THE INLAND-HEATH COMMUNITIES OF THE NETHERLANDS

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I. INTRODUCTION

The inland heath vegetations of the Netherlands consist of three main types: the dry heath complex, *Calluna vulgaris* dominant; the humid heath complex, *Calluna* and *Erica tetralix* co-dominant; and the wet heath complex, *Erica tetralix* dominant.

Each of those complexes shows some variation in its floristic composition caused by ecological and geographical factors. The water and mineral nutrient content of the soil are the two ecological master factors.

The effect of the water supply is reflected in the division into the three above-mentioned complexes. Each complex is divided into geographically determined communities: *Empetrum* heaths in the North, *Vaccinium* heaths on the hills in the centre, *Carex ericetorum* heaths in the centre, *Sarothamnus* heaths and *Erica cinerea* heaths in the South. Each of these heaths is in its turn divided into variants corresponding with the content of available mineral nutrients of the soil. Thus both the *Calluna* and the *Calluna-Erica tetralix* heaths show a floristically poor variant, one with *Festuca ovina* and one with *Festuca ovina* and *Genista pilosa*, in correlation with increasing mineral nutrient content and consequently decreasing leaching of the soil.

All variants are floristically related by the common occurrence of *Calluna vulgaris*, *Hypnum cupressiforme* var. *ericetorum*, *Cladonia impexa*, and *Cladonia pyxidata* var. *chlorophaea*. These are therefore the constant species of the Dutch acidophilous dwarfshrub communities. But even these species show some geographical differentiation; *Hypnum cupressiforme* var. *ericetorum* and *Cladonia impexa* are much more frequent and conspicuous in the North than in the South. The first-named species shows South of the great Dutch rivers a presence of 0–30% and an average coverage of 0–5%; North of the rivers these figures are 30–100% and 0.1–60%, respectively. In the South in their place *Pohlia nutans* occupies a dominant position, at least in dry heath.

Other widespread species, though less frequent are *Pleurozium schreberi*, *Cladonia uncialis*, *Clad. squamosa*, *Clad. crispata*, *Clad. sylvatica*, *Cornicularia aculeata*, *Parmelia physodes*, *Pinus sylvestris*, *Betula verrucosa*, *B. pubescens*, *Quercus robur*, *Frangula alnus*.

The *Calluna* and *Calluna-Erica tetralix* complex have a number of species in common which do not occur in the Erica tetralix complex, e.g. *Dicranum scoparium*, *Dicranum spurium*, *Campylopus flexuosus*, *C. fragilis*, *Ptilidium ciliare*, *Cladonia floerkeana*, *Cuscuta epithymum*, and *Sorbus aucuparia*.

Some cryptogams are restricted to the dry heath complex: *Cladonia cornutoradiata*, *Cl. macilenta*, *Cl. bacillaris*, and *Polytrichum piliferum*.

The phanerogamic species on the other hand, are the ones common to the moist *Callune-Erica tetralix* complex and the wet Erica tetralix complex: *Erica tetralix*, *Molinia coerulea*, *Scirpus caespitosus* ssp. *germanicus*, *Juncus squarrosus*, and *Salix repens*.

Today thousands of hectares are still covered with heathland: they

are the remnants of thousands of square kilometers that existed in the last century. At that time heathland was essential for farming on the diluvial sandy soils.

For fertilizing the fields on the poor sandy soils, the farmers had only sheep dung at their disposal. Expansion of the arable land by cultivation of the heath was only possible if more sheep dung was available. An increase of the number of sheep was necessary, and for their grazing ground the area of the heath had to be increased at the expence of the forest (*Querceto-Betuletum*). At last an equilibrium was established between the size of the heath, of the flocks of sheep, and of the arable land. A sizable heath area was also required for cutting sods which were used as litter for the stables and were later put on the fields, with the dung. A farm with 4 ha of arable land on the Veluwe used the sods from 3 ha of heath. Once in 10 years the sods could be cut; therefore a farm needed 30 ha of heath and a village with 10 farms 300 ha (OOSTING, 1942). By this treatment overgrowing of the heath by seedlings of shrubs and trees was prevented as well. Heaths from which no sods were cut was burnt once every 5 to 10 years in order to increase the production of young shoots used as sheep fodder.

In the whole area in which *Calluna* and *Erica tetralix* are the only dominant species of the heath vegetation, i.e. from Belgium to Denmark, the soil consists of sediments deposited by rivers, inland ice, or the wind.

The rivers Schelt, Maas, Rhine, Ems, Weser and Elbe brought sand and gravel. In the Riss glacial period this material was covered by inland ice South to a line extending in the Netherlands from Haarlem to Nijmegen. In many places it left a cover of boulder clay or pushed up ridges of the alluvial deposits. In the Würm period the ice did not extend southward beyond northern Germany, but to the South-West of the ice sheet the landscape was still subject to considerable change. It was covered by a layer of sand that here and there may be to several meters thick, brought from the North, together with snow, by northwesterly winds blowing from the North Sea basin (EDELMAN, 1960). It covered the Riss boulder clay and farther to the South the alluvial river deposits. The fine-grained fraction was transported farther by the wind and the snow, and consequently the cover sand in the South-East is substituted by loess deposits. The reciprocal action of rivers, ice, snow, and wind resulted in the formation of various landscape elements, each with distinctive features that are also reflected by the heath vegetations.

The southern area including North-Brabant and the Belgian Kempen, where coversand has been deposited on riversand, is poor in species and supports a low heath (30–50 cm). In contrast herewith in the localities along the Maasvalley with loess deposits *Calluna*, *Genista pilosa* and *G. anglica* grow luxuriously, reaching a height of 1.70 m, and are homogeneously intermixed with *Sarothamnus scoparius*.

Through the middle of the Netherlands extends a belt with push moraines coinciding with the southern border of the ice sheet. To this belt belong the hill ridges of Het Gooi, Utrecht, Veluwe and Salland. The material is often more or less loamy; consequently the heath

fluctuates from dry to moist and from poor in mineral nutrients to relatively rich. The push moraine near Apeldoorn is high enough to receive rain from rizing air, on its western side. This moist habitat supports a heath community with *Vaccinium myrtillus* and *Vaccinium vitis-idaea* (STOUTJESDIJK, 1959).

Where the inland ice has deposited boulder clay the heath is floristically richer. This is observed in the Achterhoek, Twente, Drente, and South-East-Friesland. Here *Arnica montana*, *Antennaria dioica* and *Orchis maculata* are much more frequent in the heath than in the central part of the country: more to the South they are virtually absent.

Empetrum nigrum is a dominant species in the dunes poor in lime north of Bergen especially on north facing slopes. In the North of the country it occurs frequently on inland heaths and on sand dunes far from the coast. *Empetrum* frequently grows in places where the soil has been disturbed, e.g. by gullies and in abandoned strips that have been plowed for fire control. Fixed sand-dunes also are a habitat for which it shows definite preference. Nevertheless, some heathlands with a well-established podzol sometimes support extensive *Empetrum* fields. This requires special conditions, as observed on the Dwingelose Heide. Between 1959 and 1964, 5–10 *Empetrum* seedlings per m^2 established themselves in the part near the sheep's pen. At present many of them have already reached a diameter of 50 cm. In the course of a few years this will develop into the largest continuous area of Empetrum heath in the Netherlands. The origin of the phenomenon dates back to 1954. In this year the heather beetle (*Lochmaea suturalis*) infested the heath in large numbers. The region was so serious afflicted that the old *Calluna* heath died almost completely. In 1958, when there was an old dead heath field, a new flock of sheep appeared on the scene after an interval of more than 50 years. In order to stimulate the growth of new shoots for sheep fodder the heath was burned over. The old heather shrubs were, however, too weak to produce new growth. Rejuvenation by seedlings was also precluded, as these perished in the following, very dry and hot summer of 1959. The drought and insolation also lead to rapid weathering of the humus layer; the bleached sand was exposed and the uppermost part became windblown. This process was hastened by the daily perambulations of 400 sheep; these, moreover, consumed the few surviving heather shoots. During four years the area had a nearly bare surface, permitting the *Empetrum* seeds to germinate and establish themselves. Seeds were present, because a number of *Empetrum* plants were growing in the heath before it was burnt. At present, after five years, an area of 50 hectares is on the way to become an *Empetrum* heath. This unique concentration of events leading to this process makes it understandable why seedlings of Empetrum are so rarely seen. Bare sandy soil appears to be essential. This is in accordance with the observation of WARTENA (1964) who found *Empetrum* seedlings on the bare sandy banks of an artificially constructed lake in the dunes near Bergen.

II. THE INFLUENCE OF THE HEATHER BEETLE (LOCHMAEA SUTURALIS)

In certain years the heather beetle devastates the heath in the Netherlands and North Germany. This occurred i.a., in the years 1952–54 and 1962–64. BETREM (1929) reported also infestations from the years 1853, 1862, 1870, 1888, and 1928.

Studies on permanent quadrats have demonstrated that the heather recovers only after several years. The extent to which *Calluna* suffers from the infestation depends on its intensity and on the age of the heather. Conversely the age of the *Calluna* plants also influences the intensity of the infestation: old *Calluna* is strongly preferred by the beetles that require a thick humus layer and a well-developed moss layer where they hide for the greater part of the day. The infestation usually starts from a patch of old heather or from a stretch of heath bordering on a forest where in the shade a thick moss cover has developed.

The intensity of the infestation and the vitality of the heather determine the mortality of the latter. Three degrees may be distinguished.

1st degree. If the infestation is slight, only a number of thin twigs is killed off. The damage may be repaired completely in the course of one year.

2nd degree. In the case of heavier infestation a number of stems is killed, the remaining ones losing the greater part of their twigs. Afterwards the surviving stems form numerous new shoots but only near the apex. This results in the formation of irregular developed, untidy heatherplants with a tuft of twigs in the top and many interspersed dead stems that give the vegetation a greyish appearance. After one year the old tufts form new shoots at the bases of the dead stems; these flower after 1–2 years and after 3–4 years equal the dead stems in height. The latter now start to decay and collapse.

3rd degree. If the infestation is very strong, all *Calluna* stems are killed. In stems of 20 years and more usually all underground parts die, too. Younger stems, however, tend to produce basal shoots in the year following the infestation, or even in the autumn of the same year. The stems should therefore not be too old, but underground parts may be dozens of years old without loss of vitality, provided the plants are regularly rejuvenated by burning, cutting, or grazing.

The course of recovery is determined by the degree of dying off and by the floristic composition.

An infestation of the Ist degree requires one or two years for complete recovery of the heather.

After an infestation of the 2nd degree the structure of the heath remains irregular and bushy for a number of years. The stems with tufts of branches in the top become prostrate after several years and may produce adventitious roots. In this manner the open places in the vegetation are filled up; they already support a number of seedlings.

This irregular structure is maintained till after the next total rejuvenation through burning.

When an infestation of the 3rd degree has taken place the dead stems fall after 3 to 4 years. The original moss layer (e.g. *Hypnum cupressiforme* var. *ericetorum*, *Dicranum scoparium*, *Pohlia nutans*, *Cladonia impexa*) dries out and decays and is replaced by pioneer mosses: *Campylopus species*, *Polytrichum piliferum*, *P. juniperinum*, *Lophozia bicrenata*, *Cladonia pyxidata* var. *chlorophaea*. Rejuvenation takes only place by means of seedlings. The young plants start flowering after 2–5 years. The formation of a 5-stemmed tuft requires about 10 years; a full-grown tuft has about 20 stems and is several dozens of years old. A *Calluna* plant can probably get hundred years or older. Under normal conditions there are very few seedlings in a mature heath field.

The floristic composition also influences the course of the recovery.

The *Calluna* variant (1.1.1) recovers after an infestation of the 3rd degree as described above, via a degeneration stage of dead *Calluna* and a dead moss layer and a pioneer stage with certain mosses and heather seedlings and the original vegetation re-appears after5–10years. In the case of degeneration a stage with dominance of *Cladonia impexa* and *Cladonia sylvatica* may be intercalated.

In the *Calluna-Festuca* variant (1.1.2) and the *Calluna-Festuca-Genista* variant (1.1.3) the first years after the devastation show a dominance of the grasses *Festuca ovina*, *Agrostis* species, and *Deschampsia flexuosa*. After 4–5 years *Calluna* reattains its dominant position.

Similar phenomena are observed in the other heath communities if co-dominant species are present, e.g. *Erica tetralix*, *Empetrum nigrum*, *Vaccinium* species, *Molinia coerulea*. They may dominate for some time but then the original situation prevails again.

It may have been this process that led STOUTJESDIJK (1959) to the supposition that cyclic processes take place in the heath, in a similar way as is known from raised bogs. He concludes this from the observation that *Calluna* seedlings were never found in mature heath vegetation, and that *Calluna* recolonizes places where it had been replaced by lichens or grass. Subsequently Stoutjesdijk describes six stages of the cyclic process. The first stage is that of a vigurous *Calluna* heath. The 2nd, 3rd, and 4th phases correspond closely to the 1st, 2nd, and 3rd degree of infestation by the heather beetle. Therefore these phases do not follow each other but occur simultaneously. Stoutjesdijk's 5th and 6th phases correspond to the pioneer stage and the stage of final recovery after devastation by beetles. The observed mosaic is interpreted by Stoutjesdijk as an assembly of stages of a cyclic, periodical series. Actually there is a number of parallel series that have different startingpoints determined by the degree of devastation by the heather beetle and by the floristic composition of the heath. The significance of the last-named factor was recognized by Stoutjesdijk; he described a cycle in the heath with *Deschampsia* and one in *Molinia* vegetation with *Calluna* and *Erica*.

III. THE COMMUNITIES

1. THE DRY HEATH COMPLEX (*Calluna vulgaris*)

This complex is characterized by species of the dry habitat: *Polytrichum piliferum, Cladonia cornutoradiata, Cl. macilenta, Cl. bacillaris.* Species which have their optimum in the wet heath are absent.

1.1. *Calluna heaths*

1.1.1. *Calluna variant*

The poverty in species is the most striking feature. *Calluna* is often the only vascular plant, sometimes accompanied by *Cuscuta epithymum* and some seedlings of *Pinus sylvestris, Betula verrucosa* or *Quercus robur.*

The soil has a well-developed heath podzol profile.

1.1.2. *Festuca variant*

To the dry heath complex belongs a variant with *Festuca ovina. Cladonia verticillata* is more frequent in this than in any other variant. The optimum of this species, however, is outside the heath formation, namely in the lichen-dominated phase succeeding *Corynephorus canescens* on resting inland dunes. There it is also often accompanied by *Festuca ovina.* The *Festuca*-variant actually often represents the phase following the lichen-dominated phase in the succession from open dune sand via *Corynephorus*, lichens, *Festuca-Agrostis* to *Calluna* heath.

The soil is only weakly leached in the upper 30 cm.

The soil may also be distinctly podzolised but then it contains a certain amount of loam, indicating that it is less poor in mineral nutrients than the preceding variant. In one occasion in the south of the country (Brunssumse heide) this variant is found on heavily podzolised soil with an exceptionally thick A-horizon of 100 cm.

1.1.3. *Festuca-Genista variant*

Species requiring a higher mineral content of the soil join those of the preceding variants: *Genista pilosa, G. anglica, Sieglingia decumbens, Carex pilulifera, Nardus stricta, Festuca ovina, Potentilla erecta, Galium hercynicum, Hieracium umbellatum,* and *Campanula rotundifolia.* In the north of the country there are in addition *Arnica montana* and *Antennaria dioica*, and in the south *Erica cinerea.*

The soil is only weakly podzolised. This is often due to the presence of fine material which prevents strong leaching.

1.2. *Calluna-Empetrum-heaths*

In the north of the country three variants occur that show a boreal influence by the presence of Empetrum nigrum. They may be regarded as the northern vicariants of the three abovementioned variants. It may, however, be objected that they also occur in well-developed

specimens in the same area. But here Empetrum approaches the southern limit of its lowland area and is consequently less common in the heath, but occurs only in locally favourable habitats.

Where it is present, it is often accompanied by *Pleurozium schreberi*, which becomes dominant in the moss layer.

1.2.1. *Empetrum variant*

This variant is the poorest in species among the *Calluna-Empetrum* heaths. The dwarfshrub layer only consists of the two dominants, while other phanerogams are normally absent. The moss layer is often dominated by *Pleurozium schreberi*; other frequent components are *Hypnum cupressiforme* var. *ericetorum*, *Dicranum scoparium*, *Dicranum polysetum* and *Cladonia impexa*.

The soil often consists of a heath podzol covered with several decimeters of blown sand. On the other hand, it may also be a well-developed heath podzol quite similar to that of the *Calluna*-variant.

This variant is common in Southeast-Friesland and North-Drente. Southward it soon becomes rare and does not extend beyond Twente and the Veluwe.

Empetrum nigrum is generally regarded as a species of resting inland dunes and coastal dunes poor in lime. It is actually a common species in these habitats, but in the northern part of the country it is equally frequent on soils with an old established heath podzol.

1.2.2. *Empetrum-Festuca variant*

This variant differs from the preceding one in the same way as the *Festuca* variant (1.1.2) differs from the floristically poor *Calluna* variant (1.1.1) through the presence of Festuca ovina.

The soil is resting dune sand, or a heath podzol covered with blown dune sand, or sometimes a normal heath podzol. The latter situation prevails less frequently than in the *Empetrum* variant. This variant has the same area as the *Empetrum* variant (1.2.1)

1.2.3. *Empetrum-Festuca-Arnica variant*

This variant is comparable with the *Calluna-Festuca-Genista* variant (1.1.3.) because it also contains the species of soils relatively rich in mineral nutrients, e.g. *Potentilla erecta*, *Sieglingia decumbens*, *Arnica montana*, *Nardus stricta*, *Galium hercynicum*, and *Hieracium umbellatum*. In contrast to the latter variant, however, both Genista species and Antennaria dioica are generally absent, whereas *Pleuzorium schreberi* and *Dicranum scoparium* are much more abundant.

The soil has a heath podzol profile, in some instances with a certain loam content, or is covered with dune sand.

The area corresponds with that of both other variants with Empetrum.

1.3. *Calluna-Vaccinium heaths*

In some parts of the country *Vaccinium myrtillus* and *V. vitis-idaea* transgress from the protection of the forest into the open heath. They are accompanied by *Melampyrum pratense*, *Leucobryum glaucum*, and sometimes *Empetrum nigrum*. *Campylopus flexuosus* and *C. fragilis* var. *pyriformis* occur frequently as a result of regular burning.

The humus production in the variants with *Vaccinium* spp. is greater than in any other variant of the dry heath, perhaps the *Empetrum* variants excepted. Consequently the soil is heavily podzolised. The humus layer is amorphous, compact, and almost peaty. The A_1 and A_2-horizons have a high humus content; the latter is not rarely coloured like the brown soils of the native forest (*Querceto-Betuletum*). The B_1 is a well-developed amorphous black humus layer. The B_2 is also well developed, but is never endured. The *Calluna-Vaccinium* heath attains dominance only in two rather small areas, namely on the western side of the glacial ridge near Apeldoorn, and on the western side of the Holterberg. These areas receive a high rainfall caught by the hills. The high humidity enables the *Vaccinium* species to leave the protecting forest (STOUTJESDIJK, 1959). Among the accompanying species there are also a few typical forest plants like *Melampyrum pratense*, *Deschampsia flexuosa*, *Leucobryum glaucum*, *Pleurozium schreberi*, and some submontane liverworts: *Orthocaulis attenuatus*, *O. kunzeanus*, and *Scapania nemorosa*. This community prefers north-facing slopes.

The *Vaccinium* species belong to the boreal-montane phytogeographical element and are frequent components of the heath communities in Scandinavia, Scotland, and the German "Mittelgebirge".

1.3.1. *Vaccinium variant*

Parallel to the *Calluna* variant (1.1.1) and the *Calluna-Empetrum* variant (1.2.1) this variant is the poorest in species. It shares the general characteristics of the *Calluna-Vaccinium* heath described above.

1.3.2. *Vaccinium-Deschampsia variant*

In this variant *Deschampsia* becomes co-dominant, *Melampyrum pratense* is of more frequent occurrence in this than in the other *Vaccinium* variants. *Pleurozium schreberi* is dominant in the moss layer, forming a dense mat up to 15 cm thick, and frequently covering more than 70 percent.

The soil profile much resembles that of the last variant, only the humus content may be somewhat higher.

This variant prefers north-facing slopes more pronouncedly than the preceding one; often they are also steeper (10–30°) (VAN DER BURGH, 1963).

1.3.3. *Vaccinium-Genista variant*

This variant differs from the preceding one by the presence of species from soils relatively rich in available mineral nutrients: *Genista pilosa*, *G. anglica*, *Sieglingia decumbens*, *Agrostis stolonifera*, *A. canina*, and *Galium hercynicum*.

The soil is only moderately podzolised with a slightly bleached upper A-horizon and an indistinctly developed B-horizon.

This variant occurs in the same area as the *Vaccinium* variant, depending on the same climatological conditions. It are the fluctuations of the mineral content which cause the differences between the three variants with *Vaccinium* species, parallel to the differentiation in communities with *Calluna* as the only dominant, in communities with *Empetrum* as dominant or co-dominant and in those with *Sarothamnus* as dominant or co-dominant.

1.4. *Calluna-Sarothamnus heaths*

In some places *Sarothamnus scoparius* is more or less homogeneously distributed in the heath fields. In our region it is not a common constituent of heath vegetation. Heaths with *Sarothamnus* differ also physiognomically considerably from the other types in the North-west European lowlands. They are dense, hardly penetrable thickets 1–1.5 m tall. *Sarothamnus* and *Calluna* grow homogeneously intermixed and are practically of the same size. The heath vegetation is here and there interrupted by shrubs of *Quercus robur* and *Quercus petraea*. *Molini coerulea* is always present in these thickets, but *Erica tetralix* is wanting. This phenomenon is only observed in the variants with *Sarothamnus*. The reverse — *Erica* without *Molinia* – is not uncommon in other regions, but hardly occurs where *Sarothamnus* heaths are found. *Pteridium aquilinum* is a faithful species within the heath formation. *Deschampsia flexuosa*, *Vaccinium myrtillus*, *Majanthemum bifolium*, and *Melampyrum pratense* are differential species providing a link with the *Vaccinium* heaths. In the moss layer *Pohlia nutans* dominates with an average coverage of 30%. Larger mosses like *Hypnum cupressiforme* var. *ericetorum*, *Pleurozium schreberi* and *Dicranum* species are wanting. The species of *Cladonia* subgenus *Cladina* are represented by depauperate specimens of *Cladonia impexa* at the most. On the other hand *Cladonia cornutoradiata* from the subgenus *Cenomyce* in the Netherlands has its optimum in the variants with *Sarothamnus* and in the floristically poor *Calluna* variant (1.1.1.) of the southern Netherlands. In the South *Pohlia nutans* is also much more abundant than elsewhere. The soil consists of fine-grained sand and contains loess or loam; it is only slightly podzolised.

Raw humus accumulation is less than in most other heath communities; the A-horizon is not much leached, the B-horizon is weakly developed. Although the phreatic level is several dozens of meters below the surface the soil may be rather humid by the high water-retaining capacity of the loess and loam.

The *Sarothamnus* heaths occur along the escarpments of the Maas valley, on deposits of the high-terrace, especially if they are overlain by a loess layer. This is particularly the case on the sides of the valley and of the tributary erosion valleys. In the Netherlands *Calluna-Sarothamnus* thickets are well developed in the Meinweg, they also occur near Mook and here and there bordering the Geul valley. A depauperate variant is formed by the Sarothamnus thickets near the Posbank, in the Gooi and along the inner border of the coastal dunes, i.a. the Vroongronden on Schouwen and the Bremakker on Tessel (WESTHOFF, 1952). The best developed specimens of *Sarothamnus* heaths in the surveyed area are to be found on the Belgian side of the Maas valley near Mechelen and Opgrimbie. Here they cover hundreds of acres on the slopes and the plateau. Recently, however, they are seriously damaged by the exploitation of vast sand pits, which threatens the whole area.

The *Sarothamnus* heath is a northern outpost of a southern montane type of heathland with *Sarothamnus*, which occurs e.g. in the Auvergne highlands and in the Cevennes. There it contains other *Ericaceae*, such as *Erica arborea*, *Erica scoparia*, and *Erica cinerea*, and a different species of oak (*Quercus pubescens*), and also mediterranean species, such as *Cistus salviaefolius*, but as a whole it is related to the Dutch-Belgian type. *Sarothamnus* and *Calluna* are also dominant in the South and *Pteridium* is present throughout, as is *Teucrium scorodonia* which grows in the Dutch-Belgian *Sarothamnus* heaths mainly at its edges and by trails and under oak shrubs. Physiognomically both kinds of *Sarothamnus* heaths are very similar. In South-France *Calluna* and *Sarothamnus* also attain the same height, 1–2 m, and form a homogeneous vegetation.

1.4.1. *Sarothamnus variant*

For the floristic composition, the soil conditions and the geographic area see above.

1.4.2. *Sarothamnus-Genista variant*

Besides the species of the *Sarothamnus* variant there occur *Genista pilosa*, *G. anglica*, *Carex pilulifera* and *Potentilla erecta; Molinia coerulea* is more conspicuous.

It is striking that in this vegetation both Genista species as well as *Calluna* reach a height of 1.70 m. The Flora of the Netherlands (HEUKELS–VAN OOSTSTROOM, 1962) describes *Genista pilosa* as 7–30 cm high. In the vegetation under discussion the plants develop into vigorous shrubs with trunks 3–4 cm thick. Insofar as I know this form of *Genista* is not met with elsewhere in the NW. European plain.

The soil contains more loess than in the *Sarothamnus* variant and consequently leaching is less strong.

This variant has the same area as the preceding one.

1.5. *Calluna-Erica cinerea heaths*

This is the only community with *Erica cinerea*. The *Genista* species have a high coverage (on the average 25–30%), *Molinia* has high constancy and *Erica tetralix* is lacking, which provides a link with the *Calluna-Sarothamnus* heaths.

The soil has a distinct profile but podzolisation is not intense. B_1 and B_2 are usually developed but often weakly. The soil contains mostly some coarse gravel.

The *Calluna-Erica cinerea* heaths occur on the West of the Maas in the Belgian Kempen. They get very close to the Dutch border but do not cross it. They grow near the *Calluna-Sarothamnus* heaths but cover the level stretches of the plateau that consist of sand and gravel deposits of the river Maas, whereas the *Sarothamnus* heaths grows on the loess covered slopes. Formerly the *Calluna-Erica cinerea* heaths occurred also in the Netherlands, viz. east of the river Maas near Echt and Roermond, but they have disappeared through land reclamation. Near Mook a station of *Erica cinerea* has disappeared about 1957 as a consequence of severe winters.

1.6. *Calluna-Carex ericetorum heaths*

This community has more faithful species within the heath formation than most of the others, viz. *Carex ericetorum*, *Poa pratensis*, *Cirsium arvense*, *Taraxacum* spec., *Epilobium angustifolium*, *Cerastium semidecandrum*, and *Veronica officinalis*. Their optimal development lies, however, outside the heath formation, and their presence can be explained as the effect of disturbance of the soil. Other frequently occurring species are *Hypochoeris radicata*, *Rumex acetosella*, *Festuca ovina*, *Carex pilulifera*, *Galium hercynicum*, and *Agrostis canina*, giving the vegetation a herb-rich aspect.

The soil consists of fine loess-like sand showing only a very weak podzol.

This type is only found in three stations on the Central Veluwe, namely east of the Compagnieberg, on the Voorste Steenberg near Kootwijk, and along the road Hoenderlo-Otterlo. *Carex ericetorum* is a continental species common in Central and East Europe in grassy heath vegetations with scattered trees of *Pinus sylvestris* (SCHUBERT, 1960).

In the same area occurs another rare species of the Dutch heath, *Scorzonera humilis*, and formerly also *Hypochoeris maculata* (UITTIEN, 1932). All three species are or were found in habitats rather strongly affected by human activity, particularly along bicycle tracks, on roadsides, and on dug-up soil. Only *Scorzonera* is met with in the undisturbed heath as well. These species here reach the western fringe of their range and apparently need gradient situations (VAN LEEUWEN, 1965) to find a suitable habitat. Along roadsides exist gradients of decreasing tread and decreasing mineral supply.

At the limits of their area these species are more specialized in their ecological requirements, a regularly observed phenomenon. Gradient situations provide the best opportunity for a suitable habitat. The western limits of the main areas of these species lie far to the east of the Netherlands. HULTÉN (1950) lists *Scorzonera humilis* and *Hypochoeris maculata* as East-European continental species, and *Carex ericetorum* as a West-Siberian continental species.

In Bretagne, however, *Scorzonera humilis* behaves differently. There it is common and of high vitality in the wettest spots of bogs, preferably on gentle slopes with flush, but it is absent from dry mineral soil. It is possible that this population consists of a special ecotype.

2. THE HUMID HEATH COMPLEX (*Calluna-Erica tetralix*)

This complex has no faithful species of its own. It is separated from the other complexes by groups of differentiating species. It differs from the dry heath complex by the constant presence of *Erica tetralix* and the frequent occurrence of *Molinia coerulea*, *Scirpus caespitosus* SSD. *germanicus* and *Juncus squarrosus*. *Calluna* has a higher cover percentage than *Erica tetralix*; this serves to distinguish the humid from the wet heath complex. This community forms the link between the dry and the wet heath complex, but is more closely related to the first. Most of the *Cladonia*, *Polytrichum* and *Campylopus* species still occur in the humid complex, but only very scantily or not at all in the wet complex. A number of *Cladonia* species occur in all three complexes.

The species from the dry heath variants with *Empetrum*, *Vaccinium*, *Festuca* or *Genista* are present again in corresponding variants of the humid heath, but they are lacking in the wet *Erica tetralix* heaths.

The community of *Calluna* and *Erica tetralix* is widespread in the Netherlands, with the exception of the Maas valley, where *Erica* is replaced by *Molinia*.

Three different types are distinguished parallel to the first three types of the *Calluna* complex. The first one is widespread in the whole diluvial part of the country, the other two have more restricted area.

2.1. *Calluna-Erica tetralix heaths*

This is the principal form of the complex, widespread on humid sandy soils in the Netherlands.

2.1.1. *Calluna-Erica tetralix variant*

This variant is poor in species and shows much resemblance to the *Calluna* variant of the dry heath. The difference is, on the one hand the absence of the species which are characteristic of the dry habitat: *Polytrichum piliferum* and *Cornicularia* aculeata, on the other hand the presence of some species which are common in the wet heath: *Erica tetralix*, *Molinia coerulea*, *Scirpus caespitosus* and *Juncus squarrosus*.

The soil shows widely divergent profiles. It fluctuates from scarcely leached dune sand on boulder clay to a strongly leached heath podzol. An important general feature is the high phreatic level which in winter may reach the surface, or at least a high moisture content, caused by the presence of loam. The B_1–horizon is normally well developed and the B_2–horizon may be endured. Sometimes an overblown peat layer is present in the upper part of the soil profile. These properties of the soil promote the retaining of the water or impede free drainage, all leading to a humid habitat.

The soil is poor in available mineral nutrients which is reflected by the floristic poverty of this community. In some instances the profile is decapitated by sod cutting and has lost the A_1–horizon. This feature it has in common with the soil of the Calluna variant of the dry soil (1.1.1.)

This variant is present in the whole Dutch heath area.

Subvariant with *Gymnocolea inflata*

Together with other liverworts, like *Odontoschisma sphagni* and *Cephalozia bicuspidata*, *Gymnocolea* may dominate in the moss layer. They are able to form a continuous layer of a few cm thick. The humus content of the A-horizon is very low, the B_1 and B_2 are well developed, the latter may be endured or of a greasy colloidal substance. The C-horizon consists of fine sand or is loamy. The *Gymnocolea*-subvariant is mainly met with in the province of Noord-Brabant in low-lying, level heath, particularly near oligotrophic heath lakes (vennen) and small watercourses.

2.1.2. *Calluna-Erica tetralix-Festuca variant*

Here *Festuca ovina* and *Carex pilulifera* join the species of the preceding variant.

The soil profile varies again in the way described for the humid conditions.

The *Festuca* variant of the *Calluna-Erica tetralix* heaths is of much less frequent occurrence than the corresponding variant of the dry heath. This may be connected with the ecology of *Festuca ovina*, which is a species of a dry rather than of a humid habitat. Only a few stands have been recorded, confined to the south and centre of the country.

2.1.3. *Calluna-Erica tetralix-Festuca-Genista variant*

Here again in some of the differentiating species of the *Festuca-Genista* variant of the dry heath come together, in the first place *Genista anglica* and *G. pilosa*, but also *Sieglingia decumbens*, *Agrostis stolonifera*, *A. canina*, *Potentilla erecta*, and *Carex pilulifera*, in the north in addition also *Arnica montana*. To the group of species that prefer soil containing available mineral nutrients belong several species which occur in the

dry heath but are absent from the humid heath, e.g. *Hieracium umbellatum*, *H. pilosella*, *H. laevigatum*, *Campanula rotundifolia*, *Agrostis tenuis*, and *Rumex acetosella*. *Genista pilosa* is more widespread and numerous in the variant of the dry heath, in contrast to *Genista anglica* which prefers the variant of the humid heath. Accordingly *Genista anglica* can grow in *Molinion* grassland, where *Genista pilosa* is never found. *Festuca ovina* has the same constancy in the corresponding dry and humid variants but in the humid variants it has a much lower covering percentrage.

These phenomena of the vegetation permit the conclusion that the soil is relatively rich in mineral nutrients. This is effected by two means, viz., a loamy substratum, or blown unleached sand on top of the leached profile. In the first case the B_1 is often absent, while the B_2 is weakly developed: in the other case there is no leaching or only its initial phase.

This variant is widespread in the Dutch heathland area, although less frequent than the *Calluna-Erica tetralix* variant.

2.1.4. *Calluna-Erica tetralix-Festuca-Genista-Orchis maculata variant*

Locally in the humid heath occurs a community with less common species which have their optimum in the *Nardo-Galion* or in the *Molinion*, viz. *Orchis maculata* var. *ericetorum*, *Potentilla erecta*, *Gentiana pneumonanthe*, *Equisetum palustre*, *E. fluviatile*, *Succisa pratensis*, *Cirsium dissectum*, *Polygala serpyllifolia*, and occasionally *Solidago virgaurea* and *Pimpinella saxifraga*.

The soil consists of fine loamy sand, loam or clay, without or with a very weak podzol or gley profile. The phreatic level rises in wintertime to 40 cm below the surface.

The variant with *Orchis maculata* occurs in Drente in the area with glacial moraine deposits and locally in Twente and the Achterhoek.

The soil is well suited for arable land and this variant has therefore greatly decreased.

2.2. *Calluna-Erica tetralix-Empetrum heaths*

In this variant *Empetrum nigrum* joins the species of the *Calluna-Erica tetralix* heaths, frequently also *Dryopteris carthusiana*.

The soil is weakly or not podzolized, wind-blown sand or a C-horizon where the A- and B-horizon have been blown off.

Sometimes both processes have subsequently taken place: first the podzol profile has been blown off and later wind-blown sand has been deposited.

Parallel to the *Calluna-Erica tetralix* heaths three variants occur:

2.2.1. *Empetrum* variant
2.2.2. *Empetrum-Festuca* variant with *Festuca ovina* and *Carex pilulifera*.
2.2.3. *Empetrum-Festuca-Genista* variant, with in addition *Genista anglica*, *G. pilosa*, *Arnica montana*, *Potentilla erecta*, *Agrostis stolonifera*, and *A. canina*.

All three variants are only found in the North of the country in Southeast-Friesland and in the province of Drente.

2.3. *Galluna-Erica tetralix-Vaccinium heaths*

As in the dry heath, a separate community with *Vaccinium myrtillus* and *V. vitis-idaea* is distinguished. *Leucobryum glaucum* and *Deschampsia flexuosa* are also frequent components.

2.3.1. *Vaccinium-variant*

This variant has no differentiating species of its own to set it off from the other variants with *Vaccinium*.

The humus layer is strongly developed, occasionally peaty, the A-horizon is a mixture of bleached sand and humus. The B_1-horizon is black, contains much humus, and is clearly separated from the underlying B_2-horizon, which may be endured.

The humid *Vaccinium* heath is not restricted to the province of Gelderland, like the dry *Vaccinium*-heath, nor is it strictly confined to north-facing slopes. Both phenomena are probably interrelated. Dry *Vaccinium* heath is restricted to heath on northfacing slopes which occurs only on the hills of Gelderland. Outside of Gelderland heath on hillsides occur only along the river Maas, viz. the *Sarothamnus* heaths which actually contain *Vaccinium*, and on the hills of the Brunssumse Heide in South Limburg. In the latter locality *Vaccinium* is lacking, probably because the soil is very permeable and well drained, and is consequently too dry.

The *Calluna-Erica tetralix-Vaccinium* heaths occur on humid soils which parallels the humidity of the north slopes. Thus level ground may be suitable for this community, which is available in Gelderland, in the eastern part of Twente, in Drente on the glacial deposits, and in South-East Friesland, where this community is found.

Subvariant of *Vaccinium uliginosum*

Occurring very rarely in the east of Gelderland near Neede and Winterswijk on boulder clay deposits.

2.3.2. *Vaccinium-Festuca-Genista-variant*

Festuca ovina, Carex pilulifera, Genista anglica, G. pilosa, Sieglingia decumbens, and *Agrostis stolonifera* are differentiating species setting it off from the preceding variants. An intermediate *Festuca*-variant has not been recorded. The soil is finer than the soil of the *Vaccinium*-variant, grain size 150–210 micron, sometimes 105–150 micron, or even 50–105 micron.

3. The wet heath complex (*Erica tetralix*)

The vegetation consists mainly of *Erica tetralix*, *Molinia coerulea*, *Scirpus caespitosus* ssp. *germanicus*; constituents of lesser importance are *Juncus squarrosus* and *Calluna vulgaris*. *Erica* is dominant; *Calluna* is not rarely co-dominant and may even be dominant. *Hypnum cupressiforme* var. *ericetorum*, *Cladonia impexa*, and *Cladonia pyxidata* var. *chlorophaea*, with *Calluna* the four constant species of all Dutch acidophilous dwarf-shrub communities, form part of the moss layer, except in the South where *Hypnum* is absent from the wet heath. Many of the mosses and lichens common in the dry and moist heath are wanting in the wet heath or occur more sparsely. *Cladonia squamosa*, *Cl. floerkeana*, *Cl. uncialis*, *Cl. crispata*, *Dicranum scoparium*, *Pohlia nutans*, and *Campylopus flexuosus* are, however, regularly met with in the wet heath. In the North, especially in Twente, they are joined by *Cetraria islandica*.

The principal difference between the wet heath complex on the one hand and the dry and humid complexes on the other hand is in the participation in the wet heath vegetation of several peat-bog plants: *Eriophorum angustifolium*, *Rhynchospora alba*, *Narthecium ossifragum*, *Drosera rotundifolia*, *Vaccinium oxycoccus*, *Andromeda polifolia*, *Sphagnum cuspidatum*, *Sph. acutifolium*, *Sph. magellanicum*, *Mylia anomala*, *Odontoschisma sphagni*. To these may be added some species of the *Nardo-Galion*: *Gentiana pneumonanthe*, *Salix repens*, *Carex nigra*, *Pedicularis sylvatica*, *Sphagnum compactum*, *Sph. tenellum*.

The *Erica tetralix* heath is found throughout the country in places that are swampy in winter and not too dry in summer. This milieu is particularly met with near small oligotrophic ponds in the heath where *Erica* often forms a belt between the water and the surrounding dry heath. It also occurs in bowl-shaped depressions that are not sufficiently deep for containing a pond; there only the *Erica* and the *Calluna* belt are present. In this way we get small areas with Erica in the *Calluna* fields or around the ponds. Extensive *Erica tetralix* heaths occur only in Twente and Drente on level till deposits left there by the inland ice which are overlain by coversand up to 1 m thick. It is this combination of a permeable sand layer with a layer of impermeable till underneath that provides the required habitat: flooded in winter and damp in summertime. Owing to the presence of loam with its great water-retaining capacity the milieu is always moist enough; on the other hand the topography and the presence of coversand render it not quite suitable for the development of a bog under the present climatic conditions. Comparable conditions are met with on the low-terrace deposits lying just above the phreatic level in the Gelderse Vallei near Appel and in the northern part of the Kampinase Heide. These areas have some extensive *Erica* fields outside of the North-East-Netherlands.

Across the Dutch border *Erica tetralix* heaths of considerable extent are very rare. In Normandy there occur, very locally, some comparable communities (Landes de Lessay), but in Brittany they are replaced by a vicariant community with *Erica ciliaris*. In Germany there is an important area with *Erica tetralix* heath in the Gildehauser Venn, just across

the border from Oldenzaal. Otherwise in N.W. Germany the *Erica* heath is only found in small patches, possibly a few localities in Schleswig-Holstein or farther to the North in Denmark excepted. Outside the Neterlands East-Friesland was the only region where the community was common before the heaths were extensively cultivated. It is described by GRAEBNER in his 2nd edition of "Die Heide Norddeutschlands" (1925), but from the first edition it is absent because by that time he had not yet visited East-Friesland. Soil conditions in East-Friesland are very similar to those in Drente: post-glacial coversand overlying glacial till deposits. The distribution of the subatlantic *Erica tetralix* heath is apparently not only due to climatic but also, and perhaps mainly, to edaphic factors.

The principal instances of *Erica tetralix* heaths in the Netherlands are situated on the Anser Veld near Dwingelo, the Eexter Veld, on the estate of Twickel near Delden and Beckum, the Boeteler Veld, the Achterveld of Neede, the Appelse Heide, and the Kampinase Heide.

3.1. *Erica tetralix heaths*

Floristic composition, ecology, and geographic distribution as described above.

3.1.1. *Erica tetralix-Cladonia-Hypnum variant*

The moss layer consists largely of *Cladonia impexa* and *Hypnum cupressiforme* var. *ericetorum*. Often one of the two species is dominant and the other may occasionally be lacking. Other constituents of the moss layer are e.g. *Cladonia sylvatica*, *Cl. squamosa*, *Cl. uncialis*, *Cornicularia aculeata*, *Dicranum scoparium*, *Pleuzorium schreberi* and *Leucobryum glaucum*.

The groundwater table is on the whole somewhat lower than in the following variants. The B_1 is often present, the B_2 is mostly not greasy.

The variant is mainly represented in Drente and Twente, to a lesser degree also in the Achterhoek and in Noord-Brabant.

3.1.2. *Erica tetralix-Sphagnum variant*

Among the wet heaths variants this one is the most distinctive because it is richest in species from the Nardo-Galion. In the moss layer peat-mosses dominate: *Sphagnum compactum* and *Sph. tenellum*; besides there are many liverworts *Odontoschisma sphagni*, *Gymnocolea inflata*, *Lophozia ventricosa*, *Scapania nemorosa*, *Telaranea setacea*, *Cephaloziella starkei*, and a single representative of the *Bryales*: *Campylopus brevipilus*. This species is rather rare in the Netherlands but is a regular component of the present community. Besides it is a frequent component of recently burnt *Calluna-Erica tetralix* heaths (J. J. Barkman, personal communication), where it reaches a height of a few mm only whereas in the *Sphagnum* variant it grows up to several cm high.

The soil is characterized by its high groundwater level that in winter exceeds the surface and in summer is not deeper than ½–1½ m. The humus layer may reach a thickness of 10 cm and is often peaty, as is the A_1. The B_1 is mostly absent, but the B_2 may be well-developed and thick and is then mostly greasy caused by the presence of colloidal iron-humus compounds. The B_2 may also be weakly developed or even wanting; this is the case when gley phenomena are manifest up to the upper horizons of the profile as a consequence of the high phreatic level. The moistness of the soil may be enhanced by the presence of loam or loamy sand.

The *Sphagnum* variant occurs throughout the area of the Dutch heath, but its best representation is in Twente, the Achterhoek and in Drente.

3.1.3. *Erica tetralix-Orchis maculata variant*

Here and there *Orchis maculata* ssp. *ericetorum* occurs also in the wet heath complex, accompanied by *Potentilla erecta, Pedicularis sylvatica, Succisa pratensis, Genista anglica, Gentiana pneumonanthe,* and *Salix repens.* This species list is proof of affinity with the *Nardo-Galion* (PREISING 1949). So many species of this alliance are, however, absent that we cannot place the community under discussion in this alliance. *Erica tetralix* is also too important a constituent, since it is predominant. We may therefore best classify this community as a variant of the *Erica tetralix* heaths.

The soil consists of clay or till with a high groundwater table and a gley profile.

The wet heath with *Orchis maculata* is one of the rarest variants. It was only found in three localities, viz. on the Eexter Veld in Drente, in the Zuid-Eschmarke near Enschede, and near Noordijk in the Achterhoek. WESTHOFF (1958) also describes it from the Beekhuizer Heide near Velp. It formerly occurred more abundantly in the Netherlands' but has become rare by cultivation; see WESTHOFF 1951, 1956; MÖRZER BRUIJNS and WESTHOFF, 1951; and DIEMONT, 1940. It also occurred in N.W. Germany; Westhoff (personal communication) still found it in the nature reserve Bordelumer Heide in Schleswig.

3.1.4. *Erica tetralix-Gymnocolea inflata variant*

Here *Gymnocolea inflata* is dominant in the moss layer, often forming very homogeneous stands. Other species may participate in the formation of this liverwort carpet, e.g. *Odontoschisma sphagni* and *Cephaloziella starkei* (SAALTINK, 1962). There are very few mosses and lichens.

This vegetation occurs in depressions in the Erica tetralix-Sphagnum heaths. The edges, at the transition from the liverworts to the Sphagna, show the optimum development of *Campylopus brevipilus.* The *Gymnocolea* variant sometimes develops in places in the *Erica tetralix*

heath where sods have been removed. In localities too wet for *Erica*, *Gymnocolea* grows with *Rhynchospora fusca*. The area of this variant coincides with that of the *Sphagnum* variant.

3.1.5. *Erica tetralix-Myrica gale variant*

Myrica gale forms a variant of which *Salix repens* is also a regular component. The moss layer contains species of the *Spagnum* as well as of the *Cladonia-Hypnum* variant, but their coverage is considerably lower. Particularly in its structure this variant is different. The dwarf shrub layer is 70–100 cm high, 30–50 cm in the other wet heath variants. This height is not only reached by *Myrica* and *Salix* but also by *Molinia coerulea*. Normally it grows homogeneously dispersed throughout the wet heath, but in this heath it forms tussocks 30–60 cm high, resulting in a rugged ground hard to penetrate. On the tops of these tussocks grow the species from the moss layer of the *Cladonia-Hypnum* variant, between the tussocks those of the *Sphagnum* variant, on the sides preferably liverworts and *Campylopus* species.

The distribution of the *Myrica* variant on a *Erica tetralix* heath is intimately connected with the local topography. *Myrica* and the *Molinia* tussocks are confined to the depressions in the terrain. The latter are often connected and run into a creek valley where *Myrica* forms a belt between the low, open *Erica* heath (*Spaghnum* and *Cladonia-Hypnum* variant) and the *Betula-Salix* wood bordering the watercourse.

The soil shows a wet podzol with gley phenomena up to the A horizon or a gley. Always distinct horizontal or vertical movements, or both, are observed in the groundwater. It is a very stable community, as shown, i.a. by the height of the *Molinia* tussocks which take many years to develop.

The *Myrica* variant occurs mainly in Twente (SAALTINK, 1962), the Achterhoek, and tributary valleys of the Maas near the Meinweg and near Opgrimbie in Belgian territory.

3.2. *Erica tetralix-Empetrum heaths*

Just like the dry and the humid heath complex, the wet heath complex has a variant with *Empetrum nigrum*. It hardly differs from the other *Erica tetralix* heaths except by the presence of *Empetrum*. In the moss layer at the one extreme *Cladonia* or *Hypnum* are dominant, at the other *Sphagnum*.

The wet *Empetrum* heats were only met with in in south-eastern Fiesland (valley of the Konings Diep and near Appelscha) and in the adjacent part of Drente near Diever.

On the West-Frisian islands the *Erica* heath is always mixed with *Empetrum*, an association described as *Empetro-Ericetum* by WESTHOFF (1947). It differs from the inland *Empetrum* variant by littoral differentiating species (i.a. *Carex trinervis*) and is connected with the coastal *Ericeta* of the German North Sea and Baltic Coasts.

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