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THE VEGETATION OF SCOTTISH PINE WOODLANDS AND DUTCH ARTIFICIAL COASTAL PINE FORESTS; WITH SOME REMARKS ON THE ECOLOGY OF LISTERA CORDATA

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1. Introduction

Coniferous woodland is not indigenous to the semi-humid and sub-atlantic temperate lowland climatic region of the Netherlands. However, extensive forests of conifers have been planted, mainly since the end of the 18th century. *Pinus sylvestris* and *Picea abies* were the main species planted up to the 20th century, but more recently *Pseudotsuga menziesii*, *Larix leptolepis*, and to a lesser extent other species have been used. In the coastal dune area, *Pinus nigra*, both ssp. *nigra* and ssp. *laricio*, is the exotic tree that is planted most frequently. From an ecological viewpoint, these forests have not so far been considered as separate plant associations. Since they were mostly lacking in faithful [2]) species, they have been classified as "cultivated forest communities" under the native deciduous woodland associations, in most cases inside the *Querceto-Betuletum* (vide e.g. Mörzer Bruijns & Westhoff 1951, Westhoff 1954b, 1955, 1957).

In the course of the last century, however, some circumboreal-montane neophytes have migrated spontaneously into these artificial forests. This has also been observed nearly in Germany (Ascherson & Gräbner 1907, Hegi, Schütt 1936 etc.). So far, in the Netherlands *Goodyera repens*, *Linnaea borealis* and *Lycopodium annotinum* were known as such neophytes, though some doubt existed as to whether these species should be considered as "glacial relics". *Goodyera repens*, which was not mentioned by Oudemans (1874), was first recorded in the Nether-

[1]) The following communication is to be regarded as a result of field work carried out during his term of office at the Laboratory of Plant Taxonomy and Plant Geography at Wageningen by Dr. V. Westhoff, which was completed by a visit to Amrum in 1958, and field work done by Dr. M. F. Mörzer Bruijns (State Forestry Service) and S. Segal (Hugo de Vries-Laboratory). The data obtained were worked out in the R.I.V.O.N. at Bilthoven by Dr. V. Westhoff in collaboration with S. Segal.

[2]) Following Poore (1955 as did Barkman (1958), we replace the term "characteristic species" in the sense of the Braun-Blanquet method (= espèce caractéristique, Charakterart, kensoort) by "faithful species", as British ecologists use the term "characteristic species" in another sense.

lands in 1880 in the Leuvenum forest near Hulshorst (Prodromus Florae Batavae ed. altera I, 4, 1916); *Linnaea borealis*, not yet mentioned in the Prodromus Florae Batavae ed. altera (I, 2, 1903), was recorded first from Appelscha in 1920 and from Hoogeveen in 1928 (BEYERINCK, 1929b). BEYERINCK (l.c.) stated that the latter pine forest dated from 1888 and concluded that *Linnaea* might have established itself there after 1888. From morphological observations, he estimated the plants to be 26 years old, which means that the species must have been present in 1903, when the pine forest was only 15 years of age. On the other hand THYEN (in BUCHENAU, 1936, p. 380) observed, that nearby in Germany *Linnaea* did not occur in woodlands before the pines fruited, the species apparently being introduced by seed devouring birds; MEYER & VAN DIEKEN (1947, p. 193) suggest that the trees must be at least 70 years old before *Linnaea* occurs. At present 12 localities of *Linnaea* are known in the North Netherlands, viz. 11 in the Drenthian District (HOOGENRAAD, 1951; VAN OOSTSTROOM, 1958, in litt.) and one on the Westfrisian island of Terschelling, where it has been discovered quite recently (1958) in Scotch pine forest (WILCKE, 1958; see § 4 and table 3). Moreover, there is one locality further to the South near Hulshorst in the Guelder District (VAN OOSTSTROOM, 1958, in litt.). For *Goodyera repens*, 17 localities are recorded in the "Plantenkaartjes van Nederland" (IV, 1937, p. 214) and are distributed throughout the mainland of the country. In 1955, mr. T. SALVERDA (Groningen) discovered *Goodyera repens* for the first time on the Westfrisian islands, viz. on the island of Ameland in an artificial forest of *Pinus nigra* ssp. *nigra*. In 1957, the present authors observed the species for the first time on the island of Terschelling in two localities, one in Austrian and the other in Corsican pine forest. In relatively old pine-forests on the Dutch mainland, these neophytes are often accompanied by other species which are, in general, characteristic of coniferous forests, but also occur in the Netherlands in old deciduous woodland, e.g. *Trientalis europaea*, *Pyrola rotundifolia*, *P. minor*, *Vaccinium myrtillus*, *V. vitis-idaea*. These species, like the neophytes themselves, are considered faithful species of the phytosociological order *Vaccinio-Piceetalia* and the alliance *Vaccinio-Piceion* (see e.g. BRAUN-BLANQUET, SISSINGH & VLIEGER 1939, OBERDORFER 1957). There is some reason, therefore, to consider the artificial pinewoods of the Netherlands and adjacent Germany as a "nascent association" of this alliance, as was suggested for dwarf shrub communities of the same alliance on the Westfrisian islands by WESTHOFF (1947).

We consider that HOOGENRAAD (1951) was wrong in designing *Goodyera repens* and *Linnaea borealis* as "glacial relics" and the same is probably true for the North-German plain. As early as 1907, ASCHERSON & GRÄBNER (p. 896) wrote about *Goodyera:* "Im nordwestdeutschen Flachlande selten, dort wie in Schleswig-Holstein und Dänemark wohl erst nach der Anpflanzung der Nadelwälder mit *Linnaea* und *Chimaphila* eingeführt. Dasselbe gilt wohl auch von dem vorkommen in den Niederlanden und Belgien und auch in der Rheinprovinz ist die Pflanze erst 1906 (abgesehen von wohl unrichtigen älteren Angaben)

aufgefunden worden". This is also the opinion of HEGI (II, 1909) and SCHÜTT (1936), and we cannot agree with MEYER & VAN DIEKEN (1947) who still consider *Linnaea borealis* in N.W.-Germany as a glacial relic.

In recent years, the number of pine forest neophytes has been further increased by the inclusion of *Listera cordata*. This small orchid had only been recorded once in the Netherlands: COMMELIN (1683, p. 82) mentioned *Listera cordata* (sub nomine *Ophris minima*, B. pin. = *Bifolium minimum* J. Bauh.) from dune valleys at Overveen near Haarlem "op opene luchtige plaatsen" (i.e. in clear, open habitat, so not in woodland); this record has been taken over by DE GORTER (1781, p. 237). No botanist ever found the species again and in later years it was considered to be no longer indigenous (at first by OUDEMANS 1874) or even an erroneous determination (Prodromus Florae Batavae, I, 4, 1916, p. 1787). However, in 1949 the species was discovered by J. WEIJER in an artificial forest of *Pinus nigra* ssp. *nigra* on the island of Ameland (WEIJER, 1949), the same forest where *Goodyera repens* occurs (see above). In 1953 it was found by J. DEELDER (State Forestry Service) in an artificial forest of *Pinus nigra* ssp. *nigra* in the Western part of the island of Terschelling; in 1955, by J. DEELDER, in similar conditions in the centre of Terschelling, and in 1956, by M. T. JANSEN and D. T. E. VAN DER PLOEG, on the island of Schiermonnikoog, again in a similar locality. Recently, *Listera cordata* has also been observed on the Dutch mainland, near Boschoord (Vledder) by G. JAGER in 1956. It was the first Dutch record in a forest of Scotch pine.[1])

As the pinewoods of Scotland are well-known to be one of the native habitats of *Listera cordata* (TANSLEY, 1949; SUMMERHAYES, 1951; CLAPHAM, TUTIN & WARBURG, 1952; etc.), we examined some Scotch pine woodlands (natural and planted,) during a trip to Scotland in 1956.

2. DISTRIBUTION AND ECOLOGY OF LISTERA CORDATA

HULTÉN (1950) assigns *Listera cordata* to his relatively small group of "boreal-circumpolar plants that are boreal-montane in Europe but with gaps in Siberia". To this group belong also *Galium trifolium*, *Botrychium lanceolatum*, *Pyrola chlorantha*, *Potamogeton filiformis*, *Isoetes tenella*, *Carex buxbaumii*, *Juncus stygius*. SUMMERHAYES (1951) lists *Listera cordata* together with two other orchids (*Gymnadenia albida* and *Goodyera repens*) as belonging to the "northern-montane" element. Several authors agree that in the Southern part of Europe the species is confined to mountains, whereas in the North it occurs also in the plains (HEGI, 1906, SUMMERHAYES, 1951, HERMANN, 1956, etc.); one may ask, however, where these Northern plains begin. Before considering this point in detail, it is necessary to look for the ecological amplitude of the species. Central European plant geographers, as well as British ecologists, have stressed, that *Listera cordata* occurs in two

[1]) During the type-setting, in May 1959, MÖRZER BRUIJNS observed Listera cordata for the first time on the island of Vlieland, near "Nieuwe Kooi", in a forest of *Pinus nigra* ssp. *nigra*, 35 years old; in June 1959, Mr. E. STAPELVELD discovered a second locality for the Dutch ∃ainland, again in the "Drenthian district", in the nature reserve "Tonckensbos", a forest of Scotch pine near Norg.

apparently rather different habitats, viz. (1) on raw humus in damp to moist woodland, with a preference for spruce forest; (2) in open wet heather moorland and in *Sphagnum* bogs (HEGI, 1906, ASCHERSON & GRÄBNER, 1907, CLAPHAM, TUTIN & WARBURG, 1952, BUCHENAU, 1894, SUMMERHAYES 1951, RAUNKIAER, 1942, TANSLEY, 1949, HERMANN, 1956, etc.). In high Savoie (France) it has been observed in mountain pastures on S. slopes (WEIJER, 1949). Though in Central Europe the woodland habitat is damp to moist, this is not necessarily so in the colder Scandinavian climate with its smaller evaporation rate. For example PALMGREN (1922) and S. SEGAL (unpublished observations) observed *Listera cordata* there in dry as well as in moist woodland. PALMGREN even remarks, that the species may be less frequent in a relatively moist habitat. As far north as Prussia, however, *Listera cordata* is still restricted to moist and wet localities (STEFFEN 1931, GROSSER 1955).

Considering the preference of *Listera cordata* for either woodland or moorland, it has been suggested, that two ecotypes could be distinguished (SUMMERHAYES, 1951). However, as the latter author points out, the two habitats may not really be so different, since the soil is usually acid in both habitats and the small plants in the open localities usually grow in the shelter of comparatively tall heather on north-facing slopes or in the wet *Sphagnum* of raised bogs (see also METCALFE, 1950). Such an ecological amplitude suggests an oceanic, humid climate, in which the difference between the microclimates in and outside the woodland is less pronounced than in a more continental and drier climate. It is strange, therefore, that OBERDORFER (1949) describes the area of *Listera cordata* as "subarctical-boreal-(continental)", whereas BUCHENAU (1936), writing from a somewhat local point of view, mentions it as "atlantic". Since *Listera cordata* is common both in Norway and Sweden (HULTÉN, 1950) and fairly common not only in the Northern half of Britain, but even throughout Ireland (PRAEGER, 1934; SUMMERHAYES, 1951) the qualification "continental" is puzzling.

It is remarkable that Central European plant sociologists (BRAUN-BLANQUET, SISSINGH & VLIEGER 1939, OBERDORFER 1949, 1957) still seem to neglect the open (moorland) habitat of *Listera cordata* and consider it a characteristic woodland species, viz. a faithful species of the alliance *Vaccinio-Piceion* or (OBERDORFER 1957) of the order *Vaccinio-Piceetalia*. Since *Listera cordata* occurs frequently in both the woodland and moorland habitats in Britain and Denmark (TANSLEY 1949, SUMMERHAYES 1951, RAUNKIAER 1942), whilst in Ireland the species is confined to the latter type (except for one record in a *Taxus* woodland; PRAEGER 1934, WEBB 1943, TANSLEY 1949), it seems that in Central Europe *Listera cordata* is much rarer in the "open" habitat than in woodland, whereas nearer to the boreo-atlantic coast there is a gradual increase in its preference for the open habitat. WEIJER (1949) mentioned, however, that in High Savoie (French Alps) *Listera cordata* was found in mountain pastures only. It is also remarkable, that Central European plant geographers stress that *Listera cordata* is limited to a true shadowy, woodland microclimate and that it disappears

when the wood had been thinned (HEGI 1906, p. 388; BUCHENAU 1894, p. 538). On the contrary SUMMERHAYES (1951, p. 173), in Britain, observed a preference for open habitat within woodland, the species evading dense shade.

In France (FOURNIER 1946) and in Germany, except for the NW. plains (HEGI, 1909), *Listera cordata* is still restricted to the mountains. In England, however, it occurs in the lowland region too; in Ireland it descends to 10 m above sea level (PRAEGER, 1934), as might be expected in an extremely oceanic climate. In Denmark (11 localities, fide HULTÉN, 1950) it occurs also in the lowland, not only in probably artificial coniferous forest (see below), but also in bogs, where it is undoubtedly native (RAUNKIAER, 1942).

STEFFEN (1931), in his description of the vegetation of East Prussia, designated *Listera cordata* as a very faithful ("besonders charakteristische") species of the "Fichtenzwischenmoore", i.e. a moist spruce woodland with a bog character. Though it appears from his table 25 that *Listera cordata* is absent if *Carex* species tend to dominate — when the swamp aspect thus predominates over the woodland aspect— it is clear that this habitat of *Listera cordata* presents a transitional community between the two major habitats previously mentioned: moorland and woodland.

In Belgium *Listera cordata* has been observed only once in the jurassic (mountain) district, but there is some doubt whether the locality of this specimen is reliable (LAWALRÉE & VANDENBERGHEN, 1946).

There has been some controversy as to the question, whether in the N.W. plains of Germany *Listera cordata* is native, or a neophyte which became established after the artificial coniferous afforestation during the last 150 years. ASCHERSON & GRÄBNER (1907) give the latter hypothesis, but HEGI (1909) states that in the Northern German plains *Listera cordata* has been found also in bogs and moorland; however, BUCHENAU (1894, 1936) and MEYER & VAN DIEKEN (1947) do not confirm the latter statement.[1])

A rather special habitat is mentioned by SUMMERHAYES (1951, p. 204), viz. "quite open . . . . , damp marshy places among sand dunes near the sea", where *Listera cordata* has been found together with *Listera ovata* and *Corallorhiza trifida!* This refers to Britain, but it is also an indication, that COMMELIN (1683), who mentioned the species from open dune valleys on the Dutch coast, might have been right.

In this connection it is interesting to know that *Listera cordata* occurs in a similar habitat on the North-Frisian island of Amrum, where it has been observed in a damp dune valley (CHRISTIANSEN, 1953). Here the species occurs spontaneously in a natural habitat, outside of conifer plantations. The locality, the only native one yet known in the

è) In May 1959, the author visited one of the two localities of *Listera cordata* in the "Land" Rheinland-Westfalen, viz. Einsiedelei near Olpe in Sauerland, in the lower mountain zone; they are the most Northern outposts of the Central European area of the species. The habitat of the visited spot, a primeval birch swamp (Betuletum pubescentis), is a remarkable one and reminds some Scottish and Scandinavian habitats of *Listera cordata* (see below).

lowland of Germany, may be considered as a southern outpost of the Scandinavian area. In 1958, the author had the opportunity to visit the spot. *Listera cordata* appeared to grow here in a dune moorland on acid sand soil, under and between tall plants of *Calluna vulgaris*, *Erica tetralix*, *Empetrum nigrum* and *Vaccinium uliginosum*. The ecological situation presented a striking resemblance to that in the moors of the Scottish highlands (see below). On the other hand, the vegetation was quite similar to that of moist dune heather formation on the Westfrisian island of

TABLE I

Dune valley moorland, habitat of Listera cordata, North Frisian island of Amrum, Germany

Number of record	1	2
Year	1958	1958
Date	19/6	21/6
Shrub + Herb layer, degree of dominance in %	90	100
Moss layer, degree of dominance in %	10	60
Surface studied, in m²	15	10
Listera cordata	1.2	+.1
Dwarf shrub species:		
Empetrum nigrum	4.2–3	3.3
Salix repens	3.2	2.2
Calluna vulgaris	3.2	2.2
Erica tetralix	2.2	2.2
Vaccinium uliginosum	2.2	2.2
Genista anglica	+.1	+.2
Betula pubescens	+.1	+.2
Herbs, grasses, mosses:		
I. Indicators of heaths, moorland and acidic grassland (Nardo-Callunetea, Nardo-Galion saxatilis):		
Molinia coerulea	2.2–3	3.2
Potentilla erecta	+.1	+.1
Luzula campestris var. congesta	+.1	1.1
Pedicularis sylvatica	+.1	(+)
Galium saxatile	—	+.2
Dicranum scoparium	—	2.3
Pleurozium schreberi	—	1.2
II. Other grassland indicators:		
Festuca ovina ssp. capillata	+.2	2.2
Anthoxanthum odoratum	1.1	1.1
Festuca rubra	+.2	—
Rumex acetosa	—	+.1
III. Swamp indicators (Scheuchzerieto-Caricetea fuscae, Caricetalia fuscae, Caricion canescentis-fuscae):		
Eriophorum angustifolium	2.1–2	2.1
Carex echinata	—	+.1
Viola palustris	—	+.1
IV. Bog indicators (Oxycocco-Sphagnetea):		
Oxycoccus paluster	—	2.2
Sphagnum papillosum	+.2	—
V. Hygrophyte companions (± indifferent):		
Pseudoscleropodium purum	1.2	3.3
Pohlia nutans	+.2	—

Terschelling. This may be shown by two sample plot analyses (records), made by the author on the Amrùm locality and given in table 1. The only species of this table which are wanting in the dune moorland of Terschelling are *Oxycoccus paluster* (there replaced by *Oxycoccus macrocarpus*) and *Listera cordata!* In comparing the two records of table 1 it is obvious that the rate of abundance and sociability of *Listera cordata* is higher in the first record. This may be due to the much denser moss cover in the second record, in combination with a dense dwarf shrub layer. Since at present *Listera cordata* thrives abundantly in artificial pine forests on the Dutch Westfrisian islands, it may be expected that the species will establish itself here also in the more natural conditions of the wet dune valleys. This seems much more probable than a movement southwards since (1) *Listera cordata* is acidiphilous and the dunes in Holland S. of Alkmaar are rich in lime ("Dune district") but N. of Alkmaar poor in lime ("Wadden district"); and (2) most of the wet dune valleys in the Dune district have been drained.

Considering the woodland habitat, we may ask in what type of woodland is *Listera cordata* likely to occur. In the Alps and the Central European secundary mountain-chains, there is a marked association with the subalpine *Picea*-forest, and to a lesser extent with the montane *Abies-Picea*-forest. BRAUN-BLANQUET, SISSINGH & VLIEGER (1939) mention it as a constant and faithful species in the *Listera cordata-Hylocomium umbratum*-woodland association in the Jura (1200–1500 m alt.) on calcareous subsoil, in the *Piceetum subalpinum* in the Alps (1200–1800 m. alt.), and in the *Picea excelsa-Hieracium rotundatum*-association in the Eastern Carpathes, whereas it occurs with a lower presence degree as a faithful species in the *Piceetum tatricum* (N. Tatra 1100–1200 m alt., S.-Tatra 1500–1650 m alt.) and in the *Mastigobryeto-Piceetum* in the Black Forest (600–1000 m alt., confirmed by OBERDORFER, 1957); all these associations belong to the subalpine sub-alliance *Rhodoreto-Vaccinion*. In all these mountains, *Listera cordata* appears to be absent from pine-woods (*Pinus sylvestris*, *P. cembra*, *P. nigra*, *P. mugo*). AICHINGER (1949), in a study of the succession types of Central-European woodland communities, comes to a similar conclusion, for he finds *Listera cordata* to be a characteristic spruce forest species and he mentioned it only once from a pine forest ("*Pinetum silvestris-basiferens*") (l.c. p. 90) in the Eastern Alps near Villach. He comments that this forest is really a secondary pioneer community, rejuvenated after the cutting down of a spruce forest and has a tendency to develope into a spruce forest again. However, in the Eastern Pyrenees, *Listera cordata* appears to be a faithful species of the *Rhododendron ferrugineum-Listera cordata*-association. in which *Pinus mugo* is the dominant tree (BRAUN-BLANQUET c.s. 1939). In view of the association of the species with pine woods in Scotland, it is possible that this Pyrenean association is of a more oceanic character. — In the montane Central European sub-alliance *Abieto-Piceion*, *Listera cordata* seems to be much rarer; it has been mentioned only in the *Aremonieto-Piceetum* of Yougoslavia (BRAUN-BLANQUET c.s. 1939) and in the *Galio-Piceetum* of the Eastern Black Forest (OBERDORFER, 1957).

The woodlands of Northern Europe are united by BRAUN-BLANQUET c.s. (1939) into the sub-alliances *Piceion septentrionale* and *Phyllodoco-Vaccinion; Listera cordata* has been observed mainly in the former. The *Piceion septentrionale* does not only include coniferous woodland, but also the boreal-subalpine and sub-arctic deciduous forest, mainly birch forests. HULTÉN (1950) describes the Scandinavian habitat of *Listera cordata* as "fugtig barrskog" (wet coniferous woodland), and BARKMAN (1951) informs us that *Listera cordata* in N.-Sweden is "more or less restricted to spruce forest". Nevertheless, BRAUN-BLANQUET c.s. (1939), following KUJALA (1929), mention *Listera cordata* as a constant and faithful species of the *Betuleto-Vaccinietum lapponicum*, a birch woodland type occurring to the North of the spruce-limit between 69° and 69°30′ (see also BEYERINCK, 1936). The species is also present in the Scandinavian spruce forest, *Piceetum fennoscandicum*, and in the *Pineto-Vaccinietum myrtilli arctostaphyletosum*, which occurs in Sweden, Finland and Estland and is essentially a Scots Pine forest. Moreover, SJÖRS (1949) reports that *Listera cordata* has been observed in an alder wood (*Alnus glutinosa* x *incana*) in Dalarna, Sweden.

Within the sub-alliance *Phyllodoco-Vaccinion*, *Listera cordata* occurs in the *Hylocomieto-Betuletum tortuosi*, a wide-spread Scandinavian mountain birch woodland on very acid raw humus. BRAUN-BLANQUET, SISSINGH & VLIEGER (l.c.) mention it only in the relatively oceanic subassociation *Hylocomieto-Betuletum tortuosi cornetosum*, with presence degree I, based on Norwegian and Finnish records from NORDHAGEN and KUJALA. SEGAL (in litt.) made a record of it near Björkliden, Sweden (1957, 450 m alt.) with some plants of *Listera cordata* in it.

In Scotland, *Listera cordata* occurs occasionally in the Caledonian pine forests of the Highlands (TANSLEY 1949, SUMMERHAYES 1951) and in Highland birchwoods, e.g. in Caithness (id.); as well as in tall *Calluna* and *Vaccinium* moorland vegetations, in damp or moist habitats and above the timber line, e.g. in the Cairngorms (METCALFE, 1950).

From these data it is obvious, that the woodland habitat (Scots pine and birch) of *Listera cordata* in Scotland corresponds more closely to that of Scandinavian than to that of Central Europe.

3. SCOTTISH PINEWOOD

During an excursion in Scotland from 29th June to 5th July 1956 we had the opportunity to see some pinewoods. Sample plot analyses records after the BRAUN-BLANQUET method were made as follows:

1. Near Fochabers, less than 200 ft (70 m) altitude. Spontaneous pinewood, age ca. 100 years, 15 m high. 30-VI-1956.

2. Culbin Sands, N. coast of Morayshire. Sea sand dunes, fixed from 1921–1951 by afforestation (OVINGTON, 1950; see also Anon., 1953). Forest of *Pinus nigra* ssp. *laricio*, age 45 years, 15–20 m high, I-VII-1956.

3. Currwood near Dulnanbridge, between Inverness and Aviemore, ca. 700 ft. (230 m) alt. Pinewood, regenerated after destruction (by fire?), several times thinned, not pastured. Age ca. 80 years, 18 m high. 1-VII-1956.

4, 5. Part of the Abernethy Forest adjoining Loch Garten near Aviemore, ca. 800 ft (270 m) alt. Old native pinewood, regenerating spontaneously. Open canopy of Scots pines, 20 m high, age ca. 200 years, alternating with groups of younger pines in varying ages, up to ca 10 m high. We were informed by the Nature Conservancy, Scotland, that this forest represented a characteristic example of group regeneration of pine at all size stages, showing the formation of dense thickets in the neighbourhood of parent trees and the natural thinning of these thickets. The pines have regenerated actively on a heather area not recently burned. This small piece of forest has attained the structure at which the Conservancy's management of pine forest is aiming in the first instance and but for any catastrophe, such as fire or wind-blow, it should maintain itself indefinitely. Pine forest with this structure is extremely rare, even in Scandinavia. The moss mat and fermentation layers are not as thick or dense as in the normal forests of these types which follow fire. 1-VII-1956.

6. Cairngorms National Nature Reserve near Aviemore, ranging from 840 ft (260 m) in altitude to 4296 ft (1309 m). The splendid Scots pine woodland still found here is, as the Nature Conservancy, Scotland, kindly informed us, the largest surviving area of the ancient Caledonian Forest, parts of which are still self-regenerating and contain their naturally associated flora and fauna. One of our analyses has been made in an open apparently primeval woodland on glacial drift, at Loch an Eilein near Rothiemurchus, a forest not managed since time immemorial. Old pines ca. 300 years of age, with heavy round crowns and far apart, alternated with younger trees of between 200–40 years old. Our second analysis was not made in a primeval woodland, but, on a west exposure on glacial drift, in a naturally regenerating forest of Scots pine, cut down (or blown down?) ca. 80 years ago and with no record of a fire. Besides the species mentioned in our analyses (see table), some other characteristic pine wood species occur in the Reserve, viz. *Linnaea borealis*, *Pyrola media* and very rarely *P. uniflora* (information by the Nature Conservancy). *Listera cordata*, however, was not mentioned nor was it seen by us here. 2-VII-1956.

The pine forest of the Cairngorms has also been described by TANSLEY (1949, p. 447–449) under the name "Rothiemurchus Forest".

7. Kinlochewe Forest near Beinn Eighe at the W.-coast of Scotland, county Ross and Cromarty. Altitude ca. 1000 ft (300 m). 3-VII-1956. In this extreme oceanic climate the annual precipitation attains one of the highest values in the United Kingdom (ca. 70 inches = 2540 mm), whilst the number of mean annual hours of bright sunshine (less than 1200) is very low; the W.-winds are very strong and continuous. Nevertheless, the natural climax of the region would be a pine forest mixed with deciduous trees and it is mainly by overgrazing by red deer and sheep that woodland has become very scarce and its regeneration difficult. Our analysis was made on a N.-exposure on a very poor soil with a wet podsol profile (30 cm. raw fermentation layer, 20–30 cm. bleached sand layer). As in the Cairngorms, the tree layer consisted of some 200–300 years old Scots

pines, ca. 30 m high, and between them trees of 150–100 years, 80–40 years, shrubs and saplings. Dr. D. Mc VEAN (The Nature Conservancy, Scotland), who studied this woodland thoroughly, kindly showed us a characteristic locality, so that nearly all species occurring in it would occur in our analysis. Dr. Mc VEAN also informed us that *Pyrola*-species do not occur here; they are confined to woodland on richer soils.

The Kinlochewe Forest has also been described by TANSLEY (1949, p. 450) under the name "pine-forest on the south-western shore of Loch Maree".

Comparing the analyses made in these localities, it became clear that the Highland pine woods of Currwood, Abernethy Forest, Cairngorms Reserve and Benn Eighe had a great similarity with respect to floristic composition, history, structure of vegetation and altitude, whereas the forests of Fochabers and Culbin Sands, both at lower altitudes, differed considerably form the former. Therefore, 6 analyses of the former woodland type are combined in table 2. A sample list of the forest of Ballochbuie at Balmoral, taken from TANSLEY's (1949) description of the Caledonian Pine Forest, has been added to the table as nr. 7. The description of the Highland Scots pine woodland type by TANSLEY suggests that nearly all important localities where this type survives are represented in our table.

TANSLEY (l.c.) points out, that the Caledonian Highland pine wood has to be considered a somewhat impoverished Southwestern outpost of the Fenno-scandinavian coniferous woodlands. In comparing table 2 with the vegetation tables of the boreal sub-alliance *Piceion septentrionale* (alliance *Vaccinio-Piceion*, order *Vaccinio-Piceetalia*) by BRAUN-BLANQUET, SISSINGH & VLIEGER (1939), it is clear, indeed, that the Highland pinewood fits very well into this sub-alliance. BRAUN-BLANQUET c.s. (l.c.) only present a short remark on the Scottish pinewoods (p. 67–68). They do not give a table of it, but consider them to be either a sub-association of the *Pineto-Vaccinietum myrtilli* or, more probably ("wohl eher aber"), a special association. Curiously enough, they state in their general outline (l.c., p. 5) that the order *Vaccinio-Piceetalia* does not occur in the humid region of Western Europe!

Compared to the Fennoscandian associations of the sub-alliance, the Scotch pinewood appears to be slightly poorer because of (1) the absence of *Picea abies*, *Lycopodium complanatum* and *Pyrola chlorantha*, which are not native at all in Britain (CLAPHAM, TUTIN & WARBURG, 1952); (2) the absence of *Lycopodium selago*, *Empetrum hermaphroditum*, *Vaccinium uliginosum* and *Lophozia lycopodioides*, because in Scotland these species do not occur in woodland, but in open moorland (CLAPHAM, TUTIN & WARBURG, 1952; MACVICAR, 1912), apparently as a consequence of the oceanic climate (cf. § 2). On the other hand, the Scotch pinewood contains at least two geographically differential eu-atlantic species, viz. *Carex binervis* and *Erica cinerea*. According to HULTÉN (1950) both occur also in the extreme S.W. part of Norway, so that it may be expected, that in Western Norway a gradual transition may be observed between the Scottish pinewood type and the *Pineto-Vaccinietum myrtilli*. The presence of *Betula pubescens* ssp. *odorata*

(Bechst.) E. F. Warburg and *Populus tremula* constitutes a difference between boreal and alpine coniferous woodland; these species are given in table 2 as differential species of the sub-alliance *Piceion septentrionale*, according to BRAUN-BLANQUET, SISSINGH & VLIEGER (1939.)

A faithful, characteristic species of the Scottish pinewood is the dominant *Pinus sylvestris* ssp. *scotica* (Schott) E. F. Warburg, which seems to be a Scottish endemic. We are not quite sure, however, that there exists a real difference between this taxon and the *Pinus sylvestris* of Norway and Sweden. For this reason and for the possibility of a gradual transition between the Scottish pinewoodland type and the *Pineto-Vaccinietum myrtilli* in S.W.-Norway (see above), we think it better not to describe as yet the Scottish pine woodland type as a new association. Provisionally we consider it as an atlantic vicariant of the *Pineto-Vaccinietum myrtilli* (*Pineto-Vaccinietum myrtilli atlanticum*).

For the sake of comparing the Scandinavian records with those of Scotland we present next vegetation record of a *Pineto-Vaccinietum myrtilli* forest near Hån (S.-Sweden), made and kindly offered to us by Mr. S. SEGAL.

Date: 30th August 1952. Surface studied: 300 m².
Tree layer: height 12 m, degree of dominance 80–90 %:

Pinus sylvestris (ssp.?)	4.1	Picea abies	2.1

Shrub layer: height to 40 cm, degree of dominance 20 %:

Vaccinium myrtillus	2.2–3	Calluna vulgaris	+.2
Vaccinium vitis-idaea	1.2		

Herb layer: 30 %

Listera cordata	+.1	Dryopteris linnaeana	+.2
Goodyera repens	+.2	Melampyrum sylvaticum	1.2
Pyrola minor	1.1	Solidago virgaurea	+.1
Pyrola chlorantha	+.1	Festuca ovina	+.2
Ramischia secunda	+.1–2	Deschampsia flexuosa	+.2
Linnaea borealis	2.2	Rumex acetosa	+.1
Lycopodium annotinum	1.2	Stellaria sp.	+.1
Trientalis europaea	2.2		

Moss layer: 40 %

Ptilium crista-castrensis	+.2	Pleurozium schreberi	2–3.2
Hylocomium splendens	1–2.2	Dicranum scoparium	2.2
Hylocomium spec.	1.2	Peltigera cf. aphtosa	+.2

Mr. SEGAL emphasizes the fact that the habitat was a dry one.

According to WHITE (1898, cit. in TANSLEY, 1949) in Scotland the following herb species may be confined to this community: *Goodyera repens*, *Corallorhiza trifida* and *Pyrola uniflora;* TANSLEY adds that these species are on the whole rare, which may be the reason why only *Goodyera repens* is represented in our table. The four taxa *Pinus sylvestris* ssp. *scotica*, *Goodyera repens*, *Corallorhiza trifida* and *Pyrola uniflora* may be considered faithful species of the community. WHITE (l.c.) also gives a number of herbs characteristic of (but not confined to) the *Pineto-Vaccinietum atlanticum;* four of them (*) occur in our table 2:

Linnaea borealis
* Listera cordata
Pyrola media
* Pyrola minor
* Pyrola rotundifolia
Pyrola secunda
* Trientalis europaea

These species occur also in birch woodland or in open moorland. It is possible, however, that some of them will present a presence optimum in the *Pineto-Vaccinietum atlanticum*, so that they may be considered faithful species of this community; this cannot be concluded on the base of the available data.
We are therefore giving the (*) species in table 2 as faithful species of the alliance, order and class, according to the classification by OBERDORFER (1957). We also put into these categories those species (phanerogams and mosses), which in the whole of their area have to be considered as such, although they (at least the phanerogams) may show no preference for pinewood in the Highlands: *Vaccinium myrtillus*, *V. vitis-idaea* and *Arctostaphylos uva-ursi*.

It is probable, that within the *Pineto-Vaccinietum atlanticum* several subassociations and (or) variants may be distinguished, e.g. a unit on poor soil lacking *Pyrola* ssp. (see also § 2) and the species indicating mild humus (*Viola riviniana*, *Luzula pilosa*), but rich in *Sphagnum* ("*sphagnetosum*"), and a unit with *Pyrola*, *Viola*, *Luzula pilosa*, but with less or no *Sphagnum* ("*pyroletosum*"). The present material, however, does not allow us to make such a distinction on the basis of table 2. It may appear from this table, that *Listera cordata* is present both in the poor "*sphagnetosum*" (record nr. 6) and in the richer variant (list from TANSLEY), but this is not certain, as in the latter list *Sphagnum* was abundant too.

The two other pinewoods visited by us situated in the lowlands, viz. at Culbin Sands and near Fochabers, do not belong to the *Pineto-Vaccinietum atlanticum*. The artificial Corsican pine afforestation at Culbin Sands showed such an interesting and striking resemblance with the artificial Corsican and Austrian pine afforestations on the Dutch Westfrisian islands, that it will be dealt with in § 4 (see table 3, nr. 7); *Listera cordata* occured there. In the Scots pine forest at Fochabers (< 70 m alt). the following record was made by us:

200 m². Tree layer: age ± 100 years, 15 m high.
Pinus sylvestris (ssp. scotica?) . . 3.1

Herb layer: 100 %

Pteridium aquilinum	4.5	Agrostis stolonifera	+.2
Erica cinerea	3.2	Veronica officinalis	+.2
Deschampsia flexuosa	2.2	Galium hercynicum	+.2
Lonicera periclymenum	2.2	Rubus fruticosus	+.2
Solidago virgaurea	1.1	Fagus sylvatica, iuv.	r
Viola riviniana	1.1	Acer pseudoplatanus, iuv. . . .	r
Teucrium scorodonia	1.2		

Moss layer: 20 %

Pleurozium schreberi	2.3	Hylocomium splendens	+.2
Pseudoscleropodium purum . . .	+.2		

Conspicuous differences with the *Pineto-Vaccinietum atlanticum* are: (1) the absence of some constant characteristics of the latter association, viz. *Vaccinium myrtillus*, *V. vitis-idaea*, *Trientalis europaea*, *Blechnum spicant*, *Melampyrum* spp., *Rhytidiadelphus triquetrus;* (2) the dominance

TABLE II

Pineto-Vaccinietum myrtilli atlanticum

Highland Scots Pine wood community.
Analyses: June–July 1956.
Alliance: Vaccinio-Piceion.
Sub-alliance: Piceion septentrionale.
Order: Vaccinio-Piceetalia.
Class: Vaccinio-Piceetea.

Cu = Currwood
AF = Abernethy Forest
Cai = Cairngorms
BE = Benn Eighe
Ba = Ballochbuie
M = Mörzer Bruijns
W = Westhoff
T = Tansley
u = unknown

Quantitative data in nrs. 1–6 after the scale of Braun-Blanquet, in nr. 7 after the British method.

Number	1	2	3	4	5	6	7
Locality	Cu	AF	AF	Cai	Cai	BE	Ba
Author	M	M	W	M	W	M	T
Date	1 VII	1 VII	1 VII	2 VII	2 VII	3 VII	—
Altitude in meters	230	270	270	>350	>350	300	>350
Tree layer(s), age in years	80	200	200	300	80	250	150
	—	—	±50	200	u	150	u
	—	u	—	80–40	u	80–40	u
Tree layer(s), height in meters	18	20	22	12–15	15–18	30	18
	—	2–10	4–10	5–10	u	20	u
						4–10	
Tree layer(s), degree of dominance in %	70	50	90	40	70	50	u
	—	10	10	20	—	20	
Shrub layer, height in meters	<1	—	1–3	—	<1	—	u
Herb layer, degree of dominance in %	60	70	90	100	100	70	u
Moss layer, degree of dominance in %	90	90	60	80	100	100	u
Surface studied, in square meters	300	250	300	250	250	500	u
Faithful species of the community:							
Pinus sylvestris ssp. scotica, upper tree layer	4.1	3.2	5.1–2	3.1	4.1	3.1	d
Idem, lower tree layer	—	+.2	+.1	2.1	—	2.1	—
Idem, shrub layer	—	—	+.1	—	—	—	—
Goodyera repens	1.1	+.1	—	—	+.1	—	—

Geographically differential species:							
Carex binervis	+.2	—	+.2	+.2	+.2	—	sp [1]
Erica cinerea	+.2	—	—	—	—	1.2	—
Differential species of the sub-alliance (compared with alpine communities):							
Betula pubescens ssp. odorata, lower tree layer	—	—	+.1	+.1	—	+.1	oc
Idem, shrub layer	+.1	—	+.1	—	—	—	—
Populus tremula	—	—	+.1	—	—	—	loc
Faithful species of the alliance:							
Melampyrum pratense ssp. + M. silvaticum	+.2	+.2	+.1–2	1.1	+.1–2	+.1	sp
Plagiothecium undulatum	+.2	—	—	—	+.2	1.2	f
Dicranum majus	—	—	—	—	1.2–3	1.3	o–f
Sphagnum girgensohnii	—	—	—	+.3	+.2	—	va
Sphagnum quinquefarium	—	—	—	—	—	2–3.4	—
Faithful species of the order:							
Trientalis europaea	2.1	+.1	+.1	+.1	+.1	—	—
Rhytidiadelphus loreus	—	—	—	—	+.2	2.2	ab
Ptilium crista-castrensis	—	—	2.3	—	—	+.2	fr
Listera cordata	—	—	—	—	—	+.2 [2]	sp
Faithful species of the class:							
Vaccinium myrtillus	1.3	3.3	4.4	3.3	5.4	3.3	ld
Vaccinium vitis-idaea	+.2	1.1	2.2	3.3	1.1–2	2.2	ld
Pyrola rotundifolia	—	—	+.2	—	—	—	—
Pyrola minor	—	—	—	+.1	—	—	—
Arctostaphylos uva-ursi	—	—	+.3	—	—	—	—
Companion species, occurring more than once:							
Deschampsia flexuosa	3–4.4	2.2	2.2	2.3	1.2	2.2	lf
Calluna vulgaris	1.3	3.4	3.3–4	1.2	+.2	3.3	ld
Sorbus aucuparia	1.1	+.1	1.1	+.1	+.1	1.1	oc
Hylocomium splendens	3.3	3.3	2.3	3.3	4.4	4.4	ab
Galium hercynicum	2.2	+.2	+.2	2.2	—	1.2	sp
Blechnum spicant	+.3	—	+.2	+.1	+.2	+.2	sp
Luzula pilosa	1.2	+.2	1.1–2	1.2	+.2	—	sp

TABLE II *(Continued)*

Number	1	2	3	4	5	6	7
Rhytidiadelphus triquetrus	3.3	3.3	3.3–4	3.3	3.3–4	—	ab
Oxalis acetosella	+.2	+.2	+.2	+.2	—	—	sp
Potentilla erecta	+.1	+.2	+.2	+.1	—	—	sp
Pleurozium schreberi	3.3	3.3	+.2	—	—	2.3	fr
Juniperus communis	—	1.2	2.1–2	2.1	+.1	+.1	—
Viola riviniana	—	+.2	+.2	+.1	—	—	sp
Dicranum scoparium	2.2	—	—	2.2	—	1.3	f
Polytrichum commune	1.3	—	—	+.2	—	—	oc
Pteridium aquilinum	—	—	—	2–3.3	+.2	2.3	—
Molinia coerulea	—	—	—	—	+.2	+.2	sp
Veronica officinalis	+.1	—	+.2	—	—	—	sp
Luzula congesta	+.1	—	—	+.2	—	—	sp
Holcus mollis	+.1	—	—	—	—	—	lf
Dryopteris phegopteris	—	—	+.2	—	—	—	sp
Dryopteris spinulosa	+.1	—	+.1	—	—	—	—
Agrostis canina	—	—	+.2	—	—	—	sp
Equisetum silvaticum	+.1	—	—	—	—	—	sp
Rumex acetosella	—	—	—	+.1	—	—	l
Anthoxanthum odoratum	—	—	+.1–2	+.1	—	—	—

Besides, next species were noted once:

in nr. 3: Anemone nemorosa, Lathyrus montanus, Athyrium filix-femina, Carex nigra, Pseudoscleropodium purum;

in nr. 6: Empetrum nigrum, Quercus robur iuv., Pleurochaete squarrosa (fide Dr. D. Mc VEAN), Thuidium tamariscinum;

in nr. 7: Deschampsia caespitosa, Solidago virgaurea, Polystichum aculeatum, Luzula silvatica, Juncus squarrosus, Nardus stricta, Euphrasia sp., Hieracium sp., Mnium hornum, Campylopus flexuosus, Sphagnum sp.

N.B. As to the large number of accidental species in nr. 7, it should be kept in mind that the author of this list, Sir ARTHUR TANSLEY, did not mention the surface studied, but that probably (according to the method used by him) this surface was very much larger than ours.

[1]) TANSLEY did not indicate Carex binervis, but C. distans; perhaps he was mistaken.

[2]) Not seen by us, but locality indicated by Dr. D. Mc VEAN within the surface studied by us.

of *Pteridium aquilinum;* (3) the occurrence of some typical lowland [1]) forest species, viz. *Lonicera periclymenum* and *Fagus sylvatica;* (4) the absence of all faithful herbs of the *Pineto-Vaccinietum atlanticum.* The Fochabers community bears hardly any resemblance to the order of *Pinetalia* (OBERDORFER, 1957), except perhaps for the hercynic association "*Pinetum variscum*". Somewhat more striking is the resemblance with the montane Central-European *Luzulo-Fagion* alliance, the beech woodland on acid soil.

4. THE PINE AFFORESTATIONS ON COASTAL DUNE SAND ON THE DUTCH WESTFRISIAN ISLANDS AND CULBIN SANDS, SCOTLAND

For understanding and interpreting the secundary vegetation of artificial pine forests on dunes, it is necessary to know the habitat and the vegetation (1) before afforestation and (2) in the dune area adjacent to the forest. A knowledge of (2) enables one to make some estimate of the former conditions which is particularly valuable if these are not known by direct observation (as in the present case). Moreover, dune species will continue to send diaspores into the forest, thus creating or maintaining there a temporary or permanent secundary population ("vicinism" sensu NORDHAGEN. 1939). The number of these migrating species will decrease gradually from the margin to the interior of a forest.

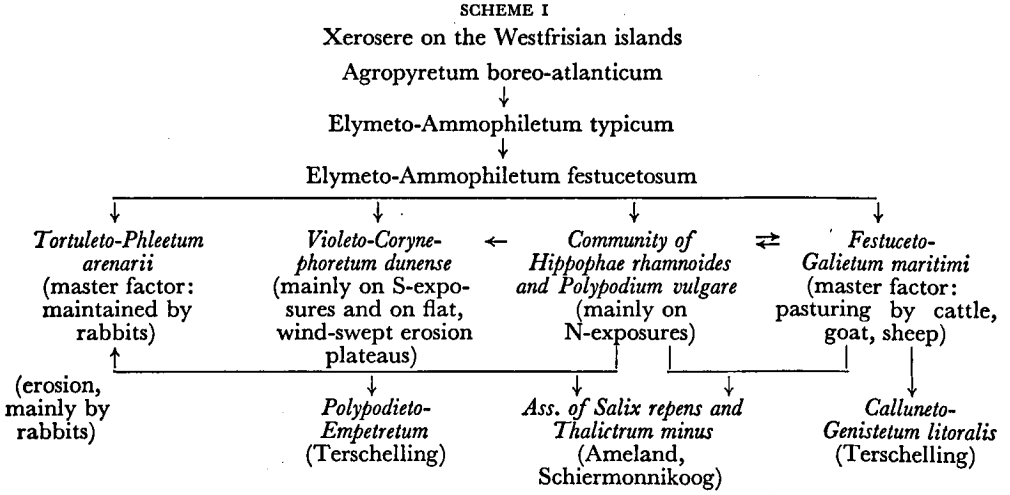
The flora and vegetation of Terschelling have been studied by VAN DIEREN (1934) and WESTHOFF (1943, 1947); the vegetation of Ameland by BRAUN-BLANQUET & DE LEEUW (1936); that of Schiermonnikoog by DEN HARTOG (1952) and WESTHOFF (1954a); and that of Culbin Sands by OVINGTON (1950). The vegetation records of all Westfrisian islands has been summarized by WESTHOFF in MÖRZER BRUIJNS & WESTHOFF (1951); the plant communities with woody species (lignosa) found in the Dutch dune area (incl. the Westfrisian islands) and its inner border have been described by WESTHOFF (1953); and the Dutch dune grasslands by BOERBOOM (1958). The forestry aspects of dune afforestation on the Westfrisian islands have been reported by BOODT (1934).

The dune sand of the islands and the adjacent Dutch dune continent ("Waddendistrict") is poor in lime ($< \pm 1$ %, on Terschelling even $< 0{,}2$ %), in contrast to the Southern "Dune District" (lime content $\pm 3 - \pm 20$ %). From Terschelling to the East, the lime content gradually increases in such a way that the flora of Schiermonnikoog has certain affinities with that of the Dune District. All islands have both a hygrosere, in the wet dune valleys, and, on the dunes, a xerosere which is independent of the phreatic water. In both seres the dunes have been partly afforested so that the wet dune valleys were drained, especially on Terschelling, and have continued to dry up as transpiration by the growing pine plantations increased.

The xerosere as far as it relates to our subject is illustrated by

[1]) Only as regard Scotland.

SCHEME I



scheme I. The names of the communities in which afforestation has taken place have been printed in italics.

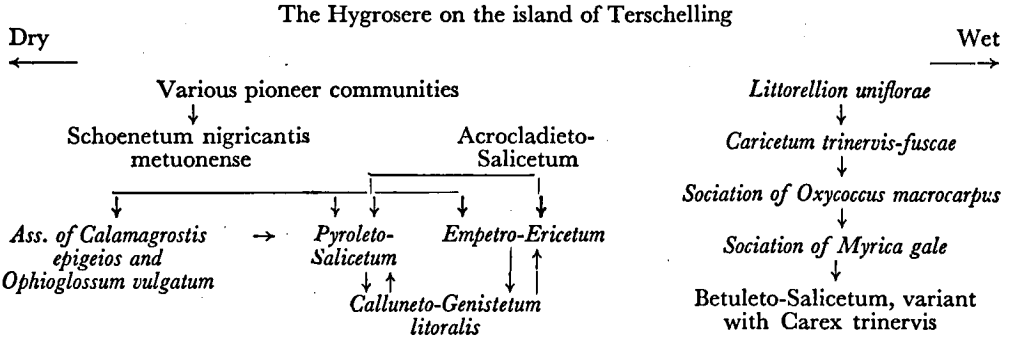
On Terschelling, the *Festuceto-Galietum maritimi* is not extensive and is only of minor importance. It has not been used for afforestation; in the xerosere, the forest has been planted mainly in the *Violeto-Corynephoretum dunense* and the *Polypodieto-Empetretum.*

On Ameland and Schiermonnikoog, however, the *Festuceto-Galietum* covers large areas; in the xerosere, afforestation has been carried out mainly in this association, and further in the *Violeto-Corynephoretum* and in the *Salix repens-Thalictrum minus*-association.

The hygrosere, as far as it relates to our subject, is given in schemes II and III. Two schemes are given, since the oligotrophic hygrosere on Terschelling, where *Empetrum nigrum, Erica tetralix, Calluna vulgaris and Myrica gale* are important constituents, differs considerably from the less oligotrophic hygrosere on Ameland and Schiermonnikoog, where these species are less common (*Calluna*) or even rare (*Erica*) or absent (*Myrica*). The names of the communities in which afforestation has taken place (mostly after draining) have been printed in italics.

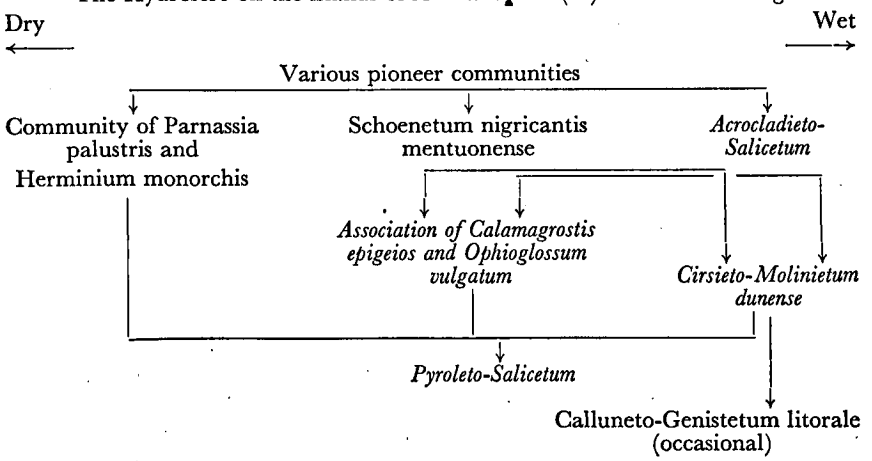
SCHEME II

The Hygrosere on the island of Terschelling



SCHEME III

The Hydrosere on the islands of Ameland and (or) Schiermonnikoog



The xero- and hygrosere mostly alternate over short distances, because of the geomorphological situation.

The undergrowth of the pine plantations differs according to the depth of the water table. In the pure xerosere, they remain very poor in species. In the first decennium, there is either no undergrowth at all, or only the mosses *Hypnum cupressiforme*, *Dicranum scoparium* and *Pleurozium schreberi*. In some cases, mainly along woodland margins, certain phanerograms may survive, though sparsely and with reduced vitality, e.g. *Ammophila arenaria*, *Carex arenaria* and *Salix repens*. In the next decennia the moss cover becomes denser and some phanerogams may either return or spread secundarily, e.g. *Agrostis canina* var. *arida*, *Polypodium vulgare*, *Epipactis helleborine*, *Empetrum nigrum*, *Hieracium umbellatum* and *Veronica officinalis* besides those mentioned previously. As yet, no *Vaccinium* species are established, and *Listera cordata* has not been found in such dry pine forests.

Pine forests in the pure hygrosere do not exist, because of the above-mentioned sylvicultural reasons. However, considerable stretches of pine forest are found in an intermediate habitat, where species of both xero- and hygrosere occur, and which may be named "mesosere" (DEN HARTOG 1952). *Listera cordata* has been observed in this habitat only. Eight sample plot vegetation analyses (records) were made by us in this biotope and are combined in table 3. The records 2 and 3 have been made on the same locality, but in different years and by different investigators.

A ninth analysis for the Culbin Sands on the Scottish coast (see § 3) was made and this agrees quite well with the other records. This may be due:

(1) to the corresponding climate: the climate of Culbin Sands is known to be relatively mild and dry for Scottish conditions, the precipitation amounting to 61–67 cm per annum (OVINGTON,

1950). Terschelling with 72 cm has a rainfall which is not considerably higher;
(2) to the similar geological and geomorphological situation;
(3) to similar history: until 1921 the Culbin Sands were a desert where the dune sand was freely blowing until it was fixed by afforestation; in the same way, only two decennia before, the dune landscape of Terschelling constituted a rather bare desert until it was fixed by various techniques, e.g. afforestation, erosion control and the abolishment of dune pasturing;
(4) to the similar ages of the forests studied: 45 years in the Culbin Sands, 30–40 years on the islands;
(5) to the fact that the dominant tree is the same.

The most constant, characteristic differential species of this community is *Pseudoscleropodium purum;* it can be said, that it is useless to look for *Listera cordata* where this moss is absent. Therefore, the present community can be indicated as a "*Pinis nigra* + *sylvestris* – *Listera cordata* – *Pseudoscleropodium purum*-consociation".

Mr. S. SEGAL kindly informed us:
(1) that he observed, that, during the years 1950–1958, in the pine-forests on Terschelling the presence and dominance of *Pseudoscleropodium purum* increased;
(2) that this moss species does not at all play the same part in the Scandinavian pinewoods, where *Listera cordata* is constantly associated by *Hylocomium splendens* and less frequently also by *Ptilium crista castrensis* and *Pleurozium schreberi.* In our table 3, the combination of these three species (and also *Pseudoscleropodium purum*) with *Listera cordata* is represented in record nr. 3 only.

A certain resemblance between the forest habitat and that of the dwarf dune scrub is obvious. Therefore in table 3 we listed separately not only the species of the xero- and the hygrosere, but also those species which occur on the islands in dune scrub or have their optimal habitat on northern exposures (which in most cases bear also a dwarf scrub community). The remaining species have been separated into a xerosere group, a hygrosere group and a (very small) group of species indifferent in this respect; besides, the "differentials" of Culbin Sands are given as a special category. Among the latter are (1) taxa which are completely wanting on the islands, viz. *Deschampsia flexuosa, Frangula alnus, Betula pubescens* ssp. *odorata,* and *Pyrola secunda;* (2) *Galium hercynicum,* which is known on the islands from only one locality on Terschelling, far from the forests; (3) *Holcus mollis,* which occurs on the islands only in alder wood.

In order to obtain a numerical expression of the position of the records between the xero- and the hygrosere, we have calculated the group quotient X/H. 100. The total cover values of the group of xerosere and hygrosere species of each record (X and H) have been calculated by addition, the cover values being made according to SCHWICKERATH (see e.g. WESTHOFF, 1947). If the total cover value of the xerosere species is lower than that of the hygrosere species, the group quotient

TABLE III

Pine forest community on the Westfrisian islands and the northern Scottish dune coast as a habitat of Listera cordata. (Pinus nigra + sylvestris — Listera cordata — Pseudoscleropodium purum-consociation).

T = Terschelling, Neth. W = West of the island Se = Segal
A = Ameland, Neth. H = Hoorn V = Vlieger
S = Schiermonnikoog, Neth. N = Nes W = Westhoff
Cs = Culbin Sands, Scotland M = Mörzer Bruijns ep. = epiphyte

Number	1	2	3	4	5	6	7	8	9
Island or region	T	T	T	T	T	T	A	S	Cs
Locality	W	W	W	W	H	W	N	—	—
Author	W	Se	M, W	Se	W	W	V, W	W	M, W
Year ('19)	'53	'55	'57	'55	'55	'58	'51	'56	'56
Date	16–6	28–6	1–8	28–6	30–6	2–9	11–7	24–8	1–7
Tree layer, age in years	32	± 30	30	30	32	30	35	40	45
Tree layer, height in meters	11	8–10	8–10	8	8–9	8	8	10	15–20
Tree layer, degree of dominance in %	80	80	80	80	80	90	80	70	80
Shrub layer, height in m	1–2	0,5–2,5	1–3	0,5–3	1–4	0,3–1	3–4	—	—
Shrub layer, degree of dominance in %	20	25	40	30	30	20	( )	—	—
Herb layer, degree of dominance in %	30	30	<5	10	20	40	80	50	<1
Moss layer, degree of dominance in %	40	30–40	60	50	20	100	80	90	100
Surface studied, in square meters	200	100	90	100	150	200	100	100	100
Tree layer (cultivated, species introduced)									
Pinus nigra ssp. nigra	5.1	5.1	—	—	5.1	—	5.1	4.1	—
Pinus nigra ssp. laricio	—	—	5.1	5.1	—	—	—	—	5.1
Pinus sylvestris	—	—	—	—	—	5.1	—	—	—
Shrub layer (cultivated, species introduced)									
Sorbus aucuparia	1.1	1.1	1.1	+–1.1	+.1	+.1	—	—	—
Quercus robur	2.1	2.1	—	1.1	3.1	2.1	—	—	—
Acer pseudoplatanus	+.1	+.1	—	—	+.1	+.1	—	—	—
Fagus sylvatica	+.1	—	—	—	+.1	+.1	—	—	—
Prunus serotina	—	+.1	3.2–3	2.2	—	2.1–2	—	—	—
Picea sitchensis	+.1	—	—	—	—	—	—	—	—
Fraxinus excelsior	+.1	+.1	—	—	—	—	—	—	—
Ilex aquifolium	—	—	+.1	+.1	—	—	—	—	—
Shrub layer (spontaneous, native species)									
Myrica gale	+.1	+.1	—	—	—	—	—	—	—
Sambucus nigra	—	—	—	—	—	—	+.1	—	—

TABLE III *(Continued)*

Number	1	2	3	4	5	6	7	8	9
Herb layer and moss layer:									
I. *Neophytes* (woodland species)									
Listera cordata	2.1	1.1	1.1†	1.1–2	1.1–2	(+.2)	1.1	1.1–2	+.3
Goodyera repens	—	—	+.2	—	—	2.2	—	—	1.1
Linnaea borealis	—	—	—	—	—	3.4	—	—	—
Lycopodium annotinum	—	—	—	—	—	—	—	+.2	—
Ptilium crista-castrensis	—	—	(+.2)	+.2	—	—	—	—	—
Plagiothecium undulatum	—	—	+.2	—	—	—	—	—	—
Cantharellus aurantiacus	—	—	+.1	—	—	—	—	—	—
II. *Species, occurring on the islands in dune shrub or having their optimal habitat on northern exposures:*									
Dryopteris spinulosa	+.2	+.2	+.2	+.2	+.2	+.1	2.2	+.1	+.1
Polypodium vulgare	+.2	1.2	1.2	+.2	—	1.2	1.2	+.2	+.1
Pyrola rotundifolia	+.2	+.2	—	+.1	+.3	—	—	+.1	—
Pyrola minor	—	+.2	—	—	1.2–3	—	2.4	—	+.1
Rubus fruticosus	+.1	+.2	—	—	+.1	—	+.1	—	—
Dicranum scoparium	—	—	+.2	+.2	—	1.2	—	1.2	2.3
Eurhynchium stokesii	—	—	+.3	—	1.2	—	+.3	—	—
Lophocolea bidentata	—	+.2–3	2.3	2.3	ep.	1.3	—	2.3	+.2
Pleurozium schreberi	—	—	+.2	+.2	—	+.3	—	3.4	—
Salix repens	—	—	—	+.1	+.1	—	—	—	—
Epipactis helleborine	—	—	—	—	—	—	+.1	+.1	1.2
Plagiothecium denticulatum	—	+.3	+.3	—	—	—	—	—	—
Brachythecium rutabulum	—	—	—	—	+.2	—	+.2	—	+.2
Calluna vulgaris	—	—	+.2	—	—	—	—	—	—
Sambucus nigra, iuv.	—	—	—	—	—	—	—	+.1	—
Hippophae rhamnoides	—	—	—	—	—	—	—	+.1	—
Rosa canina, iuv.	—	—	—	—	—	—	—	+.1	—
Crataegus monogyna, iuv.	—	—	—	—	—	—	—	+.1	—
Dryopteris filix-mas	—	—	+.2	—	—	—	—	—	—
Lonicera periclymenum	—	—	—	—	1.2	—	—	—	—
Hylocomium splendens	—	—	—	+.2	—	—	—	—	—
III. *Species of the xerosere of the dunes* (△AS: are absent from Terschelling at all)									

	Carex arenaria	2.2	1.1–2	1.1	+.1–2	1.1–2	2.1–2	3.1°	2.1	—
	Veronica officinalis	+.1	+.2	+.2	+.2	+.1	+.2	+.2	—	+.1
	Hieracium umbellatum	+.1	+.1	+.1	+.1	+.1	1.1–2	+.1	—	—
	Viola canina	—	—	+.1	+.1	—	—	2.2	+.2	—
	Senecio jacobaea	—	—	—	—	—	—	+.1	+.1	+.1
	Agrostis canina var. arida	—	+.1–2	2.2–3	2.2–3	—	2.1–2	1.2	—	—
	Epilobium angustifolium	+.2	—	—	—	—	—	—	—	+.2
△AS	Galium mollugo	—	—	—	—	—	—	+.2	+.1	—
△AS	Asparagus officinalis	—	—	—	—	—	—	+.1	+.1	—
	Ammophila arenaria	+.1°	—	—	—	—	—	—	—	—
	Rumex acetosella	—	+.1	+.2	—	—	—	—	—	—
	Galium verum	—	—	—	—	—	—	+.1	—	—
	Linaria vulgaris	—	—	—	—	—	—	1.1	—	—
	Viola tricolor var. stenochila	—	—	—	—	—	—	+.1	—	—
	Stellaria media	—	+.2	—	—	—	—	—	+.1	—
△AS	Thalictrum minus ssp. dunense	—	—	—	—	—	—	+.1	—	—
IV.	*Species of the hygrosere of the dunes* (△AS: absent from Terschelling at all)									
	Pseudoscleropodium purum	3.4	2–3.3	4.4	3.3	2.3	5.5	5.5	2.3	2.2
	Calamagrostis epigeios	—	—	+.2	—	2.1–2	1.2	2.1	2.3	—
	Lotus uliginosus	—	—	—	—	+.1	—	+.2	—	+.1
	Cirsium palustre	—	—	—	—	+.1	—	+.1	+.2	—
	Taraxacum sect. Vulgaria	—	—	—	—	+.1	—	+.1	+.1	—
	Poa pratensis	—	—	—	—	+.2	—	1.1	+.1	—
	Holcus lanatus	+.2	1.2	1.1–2	1.2	—	1.1–2	+.2	—	—
	Luzula multiflora	—	+.2	1.2	+.1	+.1	+.1	—	—	—
	Anthoxanthum odoratum	—	—	—	—	+.1	—	1.1	—	—
	Galium palustre	—	—	—	—	(+)	—	+.2	—	—
	Ranunculus repens	—	—	—	—	(+)	—	—	+.1	—
△AS	Listera ovata	—	—	—	—	—	—	+.1	—	—
	Juncus effusus	—	—	—	—	+.2	—	—	—	—
	Hydrocotyle vulgaris	—	—	—	—	+.1	—	—	—	—
	Orchis maculata	+.1	( )	—	( )	—	—	—	—	—
	Potentilla erecta	+.1	+.1	—	—	—	—	—	—	—
	Carex flacca	—	—	—	—	—	—	+.1	—	—
	Cerastium holosteoides	—	—	—	—	—	—	1.1	—	—
	Platanthera bifolia	—	—	—	—	—	+.1	—	—	—
	Ranunculus acer	—	—	—	—	—	—	+.1	—	—
	Sieglingia decumbens	—	—	—	—	—	—	+.2	—	—
V.	*Species, indifferent re xero- or hygrosere*									
	Hypochoeris radicata	+.1	—	+.1	—	+.1	+.1	+.1	—	+.1

TABLE III *(Continued)*

	Number	1	2	3	4	5	6	7	8	9
	Hypnum cupressiforme	—	—	2.2–3	2.3	—	1.3	—	3.3	4.4
	Peltigera canina	—	—	—	—	—	—	—	+.3	+.2
	Vicia angustifolia	—	—	+.2	—	(+)	—	—	—	—
	Pohlia nutans	—	—	+.2	—	—	—	—	—	—
VI.	*Species absent from the islands or only rare and local there ("differentials" of Culbin Sands)*									
	Deschampsia flexuosa	—	—	—	—	—	—	—	—	+.2
	Frangula alnus, iuv.	—	—	—	—	—	—	—	—	+.1
	Pyrola secunda	—	—	—	—	—	—	—	—	+.1
	Betula pubescens ssp. odorata	—	—	—	—	—	—	—	—	+.1
	Galium hercynicum	—	—	—	—	—	—	—	—	+.1
	Holcus mollis	—	—	—	—	—	—	—	—	+.2
VII.	*Seedlings of cultivated trees*									
	Sorbus aucuparia	+.1	+.1	1.1–2	1.1	—	+.1	—	+.1	—
	Quercus robur	+.1	+.1	+.1	+.1	—	+.1	—	—	—
	Prunus serotina	+.1	—	1.1	1.1–2	—	+.1	—	—	—
	Viburnum opulus	+.1	—	(+)	—	—	—	—	—	—
	Pinus nigra ssp. laricio	—	—	r	+.1	—	—	—	—	—
	Picea sitchensis	—	—	r	—	—	—	—	—	—
	Quercus borealis	—	—	—	—	+.1	+.1	—	—	—
	Crataegus monogyna	—	—	—	+.1	—	—	—	—	—
	Group quotient X/H. 100	75	64	64	71	25	70	75	70	60

must be < 100. Indeed, in our records it varies from 25 to 75 (see table 3), thus indicating (1) that all records belong to the hygrosere; (2) that, nevertheless, the xerosere species always remain of importance, so that it might be better to bring the *Pinus nigra* + *sylvestris* – *Listera cordata* – *Pseudoscleropodium purum*-consociation to the "mesosere".

It is interesting, that the populations of *Listera cordata* on the islands are so large; in table 3, the abundance figure 2 refers to thousands of individuals, figure 1 to many hundreds of them, on sample surfaces of circa 100 m². For the Ameland locality, WEIJER (1949) observed ca. 10,000 individuals on 20 m². SUMMERHAYES (1951) states, that the number of individuals of *Listera cordata* is rather small in most cases, and that such large populations arise only where the habitat is optimal. It is surprising, that such young and artificial pine stands with only a thin fermentation cover on sterile dune sand offer such optimal conditions for this particular species.

Comparing the difference in the dominant tree species with any difference in undergrowth vegetation, it appears from table 3, that in one record (no. 6) *Pinus sylvestris* is the dominant tree. This is exceptional: the record represents one of the very few spots on the island of Terschelling where *Pinus sylvestris* has been planted instead of *Pinus nigra*. This record is also the only locality of *Linnaea borealis* known on Terschelling; whether this correlation is accidental or real, cannot be concluded on the base of a single record. As to the subspecies of *Pinus nigra*, table 3 shows that there is no obvious correlation between the difference in the dominant tree subspecies and any of the differences in vegetation.

Comparing the *Pinus nigra* + *sylvestris* – *Listera cordata* – *Pseudoscleropodium purum*-consecciation (table 3) with the *Pineto-Vaccinietum myrtilli atlanticum* of Scotland (table 2 and context), we see that these communities have 17 species in common. Five of them are neophytes in the dune sociation: *Listera cordata*, *Goodyera repens*, *Linnaea borealis*, *Plagiothecium undulatum*, *Ptilium crista-castrensis*. Except for *Linnaea*, these are all "euchorous" species (WESTHOFF, 1947), i.e. species with a large dissemination capacity, which in this case is due to very small diaspores enabling the plants to establish themselves as soon as the habitat becomes favourable. *Linnaea borealis* is supposed to be epizoöchorous, viz. to be transported by migratory birds (GIGER 1913, BEYERINCK 1929b); in this case it would be an euchorous species too. Among the other species which both communities have in common, 8 belong to the group of species occurring on the islands in dune scrub or having their optimal habitat on northern exposures; they are, in sequence of degrees of presence in table 3: *Dryopteris spinulosa*, *Pyrola rotundifolia*, *Pyrola minor*, *Dicranum scoparium*, *Pleurozium schreberi*, *Calluna vulgaris*, *Hylocomium splendens*, *Sorbus aucuparia* (the last one in table 3 probably subspontaneous). These species, too, are euchorous. Of the four remaining species occurring in both communities, two are from the xerosere (*Veronica officinalis* and *Rumex acetosella*), one from the hygrosere (*Potentilla erecta*) and one, *Agrostis canina*, which in its main from (var. *canina?*) is hygrophilous, but in its var. *arida* not so.

The last species worth mentioning is *Dryopteris linnaeana*. It belongs to the first group, that of neophytes in the dune sociation, but it has not been considered above, as it is absent from both our tables 2 and 3. It does occur, however, in the Scotch pinewood, and it was discovered, for the first time on the Westfrisian islands, by Mr. S. SEGAL in an artificial pine forest on the island of Terschelling in the year 1955.

Finally we may ask what probability there is for a future development of the pine-consociation on the islands, from the present "nascent association", to a well-developed association of the sub-alliance *Piceion septentrionale*. This is mainly a question of accessibility. As to the dominant *Vaccinium* species, experience on the Dutch mainland has taught us that they do not establish themselves in artificial pinewoods in the first generation under 25 years of age (WESTHOFF, 1957). Assuming that it would be allowed to apply this to the islands, the establishment of these species might be expected now from an edaphic point of view. *Vaccinium myrtillus* however is completely absent from the islands as yet. *Vaccinium vitis-idaea* occurs in the dune scrub of Terschelling as a neophyte in 2 localities, probably brought by migratory birds; its establishment in the pine forest is possible, but it has been found neither on Ameland nor on Schiermonnikoog. The same is true for *Arctostaphylos uva-ursi*, a recent neophyte on Terschelling, and known there from 3 localities in open dune heath; for *Juniperus communis*, also known from Terschelling dune scrub; and for *Blechnum spicant*, a recent neophyte in one locality in dune scrub on Terschelling. *Rhytidiadelphus loreus* and *R. triquetrus* occur on Terschelling, especially in the *Polypodieto-Empetretum* on northern slopes, and we do not see any reason why they should not be able to establish themselves in the pine forest. *Sphagnum girgensohnii* and *S. quinquefarium* are montane species, not likely to be expected in a lowland dune area. *Trientalis europaea* occurs on Terschelling in alder wood where the soil is not covered with a humus layer comparable to that of the pine forests. In 1958, however, it has been observed on Terschelling also in rather open, low dune shrub in the mesosere; in a similar habitat it had been observed on the island of Vlieland as early as 1928 (DE VRIES, 1950), on which locality, however, it did not maintain itself. We do not expect a migration of *Trientalis europaea* into the Terschelling pineforests in the near future.

Summarizing, we may expect a further development of the pine forest of Terschelling into a well-defined association of the *Piceion septentrionale*. This is mainly due to the exceptionally low lime content of the Terschelling dune sand, favouring the establishment of species of the boreal coniferous woodland formation. Such a development is less probable on Ameland and Schiermonnikoog.

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