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The flora and vegetation of Ireland

By D. A. Webb, Dublin

Such interest as Ireland possesses for the student of ecology and phytogeography derives from its position at the extreme western margin of the Eurasian continent. Although the available evidence suggests that Ireland was an island for much of the Tertiary era, it was certainly joined by land connexions through Great Britain to the continent of Europe during the greater part of that period of late-glacial and post-glacial time when plant migration in northern Europe was in full swing, and when the flora was taking on the broad features of its present composition. Ireland, therefore, possesses none of the phytogeographical peculiarities that are characteristic of islands. It has very few endemic plants, and none with an indisputable claim to specific rank. In so far as its flora and its plant communities differ from those of north-western Europe in general, the differences are to be ascribed to the peculiarities of its present-day climate, and perhaps of its climate in glacial or interglacial times.

Topography

Ireland is a country of rapid and sudden changes of landscape on a small scale, but with no well-marked large-scale differentiation. The only primary regions which can be clearly recognized are the central plain, which lies below 150 m and covers nearly two thirds of the country, and the marginal hill-country. The former lies mostly on limestone of lower Carboniferous age; the latter is geologically varied, including sedimentary, metamorphic and igneous rocks, which are, however, predominantly siliceous in character. Only in the south midlands are mountains of any height found far from the sea, and only on part of the east coast (between Dublin and Dundalk) is there an extensive coastal plain. Summits upwards of 600 m are numerous all round the island, but the highest mountains are found in the southern half, and only in County Kerry do they exceed 1000 m.

As a result of this peripheral distribution of the high ground, most of the rivers are short, only the Shannon, which drains most of the central plain, attaining to any large size.

Lakes are numerous throughout the country, except in the south-east, and some of them, especially in the centre, are of large size.

The coast-line of the western half of the island is mainly rocky and very deeply indented, with numerous bays and promontories and a fringe of islands: in the eastern half it is much more regular, with considerable stretches of sand and shingle.

Soil

Most Irish soils are shallow, because they are relatively young. The Pleistocene glaciation removed the existing soils in some regions, and covered them with new deposits in others; and since the relatively cool and damp climate of Ireland does not favour the rapid development of soil, it is not surprising that in most regions (the peat-bogs forming a notable exception) the rock or glacial drift is covered by only some 25 cm of soil or less. Over considerable areas of the west (especially in the counties of Donegal, Galway and Clare) no soil at all is formed except peat, and where the steepness of the slope or some other factor has inhibited peat-formation the rock remains quite bare.

From the ecological standpoint Irish soils may be divided into the following types:—

(1) Peat of sufficient depth to form a continuous cover, and to isolate the surface from the influence of the surrounding rock. This is found throughout the country on such areas of elevated ground (over 250—300 m) as are fairly flat; on low-lying ground near the west coast; and covering the sites of former glacial lakes in the central plain. These last areas are distinguished as *raised bogs* (their contour being slightly convex): the other two are grouped together as *blanket-bog*.

This peat is acid, though less acid than in some other countries, pH values between 4.0 and 4.4 being usual. A small quantity of fen peat (neutral or alkaline) is found by Lough Neagh, in the north-east.

(2) Mountain soils on siliceous rocks. These are usually shallow and always heavily podsolized, with a superficial peaty layer. They merge insensibly into the thinner types of blanket-bog. They are characteristic of the foot-hills and the moderately steep slopes of most Irish mountains. Their vegetation may be heath, mountain grassland, *Ulicetum* or *Pteridietum*.

(3) Clay soils. These are found chiefly on impermeable stretches of glacial boulder-clay, but somewhat similar soils have developed independently of glacial action over Carboniferous shales, as in County Limerick. These clay soils are partly waterlogged, even when on a fairly steep slope, and are characterized by an abundance of *Juncus* spp. (*J. inflexus* if alkaline, *J. acutiflorus* and *J. effusus* if acid).

(4) Calcareous loams. These are for the most part found overlying sandy or gravelly drift which has been derived from Carboniferous limestone; they are also developed over the less exposed areas of drift-free limestone. They cover a large part of central Ireland, and include most of the best grazing land. At the one extreme they merge into calcareous clay soils; at the other they may be very dry and gravelly, as on esker ridges.

The soils which develop on the basalt of north-east Ireland are broadly similar, and may be included under this head.

(5) Non-calcareous loams. These are found chiefly in the east, and are mainly derived from Silurian shales and slates. They constitute the best tillage land in Ireland and most of their natural vegetation has therefore been destroyed.

It may be noted that sandy soils are practically unknown in Ireland, except in the neighbourhood of the coast.

Although the principal characteristics of the vegetation and flora of Ireland as a whole are determined almost wholly by climatic factors, the distribution of plants within Ireland is influenced at least as much by differences in soil as by differences in climate between the various districts. The two soil characters which are of importance are its water-holding capacity and its base content. As a result of the generally damp conditions one finds that many plants which in England or on the continent are of general occurrence are restricted in Ireland to the rather limited areas of especially permeable and well-drained soils. Much more striking, however, is the contrast between the calcicole and

calcifuge floras. The former is confined to regions where the influence of the limestone or basalt (or in a few cases of very calcareous sea-sand) is paramount. The latter is confined in the east and centre to regions of siliceous rocks or drift, to limestone soils that have been thoroughly leached, or to areas of continuous peat-cover; but in the west, as a result of factors that are not properly understood, the calcifuge flora transgresses much more freely on to the limestone, even when the latter is covered only by the thinnest skin of peaty soil, which would seem quite insufficient to insulate the plant-roots from the rock.

Plants which are calcifuge or calcicole in Ireland do not always show the same preferences in England and France. The following list gives those species whose distribution in Ireland indicates an unmistakable preference for calcareous or for non-calcareous soils. Certain species which are almost always found on one type of soil have been excluded because their restricted distribution or their peculiar ecological requirements leave it open to doubt whether or not the base content of the soil is a primary factor in determining their distribution. As examples of species of this type *Gentiana verna* and *Neotinea intacta* may be cited on the one side, and *Erica mackaiana* and *Simethis planifolia* on the other.

Species calcicole in Ireland

<i>Ranunculus circinatus</i>	<i>Euphrasia salisburgensis</i>
<i>Reseda luteola</i>	<i>Origanum vulgare</i>
<i>Hypericum perforatum</i>	<i>Spiranthes spiralis</i>
<i>Geranium lucidum</i>	<i>Anacamptis pyramidalis</i>
<i>Evonymus europaeus</i>	<i>Orchis morio</i>
<i>Poterium sanguisorba</i>	<i>Ophrys apifera</i>
<i>Sedum acre</i>	<i>O. muscifera</i>
<i>Galium pumilum</i>	<i>Juncus inflexus</i>
<i>Asperula cynanchica</i>	<i>J. subnodulosus</i>
<i>Tussilago farfara</i>	<i>Potamogeton coloratus</i>
<i>Carlina vulgaris</i>	<i>Trisetum flavescens</i>
<i>Centaurea scabiosa</i>	<i>Helictotrichon pubescens</i>
<i>Leontodon hispidus</i>	<i>Sesleria caerulea</i>
<i>Blackstonia perfoliata</i>	<i>Briza media</i>
<i>Gentiana amarella</i>	<i>Ceterach officinarum</i>

Species calcifuge in Ireland

<i>Ranunculus lenormandi</i>	<i>Hypericum humifusum</i>
<i>Lepidium heterophyllum</i>	<i>H. elodes</i>
<i>Viola palustris</i>	<i>Radiola linoides</i>
<i>Polygala serpyllacea</i>	<i>Ulex gallii</i>
<i>Montia fontana</i>	<i>Sarothamnus scoparius</i>

Saxifraga stellaris
S. spathularis
Sedum anglicum
Umbilicus pendulinus
Drosera spp.
Peplis portula
Galium saxatile
Chrysanthemum segetum
Senecio sylvaticus
Jasione montana
Vaccinium myrtillus
Calluna vulgaris
Erica tetralix
E. cinerea
Daboecia cantabrica
Digitalis purpurea
Polygonum hydropiper
Rumex acetosella

Narthecium ossifragum
Juncus squarrosus
J. bulbosus
Luzula sylvatica
L. multiflora
Potamogeton polygonifolius
Scirpus caespitosus
S. fluitans
Eriophorum vaginatum
E. angustifolium
Rhynchospora alba
R. fusca
Carex binervis
Deschampsia flexuosa
Nardus stricta
Blechnum spicant
Athyrium filix-femina
Equisetum sylvaticum

Climate

The climate of Ireland is determined partly by its position on the western fringe of the Eurasian continent, where it is exposed to the full effects of the prevailing westerly and south-westerly winds which blow from the relatively warm waters of the north Atlantic. As a result the climate of Ireland is not only more constant and equable, but is also generally warmer than other parts of the northern hemisphere in the same latitude, such as northern Poland, Lake Baikal, Kamchatka, and southern Labrador. In comparison with central Europe the most notable features of the Irish climate are the mild winters with very little frost and snow, the cool summers with frequent cloudy skies, the constant winds, the high relative humidity of the air, and the even distribution of rainfall throughout the year. Before discussing the effect of these on the vegetation, a few of the meteorological data will be presented in summary form, so as to afford the reader a basis for comparison with other climates with which he is familiar.

Temperature. The mean temperature throughout the year is about 9° in the extreme north-east and 10.5° in the extreme south-west. The range of seasonal variation from this mean is remarkably restricted, the mean temperature for the coldest month (January) being from 5° to 7°, and for the warmest month (July) from 14° to 16°. Nowhere in Ireland does the annual range of mean monthly temperatures exceed 10.5°, and on parts of the west coast it is only 8.5°. Ireland, therefore, enjoys a climate

which combines winter temperatures characteristic of Bordeaux, Marseilles and Florence, with summer temperatures characteristic of Edinburgh, Göteborg and central Finland. Moreover, in summer and winter alike the daily range of temperature is small; it averages about 6.5° over the whole year.

Although frost is of frequent occurrence from November to April in most parts of Ireland, it is seldom severe and seldom prolonged. Temperatures of -10° are recorded perhaps every fourth or fifth winter, but they never persist for more than two or three successive nights. On the western seaboard the frosts are very mild and transient. Snow falls on 3 or 4 days in an average winter in the west, and perhaps on 8 or 10 days in the east; but it nearly always melts quickly, and even on the highest mountains it is exceptional for it to lie for more than 2 weeks. With regard to extremes of heat, the mean daily maximum for July nowhere exceeds 20° . Temperatures above 25° are usually experienced on only 2 or 3 days in the year.

Rainfall. Ireland has not such an unusually high rainfall as is commonly supposed: it is no higher than that of the Alps and the adjacent regions, and it is rather lower, judging the countries as a whole, than that of Scotland or Norway. 1000 mm per annum is a fair average for the whole island. On the driest parts of the east coast it is as low as 750 mm, and in the mountainous regions of some of the western counties (Donegal, Mayo, Galway, Kerry) it exceeds 1500 mm.

The most striking feature of the rainfall, however, is its even distribution throughout the year. The driest months are April and May, but even in each of these there is an average fall of 45 mm in the driest districts; nowhere, in fact, does the rate of precipitation in the driest month amount to less than two thirds of the average. August, November and December are as a rule the wettest months, but there is no clearly marked maximum.

The number of days on which a recordable quantity of rain falls exceeds 200 per annum over most of the country, and is over 240 per annum on many parts of the west coast. It is this very frequent occurrence of relatively light rain that is one of the most characteristic features of the Irish climate.

Not only is the incidence of rain rather constant through the year; it is also constant from year to year. Prolonged drought is

rare, especially in the northern half of the island, and it is a most exceptional occurrence for the rainfall of any one year to differ from the normal by more than 25%.

Humidity. The recorded data for humidity of the air are, unfortunately, very scanty, but it is certain that the constancy of a relatively high content of water vapour in the air is an important feature of the Irish climate. This is particularly true of the west, where the moist and «balmy» quality of the air is readily perceived without instruments. Records from Valentia, County Kerry, show that the average saturation-deficit of the air through the year there is only 2.0 millibars, and that even in June, the month in which it is highest, the average is only 2.9 millibars. These figures are probably typical for the west coast.

Sunshine and cloud. Frequent rain is naturally associated with cloudy skies, and even in fine weather the persistence of completely clear skies for several consecutive days is rather unusual. On low ground the average daily duration of sunshine in the midlands is about $5\frac{3}{4}$ hours in June and $1\frac{1}{4}$ hours in December, the annual average being about $3\frac{3}{4}$ hours, or 31% of the possible. In other words the sun is obscured by cloud for at least two thirds of its time above the horizon. The south-east of Ireland is the sunniest part and the north-west the most cloudy.

The cloud is frequently at a low level, so that on the mountains mist is very frequent and persistent.

Wind. Gales are fairly frequent, especially in winter, on the west and north coasts, but of greater importance to the vegetation is the great frequency of moderate winds and the rarity of any prolonged periods of calm.

Effect on the vegetation

These climatic conditions are, with the exception of the wind, generally favourable for the growth of the vegetation as a whole, and especially of chamaephyte and hemicryptophyte species; and accordingly the vegetation of Ireland develops, under suitable conditions of shelter, a quality of lushness and of greenness throughout the year which is not readily paralleled in the north temperate zone, and which is in some respects comparable to the characteristic facies of the temperate rain-forest of the southern he-

misphere. The continuous growth of grasses in particular is favoured by the mild winters and the wet summers, so that there are seldom more than 3 or 4 months in the year in which active growth of grass may not be observed. To this fact Ireland owes its importance as a grazing country for cattle and horses, as well as its sobriquet of «the Emerald Isle», for the bright green aspect which the countryside preserves through every normal summer makes an immediate impression on visitors from other countries.

Woody evergreen species, such as *Ilex aquifolium*, *Hedera helix* and *Arbutus unedo* (as well as such exotics as *Rhododendron ponticum*, *Prunus lusitanica* and *P. laurocerasus*, which flourish exuberantly and freely naturalize themselves in woods in which they have been planted) are favoured by the rarity of cold, dry weather; for even the east winds of spring, which are such a regular feature of the climate of the British Isles, are less desiccating and destructive in most parts of Ireland than they are in Great Britain. *Hedera helix* and *Arbutus unedo*, both of which flower in late autumn, are further favoured by the climate, in that even in November there are usually some insects on the wing for pollination, and the maturation of the fruit can proceed at the normal winter temperatures.

Woodland species as a whole are favoured by the low saturation-deficit of the air. This is especially true of ferns, bryophytes and epidendric lichens, which form a notable and conspicuous element in the vegetation of Ireland, and especially of the western half. But it may also be noted that despite the very small area of woodland in the country many phanerogamic species which on the continent and even in Great Britain are regarded as characteristic of woodland, or at least of hedgerows and wood-margins, are abundant in Ireland, where they grow freely in open country. Such species include *Conopodium majus*, *Viola riviniana*, *Primula vulgaris*, *Fragaria vesca*, *Lysimachia nemorum* and *Luzula sylvatica*. This tendency becomes more and more marked as one travels north-westwards, and in the counties of Sligo and Donegal even such species as *Ranunculus auricomus*, *R. ficaria* and *Anemone nemorosa* are frequently to be seen growing in situations in which the only shelter is that afforded by a gentle north-facing slope. Other species again, such as *Oxalis acetosella* are satisfied with the shelter that may be obtained from the fronds of *Pteri-*

dium aquilinum, and, given this, will grow freely on exposed sea-cliffs.

It is, of course, true that many of the stations where these woodland plants are found represent the sites of former woods, so that the plants are in that sense relict; but their power of persistence after the clearing of the wood is much greater than would be possible in a drier or sunnier climate.

Against all these favourable factors there must, however, be set the destructive power of the wind, which, except in sheltered pockets here and there, is a climatic factor of major importance in all the western counties. Although the wind in Ireland is seldom very desiccating, its persistence and frequent strength more than compensate for its high humidity in enabling it to kill young shoots that are exposed to its full force. It must also be remembered that the prevailing winds blow inland from a turbulent sea whose waves are breaking against a rocky and much-dissected coast-line, so that, even for some miles inland, the droplets of salt spray carried in the wind add greatly to its destructive powers. Wind-shorn trees, with their crowns produced unilaterally and almost horizontally towards the east, are a familiar feature of the western landscape; and it is certain that there are large areas of the west which, though they might perhaps be covered with scrub if biotic interference was removed, are incapable of developing naturally under modern climatic conditions a vegetation that really deserves the name of woodland. In the most exposed areas even the herbaceous vegetation is strikingly dwarfed by the joint action of wind and spray, the community described by P r a e g e r as «*Plantago-sward*», found here and there along the west coast, consisting of *Plantago maritima*, *P. coronopus*, *Euphrasia* spp., *Daucus carota*, *Succisa pratensis* and other plants all reduced to a height of 3 cm or less.

The principal communities, and their relation to the climatic climax

Characteristic plant communities of a more or less specialized type may be found in Ireland, as in other countries, in particular habitats such as salt-marshes, sand-dunes, cliffs or lake-shores. But these habitats cover between them only a minute fraction of

the total area of Ireland, and in a brief general survey of the vegetation even a cursory mention of them is impossible. There are, if one omits these small areas and also cultivated land and other regions in which the native vegetation has been wholly destroyed, three types of natural or semi-natural plant community which between them cover practically all the rest of the country; and these alone can be considered here. They are grassland, heath and bog.

Grassland dominates all the lowlands of Ireland, except for a few tillage areas in the east, parts of the central plain where extensive raised bogs are found, and parts of the west coast where blanket bog or heath descends to sea-level. It usually overlies glacial drift, but in parts of the west midlands good grassland is developed over drift-free limestone. It passes over into heath at an altitude that varies considerably from place to place, but is usually between 100 and 225 m. The level of transition is lower in the west than in the east, lower on siliceous rocks than on limestone, and lower on the coast or other exposed situations than on sheltered slopes. More rarely the grassland passes over through *Molinietum* into bog; this can be seen in places near the west coast, and at the margins of some of the large midland bogs.

The areas at present occupied by this grassland would, almost without exception, bear woodland as their natural climatic climax—*Quercetum sessiliflorae* on siliceous rocks and *Fraxinetum excelsioris* (perhaps with some admixture of *Quercus*) on the limestone. There is no doubt that even today, when conditions for forest growth in Ireland are not as favourable as they have been in the past, most of these areas would pass rapidly into scrub and eventually into woodland if they were rigorously protected from grazing. Destruction of the native woodland, which was begun by neolithic farmers and completed during the seventeenth and eighteenth centuries, has been very complete in Ireland, and the fragments that remain are barely sufficient to give us an idea of what would be the nature of this climax woodland, especially on the limestone plain. It has been accomplished largely in the interests of grazing, which has always been the focal point of Irish agriculture; and it has been assisted by the fact that the Irish soil and climate, at any rate in historic times, are not favourable for the production of timber of good enough quality to make it an

attractive economic proposition. For these reasons the semi-natural, managed woodland which is so common in England is almost unknown in Ireland, and the fragments of woodland that remain are mostly on steep and rocky ground unsuited for grazing. A minor biotic factor, due also to human agency, results from the introduction of the rabbit to Ireland some 600 years ago. It is now common in all parts of the country where the soil is not waterlogged, and its grazing in some regions (especially eskers and stabilized sand-dunes) is of as great importance as that of sheep and cattle.

The first stages of the reversion of grassland to woodland can sometimes be seen in undergrazed fields, which become colonized by scattered bushes of *Prunus spinosa*, *Crataegus monogyna*, and *Ulex europaeus* (all spiny plants), but it is seldom allowed to proceed further. There is little doubt that on limestone soils *Corylus avellana* would be prominent in later stages of the succession.

The degree of management to which the grassland is subjected varies greatly according to the situation; but as a rule the human interference is limited to grazing, manuring by the beasts that graze, and in some cases draining. Nearly all the grassland of Ireland is permanent pasture, and the sowing of grass as a short-term crop to be alternated with others is as yet practised on a very small scale. Nor is the application of chemical manures (apart from the fairly widespread use of lime) a factor of much importance. The grassland, therefore, and especially its more upland and less intensively grazed fraction, can be fairly regarded as a semi-natural community, of the nature of a plagioclimax, in which the constituent species are selected mainly by the various responses of the native flora to the deflecting factor of grazing.

Irish grasslands are, as a rule, poor in species. The following are the species most constantly represented in fair abundance; all others may be regarded either as minor ingredients or as distinctly local in their occurrence, or as confined to basic or acidic soils.

Grasses

Anthoxanthum odoratum
Agrostis tenuis
A. stolonifera
Holcus lanatus
Arrhenatherum elatius
Cynosurus cristatus

Dactylis glomerata
Poa pratensis
P. trivialis
Festuca arundinacea
F. ovina
Lolium perenne

Other Monocotyledons

Juncus effusus
Luzula campestris
Carex flacca
C. caryophyllea

Dicotyledons

Ranunculus repens
R. acris
Polygala vulgaris
Cerastium vulgatum
Sagina procumbens
Linum catharticum
Trifolium pratense
T. repens
T. dubium
Lotus corniculatus
Conopodium majus

Heracleum sphondylium
Scabiosa succisa
Bellis perennis
Achillea millefolium
Chrysanthemum leucanthemum
Senecio jacobaea *
Cirsium vulgare
C. palustre
C. arvense
Centaurea nigra
Crepis capillaris
Hypochoeris radicata
Leontodon autumnalis
Veronica serpyllifolia
Euphrasia spp.
Rhinanthus minor
Prunella vulgaris
Plantago lanceolata
Rumex acetosa

Heath is in Ireland mainly a transitional community, which links the more upland types of grassland with the drier types of mountain blanket-bog. It is developed chiefly on the hills and on the lower parts of the mountains (usually between about 150 m and 300 m), but it is also found on exposed areas at all levels near the coasts, especially in the west, and on occasional patches of low ground in the midlands. It usually occurs on shallow, podsolized, acid and rather peaty soils—more acid and peaty than grassland will usually tolerate, but shallower and with a higher mineral content than in the true peat characteristic of bog.

Floristically this community is somewhat heterogeneous. It may be dominated in different areas by *Pteridium aquilinum*, by *Vaccinium myrtillus*, by *Luzula sylvatica*, by *Ulex gallii*, by *Erica cinerea*, by dwarfed *Calluna vulgaris*, or by grasses. The dominance of any one of these is the result of a complex interaction of aspect, drainage, grazing, base-content and doubtless other factors that are not well understood. If *Calluna* is dominant it usually indicates a fairly solid peat-cover, and the community may be regarded as transitional to thin blanket-bog. If grasses are dominant it is obviously transitional to grassland, but if *Sieglingia decumbens*, *Festuca ovina*, *Nardus stricta* or *Deschampsia*

* Replaced in the west by *Senecio aquaticus*.

flexuosa are present in any quantity, then it will usually be found that the rest of the flora relates the community rather to heath.

Among the species that are commonly found in heath communities of one type or another are the following:

<i>Viola riviniana</i>	<i>Digitalis purpurea</i>	<i>Carex pulicaris</i>
<i>Polygala serpyllacea</i>	<i>Veronica chamaedrys</i>	<i>C. flacca</i>
<i>Cerastium vulgatum</i>	<i>V. officinalis</i>	<i>C. pilulifera</i>
<i>Stellaria graminea</i>	<i>Euphrasia</i> spp.	<i>C. binervis</i>
<i>Hypericum pulchrum</i>	<i>Pedicularis sylvatica</i>	<i>Anthoxanthum odoratum</i>
<i>Ulex gallii</i>	<i>Melampyrum pratense</i>	<i>Agrostis canina</i>
<i>Vicia sepium</i>	<i>Thymus serpyllum</i>	<i>A. tenuis</i>
<i>Potentilla erecta</i>	<i>Nepeta hederacea</i>	<i>Deschampsia flexuosa</i>
<i>Conopodium majus</i>	<i>Prunella vulgaris</i>	<i>Sieglingia decumbens</i>
<i>Galium saxatile</i>	<i>Teucrium scorodonia</i>	<i>Molinia caerulea</i>
<i>Scabiosa succisa</i>	<i>Rumex acetosella</i>	<i>Festuca ovina</i>
<i>Solidago virgaurea</i>	<i>Juncus squarrosus</i>	<i>Nardus stricta</i>
<i>Hypochoeris radicata</i>	<i>Luzula sylvatica</i>	<i>Pteridium aquilinum</i>
<i>Vaccinium myrtillus</i>	<i>L. campestris</i>	<i>Blechnum spicant</i>
<i>Calluna vulgaris</i>	<i>L. multiflora</i>	<i>Dryopteris dilatata</i>
<i>Erica cinerea</i>		

The relation of this heath vegetation to the natural climax of the areas that bear it is a rather obscure. Most heaths are grazed to a greater or less extent—though much less intensively than the grassland—and a large number of them are periodically burnt in order to improve the grazing. Both these processes obviously affect the floristic composition of the community, and tend to restrict the stature of the larger shrubs such as *Ulex gallii* and *Calluna vulgaris*. But whether they radically change the character of the vegetation is a matter about which we have not enough evidence to speak with certainty. There is little doubt that many inland areas which are at present under heath would, if they were not grazed and fired, become colonized by *Sorbus aucuparia*, *Betula pubescens*, *Ilex aquifolium*, *Salix atrocinerea*, and perhaps other woody species, and would develop into woodland of a sort, in which no doubt *Quercus sessiliflora* would eventually establish itself as a prominent and perhaps dominant ingredient. But it seems equally clear that certain exposed areas of heath, especially near the coast, are maintained in this condition at least as much by climatic as by biotic factors, and that in the absence of grazing reversion to woodland be slow, uncertain and incomplete. Where the line is to be drawn between these two cases is very much a matter of personal judgment.

It should be remembered in considering this problem, which is but one aspect of the problem of locating the natural Baumgrenze on the Irish mountains, that the recognition of the importance of biotic factors should not make one forget all about climate. The treelessness of many tracts of hill country in Ireland may well represent the interaction of the two, in that a low intensity of grazing, which in central Europe would be quite inadequate to prevent tree growth, may here bring about the final elimination of seedlings which are, as a result of the shallow soil and the Atlantic climate, making very poor growth at the best.

These considerations apply in some measure to the bog communities as well, for occasional burning and grazing makes them even more treeless than they otherwise would be. But they approximate much more nearly to a natural climax, since most arboreal species are unable to compete with the bog vegetation of herbs and ericaceous undershrubs when the soil is pure, waterlogged peat.

Bog communities have received more study in Ireland than have heath or grassland, and as a fairly full account of them has been given by Tansley (The British Islands and their vegetation, 686—697, 714—718) they will be very briefly treated here. They may be divided into raised bog, which occupies the site of former lake basins, usually at a fairly low altitude in the central plain, and blanket bog, which is climatically and not topographically determined, and clothes all the level and gently sloping areas overlying siliceous rock both on the mountains and near the west coast down to sea levels. The drier regions of the mountain blanket-bog are usually referred to as moorland, and are classified by Tansley with heaths. They are, of course, transitional between heath and bog, and cannot be sharply separated from either. The boundary is best recognized by the falling off in floristic variety which accompanies the development of a solid blanket of peat.

This floristic monotony, which is very characteristic of the bog associations of Ireland, is indeed developed most highly in the drier upland blanket-bogs, where one may walk for several kilometres without seeing more than 25 phanerogamic species. On moors of this type *Calluna vulgaris* is always dominant. It depends for its successful growth on a fair degree of drainage, and

although it is nearly always present in some quantity even on very wet bogs, it only attains in such situations a height of 5—10 cm and is unable to become an effective dominant. Well-grown Callunetum is often astonishingly pure, with the other species making only an insignificant contribution to the vegetation. The most frequent of these are:

<i>Potentilla erecta</i>	<i>Carex binervis</i>
<i>Galium saxatile</i>	<i>Scirpus caespitosus</i>
<i>Erica cinerea</i>	<i>Deschampsia flexuosa</i>
<i>Vaccinium myrtillus</i>	<i>Molinia caerulea</i>
<i>Juncus squarrosus</i>	<i>Nardus stricta</i>
<i>Luzula multiflora</i>	<i>Rhacomitrium lanuginosum</i>
	<i>Cladonia sylvatica</i>

The wetter areas of mountain bog, the lowland blanket-bog of the west, and the raised bogs of the centre may have *Scirpus caespitosus*, *Eriophorum angustifolium*, *Molinia caerulea* or stunted *Calluna vulgaris* as dominant, or, more frequently, a fluctuating mixture of any or all of these, together with much *Erica tetralix*, *Narthecium ossifragum*, *Eriophorum vaginatum*, *Carex panicea*, and, in the west, *Rhynchospora alba* and *Schoenus nigricans*. The presence of this last-named species in abundance is a curious feature of the low-lying blanket-bog of the west, and has yet to receive a convincing explanation, in view of the otherwise constant association of *Schoenus* with calcareous or at least base-rich soils.

In all these wet bogs *Sphagnum* spp. are plentiful, and are mainly responsible for the growth of the peat, with the well-known cycle of hummock and hollow formation. The most conspicuous species are *Sphagnum rubellum*, *S. magellanicum*, *S. papillosum* and *S. cuspidatum*. *Leucobryum glaucum* is also plentiful on the lowland bogs, and *Rhacomitrium lanuginosum* on the upland ones; *Cladonia* spp. are often abundant on both. Minor but characteristic ingredients of the flora, some of them confined to the lowland bogs, are *Drosera* spp., *Andromeda polifolia*, *Oxycoccus quadripetala*, and *Anagallis tenella*.

The limitations of the Irish Flora

The vascular plants native to Ireland comprise about 1250 species, which is much less than would be found in any continen-

tal area of the same size in western Europe. It is less than two thirds of the number to be found in Great Britain. This discrepancy may be accounted for partly by the fact that Ireland is considerably the smaller of the two islands, and extends through only half as many degrees of latitude as does Great Britain, with a consequent lack of climatic variety. It also arises partly from the relative homogeneity of Ireland from the ecological point of view: it has no contrast to equal that afforded by the younger rocks of south and east England and the Palaeozoic regions of Scotland and Wales. But when due allowance has been made for these features there still remains a discrepancy which can be explained only in terms of the insularity of Ireland, by supposing that it became effectively isolated from Great Britain and thereby from the Continent while the later stages of the post-glacial floral migrations were still in progress.

It is, unfortunately, impossible to say with any confidence at what date the isolation of Ireland became effectively complete. The most reasonable hypothesis would seem to be that the southern part of the Irish Sea, which separates southern Ireland from south Wales and south-west England, became flooded relatively early in post-glacial time (probably during the Boreal period), but that a land connexion further north, linking northern Ireland with south-west Scotland, persisted for some centuries after this, and may have lasted into the Atlantic period. If this is true it follows that out of the last substantial contingent of the west-central European flora which was immigrating into Great Britain, a good many species would have been checked, either by a sea barrier or by the stabilization brought about by the extensive development of forest and bog, before they had a chance to reach Ireland.

It is not very easy to discriminate between these species, which are presumed to be absent from Ireland as a result of purely historical causes, and others which, though fairly widespread in Great Britain, find there the north-western limit of the conditions to which they are adapted and are ecologically unfit to colonize Ireland even if they were given a chance to do so. It is obvious, however, that since the western parts of Great Britain are, in climate and soil alike, closely comparable to many parts of Ireland, any species which is reasonably widespread in

these western areas of Great Britain may be presumed to have been capable of establishing and maintaining itself in some part of Ireland if it had ever had an opportunity of immigrating in sufficient quantity. The British species which, judged by this criterion, are well adapted to Irish conditions but are nevertheless absent from Ireland except as obvious introductions are listed below.

Species widespread in Great Britain
(including the western parts) but not native to Ireland

* <i>Clematis vitalba</i>	<i>Genista anglica</i>
<i>Dianthus deltoides</i>	<i>G. pilosa</i>
* <i>Moenchia erecta</i>	<i>Ononis spinosa</i>
<i>Stellaria nemorum</i>	<i>Lathyrus sylvestris</i>
<i>Hypericum montanum</i>	* <i>Sorbus torminalis</i>
* <i>Acer campestre</i>	* <i>Petroselinum segetum</i>
* <i>Sison amomum</i>	<i>Plantago media</i>
<i>Silaum silaus</i>	* <i>Daphne laureola</i>
<i>Valeriana dioica</i>	* <i>Viscum album</i>
<i>Scabiosa columbaria</i>	* <i>Narcissus pseudo-narcissus</i>
* <i>Inula conyza</i>	* <i>Polygonatum multiflorum</i>
** <i>Campanula latifolia</i>	<i>Convallaria majalis</i>
<i>Limonium vulgare</i>	<i>Blysmus compressus</i>
<i>Centaureum littorale</i>	** <i>Melica nutans</i>
** <i>Myosotis sylvatica</i>	

The species marked with an asterisk (*) do not penetrate as natives as far north as Scotland. It is reasonable to suppose, therefore, that they arrived in Wales or south-west England after the southern part of the Irish Sea had been flooded, and were prevented by climatic limitations from spreading to Ireland along the more northerly route, which may still have been open. The species with two asterisks (**) are, on the other hand, distinctly northern in their British distribution, so that their absence from Ireland cannot be explained in this way: whatever factor has excluded them from southern England has presumably also excluded them from Ireland. The remaining species are fairly generally distributed in Britain, and one must suppose that they represent more tolerant late arrivals which had not yet established themselves in south-west Scotland at the time of the final severance of Ireland from Britain.

It will be noticed that this list contains only two maritime species. All the evidence suggest that the maritime species of the British Isles were for the most part early post-glacial arrivals, and that any anomalies in their present distribution arise from local extinction—a process which is in many cases still proceeding today without any obvious human interference.

Attention must also be drawn to the existence of a number of species, obviously related to those that have been discussed above, which once more are widespread in Great Britain, including its western seaboard, and which occur in Ireland, but only over an extremely limited area, being in many cases restricted to a single station. These species include the following:

Species widespread in Great Britain (including the western parts) but confined to one or two very restricted localities in Ireland

<i>Helianthemum nummularium</i>	<i>Adoxa moschatellina</i>
** <i>Geranium sylvaticum</i>	<i>Galium cruciata</i>
<i>G. pratense</i>	<i>Serratula tinctoria</i>
* <i>Trifolium subterraneum</i>	<i>Hypochoeris glabra</i>
** <i>Astragalus danicus</i>	** <i>Cirsium heterophyllum</i>
** <i>Rubus chamaemorus</i>	<i>Limosella aquatica</i>

(The significance of asteriks is the same as in the previous list.)

Astragalus danicus, *Rubus chamaemorus* and *Cirsium heterophyllum* may reasonably be regarded as boreal relicts of post-glacial times which have happened to fare worse in Ireland than in Great Britain; and *Geranium sylvaticum*, and *Galium cruciata* are probably recent arrivals in Ireland. But why the other species, once they had reached Ireland, were not more successful in establishing themselves there is very difficult to explain.

The emphasis that has been laid above on the isolation of Ireland from Great Britain relatively early in post-glacial times as a primary factor in limiting the variety of the Irish flora must not be allowed to obscure the fact that there are number of species widespread in Great Britain and in north-western continental Europe whose absence from Ireland is to be attributed rather to ecological factors. The following may be cited as examples:

Species absent from Ireland and widespread in Great Britain, but with a distinct easterly tendency

<i>Myosoton aquaticum</i>	<i>Bryonia dioica</i>
<i>Astragalus glycyphyllos</i>	<i>Viburnum lantana</i>
<i>Hippocrepis comosa</i>	<i>Cirsium eriophorum</i>
<i>Chrysosplenium alternifolium</i>	<i>Paris quadrifolia</i>

These are plants which, though widespread in Great Britain, show an unmistakable easterly bias, being rare in or absent from Wales, western England and south-west Scotland. It is clear that their north-westward migration has been stopped not by the barrier of the Irish Sea, but by climatic or edaphic factors which become critical in the neighbourhood of the line that separates the Mesozoic and Tertiary area of south and east England from the Palaeozoic areas of the north and west. The list is very diverse ecologically, but most of the species, though generally distributed over Europe, are absent from some of the peripheral countries such as Scandinavia, Greece and the Iberian peninsula. It is reasonable therefore to suppose that Ireland lacks such species as these simply as a result of its marginal position, quite apart from its insularity.

Two more points demand brief mention in connexion with the subject of species absent from the Irish flora. The first relates to woodland plants. *Praeger* has drawn attention to the particularly striking gaps that are to be found in the Irish list when one comes to consider the ground flora of woodlands. *Helleborus*, *Linnaea*, *Trientalis*, *Daphne*, *Corallorhiza*, *Goodyera*, *Maianthemum*, *Ruscus*, *Convallaria*, *Paris*—all are missing. He suggests that this is due partly to the extensive destruction of native forest, and that some of these plants were formerly to be found in Ireland. This may be true, but it should be realized that the list of trees and shrubs which one might expect to find in Ireland but which are absent from it is almost equally striking. These include *Tilia* spp., *Acer* spp., *Sorbus torminalis*, *Ribes* spp., *Viburnum lantana*, *Ulmus* (all species except *U. glabra*), *Fagus sylvatica*, *Populus nigra*, *P. canescens*, *Pinus sylvestris*. None of these, except the last, is believed to have been formerly native to Ireland. It would appear probable, therefore, that although considerable forests of *Pinus*, *Betula*, *Corylus* and *Ulmus* may have existed

in Ireland before its isolation, the spread and development of the mixed-oak-forest, with its associated ground-flora, was a later development, and that the isolation of Ireland may have been early enough for it to have received only a meagre selection of its characteristic species, both woody and herbaceous.

The second point relates to the establishment of aliens in Ireland. Although some 150 species have been added to the Irish flora by human agency the majority of these are either transitory and uncertain, little more than casuals, or else are confined to a small area closely surrounding their centre of introduction. This is partly because the greater part of Irish trade is carried on with Great Britain, and the opportunities for introduction of plants from more remote regions are not as numerous as in most other countries. But the failure of a large number of aliens to establish themselves must be ascribed to the ecological peculiarities of Ireland. In particular, the ruderal species from the Mediterranean and other warm-temperate regions, which constitute a large proportion of the adventive flora of many north-European countries, find themselves severely handicapped in Ireland by the rarity of light soils and by the lack of sufficient sunshine in summer to enable them to ripen their seeds.

A list of the more conspicuous and successful naturalized species is given later in this article.

The Atlantic Flora

The main path of immigration into the British Isles in late-glacial and post-glacial times is presumed to have been across what is now the North Sea and the straits of Dover, from the Low Countries, north-west Germany, and the Rhine basin in general. But a substantial fraction of the Britannic flora shows a Continental distribution of the type usually referred to as Atlantic: limited, that is to say, to the western fringe of Europe and penetrating scarcely or not at all into Switzerland, Germany, Holland, Denmark or Sweden. Unless one presumes that these species at one time ranged further east in Europe (for which there is in most cases no evidence) it is clear that they must have reached the British Isles by a rather more westerly route, namely from northern or north-western France to southern England, south

Wales or southern Ireland. The facilities which they possess for distribution across marine barriers vary greatly from one species to another, but as far as we can tell the majority of them must have reached the British Isles at a time when the seas in this region were at any rate much narrower than they are today.

The precise delimitation of this Atlantic flora is impossible. On the one hand it shades off imperceptibly into a group of species which, though primarily western, penetrate to some small extent into central Europe, and may be described as sub-Atlantic. On the other hand it is neither possible nor profitable to delimit sharply purely Atlantic species from those which extend eastwards in the Mediterranean. From the point of view of its significance in northern Europe it makes little difference whether an Atlantic species is also Mediterranean or not. For the purposes of the present discussion I shall designate as Atlantic any species which, if it transgresses at all to the eastward the meridian of 5° E. longitude (other than along the shores of the Mediterranean) is found to the east of it only in relatively small and discontinuous areas.

On this definition (which is a rather restricted one) there are some 58 Atlantic species in the Irish flora. In the degree to which they are closely bound to the western shores of Europe they vary from extreme western types like *Euphorbia portlandica*, *Daboecia cantabrica* and *Saxifraga spathularis* (none of which comes as far east as London or Toulouse) to others such as *Carum verticillatum*, *Erica cinerea* and *Wahlenbergia hederacea*, whose distribution is only slightly more western than that of such subatlantic species as *Ulex europaeus* and *Digitalis purpurea*. The former category includes, of course, the well-known group of species which is variously referred to as Hiberno-Lusitanian, Hiberno-Pyrenean or Hiberno-Cantabrian. (None of the names is entirely satisfactory, but the last is the best.) These are species which are found in Ireland as well as in Portugal, Northern Spain or western France, but are unknown in Great Britain. They have been the subject of a great deal of discussion and speculation, because of the light that they may be held to throw on the botanical history of the British Isles during the glacial period.

Only two possible explanations of their discontinuous distribution are seriously considered to-day. One is that these species

are, in Ireland, pre-glacial or at least inter-glacial relicts, having managed to survive the final glaciation, or perhaps all the glaciations, on the extreme western fringe of the country (perhaps in areas now submerged) where oceanic influences mitigated the rigours of the glacial climate. The other theory holds that these species shared in the main northward migration (though along a very westerly route) in late-glacial and early post-glacial time, and have suffered disintegration of area since that time. According to this latter theory, then, the extinction of these species in the south-western parts of Great Britain has been comparatively recent.

Either theory presents grave difficulties if applied to the whole group of species. It is very difficult to believe, on the one hand, that *Arbutus unedo* could have survived the last glaciation anywhere in northern Europe. It seems almost equally improbable that *Saxifraga spathularis*, having been widespread along the Atlantic littoral in early Boreal times, should have been totally exterminated throughout the Basque Provinces of Spain, the whole west coast of France, south-west England and south Wales.

I do not wish to pronounce on this controversy here, but to draw attention to two relevant points that are sometimes overlooked. The first is the necessity of considering this discontinuity in distribution in conjunction with other examples furnished by the Atlantic flora. A list of Atlantic species found in the British Isles which show some degree of discontinuity in their distribution is given in the accompanying table. It will be seen that although the Hiberno-Cantabrian plants furnish all the most striking examples, there are certain other species, such as *Ulex gallii* and, in a different way, *Carex punctata* and *Erodium maritimum*, whose distribution is curiously discontinuous. *Otanthus maritimus*, which had a relatively continuous, if sparse, distribution a century ago, has now become extinct in Great Britain, and serves as a reminder of the necessity of discriminating between species that are so rare that the obliteration of a few stations can radically alter the pattern of their distribution (*Trichomanes* provides another instance of this) and those like *Pinguicula grandiflora*, *Ulex gallii* and *Saxifraga spathularis* that are sufficiently common in those areas in which they occur to make it unlikely that the gaps which separate those areas are of very recent origin.

	Ireland				Gr. Britain				France			Spain		Portugal	Mediterranean coasts.
	North-west	West	South-west	South-east	North-west	West	South-west	South-east	North-west	West	South-west	North	North-west		
<i>Erica mackaiana</i>	—	+	—	—	—	—	—	—	—	—	—	—	+	—	—
<i>Neotinea intacta</i>	—	+	—	—	—	—	—	—	—	—	—	+	+	+	+
<i>Erica mediterranea</i>	—	+	—	—	—	—	—	—	—	—	+	+	+	+	+
<i>Saxifraga spathularis</i>	+	+	+	+	—	—	—	—	—	—	—	—	+	+	—
<i>S. hirsuta</i>	—	(+)	+	—	—	—	—	—	—	—	+	+	+	—	—
<i>Pinguicula grandiflora</i>	—	+	+	—	—	—	—	—	—	—	+	+	+	—	—
<i>Carex punctata</i>	—	—	+	—	+	+	+	—	+	+	+	—	—	—	+
<i>Erodium maritimum</i>	—	+	+	+	+	+	+	+	+	+	—	—	—	—	+
<i>Trichomanes speciosum</i>	+	+	+	+	+	+	—	—	—	—	+	—	+	+	—
<i>Daboecia cantabrica</i>	—	+	—	—	—	—	—	—	+	+	+	+	+	+	—
<i>Arbutus unedo</i>	+	—	+	—	—	—	—	—	+	+	+	+	+	+	+
<i>Spergularia rupicola</i>	+	+	+	+	+	+	+	+	+	+	—	—	+	+	—
<i>Erica vagans</i>	—	—	—	—	—	—	+	—	+	+	+	+	+	+	—
<i>E. ciliaris</i>	—	—	—	—	—	—	+	—	—	+	+	+	+	+	—
<i>Meconopsis cambrica</i>	+	+	—	+	—	+	+	—	+	+	+	+	+	—	—
<i>Ulex gallii</i>	+	+	+	+	+	+	+	+	+	—	+	—	+	—	—
<i>Simethis planifolia</i>	—	—	+	—	—	—	+	—	+	+	+	+	+	+	+
<i>Euphorbia hiberna</i>	+	+	+	+	—	—	+	—	+	+	+	+	+	+	—
<i>Sibthorpia europaea</i>	—	—	+	—	—	+	+	+	+	+	+	+	+	+	—
<i>Otanthus maritimus</i>	—	—	—	+	—	(+)	(+)	(+)	+	+	+	+	+	+	+

(+) indicates extinct.

It must be admitted, however, that all the most striking examples of discontinuity are furnished by plants which are found in Ireland (whether they are also represented in Great Britain or not); and that Atlantic species which find their northern limit in south-west England have a relatively continuous distribution south of this. This argument, as far as it goes, would seem to favour the survival hypothesis.

The other point to be considered is the distribution in Ireland of Atlantic species. Since the climate of all parts of Ireland is, in comparison with that of central Europe, decidedly Atlantic, it is not surprising to find that a considerable number of species that are indubitably Atlantic are generally distributed over Ireland. Some of these, such as *Carex binervis*, *Conopodium majus* and *Erica cinerea*, are also very widespread in Great Britain; others, such as *Pinguicula lusitanica*, *Ulex gallii* and *Spergularia rupicola*, though widespread in Ireland are distinctly western in Great Britain; others again show a curious distribution centred round

the Irish sea, being western in Great Britain but somewhat eastern in Ireland, such as *Asparagus maritimus*, *Scilla verna* and *Inula crithmoides*.

Distribution in Ireland		Distribution in Great Britain
General	<i>Hypericum androsaemum</i>	South
»	<i>H. elodes</i>	South-west
»	<i>Ulex gallii</i>	South-west
»	<i>Umbilicus pendulinus</i>	South-west
»	<i>Sedum anglicum</i>	West
»	<i>Conopodium majus</i>	General
»	<i>Oenanthe crocata</i>	General
»	<i>Anthemis nobilis</i>	South
»	<i>Erica cinerea</i>	General
»	<i>Pinguicula lusitanica</i>	West
»	<i>Carex binervis</i>	General
»	<i>Hymenophyllum peltatum</i>	North-west
»	<i>Dryopteris aemula</i>	West
General (maritime)	<i>Raphanus maritimus</i>	South-west
»	<i>Spergularia rupicola</i>	West
»	<i>Crithmum maritimum</i>	West
»	<i>Limonium binervosum</i>	South
»	<i>Beta maritima</i>	General
»	<i>Polygonum raii</i>	General
»	<i>Euphorbia paralias</i>	South
»	<i>E. portlandica</i>	West
»	<i>Scirpus cernuus</i>	West
»	<i>Agropyron junceum</i>	General
»	<i>Asplenium marinum</i>	North-west
West	<i>Saxifraga spathularis</i>	—
»	<i>Arbutus unedo</i>	—
»	<i>Erica mackaiana</i>	—
»	<i>E. mediterranea</i>	—
»	<i>Daboecia cantabrica</i>	—
»	<i>Bartsia viscosa</i>	West
»	<i>Euphorbia hiberna</i>	South-west
»	<i>Neotinea intacta</i>	—
»	<i>Adiantum capillus-veneris</i>	South-west
South-west	<i>Saxifraga hirsuta</i>	—
»	<i>Cicendia filiformis</i>	South
»	<i>Sibthorpia europaea</i>	South-west
»	<i>Orobancha hederæ</i>	South-west
»	<i>Pinguicula grandiflora</i>	—
»	<i>Simethis planifolia</i>	South
»	<i>Trichomanes speciosa</i>	West
South-west (maritime)	<i>Carex punctata</i>	West
South	<i>Ranunculus lenormandi</i>	West
»	<i>Rubia peregrina</i>	South-west
»	<i>Wahlenbergia hederacea</i>	South-west
»	<i>Asplenium lanceolatum</i>	South-west
South (maritime)	<i>Matthiola sinuata</i>	South-west
»	<i>Juncus acutus</i>	South
»	<i>Agropyron pungens</i>	General
South-east	<i>Corydalis claviculata</i>	General
»	<i>Lepidium heterophyllum</i>	General

South-east (maritime)	<i>Lavatera arborea</i>	West
»	<i>Erodium maritimum</i>	South-west
»	<i>Otanthus maritimus</i>	South
»	<i>Inula crithmoides</i>	South-west
»	<i>Asparagus maritimus</i>	South-west
East (maritime)	<i>Scilla verna</i>	North-west
Disjunct and scattered	<i>Meconopsis cambrica</i>	South-west
»	<i>Carum verticillatum</i>	West

There remains, however, a considerable number of Atlantic species which even in Ireland show a southern or western distribution. A few of these, such as *Trichomanes speciosum* and *Saxifraga hirsuta*, are so clearly adapted to very damp situations

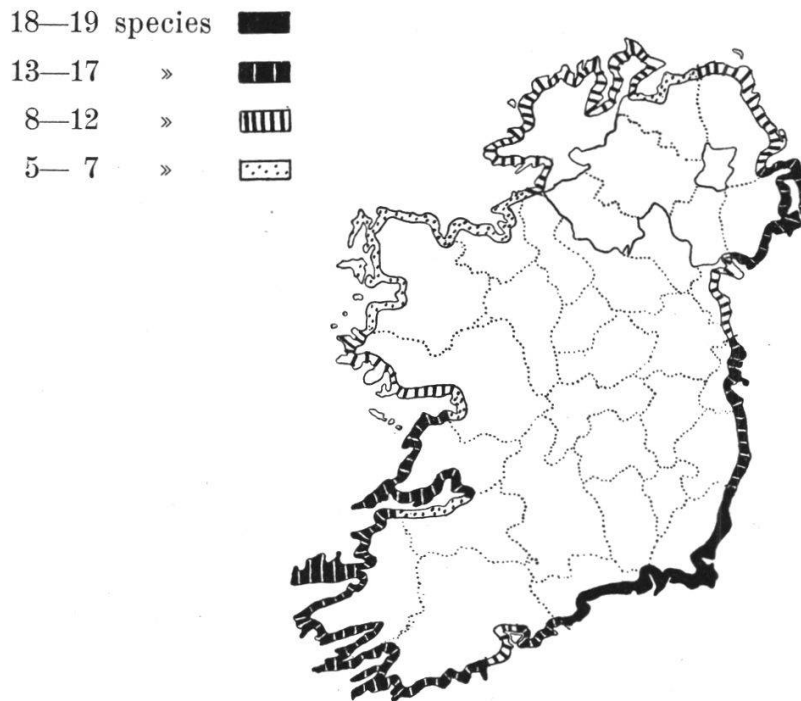


Fig. 1. Distribution in Ireland of 21 maritime Atlantic species.

that a climatic explanation is obvious, but there are many others whose restricted range is not so easily explicable on purely ecological grounds. The distribution of all Irish species which are Atlantic according to the criteria adopted earlier in this section is summarized in the accompanying table and maps. Attention may be drawn especially to two features of this distribution. The first is the fact that the maritime species show a pronounced south-easterly trend, finding their maximum frequency in Wexford and Waterford and their minimum in Mayo and Sligo. This

is very suggestive of relatively recent arrival along a former coast-line, now drowned, which ran from Brittany past Land's End (Cornwall) and Pembrokeshire (South Wales) to reach Ireland near what is now its south-east corner. The second is the equally pronounced coastal and south-western tendency shown by the non-maritime species. The greater variety of soil, elevation and situation to be found in the coastal counties of Ireland may partly account for this coastal distribution, but would hardly have been expected to produce such a striking result. However, it is not only Atlantic species which show, in the British Isles

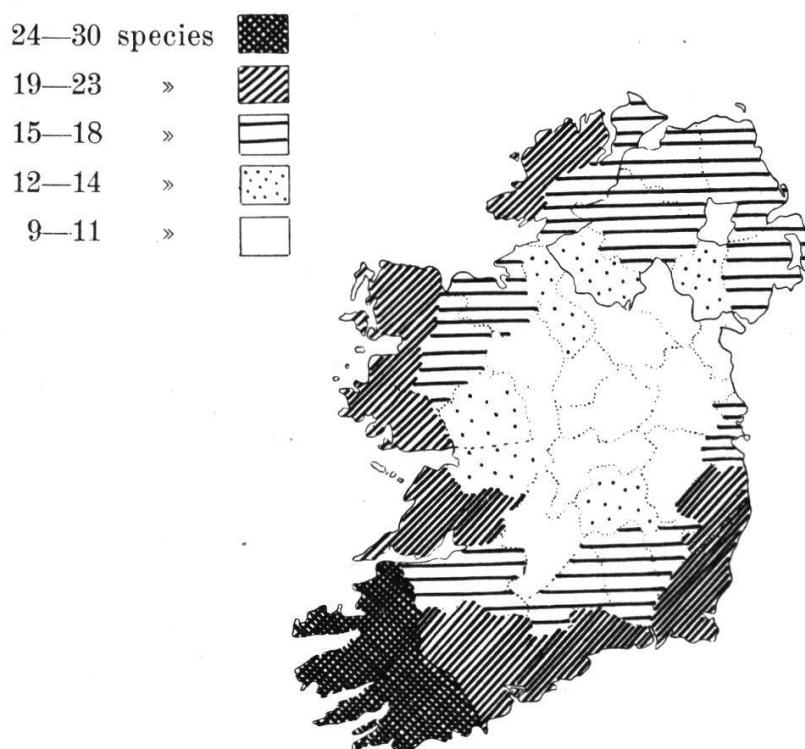


Fig. 2. Distribution in Ireland of 37 non-maritime Atlantic species.

and especially in Ireland, this curious type of «submaritime» distribution, being found not on or very near the shore, but seldom more than 10 km from the sea. Species of this type present a very baffling problem in distributional ecology.

Finally, attention may be directed to a fact which emerges clearly from this table: that in spite of the general south-westerly trend of the Atlantic species in Ireland, the Hiberno-Cantabrian group is centred not on the south-west but on the west of island. *Pinguicula grandiflora*, which is not found further north than

Clare, forms an exception, but *Saxifraga hirsuta*, though now confined to the south-west, must have existed formerly in Mayo and Galway, as it has left hybrid descendants there. *Euphorbia hiberna* may soon be in similar case: it is abundant in the south-west, and has only three or four precarious relict stations scattered up the rest of the west coast. It seems clear that the west coast as a whole was the original Irish centre for this group of extreme Atlantic species, and that in recent centuries, presumably under the influence of climatic changes, some of them, but by no means all, have contracted their range so as to confine it to the south-west.

The Boreal Flora

The flora of Ireland in late-glacial times is believed to have been composed mainly of species which are now found principally in the arctic and sub-arctic regions of Europe (extending in many cases to Arctic Asia or America), and on the higher parts of the principal mountain ranges of Central and Southern Europe. The present restriction of their distribution is, of course, a result of their retreat before the invasion of the temperate flora in early post-glacial times. In most countries of central and north-central Europe small relict populations of this late-glacial flora persist here and there, either on mountains of moderate height or in other districts which for one reason or another have favoured their survival.

To this group may be assigned some 50 members of the present Irish flora, apart from a number of critical species (including the *Hieracia*) in which taxonomic difficulties render uncertain the accurate assessment of geographical range. Two of them are alpine rather than boreal: they are unknown in Scandinavia or the Arctic, and find their northern limit in the British Isles. These are *Gentiana verna* and *Arenaria ciliata*. The populations which exist in Ireland to-day must be regarded as detached fragments of a northerly migration from their primary centre in the mountains of Central Europe. *Rubus chamaemorus*, *Ligusticum scoticum*, *Mertensia maritima* and *Carex aquatilis* are, on the other hand, essentially subarctic species, which do not reappear in the Alps (two of them being, of course, debarred from doing so by their

maritime habit); and all, in fact, except *Rubus chamaemorus*, find in Ireland their southern European limit.

For the remaining 42 species, however, the Irish stations form merely one of a number of links which help to connect their main populations in Scandinavia and the Arctic with the considerable populations that exist also in the Alps and other major mountain ranges of Europe. Many of these species may be fairly classified as Arctic-Alpine, but others, which exhibit a fundamentally similar distribution in less extreme form, are best considered with them and it is best to adopt for the whole group Matthews's term of «boreal-montane». They connect on the one hand, through such species as *Meconopsis cambrica* and *Pinguicula grandiflora*, to the Atlantic flora, and on the other hand through distinctly, but less exclusively boreal species such as *Gentiana campestris* and *Andromeda polifolia* to the main mass of the central European flora.

Most of these boreal-montane species are distinctly rare in Ireland, as conditions have favoured there a more complete obliteration of this boreal-montane flora by the growth of forest and bog than has taken place in Scotland, or even in northern England and North Wales, where one finds in abundance, on mountains no higher than those of Ireland, species such as *Lycopodium alpinum*, *Alchemilla alpina* and *Cryptogramme crispa* which are extremely rare in Ireland. There is no doubt that a considerable number of boreal-montane species which are still widespread in the Scottish Highlands, and which in many cases still persist in small quantity in northern England, were found in Ireland in late-glacial times but have since then become extinct. *Betula nana* is the only species of which this can be said with confidence, but further exploration of fossil material may be expected to produce additions to the list. At present there are many species such as *Rubus chamaemorus*, *Saxifraga nivalis*, *S. hirculus*, *Arabis petraea* and *Carex pauciflora* which are so rare in Ireland that they may be said to be trembling on the verge of extinction; and there are others such as *Poa alpina*, *Alchemilla alpina*, *Epilobium alsinifolium*, *Arenaria ciliata* and *Carex magellanica*, which, though well established and flourishing in their known stations are confined to one or two extremely small areas.

It is all the more remarkable therefore that in certain parts of Ireland arctic-alpine or cognate species show a quite unexpected

degree of tolerance, by descending almost to sea-level. The same phenomenon is seen in north-west Scotland, but it takes place on at least as large a scale in County Donegal, some 3° further south, and to an even more unexpected extent in the Aran Islands and the Burren country of Clare. Whether the karst-like nature of the country which enables the arctic-alpine species to sieze possession of this low-lying land exposed to the full influence of warm Atlantic winds is the result of purely climatic factors, or of accidents of post-glacial history, is a matter on which it is impossible to pronounce with any confidence.

The accompanying table lists the boreal-montane species found in Ireland, with an indication of their altitudinal range and their general distribution in the country. It will be seen that more than half of them descend to a height of 150 m or less. Thanks to the relative climatic homogeneity of Ireland the tendency to favour the northern rather than the southern half of the island is not very strongly marked. Most of the single-station plants have that station in the north; *Cryptogramme crispa* makes its uncertain and fleeting appearances only in the northern half; and of the two coastal species *Ligusticum scoticum* has a northern and *Mertensia maritima* a north-eastern distribution. But a considerable number of the montane species have a north-western, or in some cases purely western distribution. The abundance of high mountains in Kerry is one factor that influences this pattern, but there is no doubt that the western mountains—probably by a combination of climatic and edaphic influences—provide a much more favourable habitat for plants of this type than do the mountains of Wicklow or Down. Finally, it may be noted that over a third of the species are generally distributed through the country.

Boreal-montane and related species in Ireland

	Distribution in Ireland	Altitudinal range in Ireland (metres)
Alpine only		
<i>Arenaria ciliata</i>	north-west (one station)	360— 590
<i>Gentiana verna</i>	west	0— 300
Boreal only		
<i>Rubus chamaemorus</i>	north (one station)	550
<i>Ligusticum scoticum</i>	north	maritime
<i>Mertensia maritima</i>	north-east	maritime
<i>Carex aquatilis</i>	scattered	lowland

Boreal-montane

(1) Very restricted distribution

	Distribution in Ireland	Altitudinal range in Ireland (metres)
<i>Arabis petraea</i>	two separate stations	400— 800
<i>Epilobium alsinefolium</i>	north-west (one station)	300— 360
<i>Saxifraga nivalis</i>	north-west (one station)	590
<i>Alchemilla alpina</i>	south (three stations)	600— 800
<i>Carex pauciflora</i>	north-east (one station)	300
<i>C. magellanica</i>	north-east (one station)	300
<i>Calamagrostis neglecta</i>	north-east (one area)	lowland
<i>Poa alpina</i>	west (two stations)	450— 950
<i>Cryptogramme crispa</i>	north (isolated single plants)	90— 520

(2) Less restricted distribution

<i>Thalictrum alpinum</i>	west	270— 640
<i>Trollius europaeus</i>	north-west	0— 75
<i>Draba incana</i>	west (mainly north-west)	0— 770
<i>Subularia aquatica</i>	west (extinct in north)	0— 370
<i>Silene acaulis</i>	north-west	120— 480
<i>Arenaria verna</i>	disjunct	0— 430
<i>Rubus saxatilis</i>	general (rare in south)	0— 550
<i>Dryas octopetala</i>	north-west	0— 390
<i>Potentilla fruticosa</i>	west	lowland
<i>Saxifraga oppositifolia</i>	north-west	0— 720
<i>S. aizoides</i>	north-west	0— 480
<i>S. hirculus</i>	scattered sparsely	80— 300
<i>S. stellaris</i>	general	150—1030
<i>S. rosacea</i>	west	0— 950
<i>S. hypnoides</i>	mainly north and west	0— 550
<i>Sedum rosea</i>	general	0— 950
<i>Antennaria dioica</i>	general	0— 800
<i>Saussurea alpina</i>	scattered sparsely	300— 840
<i>Vaccinium vitis-idaea</i>	general	30— 880
<i>Arctostaphylos uva-ursi</i>	north-west	0— 575
<i>Polygonum viviparum</i>	west (mainly north-west)	150— 720
<i>Oxyria digyna</i>	west	170— 950
<i>Empetrum nigrum</i>	general	0—1000
<i>Salix phylicifolia</i>	north-west	170— 300
<i>S. herbacea</i>	general	260— 920
<i>Listera cordata</i>	scattered	50— 600
<i>Leucorchis albida</i>	marginal	0— 250
<i>Eriophorum vaginatum</i>	general	0— 910
<i>E. angustifolium</i>	general	0— 850
<i>Carex rigida</i>	general	300—1000
<i>Asplenium viride</i>	west	210— 950
<i>Polystichum lonchitis</i>	west	350— 850
<i>Lycopodium alpinum</i>	scattered sparsely	430— 900
<i>Selaginella selaginoides</i>	general (rare in south)	0— 630
<i>Isoetes lacustris</i>	general	0— 710

Such boreal-montane species as are largely confined to mountain situations in Ireland are seldom found on the actual summits, *Carex rigida* and *Salix herbacea* providing the only exceptions. They are chiefly concentrated on north-facing cliffs. Confirmation has, of course, ensured that the majority of the cliffs

on Irish mountains are north-facing, but the scarcity of these specifically mountain plants on such south-facing cliffs as do exist shows that shading and constant moisture are generally required, as well as a reduced intensity of competition.

The Hiberno-American flora

A few species found in Ireland are primarily American rather than European. Two of these—*Juncus macer (tenuis)* and *Sisyrinchium bermudiana*—are under some suspicion as recently introduced by human agency, since both have freely established themselves as colonists in Great Britain and elsewhere in western Europe. Their Irish centres of distribution are, however, in rather remote regions of the west, and there would seem to be a strong possibility that they are native to Ireland. For the other three species there is no reason to suspect that they have been distributed by human agency. These are *Eriocaulon septangulare*, *Naias flexilis* and *Spiranthes gemmipara*. They are confined to the western fringe of Ireland, except for the colony of *Spiranthes* in the Lough Neagh region in the north-east. This has usually been listed as a different species (*S. stricta*), but it would seem to differ only varietally from the *S. gemmipara* of the south-west.

Naias flexilis is found also in a few stations in Great Britain, and here and there round the Baltic and in Switzerland (Bodensee). It has, however, a fairly wide distribution in northern Europe as a fossil, and it is clearly to be regarded as a circumpolar species whose range has contracted recently, till it has become almost exclusively American. It would seem probable that *Eriocaulon* and *Spiranthes* represent a more extreme development of the same process; each of them has now a European distribution that is confined to Ireland and one or two islands of the west of Scotland. Whatever the details of the quaternary history of these species may be, it seems almost certain that their Irish and Scottish populations are relict rather than recently arrived.

The Alien Flora

It has been mentioned earlier that conditions in Ireland are not such as favour the introduction and establishment of large numbers of alien species. But these are partly counterbalanced by

the poverty of the native flora, which means that certain ecological niches are not completely filled, and that the adventive species finds, therefore, less intense competition than it might elsewhere. The principal adventive species are listed below, the list being restricted to include only those that have established themselves in several different localities, that seem to be fairly permanently established, and that show some power of dispersal from their original centres of introduction. Among recent arrivals the most strikingly successful have been *Elodea canadensis*, *Crepis biennis*, *Matricaria matricarioides* (which spread all through the country in the first thirty years of this century) and *Epilobium pedunculare* (which arrived barely twenty years ago and is already abundant on wet stony ground in the mountains, miles from human habitations).

Ruderals

Papaver rhoeas
P. dubium
Fumaria officinalis
Coronopus didymus
Raphanus raphanistrum
Silene anglica
Melandrium album
Spergula arvensis
Malva moschata
M. rotundifolia
Melilotus officinalis
Scandix pecten-veneris
Foeniculum vulgare
Aethusa cynapium
Matricaria matricarioides
Veronica persica
Chenopodium bonus-henricus
Euphorbia helioscopia
E. peplus
E. exigua
Lolium temulentum
Hordeum murinum

Spreading along railway tracks

Diplotaxis muralis
Arenaria tenuifolia
Linaria minor

Spreading along roadsides

Smyrniolum olusatrum
Petasites fragrans

Established in hedges and woods

Clematis vitalba
Acer pseudoplatanus
Prunus insititia
P. cerasus
Humulus lupulus
Fagus sylvatica

In other habitats

Impatiens glandulifera
Cotoneaster microphyllus
Sedum fabaria
S. album
Epilobium pedunculare
Centranthus ruber
Crepis biennis
Lactuca muralis
Symphytum officinale
Erinus alpinus
Linaria cymbalaria
Mimulus guttatus
Orobanche minor
Mentha piperita
M. rotundifolia
Lamium album
Salix fragilis
S. viminalis
Elodea canadensis
Pinus sylvestris

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