristic species of the Salicornieto-Spartinetum: a striking case of "introgressive hybridization" (ssp. glabra is considered a hybrid). Contrary to the situation in the North, in the South Limonium vulgare is an abundant species in Puccinellietum maritimae, colouring large stretches of the latter with its violet flowers. The large tidal range brings about the penetration of deep creeks throughout the salt marsh; they are bounded by low banks, overgrown with a closed sociation of Obione portulacoides and Bostrychia scorpioides, which is almost wanting any other species. Artemisietum maritimae is well-developed, but Armerieto-Festucetum is rather scarce on account of the clayey soil; Junceto-Caricetum extensae has never been observed, but the stage with Trifolium fragiferum does occur, at least at the inland side of the sea dikes; e.g. on the island of Schouwen (Westenschouwense Inlagen). In the latter case the halosere is

terminated by a community of Orchis morio, Ophioglossum vulgatum and Briza media. Outside of the dikes, a conspicuous community of the tall Juncus maritimus, together with Oenanthe lachenalii, Glaux maritima, Juncus gerardi, Potentilla anserina, Bupleurum tenuissimum and Triticum litorale, may be considered the desalinating stage of Armerion and the end of halosere in this region (e.g. Oosterschelde near Bergen op Zoom).

IV. SEA DUNES

a. Introduction and generalities

Taken as a whole, the sea dune landscape of the Netherlands may be considered the most extended and the best developed dune area of Europe. Its importance is increased by its differentiation. It may be divided into a region in the Northern part of the country, including the West-Frisian islands and corresponding with the type of dune area up to Denmark, where the dune sand is poor in lime (content of $CO_3 < \pm 1\%$, mostly $< \pm 0{,}2\%$), and a region in the Southern part of the country, including the estuary islands of Rhine, Meuse and Scheldt and comparable to the Flemish and French dunes, where the dune sand is rich in lime (content of $CO_3 \pm 3 - \pm 20\%$). It is not the place here to discuss the cause of this difference. It may be sufficient to comment: 1. that the relatively high lime content is correlated with a high content in iron salts, inducing the sand to cohere more firmly and to present a more yellow colour than the loose, white sand poor in CO_3 and in iron; 2. that the border zone between the two areas is rather small, extending over about 2 km, and that it is situated near the village of Bergen (near to the town of Alkmaar), some miles south of the dunes of Schoorl, which will be visited by the Congress; 3. that the differences mentioned present such a great difference in habitat, that these two dune areas are considered two plant geographical "districts": the Dune District being the southern, the Wadden District the northern one.

There are, however, several other aspects of habitat variation within the dune area. We may mention three of them:

1. The climate gradient from S. to N. (see p. 9). Important factors in it seem to be: a. the limiting extreme factor of the number of ice days and frost days and of the period between first and last of these days in winter: these numbers increase rapidly from S. to N. and may limit the area of such mediterranean-atlantic species as Euphorbia paralias, Tuberaria guttata and Catapodium loliaceum.

2. The variation in age and in the initial causes for the development of the dunes. E.g.: the young and therefore low dunes of the island of Voorne were built up from a marine estuary and therefore are marked by a relatively high salt content, which has influenced flora, vegetation and fauna.

3. The situation of the water in the dunes. Up to about a century ago dune ranges alternated with more or less extended wet dune valleys. The latter presented an oscillating phreatic level, but most of them were submerged in

winter; their flora, vegetation and fauna formed a very interesting hygrosere. In present times, nearly all the dune valleys of the continent and many of them on the islands have run dry by several causes (water extraction by water companies, afforestation of the dunes, drainage by agricultural management at the inner boundaries of the dune area, etc.). A well-developed hygrosere still can be studied only on the islands of Voorne, Texel and Terschelling; none of them will be visited during the excursions, however. A fragmentary hygrosere has remained on the islands of Schouwen, Vlieland, Ameland and Schiermonnikoog, in the nature reserve "De Beer" near Hook of Holland, and in the most northern continental dunes of Holland (between Bergen and Helder).

The dunes of the Dune District and the Wadden District have in common especially two categories of habitats, therefore two assemblages of plant and animal species and biotic communities:

1. The plant and communities of the coastal range, where the influence of the factor "wind" predominates over that of the factor "lime". Young dunes are built up here by the grass Agropyron junceum, constituting the Agropyretum boreo-atlanticum together with Honckenya peploides and summer therophytes like Cakile maritima. Here we may encounter the following insect species: *Chersodromia arenaria* Fall. (Dipt.), *Aegialia arenaria* F. (Col.), *Cicindela maritima* Latr. (Col.). The "embryonal" dunes attain a height of about 1–3 m (dependent on the tidal range); as soon as a reservoir of fresh water forms itself in the dunes, the marram grass, Ammophila arenaria, establishes itself and it soon tends to dominate, forming the association Elymeto-Ammophiletum. Among the 12 characteristic plant taxa of the latter, Elymus arenarius, Eryngium maritimum, Calystegia soldanella, Sonchus arvensis var. maritimus may be mentioned. Both communities need a considerable supply of shifting sea sand by the wind, this sand containing the mineral nutrients necessary for the plants: the latter being autotrophic, contrary to the later succession stages, in which the plants are heterotrophic (mycorrhiza symbionts) for the greater part, thriving indirectly on the humus. The following insects are typical for this plant community: *Meromyza pratorum* Mg., *Tetanops myopina* Fall., *Chortophila angustifrons* Mg., *Chortophila albula* Fall., *Dexiopsis lacteipennis* Zett., *Rhicnoessa grisea* Fall. (Dipt.), *Demetrias monistigma* Sam., *Dromius linearis* Ol. (Col.), *Trigonotylus psammaecolor* Reut. (Heteropt.), *Arenostola elymi* Tr., *Leucania litoralis* Curtus (Lep.), *Liodes ciliaris* Schmidt., *Liodes furva* Er. (Col.).

2. The plant communities of the young wet dune valleys with more or less calcareous soil water. They are manifold; only some of them may be mentioned here. In shallow, oligohalinic to almost oligohalinic water with fluctuating level (in summer the floor can run dry for several weeks or even months) the Samoleto-Littorelletum is found, characterized by dominance of Littorella uniflora together with the occurrence of Echinodorus ranunculoides, Batrachium salinum, Carex trinervis, Samolus valerandi etc. It is photophilous and may soon be replaced by a reed community, a consociation of Phragmites communis above Mentha aquatica and Hydrocotyle vulgaris. Moist, but not or only

temporarily submerged bare dune soil may be occupied by Centaurium vulgare, Sagina nodosa var. moniliformis, Bryum pendulovatum, etc. This community is named Centaurieto-Saginetum; here *Cicindela trisignata* Latr. (Col.) occurs but only south of the Hook of Holland. In this rather ephemeral community taller plants tend to establish themselves, at first Parnassia palustris, Juncus anceps, Lythrum salicaria etc. The latter ones present the initial stage of the Schoenetum nigricantis metuonense, the most interesting association of the wet dune valleys, turning the young haloid soil into a geloid one by building a 2–10 cm deep horizon of black sand containing a considerable amount of mild humus with a crumb structure. The black sedge Schoenus nigricans is dominant in this community and it is characteristic of it, together with some orchids (Liparis loeselii, Orchis incarnata, Epipactis palustris) and Equisetum variegatum. Salix repens is often codominant and Hippophae rhamnoides soon may enter. The following Diptera may be found here: *Lasiops semicinereus* Wied., *Herina palustris* Mg., *Herina Frondescentiae* L.

In several cases, Schoenus nigricans is absent. The habitat where it might be expected is sometimes occupied, then, by the community Acrocladieto-Salicetum (named after Salix repens and the moss Acrocladium cuspidatum), much resembling Schoenetum as for its specific assemblage, but marked e.g. by Gentiana uliginosa. This community is mentioned here because it is frequently found on the island of Ameland.

In present times, the hygrosere of the dune valleys can be studied especially in the "Wadden District", the dune area there being not so much drained as that of the "Dune District". In the latter only the dunes of the southern estuary islands (e.g. Voorne) present some well-developed hygrosere. Generally Schoenetum nigricantis is replaced here by a vicariant closely allied to it, described as "association of Carex trinervis and Drepanocladus aduncus" for the Belgian coast (Duvigneaud 1947). Some characteristic species to be found in this southern community are Blysmus compressus and (locally) Herminium monorchis. The latter species however, a rare orchid, presents a sudden optimum on the island of Schiermonnikoog, the most outlying N.E. part of the Netherlands. This disjunct area may be explained by the fact, that the dunes of Schiermonnikoog are the most calcareous ones of the "Wadden district".

For the reasons mentioned above, the xerosere will be pursued here for the Dune District and the Wadden District separately, but the further course of the hygrosere will be dealt with respect tot he latter district only.

b. Dune District (calcareous dunes)

The marram grass community of the coastal range (Elymeto-Ammophiletum) is soon invaded by the spiny shrub Hippophae rhamnoides, building up a veritable "macchia" (a nearly impenetrable thicket often to more than a man's height), which covers large areas. Taken as a plant community, this scrub is named Hippophaeto-Ligustretum. Its initial stage on sand poor in humus and relatively rich in nitrates is marked by Sambucus nigra and by a number of

photophilous, mostly annual herbs such as Stellaria media, Taraxacum sect. Erythrosperma and Cardamine hirsuta; however, some more characteristic species like Cynoglossum officinale are already found in it. Interesting insects are: *Psylla hippophaes* Foerster (Hem.), *Polyphylla fullo* F. (Col.). This stage ends by the entering of a number of shrubs, a.o. Rosa eglanteria, Ligustrum vulgare, Crataegus monogyna and later on Berberis vulgaris and Rhamnus cathartica, accompanied by an undergrowth poor in individuals but rich in species; we only mention Inula conyza, Asparagus officinalis, Polygonatum odoratum, Lithospermum officinale, Viola hirta, and, besides, lianes like Bryonia dioica and Solanum dulcamara var. litorale. This stage is known as Hippophaeto-Ligustretum asparagetosum. The final stage, Hippophaeto-Ligustretum betuletosum, is a low birch wood, much more open than the previous scrub, and sometimes dominated by Berberis vulgaris; also Quercus robur may enter and even dominate in it. It presents a remarkable soil horizon of mild humus and a number of species from rich wood soil, such as Listera ovata, Fragaria vesca and Ajuga reptans.

Not all the dunes within the coastal range are covered by this scrub or wood community, however. Large stretches are covered with dune grassland, which is due mainly to the action of rabbits, sheep, goat, wood burning, influences reinforced by the action of wind and by draining (trees often die when the phreatic level changes considerably). A common pioneer community is the Tortuleto-Phleetum, rich in tiny winter therophytes and in xerophytic mosses, and named after the characteristic species Tortula ruralis var. arenicola and Phleum arenarium. Among the other characteristic plants Saxifraga tridactylites and Silene conica may be mentioned; Sedum acre, Koeleria albescens, Carex arenaria and Ononis repens are some of the constant perennial species. The association has a small ecological amplitude (microclimate with high temperature of the superficial soil-layers and the lowest layer of air, especially in winter and in spring; hardly shifting, loose sand containing at least 0.2 % $CaCO_3$), but under favourable conditions it may flourish for a number of years on the same spot. In most cases, however, it is more rapidly succeeded by a more closed vegetation or by an open community of decalcified soil. On sufficiently calcareous dune soil (lime content $\pm$ 2 %) this vegetation, very rich in species, is known as Anthyllideto-Silenetum, named after Anthyllis vulneraria ssp. maritima and Silene otitis (alliance of Bromion erecti); this association presents a rather strong variation according to minor differences in habitat. In the dunes N. of Haarlem and along the Flemish (Belgian) coast Rosa spinosissima is dominant, but it does not occur elsewhere; in the most calcareous dunes (between the Hague and Haarlem) Ligustrum vulgare has a great importance. Characteristic species with a large distribution are a.o. Arabis hirsuta, Orobanche vulgaris, Thalictrum minus ssp. dunense and Satureia acinos; among the constant companion species we mention Rubus caesius, Galium mollugo, G. verum. Interesting species confined to the environment of Haarlem are the orchid Anacamptis pyramidalis and Sanguisorba minor.

On Northern slopes (cool microclimate, more humus), this community presents a variant rich in Salix repens, Polypodium vulgare, Pyrola rotundifolia and many mosses, developing into a special form of Hippophaeto-Ligustretum.

Where the lime content of the soil is lower, a somewhat more acidophilous grassmat is found: Festuceto-Galietum maritimi, named after Festuca ovina and Galium verum var. maritimum. In the Dune District it is developed as a subassociation rich in Koeleria albescens and Rosa spinosissima (F.-G. koelerietosum). Among the Lepidoptera, *Colostygia multistrigaria* Hw. is an interesting species of this association. The community has a number of interesting mostly basiphilous species in common with the Anthyllideto-Silenetum; from those not yet mentioned we choose Botrychium lunaria, Viola rupestris var. arenaria and Carlina vulgaris.

c. Wadden District (dunes poor in lime)

In the Wadden District a tendency for shrub vegetation to develop can be observed, but much more feebly than in the Dune District. Hippophae rhamnoides, distinctly calciphilous, establishes itself less rapidly, attains to a lower vitality and a smaller size (max. 0.5–1.5 m, depending on the degree of lime of the soil) and decays sooner. For this reason, as well as through the much looser coherence of the (therefore longer shifting) sand and by climatic influences the Elymeto-Ammophiletum in this district presents a larger expansion and a differentiation between the wind-exposed weather side of the coastal dune range (Elymeto-Ammophiletum typicum) and the more wind-protected, inner lee side of it: Elymeto-Ammophiletum festucetosum. In the latter community, differentiated by Eryngium maritimum and Calystegia soldanella (which in the Dune District cover the whole amplitude of the Elymeto-Ammophiletum) and further by Festuca rubra, Hieracium umbellatum and Oenothera muricata var. ammophila etc., the microclimate is milder, the sand less shifting; content of nitrates being a limiting factor, mycorrhiza species are yet appearing (e.g. Festuca rubra). The structure is more developed and the insect fauna, too, differs distinctly from that in the pioneer community. Characteristic insects are: *Sciopus maritimus* Lichtw., *Dorylas mimimum* Beck., *Chersodromia arenaria* Fall., *Dexiopsis littoralis* Zett. (Dipt.), *Phylan gibbus* F. (Col.).

In Elymeto-Ammophilatum festucetosum, Hippophae rhamnoides and Salix repens may enter, closing up to a dwarf shrub community, which has been described as "Hippophaeto-Salicetum", but which, presenting no characteristic species, is better considered "a stage with Polypodium and Hippophae". On the relatively more calcareous dune soil of the island of Texel this stage shows some affinity to the Hippophaeto-Ligustretum of the Dune District; elsewhere, this resemblance is not obvious. The stage often attains an age of no more than 20 years. When the soil decalcifies to below the minimal tolerance point for Hippophae, the latter dies. On slopes with N-exposure, in the greater part of the "Wadden district", it is succeeded by dominant Empetrum nigrum, which remains accompanied by Polypodium vulgare; humus horizon and moss layer

get thicker resp. denser, pH diminishes: the new community is named Polypodieto-Empetretum and shows a certain affinity to the Scandinavian dwarf shrub communities. (However, in the more calcareous dunes of the islands of Ameland and Schiermonnikoog this development is less clearly pronounced, Empetrum nigra being very rare here). On slopes with S-exposure, in the contrary, a regression takes place: the dying Hippophae shrub stage is replaced by an open community of a much simpler structure, adapted to extreme microclimate: the Violeto-Corynephoretum dunense, a vicariant of the inland Corynephoretum dealt with in § 2. It is marked by Corynephorus canescens, Viola canina var. dunensis, Teesdalia nudicaulis and an often dominant layer of lichens. Important Diptera of this plant community are: *Geomyza apilcalis* Mg., *Meromyza pratorum* Mg., *Meromyza saltatrix* L., *Noesta pupillata* Fall., *Trichoscelis obscurella* Fall.

In the Wadden District the stage of Hippophae is wanting rather often. In such cases Elymeto-Ammophiletum is replaced by a relatively acidophilous subassociation of Tortuleto-Phleetum (T.–P. jasionetosum) without Saxifraga tridactylites and often without Koeleria albescens; in its turn this community is replaced again by Violeto-Corynephoretum.

Pastured dry dune slopes, especially in regions with somewhat more coherent sand, often do not bear Violeto-Corynephoretum, but Festuceto-Galietum in an acidophilous subassociation, the F.–G. agrostidetosum. It is found on large stretches on the islands of Texel, Vlieland and Ameland, but it is relatively scarce in the dunes poorest in lime, viz. those near Schoorl and those on the island of Terschelling. The contact zone between this Festuceto-Galietum and the communities of the older hygrosere is marked by Empetrum nigrum, Orchis morio, Botrychium lunaria and Gentiana campestris ssp. baltica.

In the hygrosere of the Wadden District, Schoenetum and Acrocladieto-Salicetum (see A) do not stay for a longer time than a few decennia. Decalcification of the soil together with supply of shifting sand on it (causing the habitat to run drier) lead to a dominance of Calamagrostis epigeios, in some cases (acid dune valleys far from the sea) together with Molinia coerulea; nearly always accompanied by Ophioglossum vulgatum, being characteristic of this community. In the course of time this stage is succeeded by a community marked by Pyrola rotundifolia and named Pyroleto-Salicetum; the latter may also be the direct succession stage of Schoenetum and of Acrocladieto-Salicetum. On the islands of Texel, Vlieland and Terschelling, Empetrum nigrum is the dominant dwarf shrub in this community, but this is not the case on the islands of Ameland and Schiermonnikoog, with more calcareous dune sand.

Both xero- and hygroseres may submerge in a mesophilous dune heath vegetation, the Calluneto-Genistetum litoralis with Calluna vulgaris, Genista anglica, G. tinctoria, Hieracium umbellatum etc. Like Pyroleto-Salicetum and Polydieto-Empetretum this association contains a certain number of boreal elements, as well among plants (Arctostaphylos uva-ursi, Juniperus communis "var. nana", Vaccinium uliginosum, V. vitis-idaea) as among insects (e.g.

Formica exsecta Nyl. and *F. pressilabris* Nyl.). This dune heath seems to have the character of a local climax, but it is not one. It is only permanent under the influence of man (burning, grazing and cutting of sods); otherwise it is succeeded by regression stages, in some favourable cases by a low open forest or savanna of Betula pubescens or Populus tremula. Cutting of sods in moist heath habitat leads to a temporary Empetro-Ericetum with Erica tetralix, Gentiana pneumonanthe, Platanthera bifolia, Orchis maculata etc., succeeded again by Calluneto-Genistetum.

The wettest spots of the dune valleys, nearly all the year submerged, become finally settled by an acidophilous dune fen community, Caricetum trinervis-fuscae, vicarious with the inland Caricetum canescentis-fuscae (see § 1). Here, too, a tendance to wood growth can be observed: Salix cinerea, S. aurita, on the island of Terschelling and near Schoorl also Myrica gale.

V. WOODLANDS

a. Introduction

The Netherlands are with two exceptions, the country of Europe which is poorest in forests: only 8 % of their surface is occupied by woodland. By far the greater part of these woods are, moreover, artificial plantations of exotes, mostly Pinus silvestris, Larix leptolepis, Pseudotsuga taxifolia and Quercus borealis var. maxima. These "crop woods" constitute no separate plant communities; their undergrowth corresponds to that of the respective deciduous natural woodlands peculiar to each habitat. Left to their own development, such artificial forests gradually change into more natural types of deciduous woodland. Only the latter will be dealt with here. Many of them have been planted too; the greater part, however, on the sites of old woodlands. A plantation of the natural indigenous trees on their own soil will in course of time assume most of the characters of a natural wood, e.g. as to the floristic composition of the shrub- and herblayers and as to the fauna. There are also some non-indigenous trees which do not spoil the character of the wood in which they are planted; they will be mentioned below. On the other hand, some indigenous trees may exercise a very unfavourable influence both on soil and vegetation of the wood, if they are planted in dominance on a soil not suited to them; the best example is Fagus silvatica.

The native woodlands may be divided into two categories in two different ways: firstly, according to the height of the phreatic water, viz. whether or not the latter attains – constantly or periodically – the rhizosphere; secondly with respect to the content of nutrients of the soil. From a pedological viewpoint, the first difference is the more important one; as regards the difference in vegetation, however, the chemical composition of the soil is the master factor. In this outline the usual ecological method is followed, starting from the variation in vegetation itself, which brings about, in this case, a classification based upon chemical variance.

b. Woodlands on rich soils

The rich soils of the Netherlands are most of the clay soils (river clay and marine clay), the residual soils of Senonian limestones (only in Southern Limburg), the loess-loam soils, and some sandy and peaty soils, especially those which are influenced by rich subsoil water (loamy brook soils, some moist sandy soils etc.). All these soils having a high agricultural value, only a small part of them is still occupied with woodland; these forests, generally very small, are scattered throughout the country. Although most of them have been more or less degraded and vitiated, owing to their small size, there have been left enough of them to get an idea of their natural character. On the whole, they constitute an association named Querceto-Carpinetum, which is widely spread in Europe from England to Russia and from Denmark to N.-Italy and the Balkans, presenting a clear geographic variation. The dominant tree is, in the most cases, Quercus robur; the hornbeam, Carpinus betulus, is often subdominant: in the Netherlands it is indigenous only in the Eastern and Southeastern part of the country. Other trees occurring in this community are Fraxinus excelsior (especially on humid soil, on wet soil sometimes dominant), Prunus avium, Acer pseudoplatanus, Taxus baccata, Tilia cordata and Fagus silvatica, in wet places also Alnus glutinosa. A number of trees often planted in this community are not native ones: e.g. Populus div. spp., Aesculus hippocastanum, Tilia platyphyllos, Acer platanoides; but they have no adverse influence on it, not even when they are dominant. Plantation of most conifers and of Quercus borealis on the contrary causes this wood to degenerate. So does Fagus silvatica, if dominant, except in the subassociation Querceto-Carpinetum asperuletosum.

The shrub-layer of the Querceto-Carpinetum is rich in species; we mention Corylus avellana, Crataegus monogyna, C. oxyacantha, Evonymus europaeus, Cornus sanguinea, Rhamnus cathartica, Rosa canina, Prunus spinosa, Acer campestre, Malus silvestris.

The floristic composition of the herb layer is very complex. It numbers more than a hundred species, which appear in several seasonal aspects or periods. Among the most common and often frequent species we mention: in the vernal aspect Anemone nemorosa, Corydalis solida, Ficaria verna, Adoxa moschatellina, Veronica hederifolia (all of them dying back in summer except for their subterranean parts); in the early flowering aspect (plants remaining green in summer): Primula elatior, Geum urbanum, Poa nemoralis, Stachys silvaticus, Polygonatum multiflorum; in the later flowering aspect: Scrophularia nodosa, Festuca gigantea, Circaea lutetiana, Brachypodium silvaticum; and from the species remaining green in winter too: Oxalis acetosella, Viola riviniana, Lamium galeobdolon, Stellaria holostea, Glechoma hederacea, Milium effusum.

For lepidopterists the occurrence of *Asthena anseraria* N.S. in this association is of importance.

In the Netherlands at least seven subassociations of Querceto-Carpinetum can be distinguished, each of them characteristic of a special habitat. They fall

into a more "dry" group on soils where the roots are not reached by subsoil water, and a more "wet" group on humid or wet soils. One of the "dry" subassociations, Querceto-Carpinetum orchidetosum (with Clematis vitalba, Orchis mascula, O. purpurea etc.) is limited to the residual limestone soil in Southern Limburg; the other communities of this group are the Querceto-Carpinetum typicum, mainly on loess-loam soil, and the more acidophilous Querceto-Carpinetum stellarietosum, occurring on loess-loam soil which is leached out and on brown forest soils on not too poor pleistocene sands (e.g. sandy push moraines complex, at least in some cases).

The "wet" subassociations of Querceto-Carpinetum are distinguished by hygrophilous differential species such as Urtica dioica, Athyrium filix-femina, Impatiens noli-tangere and Ribes uva-crispa. The most widely spread community of them is the Querceto-Carpinetum stachyetosum, mainly occurring on loamy brook soils. In the Western, holocene part of the country, mainly on calcareous river levée soils, it is developed in a special variant, conspicuous by the dominance of Anthriscus silvestris (Umbelliferae). Moister spots, where in winter phreatic water attains the top soil or submerges it, bear the Querceto-Carpinetum filipenduletosum, distinguished by Alnus glutinosa, Filipendula ulmaria, Humulus lupulus etc. Moist loamy soils, especially on slopes, may be occupied by the Querceto-Carpinetum asperuletosum, which, however, also requires more continental climate, being nearly confined to the Cretaceous and the Subcentral European Districts. Among the insect species, *Penthesilea berberina* F., *ranunculi* Panz., *Brachypalpus vulgus* Panz., *Hydrotaea ciliata* F., *Hydrotaea palaestrica* Mg. (Dipt.), *Psallus variabilis* Fall., *quercus* Kbm., *varians* H.S., *Orthothylus senellus* Fall. (Heteropt.) may be found here.

On wet rich sandy or peaty soils continuously saturated with water, Querceto-Carpinetum is no more able to thrive. It is replaced here by the Alnetum glutinosae, which has been dealt with in § 1. The interesting wood communities of "spring soils", where the subsoil water wells up and is running through and over the top soil, cannot be considered here. It is, however, necessary to say some words relating to the woods of the river foreland clay soils, especially those in the estuary region of the tidal rivers, the Biesbosch, which will be visited by an excursion during the Congress. Here we have to do with the almost unique case of a fresh water "tidal delta" which is still "alive" and which has not yet been wholly reclaimed. The forests of this landscape are periodically submerged by high tide. They consist of Salix species (mostly S. fragilis, S. purpurea, S. alba, S. triandra and S. dasyclados) and Populus species, of which P. nigra is a native tree. Alnus glutinosa is almost completely wanting, except for some planted trees. These forests are most remarkable for the luxurious undergrowth of giant plants: e.g. Angelica silvestris attaining to 3 m, Caltha palustris and Ranunculus repens to 1 m high! The community has been described as Saliceto-Populetum and it may be designed to the "river wood alliance" of Alneto-Ulmion. Characteristic non-woody species of it are Angelica archangelica (attaining a height of 4 m), Rumex obtusifolius var. sil-

vester, Cardamine amara. Several subassociations can be distinguished, according to the situation with respect to the submerging water (top of river bank, slope of it, river basin). The river basin wood is marked by the occurrence of supraterranean roots ("air roots") of the different Salix species, which may be considered an adaptation to the sticky anaerobic substrate of silt and organic ooze (cf. tropical tidal forests). It is probable that a great part of the ancient heavy woods of the holocene Netherlands has belonged to this type, together with the Querceto-Carpinetum filipenduletosum. The rich woodland of the calcareous dunes has been dealt with in § 4.

c. Woodlands on poor ('sour') soils

It is a wide-spread, but nevertheless a false conception, that the rich woodlands of the previous group thrive on alkaline to subneutral soils, whereas only the poor forest soils would show a stronger acidity. It must not be supposed that because a soil is distinctly acid in reaction it is necessarily poor in basic ions. It has been shown that many of the loam soils of the "dry" subassociations of the Querceto-Carpinetum are decidedly acid – pH value between 4 and 6 –, although they may have a high "base status", being rich in calcium ions adsorbed by the colloids of the weathering complex. The same is true for Querceto-Carpinetum asperuletosum. Only the wet alluvial deposits on which Querceto-Carpinetum filipenduletosum is thriving, present a pH value of between 6 and 7. The humus of all these woods is known as mull (mild humus). Its turnover is quick because of the favourable conditions for the activity of the soil organisms. This fact has a major influence on the specific composition of the insect fauna of the litter.

On the other hand there are woods with extremely acid soils, with pH values mostly between 3 and 4, in the more favourable cases up to 5. These soils, called "sour" by agriculturists, are in fact very poor in bases. The slow decaying raw humus of such forests is known as "mor"; it offers quite another habitat for the insect fauna of the litter and the top soil horizon.

The bulk of the forests of these really poor soils is formed by the association of Querceto-Betuletum, named after Quercus robur, Q. petraea (= Q. sessiliflora) and Betula alba. The latter species can be split up into Betula pendula (= B. verrucosa), preferring dry habitat, and B. pubescens, more common on moist and wet soil. The association is not so wide-spread as the Querceto-Carpinetum is; it presents an atlantic and subatlantic distribution, from England to Switzerland and from Denmark to Belgium; in France it is replaced by vicarious communities closely allied to it. Compared with Querceto-Carpinetum it is rather poor in species. Among the characteristic plants we name Quercus sessiliflora, Pteridium aquilinum, Teucrium scorodonia, Holcus mollis, Majanthemum bifolium, Melampyrum pratense, Hieracium umbellatum, Vaccinium myrtillus and V. vitis-idaea. The grass Deschampsia flexuosa, often dominant and hardly ever absent, is a differential species with respect to Querceto-Carpinetum, but it is equally found in the heaths (see § 2). Among the shrubs and lianes Populus tremula, Sorbus aucuparia, Frangula alnus and Lonicera periclymenum

are of interest; introduced shrubs, often run wild in masses, are Amelanchier laevis and Prunus serotina. The moss layer, often dominant, is much more developed than it is the case in Querceto-Carpinetum, at least in quantitative respect.

In far the most cases the shrub-layer of this community is coppiced; a few standard oak trees only may be present, but a close canopy of it is very rare, except for Southern Limburg.

The poverty of the soil is in many cases a primary one, but often it is caused by human influence, viz. by predatory forest culture during many centuries: grazing, pannage (acorn grazing by pigs), repeated clear felling with too short rotation, coppice-system, removal of litter. Such Querceto-Betuletum has arisen by degradation of a previous Querceto-Carpinetum stellarietosum.

Among the many insects characteristic for the Querceto-Betuletum, the following species may be mentioned: *Meconema thalassina* de G., *Ephippigera ephippigera* Fieb., *Nemobius sylvestris* Bosc. (*Orthoptera*), *Elasmucha grisea* L., *Elasmostethus interstinctus* L., *Psallus betuli* Fall., *Calocoris ochromelas* Gmel., *Acanthosoma haemorrhoidale* L. (*Hemiptera*), *Carabus catenulatus* Scop., *Rhizotrogus solstitialis* L., *Clytra quadripunctata* L., *Deporaus betulae* L., *Telephorus fuscus* L., (*Coleoptera*), *Gonepteryx rhamni* L., *Limenitis camilla* L., *Pararge aegaria* L., *Zephyrus quercus* L., *Hoplitis milhauseri* F., *Dasychira pudibunda* L., *Endromis versicolora* L., *Drepana binaria* Hufn., *Tortrix viridana* L., *Adela* sp. (*Lepidoptera*), *Laphria flava* L., *Dioctria cothurnata* Mg., *rufipes* de G., *Empis tessellata* F., *Pelecocera tricincta* Mg., *Doros conopeus* F., *Sicus ferrugineus* L. (*Diptera*), *Stenamma westwoodi* Westw., *Leptothorax nylanderi* Först., *muscorum* Nyl., *Trichiosoma lucorum* L., *Vespa crabro* L., *sylvestris* Scop., and many *Cynipids* (*Hymenoptera*).

Like woodlands in general, Querceto-Betuletum can be divided into minor units according to two viewpoints: the average height of subsoil water, and the degree of content of nutrients in the soil. Based upon the floristic differences, both subdivisions are equally justified. At first, we may consider the division into Querceto sessiliflorae-Betuletum and Querceto roboris-Betuletum. These names do not alter the fact that both Quercus species occur in both of these "subassociation-groups", although Quercus petraea has a relative optimum in the former.

Querceto sessiliflorae-Betuletum, the community of the relatively best soils, in its best developed form is marked by Mespilus germanica, Ilex aquifolium, Luzula nemorosa, Hypericum pulchrum, Solidago virgaurea etc. This form is limited to loess-loam soil and to a relatively wet climate (annual precipitation more than 750 mm); in the Netherlands it is only known from Southern Limburg, where it occupies rather large stretches. In a less typical form, however, the community is scattered throughout the plistocene parts of the country, viz. on brown forest soils, found on pre-(Riss-) glacial sands, and on the richer soils of the sandy push moraines complex. Here it can be distinguished from the Querceto roboris-Betuletum by the occurrence of Convallaria majalis, Hypericum pulchrum, Polygonatum multiflorum and some other species. On the

richest of this type transitions to Querceto-Carpinetum stellarietosum occur, marked e.g. by Anemone nemorosa and Stellaria holostea.

So far, the Querceto sessiliflorae-Betuletum has been described in its form "typicum", found on dry soils with deep subsoil water. Where subsoil water poor in nutrients attains the rhizosfere, another subassociation is developed, Querceto sessiliflorae-Betuletum molinietosum, marked by Molinia coerulea and Agrostis stolonifera; it is wanting on the Veluwe, but it can be observed on high but moist loamy-sandy soils in the Drenhte and Subcentral European districts. A third subassociation, Querceto sessiliflorae-Betuletum violetosum rivinianae, is characteristic of the thick boulderclay soil in the glacial plistocene of the Drenthe District.

The second subassociation-group, Querceto roboris-Betuletum, is found on the poorest soils of the country; grey forest soils, more or less podzolised, on stratified drift and on the poor parts of the sandy push moraines complex, sometimes on fixed shifting sands. These communities distinguish themselves from the previous group e.g. by Vaccinium vitis-idaea and the moss Leucobryum glaucum. They are by far the commonest woods of Querceto-Betuletum in the centre of the country, especially on the Veluwe, but they owe their predominance largely to degradation by man (see above). A transitional form to the Querceto sessiliflorae-Betuletum is presented by the "variant with Pteridium and Teucrium scodonia", marked by a more or less pronounced layer of the often dominant fern Pteridium aquilinum; in the poorest form of Querceto roboris-Betuletum, contrarily, Vaccinium myrtillus and Deschampsia flexuosa are the only possible dominants (except for mosses). This Pteridium variant is rather common on the Veluwe.

Querceto roboris-Betuletum, too, may occur in a "wet form" on moist sandy soils with subsoil water poor in nutrients: Querceto roboris-Betuletum molinietosum. On the Veluwe such soils, and therefore, this community, are very rare, but in the Eastern parts of the country this subassociation is much more common than Querceto-Betuletum typicum, the "dry form" of the community.

Contrary to other woodlands, Querceto roboris-Betuletum typicum (and equally the dune shrubs and dune wood dealt within § 4) is rather rich in thermophilous insect species, a feature due to its light structure and, therefore, the relatively dry and warm toplayer of its soil.

Some words may be said on geographic (climatic) differences which do not appear to advantage within the classification dealt with above. Thus the woods of the northern Querceto-Betuletum (Drenthe district) are marked by some boreal species, be it rare ones: Trientalis europaea and Cornus suecica. The boreal species Vaccinium vitis-idaea is still common in the centre of the country, but it is completely wanting in the Southern plistocene (Campine District). The Eastern Querceto-Betuletum of the Subcentral European District presents a somewhat richer floristic composition, e.g. by the occurrence of Hieracium sabaudum, Equisetum silvaticum, Genista germanica and Betonica officinalis.

The development (succession) of Querceto-Betuletum out of the heather community has been dealt with in § 2.

LITERATURE

Nearly all of the publications relating to the vegetation of the Netherlands have been written in Dutch, in general without summaries in congress languages; therefore, they have been omitted here, with one exception (nr 22), giving an account of the plant associations and subassociations of the Netherlands with their characteristic species. From the few studies written or summarized in other languages a number is mentioned below, together with some foreign publications dealing with similar vegetation types (nrs 7, 11, 15 17) and some more general resp. edaphical, geological and climatological works.

1. ADRIANI, M. J.: Sur la phytosociologie, la synécologie et le bilan d'eau de halophytes. Thesis, Amsterdam. Groningen 1945, 214 pp.
2. BRAAK, C.: The Climate of the Netherlands, Med. en Verh. Kon. Ned. Met. Instituut, nrs **32**, **39**, **41**, **43** and **46**. 's-Gravenhage, 1929–1942.
3. BRAUN BLANQUET, J.: Pflanzensoziologie. Berlin, 1928, 2nd ed.: Vienna, 1951.
4. BRAUN-BLANQUET, J. and LEEUW, W. C. DE: Vegetationsskizze von Ameland. "Nederlands Kruidkundig Archief" **46**, p. 359–393, 1936.
5. DIEREN, J. W. VAN: Organogene Dünenbildung, eine geomorphologische Analyse der Westfriesischen Insel Terschelling mit pflanzensoziologischen Methoden. Thesis, Amsterdam. The Hague 1934. 304 pp.
6. EDELMAN, C. H.: Soils of the Netherlands. Amsterdam 1950. 170 pp.
7. ELLENBERG, H.: Ueber Zusammensetzung, Standort und Stoffproduktion bodenfeuchter Eichen- und Buchenmischwaldgesellschaften Norddeutschlands. Mitt. d. flor.-soz. Arbeitsgemeinschaft in Niedersachsen, **5**, p. 1–135, 1939.
8. FABER, F. J.: Geologie van Nederland. 's-Gravenhage, 1933.
9. FABER, F. J.: Nederlandsche Landschappen. Gorinchem, 1942.
10. LABRIJN, A.: The Climate of the Netherlands during the last two and a half centuries. Med. en Verh. Kon. Ned. Met. Instituut, nr **49**, 's-Gravenhage, 1945.
11. LEBRUN, J., NOIRFALISE, A., HEINEMANN, P. and VANDENBERGHEN, C.: Les associations végétales de Belgique. Bull. de la Soc. royale de Botanique de Belgique, **8**, p. 105–207, 1949.
12. LEEUW, W. C. DE: The Netherlands as an environment for plant life. 19 pp. + 46 fig. Leiden 1935.
13. MELTZER, J.: Die Sanddorn-Liguster-Assoziation. „Nederlands Kruidkundig Archief" **51**, p. 385–395, 1941.
14. SOEST, J. VAN: see: HEUKELS-WACHTER, Schoolflora voor Nederland.
15. TANSLEY, A. G.: The British Islands and their Vegetation. 2nd edition. Cambridge 1951.
16. THORNTHWAITE, C.W.: The Climates of the Earth. The geographical Review, Vol. 33, 1933.
17. TÜXEN, R.: Die Pflanzengesellschaften Nordwestdeutschlands. Mitt. d. flor.-soz. Arbeitsgemeinschaft in Niedersachsen, **3**, p. 1–170, 1937.
18. VEEN, B.: Climatological classifications applied to the Netherlands. Med. v. d. Landbouwhogeschool te Wageningen, Nederland, 1949.

19. VLIEGER, J.: Ueber einige Waldassoziationen der Veluwe. Mitt. d. flor.-soz. Arbeitsgemeinschaft in Niedersachsen, 3, p. 193–203, 1937.
20. WESTHOFF, V.: The vegetation of dunes and salt marshes on the Dutch islands of Terschelling, Vlieland and Texel. Thesis, Utrecht. The Hague 1947, 131 pp.
21. WESTHOFF, V., and WESTHOFF–DE JONCHEERE, J. N.: Verspreiding en nestoecologie van de mieren in de Nederlandsche bosschen (Distribution and ecology of ant species in the woods of the Netherlands). With a summary in English. "Tijdschrift over Plantenziekten", Sept.–Oct. 1942, 76 pp. (Summary p. 47–49).
22. WESTHOFF, V., DIJK, J. W. v., PASSCHIER, H., and SISSINGH, G.: Overzicht der Plantengemeenschappen in Nederland. 2nd edition. Amsterdam 1946, 118 pp.

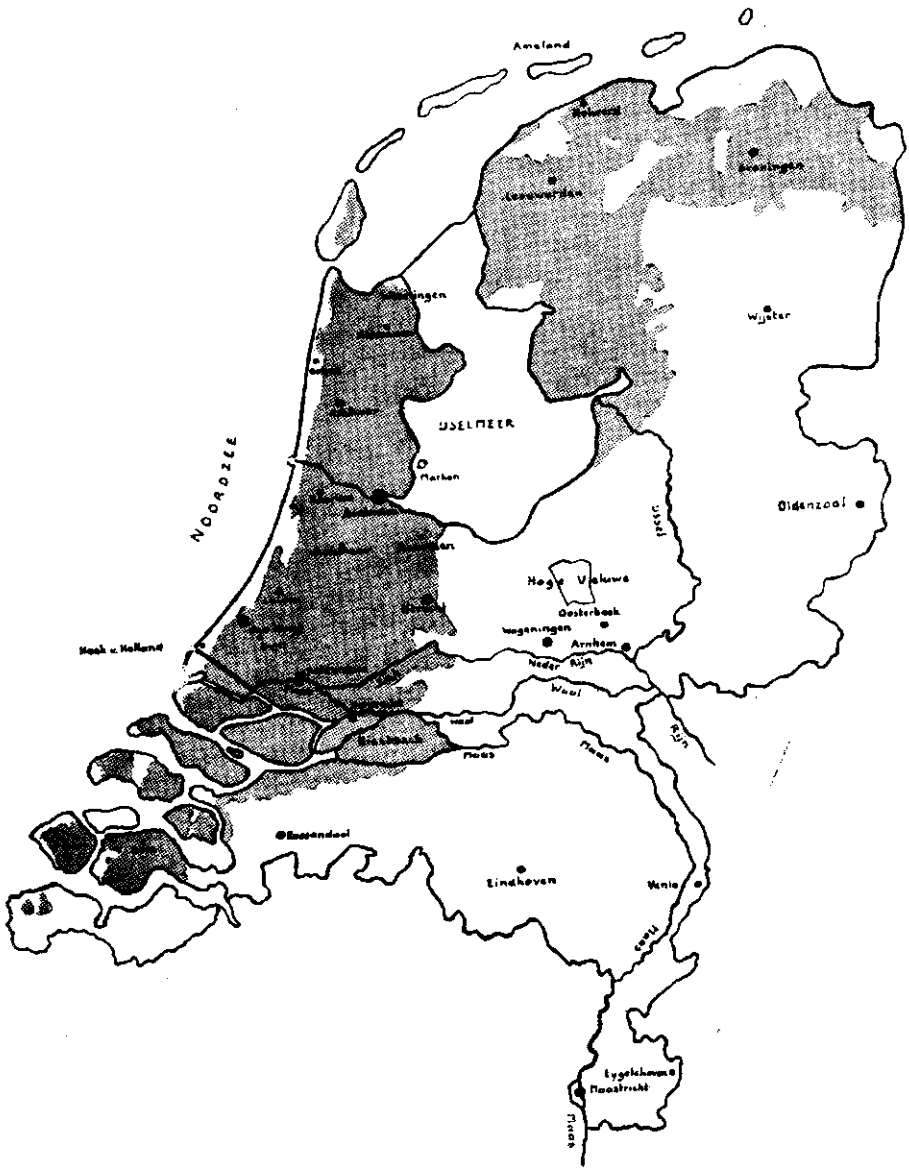


Fig. 1. The Netherlands. The regions below sea level are grey.

Fig. 2. The Netherlands without dykes. Black: inundated by sea water. Grey: Inundated by water of the great rivers. The small rivers have not been drawn. (From FABER: Geologie van Nederland)

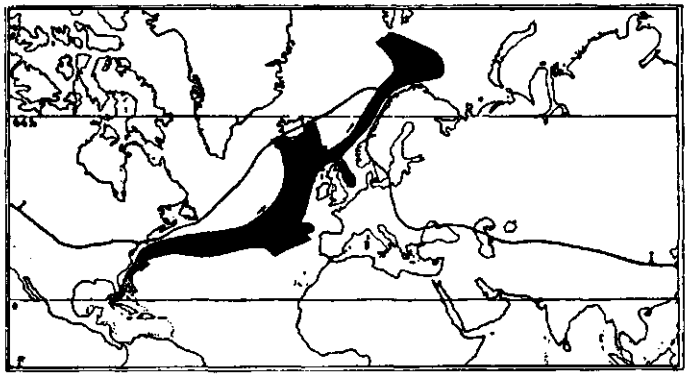


Fig. 3. The gulfstream (grey) and its influence on the January isotherm of 0° C. (from FABER: Geologie van Nederland)

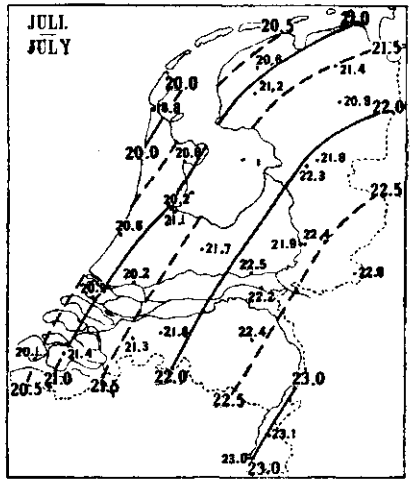


Fig. 4. Air temperature: Mean daily maximum for July. (Comm. 33 of the Royal Meteorological Institute, de Bilt)

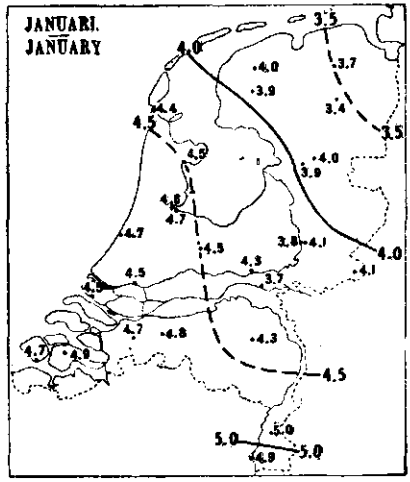


Fig. 5. Air temperature: Mean daily maximum for January. (Comm. 33 of the R.M.I., de Bilt)

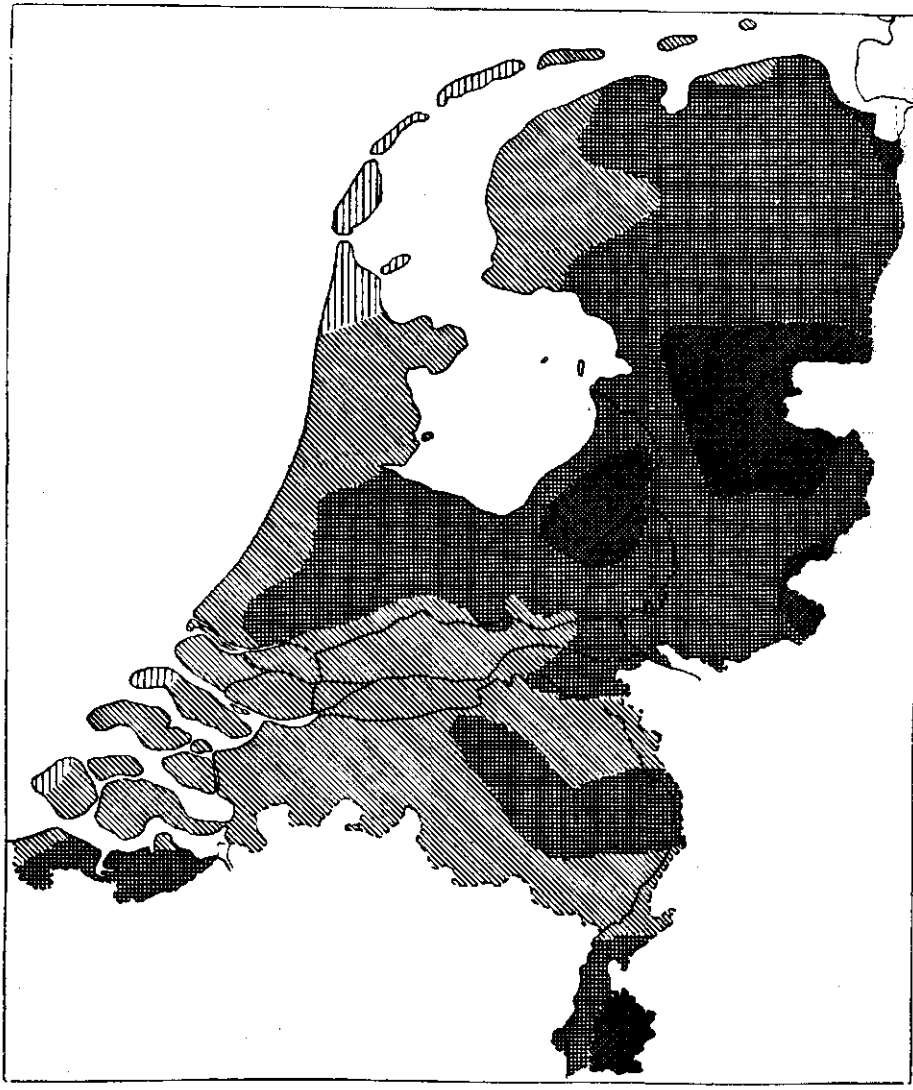


Fig. 6. Mean precipitation in July, 1891–1930. Note region of summer rains in the middle eastern parts. (Comm. 34a of the Royal Meteorological Institute, de Bilt)

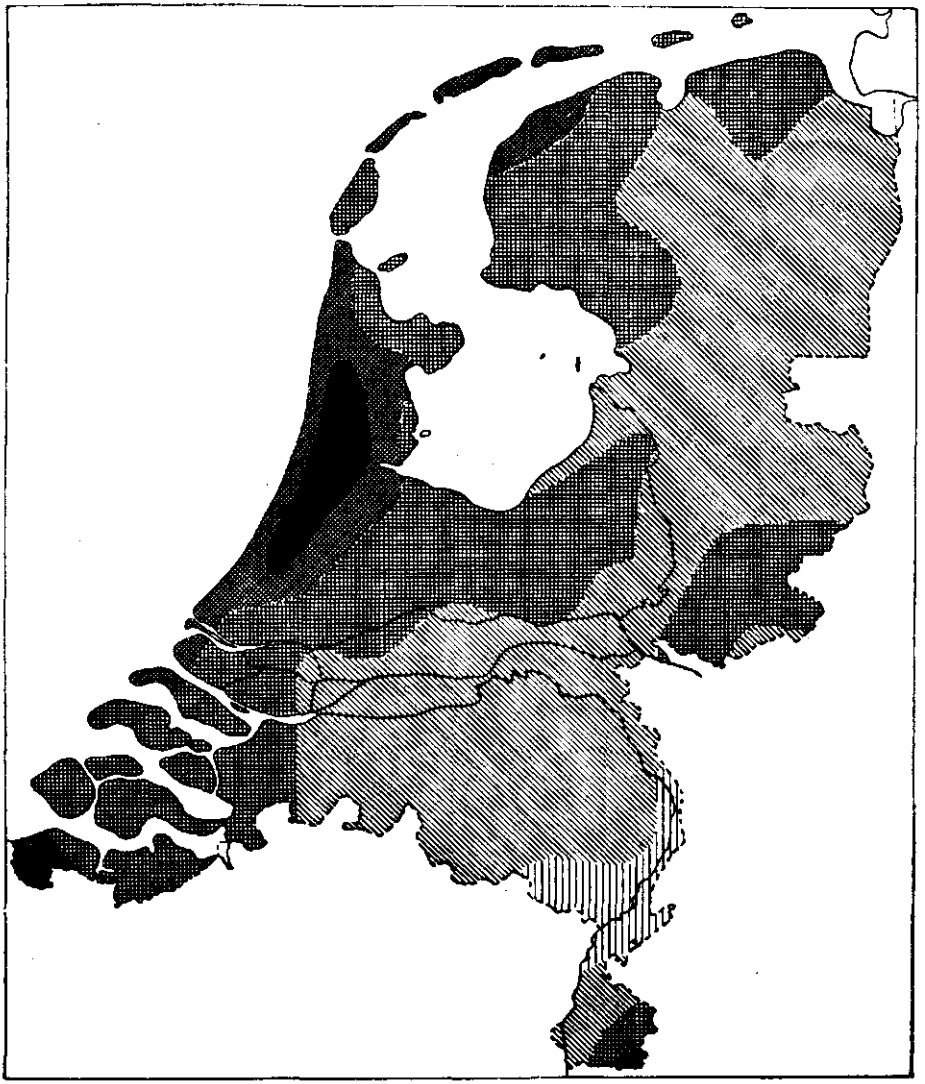


Fig. 7. Mean precipitation in October, 1891–1930. Note high precipitation behind dunes. (Comm. 34a of the R.M.I., de Bilt)

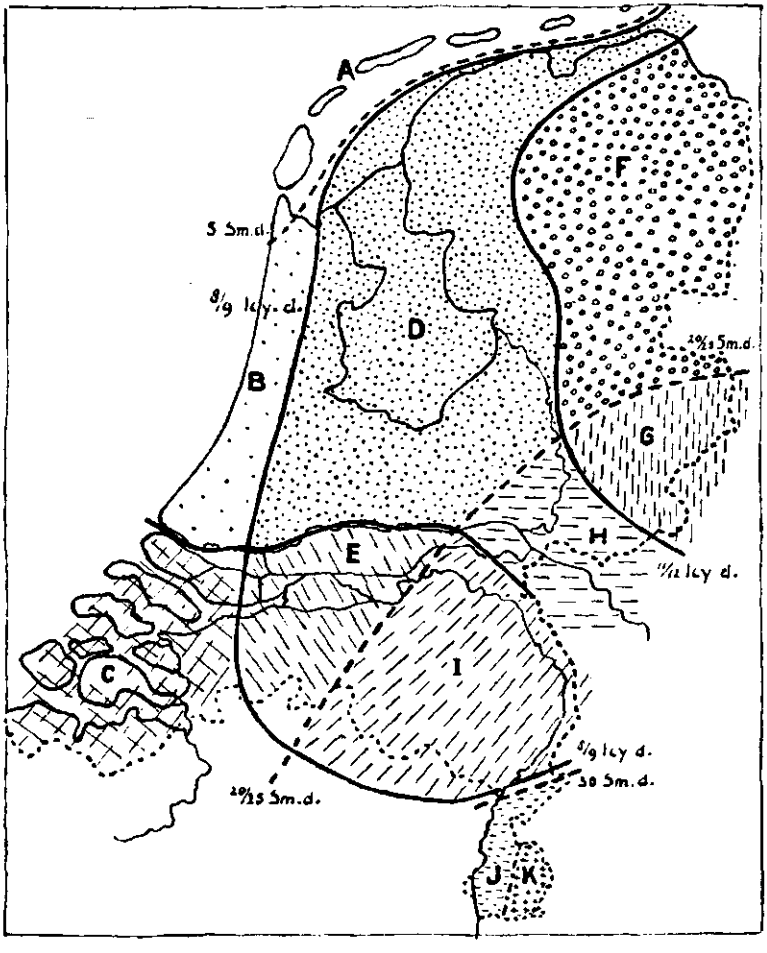


Fig. 8. Climatic regions in the Netherlands. Explanation see text p. 9.

Fig. 9. The Holocene in the Netherlands (grey) (from FABER: Geologie van Nederland)

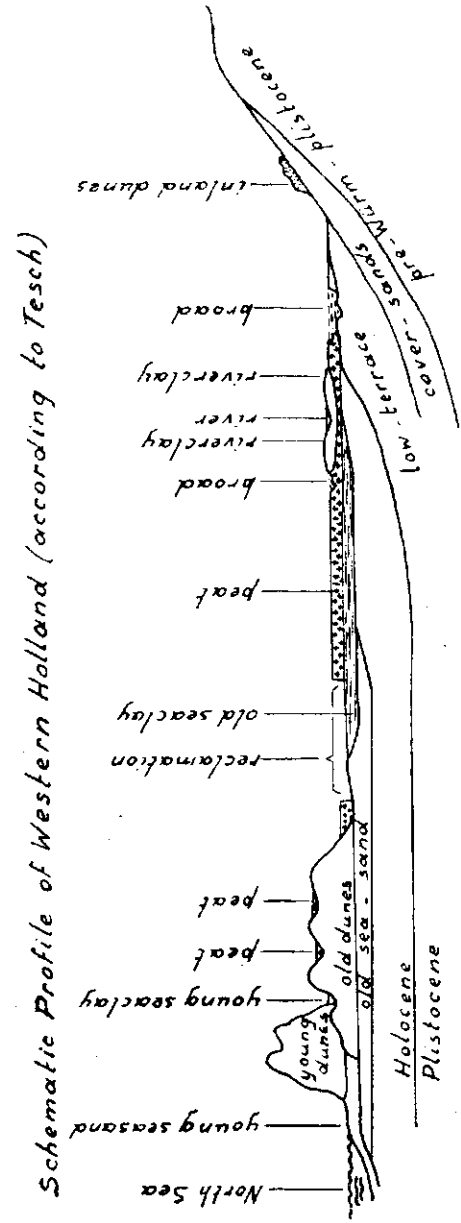

Schematic Profile of Western Holland (according to Tesch)
North Sea
young seasand
young seaclay
peat
peat
reclamation
old seaclay
peat
broad
riverclay
river
riverclay
broad
riverclay
inland dunes
young dunes
old dunes
old sea - sand
Holocene
Pleistocene
low terrace
coaver - sands
pre - Wurm - pleistocene

Fig. 10.

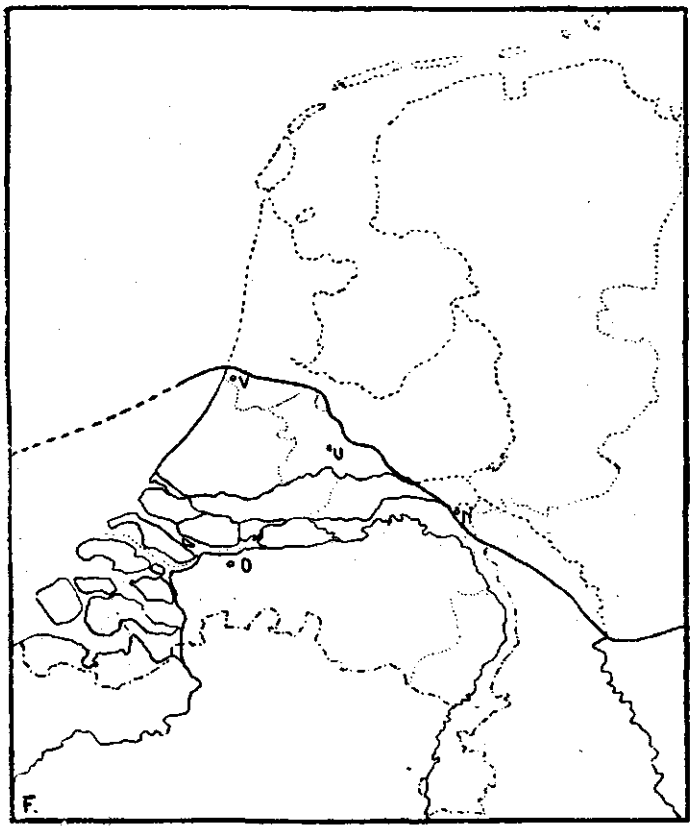


Fig. 11. Southern edge of the ice cap in the Netherlands (from FABER, Geologie van Nederland)

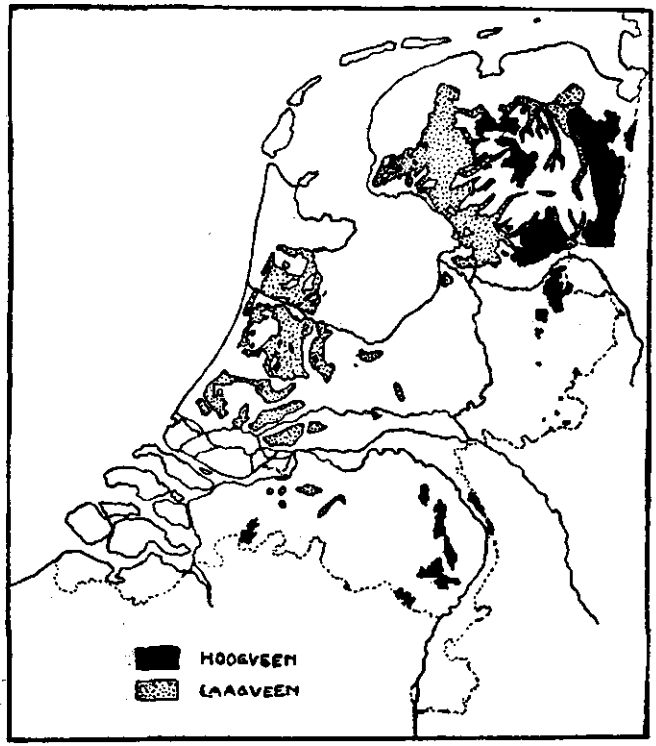


Fig. 12. Distribution of peat in the Netherlands. Dotted: fens and swamps. Black: former extension of bogs (from FABER: Geologie van Nederland) Compare fig. 13

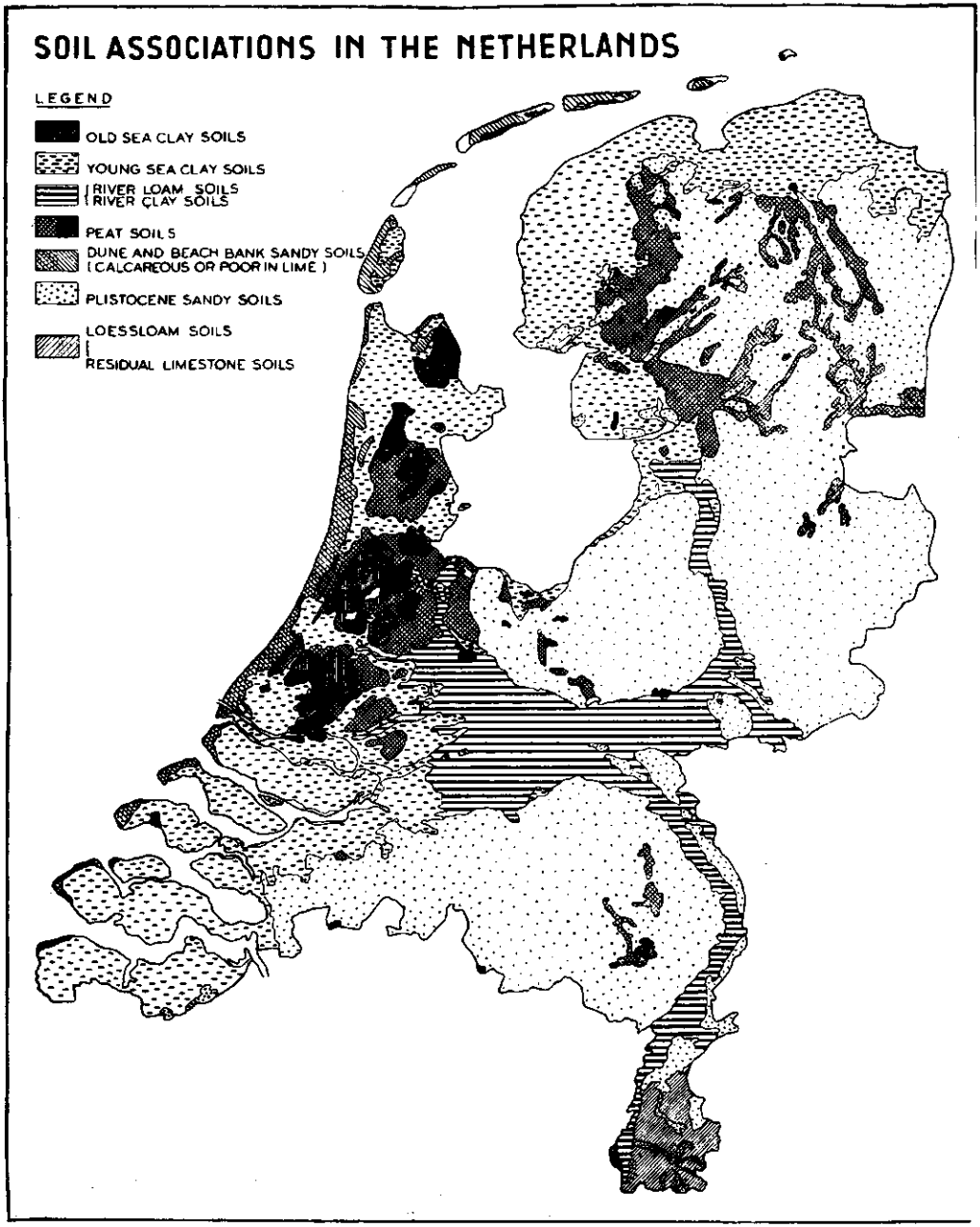
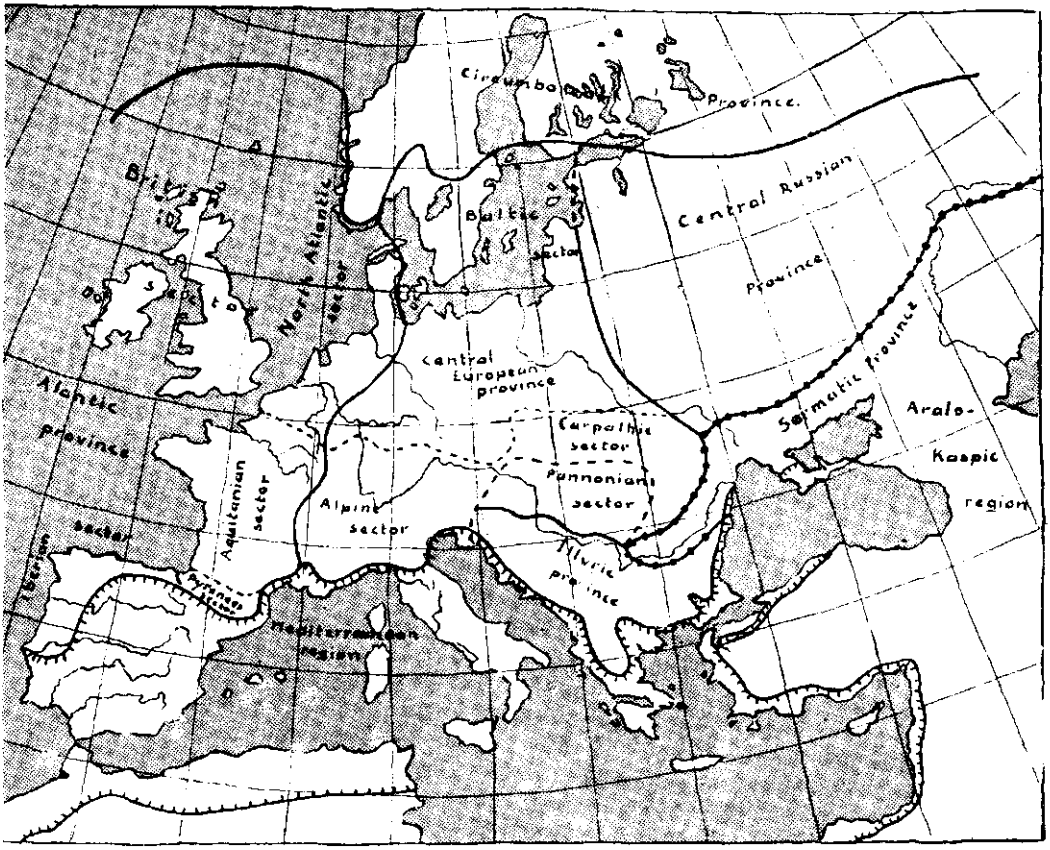


Fig. 13. Soil associations in the Netherlands, according to the Provisional Soil Map, Soil Survey Institute, Wageningen



ig. 14. Map of the principal floristic and vegetational regions of Europe. Atlantic province comprises: . British sector. 2. North Atlantic sector. 3. Aquitanian sector. 4. Pyrenees sector. 5. Iberian sector (after Braun Blanquet)

Fig. 15. The floristic and vegetational sub-districts of the Netherlands, according to van Soest (from HEUKELS' Flora, NOORDHOFF, Groningen)

Wadden

Dune

Haf

Drenthe

Gueldern

Flemish

Subcentreuropean

Cretaceous

Campina

Fluviatile