A bridge too far – the non-Irish element in the British flora

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ABSTRACT

Native British vascular plants which do not occur in Ireland were assessed by examining all those which occur in eight selected areas: St David's, Lleyn, West Anglesey, Isle of Man, Mull of Galloway, Mull of Kintyre, Arran and Islay. The 58 candidate species which emerged were analysed in relation to their distribution in Britain and Europe and their biogeographical elements, their habitats, Quaternary history and ability to become established in Ireland or elsewhere beyond their native range. This analysis reduced the list to 22 species which fell into two distinct groups: 17 of woodlands and woodland margins, and five of dry, open grassland or cliffs. It is argued that these species, nearly all of which are thermophilous and belong to Continental or Continental Southern elements in the British flora, did not arrive in Britain until the climatic amelioration of the Boreal period of the Flandrian post-glacial, about 9,000 BP, by which time the land bridge to Ireland had already gone, or would have gone, before these slow-moving forest species reached the coast. The small number of the candidate species is compared with other similar situations in Britain.

KEYWORDS: biogeography, floral history, plant distribution.

INTRODUCTION

The first extensive use of the maps being produced by the Distribution Maps Scheme of the B.S.B.I. was by David Webb in an account of the vegetation and flora of Ireland which he wrote for the British Association in preparation for their visit to Dublin in 1957 (Meenan & Webb 1957), in which he discussed the possible explanation of the fact that there are 460 species which are native to Britain which are not found in Ireland. Whilst acknowledging that for the majority no special explanation is needed – Ireland is outside the geographical range of the higher Scottish mountain plants, the steppe species of East Anglia, the Mediterranean element of the Lizard Peninsula, or that large number of species more or less confined to the area south-east of a line joining the Severn to the Humber such as *Cirsium acaule** and *Viburnum lantana* – he drew attention to species like *Genista anglica*, *Helictotrichon pratense* and *Chrysosplenium alternifolium* for which this explanation is inadequate. He suggested that there were both historical and ecological reasons for these absences: *Genista anglica* is an Oceanic West European species according to Matthews (1955) which, on biogeographical grounds, ought to be in Ireland, the most Atlantic country of all, where the acid habitats it grows on are abundant, but it was probably a late arrival in Britain and, by the time it arrived in Wales and south-west Scotland, the land bridges which formerly connected Britain and Ireland had already gone. *Helictotrichon pratense*, in contrast (see Fig. 1), belongs to the Continental element in our flora (Perring 1985), and was probably established early in post-glacial times in eastern England and the midlands but advanced so slowly along the restricted routes open to this base demanding species that it was never common on the west coast area and was not able to cross to Ireland before the waters inundated the bridge. He pointed out that *Chrysosplenium alternifolium* had a distribution showing the same feature (Fig. 2).

Webb was not the first to address this subject. Praeger (1934) suggested nine species which failed to reach Ireland: *Genista anglica*, *Ononis spinosa*, *Astragalus glycyphyllos*, *Lathyrus sylvestris*, *Chrysosplenium alternifolium*, *Scabiosa columbaria*, *Paris quadrifolia*, *Convallaria majalis* and *Helictotrichon pratense*. Godwin (1975) included the same list when discussing the impoverished nature of the Irish flora and fauna. It will be noted that all three species selected for discussion by Webb are in this list. However he did not at that time have the access to the completed maps of the

* Nomenclature follows Kent (1992).

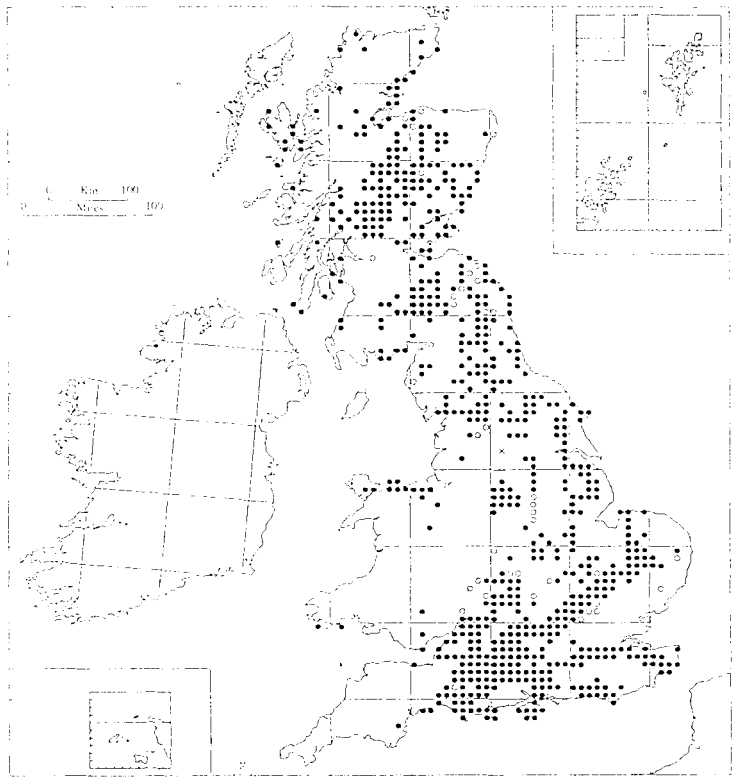

FIGURE 1. The distribution of *Helictotrichon pratense* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record, × = introduction. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

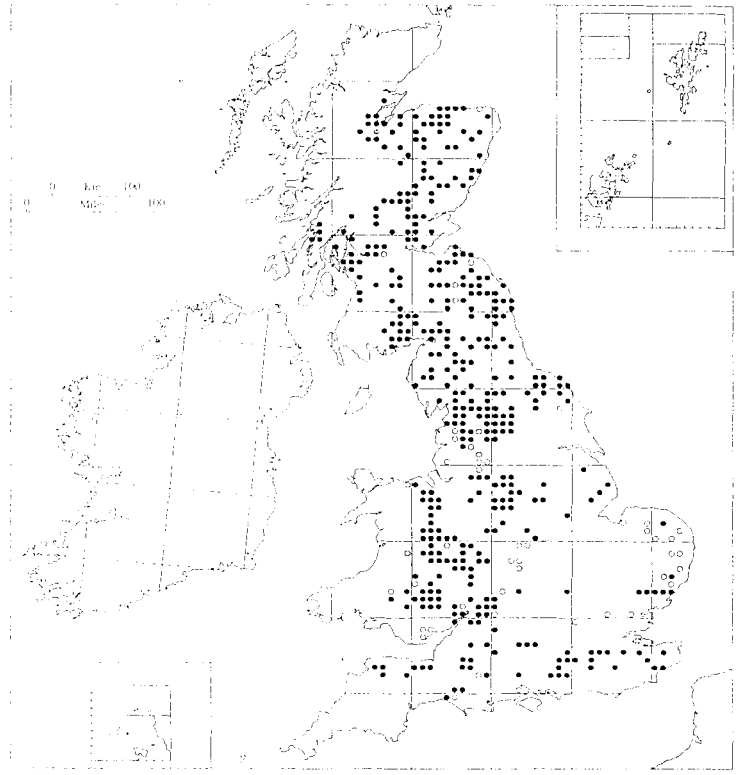

FIGURE 2. The distribution of *Chrysosplenium alternifolium* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

Atlas of the British flora (Perring & Walters 1962) or the other sources of information which have followed it including many local floras. In a later paper (Webb 1983) he did return to the subject and concluded that there are 186 species "of which it may be said with reasonable confidence that their absence from Ireland is due, principally if not entirely, to the opening of the Irish Sea before they had completed their north-westward migration". However he did not consider the distribution of these species in detail or publish a list, though he implied that they all occur in Britain close to the bridge-heads from which an invasion of Ireland must have started.

It therefore seems timely to assess the list of species in the flora of Great Britain which are absent from Ireland and review them in the light of up-to-date information on their present and, where it is known, past distribution, and recent evidence on the existence of land bridges between Britain and Ireland and the time when they ceased to exist.

To do this all the native species of Britain which are not recorded as native in Ireland but which grow or have grown recently in the areas of the British coast closest to Ireland have been considered. Critical species in the *Critical Supplement* (Perring & Sell 1968) and the brambles covered by Edees & Newton (1988) were also considered but narrow endemics were excluded on the grounds that the majority will have evolved in situ in habitats like cliffs from which they are unable to spread or that they are so local that even if they do occur in Ireland they have not yet been detected.

The areas selected were: St David's Peninsula, Lleyn, West Anglesey, Isle of Man, Mull of Galloway, Mull of Kintyre, Arran and Islay. These are defined by the 10-km squares shown on the map (Fig. 3).

THE LAND BRIDGES

Godwin (1975) placed the separation of Ireland from Great Britain in the Boreal period about 8,500 BP when the bridges were flooded by a major eustatic rise in the sea level. More recently Synge (1985) has postulated a much earlier date suggesting that the last land bridge, the Bardsey Ridge between Wicklow and Lleyn, was breached during the Allerød about 12,000 BP.

This large difference of date is critical for, as Godwin remarked, during the earlier stages of the retreat of the ice, in the Allerød for example, the conditions favoured species of open habitats but the later stages were within a period of rapidly intensifying forest dominance. A bridge in the Boreal would have allowed many forest species to cross: a bridge in the Allerød would have been available only for species of open vegetation.

Both authors agreed that the separation of Ireland from Britain was earlier than the separation of England from northern France which was placed by Pennington (1969) at about 7,500 BP. The separation of the Isle of Man from Britain appears to have been later than the separation from Ireland but earlier than the separation from France and is placed by Allen (1984) at 9,000 BP.

NATIVE WEST COAST SPECIES OF BRITAIN ABSENT FROM IRELAND

The native British species which occur in these eight areas on the west coast but which do not occur as natives in Ireland are listed in Table 1. They may be regarded as candidate species. A few general points are noteworthy:

1. The small number of candidates – 52 macro and six critical species – this represents only about 28% of the 186 macrospecies absent from Ireland suggested by Webb (1983).
2. The absence of any pteridophytes or member of the Ericaceae and the presence of only two orchids in the list – light-propaguled species can cross the sea without bridges.
3. That the largest number of species which may have failed to cross is in St David's (31) with Anglesey (28) a close second whilst the smallest numbers are in Arran (3) and on the Mull of Kintyre (5) but there are no species in Islay which do not occur in Ireland.
4. That these numbers tend to be correlated with the present distance between these areas and the nearest Irish coast (Fig. 4). However, though there is a general correlation there are two major discrepancies:
   i) All four islands fall well below the line, suggesting that they too have impoverished floras because of early separation from the mainland of Britain.

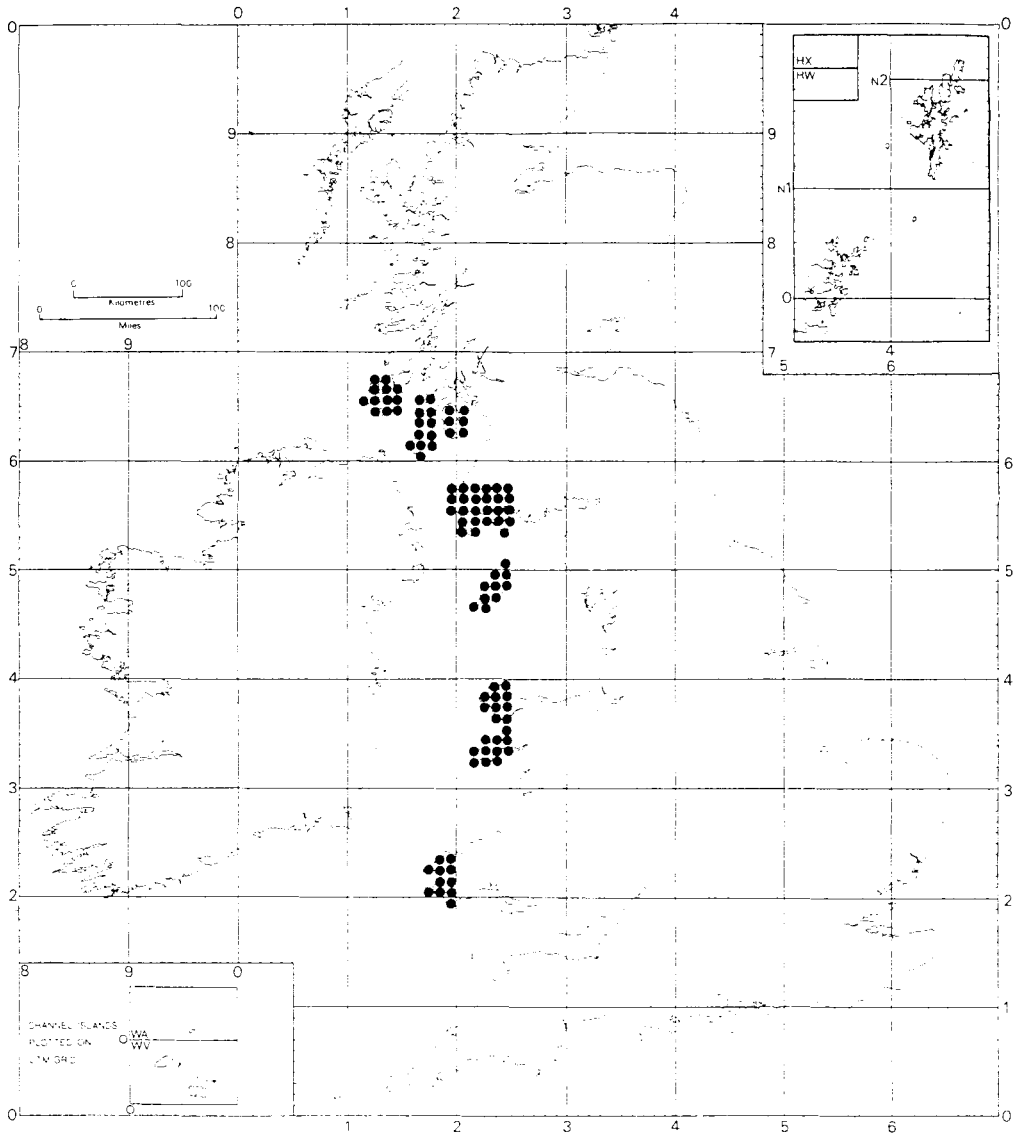

FIGURE 3. Map showing selected areas by 10-km squares used in the study.

ii) Lleyn has many fewer absent taxa than St David's or Anglesey which may be correlated with the location of the last land bridge being between Lleyn and Wicklow (Synge 1985) but may also be related to the scarcity of base-rich habitats there compared to these other two areas.

5. Most of the taxa (49) occur in only one or two of the eight areas, six occur in three areas, whilst there is only one in four and two in five areas and none in more than that.
6. Whilst of the nine species which failed to reach Ireland suggested by Praeger (1934) *Lathyrus sylvestris* (5), *Helictotrichon pratense* (4) and *Genista anglica* are in the top nine here, *Astragalus glycyphyllos*, *Paris quadrifolia* and *Scabiosa columbaria* occur in only one area whilst *Chrysosplenium alternifolium*, *Convallaria majalis* and *Ononis spinosa* do not occur in any.

TABLE 1. SPECIES WHICH OCCUR IN BRITAIN AS NATIVES IN EIGHT GEOGRAPHICAL AREAS BUT WHICH DO NOT OCCUR AS NATIVES IN IRELAND

S = St David's; L = Lleyn; An = W. Anglesey; M = Isle of Man; G = Mull of Galloway; K = Mull of Kintyre; Ar = Arran; I = Islay; (+) = extinct or no records from 1930 onwards

Species	Geographical area								Total
	S	L	An	M	G	K	Ar	I	
Acer campestre	+								1
Allium schoenoprasum	+								1
Astragalus glycyphyllos					(+)				1
Campanula latifolia					+	+			2
Clematis vitalba	+		+						2
Coincya monensis				+			+		2
Cruciata laevipes					+	+			2
Cyperus longus	(+)	+							2
Dactylorhiza praetermissa	+	+							2
Daphne laureola	+	+	+						3
Epipactis leptochila			+						1
Genista anglica	+	+	+						3
G. pilosa	+								1
G. tinctoria			(+)	+	+				3
subsp. *littoralis*	+								1
Gentiana pneumonanthe			+						1
Helictotrichon pratense	+		+			+	+		4
Hornungia petraea	+	+							2
Hottonia palustris			+						1
Hypericum linariifolium		+	(+)						2
H. montanum	+								1
H. undulatum	+								1
Inula conyzae	+	+	+						3
Iris foetidissima	+		+						2
Juncus capitatus			+						1
Lathyrus sylvestris	+	+	(+)		+		(+)		5
Limonium vulgare			+	+					2
Luronium natans	+		+						2
Meum athamanticum					+				1
Mibora minima			+						1
Moenchia erecta	+		+						2
Nepeta cataria		+							1
Ononis reclinata	+				+				2
Oxytropis campestris						+			1
O. halleri					+				1
Paris quadrifolia			+						1
Petroselinum segetum	+								1
Potamogeton trichoides			+						1
Puccinellia rupestris	+								1
Ranunculus sardous	+				(+)				2
Rhinanthus angustifolius			(+)						1
Ruscus aculeatus	+								1
Scabiosa columbaria	+								1
Sedum telephium subsp. *fabaria*	+	+	+		+	+			5
Sison amomum	+		(+)						2
Tamus communis	+	+	+						3
Tephroseris integrifolia subsp. *maritima*			+						1
Trifolium strictum			(+)						1
Valeriana dioica			(+)	(+)					2
Veronica spicata subsp. *hybrida*	+								1
Vicia lutea				(+)	+				2
V. tetrasperma	+	(+)							2
Totals	29	12	26	5	11	5	3	0	

TABLE 1. *continued*

Species	Geographical area								Total
	S	L	An	M	G	K	Ar	I	
Critical genera – excluding narrow endemics									
Hieracium caesiomurorum						+			1
H. sarcophylloides						+			1
H. vagum		+	+						2
Rubus bertramii	+								1
R. lindebergii				+	+				2
R. silurum	+	+	+						3
Grand totals	31	14	28	6	12	7	3	0	

Notes:
The following species were omitted on the grounds that all the evidence suggests that they were never more than colonists in west Britain: *Medicago arabica*, *Rumex pulcher*, *Verbascum nigrum*, *Kickxia spuria*. *Brassica oleracea* has been omitted because recent opinion suggests that it was introduced by the Romans long after the bridge to Ireland was flooded (Stewart *et al.* 1994).
Sources:
The data presented in this table have been taken from the following:
General
Atlas of the British flora (Perring & Walters 1982). *Critical supplement to the atlas of the British flora* (Perring & Sell 1968). *British red data books: 1 – Vascular plants* (Perring & Farrell 1983). *Scarce plants in Britain* (Stewart *et al.* 1994). *Brambles of the British Isles* (Edees & Newton 1988). *Flowering plants of Wales* (Ellis 1983). *Census Catalogue of the flora of Ireland* (Scannell & Synnott 1987). *Flora of North-east Ireland* (Hackney 1992).
Specific
St David's: *Plants of Pembrokeshire* (Davis 1970). Anglesey: *The flowering plants and ferns of Anglesey* (Roberts 1982). Isle of Man: *Flora of the Isle of Man* (Allen 1984). Mull of Kintyre: *The flora of Kintyre* (Cunningham & Kenneth 1979). *Additions to the Flora of Kintyre* (Kenneth 1985). Arran: *Arran's flora* (Church & Smith 1991). Islay: *The wild flowers of Islay* (Ogilvie 1995).

Clearly further analysis is required to distinguish between those species for which the absence of a bridge explains their absence from Ireland and those species which, even if there were a bridge, would not find the climatic or edaphic conditions in Ireland suitable.

To make this analysis the following features of each species have been examined:

1. Distribution inside Britain; 2. Distribution outside Britain; 3. Habitat; 4. Any known glacial and post-glacial record in Britain or Ireland; and 5. Behaviour if introduced to Ireland.

DETAILED ANALYSIS

RELICT SPECIES

Firstly there is a group of 14 species (Table 2) which can be dismissed as candidates because they are clearly not taxa which have been prevented from moving westwards into Ireland. All occur in only one of the selected areas, with the exception of *Luronium natans* and *Vicia lutea* which are recorded in two, though the latter was probably introduced to the Isle of Man by gulls and did not persist (Allen 1984). They are Continental or Northern Continental in distribution outside Britain and are at the extreme edge of their range here. They are rare or scarce plants, according to the list in Stewart, Pearman & Preston (1994), which have disjunct distributions suggesting they are relicts which have declined but were more widespread when climatic and habitat conditions were more suitable. They include such taxa as *Veronica spicata* subsp. *hybrida* (Fig. 5) regarded by Pigott & Walters (1954) as having survived in their present scattered refuge sites since the late-glacial period about 10,000 BP.

Material of three of these species has been found in Quaternary deposits (Godwin 1975). *Potamogeton trichoides* has records from interglacials and the post-glacial and the overall record

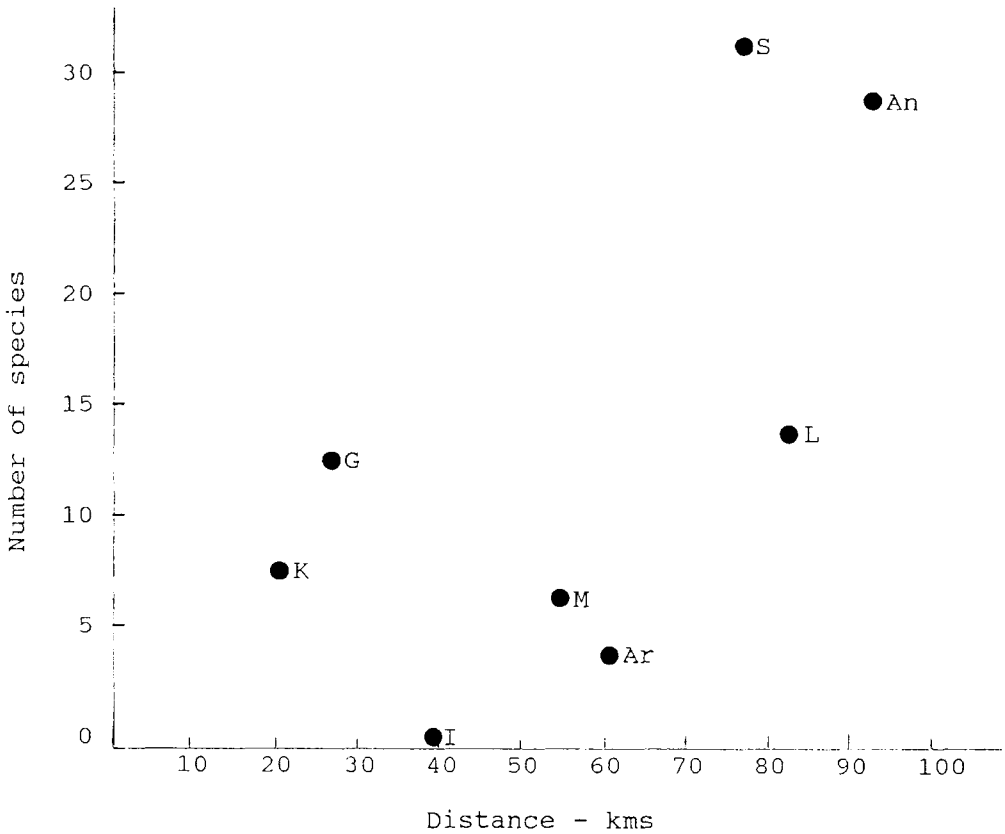

FIGURE 4. Correlation between numbers of species in each coastal area absent from Ireland and distance to the nearest part of Ireland. An = W. Anglesey, Ar = Arran, G = Mull of Galloway, I = Islay, K = Mull of Kintyre, L = Lleyn, M = Isle of Man, S = St David's.

suggests permanent occupation of the British Isles. *Allium schoenoprasum* has been found in the Middle Weichselian about 15,000 BP, long before Ireland was separated from Britain, whilst *Gentiana pneumonanthe* was found in Boreal remains from Cheshire, about the time the land bridge was breached if we accept the later date of Godwin (1975) of 8,500 BP.

Gentiana pneumonanthe and *Potamogeton trichoides* are species of wet habitats, and *Allium schoenoprasum* often grows close to such habitats in its upland sites: they are more likely to have material preserved than some of the others in this group, especially dry heath, cliff or grassland species like *Genista pilosa*, *Hieracium* sp., *Meum athamanticum*, *Oxytropis* sp., *Tephroseris integrifolia*, *Veronica spicata* and *Vicia lutea* which may, nevertheless have had a similar history.

TABLE 2. RELICT SPECIES — SPECIES WHICH HAVE DECLINED IN BRITAIN BUT WHICH WERE FORMERLY MORE WIDESPREAD

Allium schoenoprasum	*Meum athamanticum*
Genista pilosa	*Oxytropis campestris*
Gentiana pneumonanthe	*O. halleri*
Hieracium cacsiomurorum	*Potamogeton trichoides*
H. sarcophylloides	*Tephroseris integrifolia* subsp. *maritima*
Juncus capitatus	*Veronica spicata* subsp. *hybrida*
Luronium natans	*Vicia lutea*

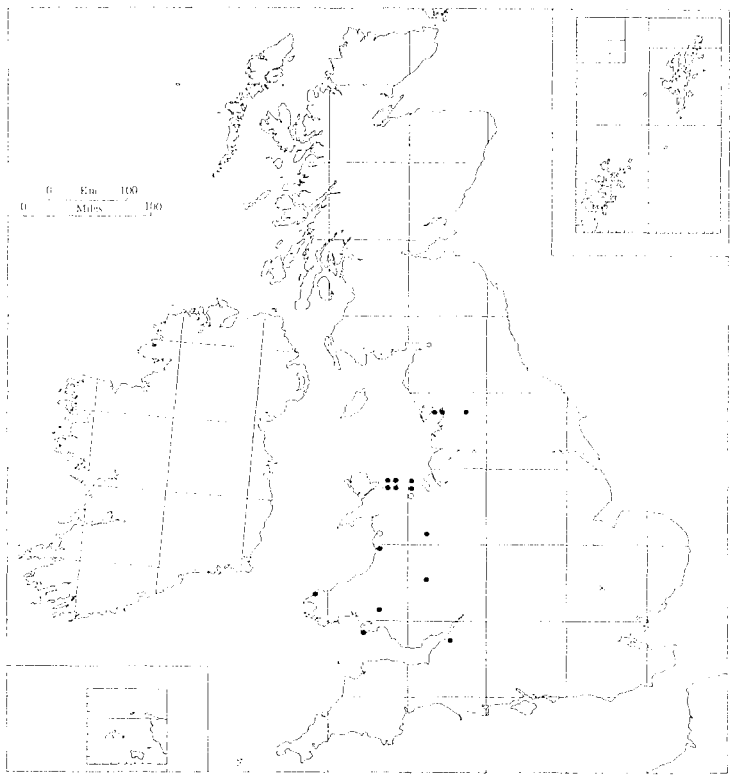

FIGURE 5. The distribution of *Veronica spicata* subsp. *hybrida* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1970 onwards record, ○ = pre-1970 record, × = introduction. Based on Stewart, Pearman & Preston (1994) and prepared by the Biological Records Centre, Institute of Terrestrial Ecology.

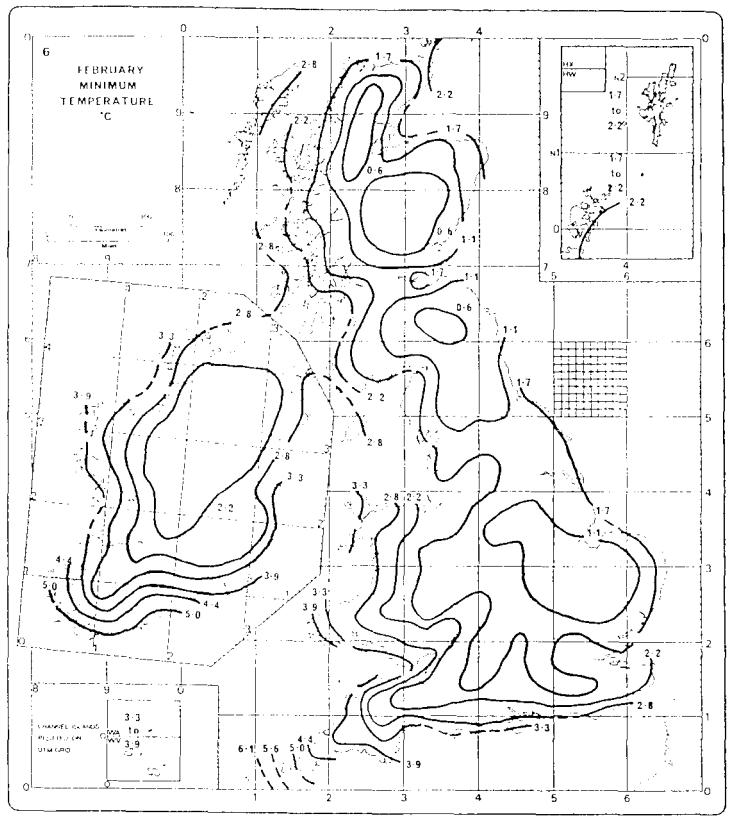

FIGURE 6. February minimum temperature. Isotherms show the mean minimum temperature in °C based on 1941–70 average for Britain and the 1931–60 average for Ireland. From Institute of Terrestrial Ecology (1978).

In order to consider taxa with similar distribution patterns and climatic relationships together the 44 remaining taxa have been grouped according to their biogeographical elements following Matthews (1955), Perring (1985) or other information. Wide and Eurasian taxa which do not fall within one of the 'European' elements have been placed in the element which most conforms with their distribution within Europe – these are marked (W) in Tables 3–7.

CONTINENTAL ELEMENT

Details of the 14 members of the Continental element which occur in the selected areas are given in Table 3. They all have a similar distribution in Europe and in Britain. In Europe they generally reach southern Scandinavia in the north and extend as far south as central Italy and the Balkans but are usually confined to the mountains there. They are absent from most of the Mediterranean islands and tend to be scarce or absent from Spain or Portugal, and western France.

In Britain they are mainly eastern in distribution and are rare or absent from Devon and Cornwall and most of Wales though, if they are calcicoles, they occur on the limestones of North and South Wales. If they reach the west coast it is usually only in the north – the Lake District and western Scotland. *Helictotrichon pratense* (Fig. 1) is a typical example.

This distribution pattern correlates with the mean February minimum temperature isotherm of 2.2°C (Fig. 6) and is characteristic of species which require low winter temperatures to complete their life cycles. Being 'Continental' species they also require warm summers and their northern limits may be an indication of the level of that requirement.

Valeriana dioica (Fig. 7) only reaches southern Scotland in the area with a July mean of 15.5°C (see Fig. 8) whereas *Helictotrichon pratense* (Fig. 1) reaches Orkney with a July mean of 12.5°C.

The most 'Continental' part of Ireland is in the north-east which has the lowest winter temperatures of under 2.2°C which are similar to those of the Lake District and south-west Scotland whilst the summer temperatures are comparable with those of southern Scotland.

Of the 14 taxa *Rhinanthus angustifolius* has the slenderest claim for recognition and has been omitted on the grounds that the single record by Druce from Anglesey, which has not been seen since, may have been another error for a species much over-recorded in the past (Perring & Farrell 1983).

Nepeta cataria can be excluded because it was almost certainly introduced to Britain as a herb after the land bridge was severed. The first record is from a Roman site in Nottinghamshire.

Epipactis leptochila is an orchid which has the ability to spread westwards, as its recent discovery in the Glasgow area demonstrates and, if climatic and other conditions had been suitable, it would no doubt have spread to Ireland without the presence of a land bridge.

Two other species which can be omitted on the basis that they had the opportunity to reach Ireland are *Scabiosa columbaria* and *Valeriana dioica* (Fig. 7). They both have extensive interglacial and post-glacial Quaternary material and were widely distributed in Britain when it was connected to Ireland. They either existed in Ireland but have since died out because the climate and other conditions have become unsuitable, or failed to cross the bridge because the conditions never were suitable for these two generally base demanding species which do not go far north in Scotland and may need warmer summer temperatures than have prevailed in Ireland.

A species with a similar distribution to *Scabiosa columbaria* and *Valeriana dioica*, though much more restricted, is *Hypericum montanum* (Fig. 9). It has only qualified for consideration because of two 10-km square records on the east side of St David's and, with its northern limit well south of the Scottish border, is probably too warmth demanding to extend its range to Ireland and is therefore omitted.

The same argument might be applied to *Hottonia palustris*. Like *Hypericum maculatum* it too reaches its northern limit near the Tyne and it is even more restricted in the west and is in only one of the eight areas, Anglesey. It too could be omitted from the list of candidates were it not recorded from Northern Ireland where it has been established and persisted since 1810. However the absence of any Quaternary records for this aquatic species, where preservation might have been expected had the species been here (cf. *Potamogeton trichoides* above) strongly suggest that it was a late arrival in the British Isles and not a good candidate.

Too high a temperature in winter is the most likely explanation for the absence of *Astragalus glycyphyllos* and *Paris quadrifolia* from Ireland. The former only qualified because of a single old record on the Isle of Whithorn well east of the Mull of Galloway, whilst the latter relies on a

TABLE 3. CONTINENTAL SPECIES

1 = distribution inside Britain; 2 = distribution outside Britain; 3 = habitat; 4 = glacial/post-glacial records; and 5 = behaviour if introduced into Ireland or other part of the selected areas. W = widespread taxa placed in the element which most conforms with their distribution in Europe.

Astragalus glycyphyllos
1. A species of central and eastern Britain almost absent from Devon and Cornwall, Wales and the western half of Scotland. Only in one area (Galloway) and that a pre-1930 record.
2. Continental (Matthews 1955). Most of Europe but only in southern Scandinavia and the mountains in the south. Absent from north-west France.
3. Rough grassland and bushy places on basic to neutral soils.
4. –
5. –

Campanula latifolia
1. A somewhat northern species absent from most of Wales but reaching the west coast of Scotland on Mulls of Galloway and Kintyre.
2. Continental element (Perring 1985). Although widespread in Europe absent from parts of the north, much of the south-west (in Spain but not in Portugal), and from most of the Mediterranean.
3. Woodland rides and glades, shady hedgebanks and river sides on moderately acid soils.
4. –
5. Very well established in numerous localities in north-east Ireland (Hackney 1992); also an established introduction in Anglesey (Roberts 1982), Islay (Ogilvie 1995) and Man (Allen 1984).

Epipactis leptochila
1. Mainly a southern and eastern species but with scattered localities on the north-west coast of England and in Anglesey where it occurs in two 10-km squares. Has recently spread westwards to the Glasgow area (Richards 1989).
2. Continental (Stewart *et al.* 1994). From Belgium and central France through the Alps to Hungary and northern Greece.
3. Beechwoods on calcareous soil in deep shade; under birch on lead and zinc rich soils, old runways and coal spoil; edges of dune slacks and stabilised sides of sandhills (Richards & Swann 1976).
4. –
5. Though not introduced by man has recently spread westwards to new, man-made, habitats in northern England and Scotland.

Genista tinctoria
1. Throughout England and Wales and southern Scotland reaching the west coast in many places. Subsp. *littoralis* grows on St David's. Subsp. *tinctoria* was in Anglesey but is thought to be extinct there; it is common in a small area of the Isle of Man but there is doubt about its status there (Allen 1984) where it was not recorded until 1888; it grows on the cliffs of Wigtownshire where it is clearly native.
2. Continental (Matthews 1955). Most of Europe north to Denmark but absent from Portugal.
3. Old pastures, heath and open scrub on acid to base rich soils.
4. –
5. –

Helictotrichon pratense
1. Nearing its western limit on west coast of Britain: absent from almost all Devon and Cornwall but occurs in four of the eight areas including St David's (Ellis 1983). (See Fig. 1)
2. Continental (Perring 1985). West and central Europe from western and southern Fennoscandia to north-east Spain, but not in Portugal.
3. Base rich grasslands and cliff-top turf; up to 825 m on Scottish mountains (Wilson 1956).
4. –
5. –

Hieracium vagum
1. Frequent in central and northern England and North Wales but absent from South Wales, Devon and Cornwall and most of Scotland though it does reach the west coast just north of the Mull of Galloway.
2. Continental (Perring & Sell 1968). Absent from Scandinavia and Portugal but extending east to Poland, Hungary and Romania.
3. Open woodland and hedgebanks.
4. –
5. Established in the Isle of Man since c. 1899 or before. "Abundant round Laxey, recurring S to Baldrine, on railway banks and adjacent roadsides and cliffs" (Allen 1984).

TABLE 3. *continued*

Hottonia palustris
1. Almost confined to central and eastern England but reaching the west coast in Lancashire and North Wales where it still occurs in Anglesey.
2. Continental (Perring 1985). Central Sweden southwards to central Italy and Romania; absent from most of the west of France and from Spain and Portugal.
3. Ponds, wide ditches in standing, fairly shallow, waters.
4. –
5. Established introduction in Co. Down (v.c. H38) where it has been known since 1810 and was thought by Praeger to be native there (Hackney 1992). Also reported from S. Tipperary (v.c. H7), Meath (v.c. H22), Fermanagh (v.c. H3), and other parts of Down but rarely persistent.

Hypericum montanum
1. Confined to lowland England and Wales just reaching the west coast on limestone in North Wales and the Morecambe Bay area and only qualifying because it occurs in two 10-km squares on the east side of St David's. (See Fig. 9).
2. Continental (Matthews 1933). Southern Scandinavia, south to central Spain, Italy and northern Balkans and east to the Ukraine.
3. Tall herb community on dry base rich soils.
4. –
5. –

Nepeta cataria
1. Only in one selected area, Lleyn, though it also occurs in east Anglesey. Confined to lowland England and Wales but reaching the west coast on the limestone in North and South Wales and in Devon and Cornwall. Doubtfully native (Clapham, Tutin & Moore 1987) and probably introduced as a herb.
2. Continental (Perring 1985). South, east and east central Europe but regarded as naturalised in Belgium and Holland.
3. Roadside verges and hedgebanks usually on lime-rich soils.
4. Material found at a Roman site in Nottinghamshire (Godwin 1975).
5. Widespread as a garden escape in Ireland and persisted in the Magilligan – Benone – Downhill area of Co. Londonderry (v.c. H40) from 1830s to 1940s (Hackney 1992).

Paris quadrifolia
1. Generally an eastern species in Britain only reaching the west coast in the Lake District, Anglesey and in south-west Scotland. Only occurs in one of the selected areas, Anglesey.
2. Continental (W). Throughout most of Europe but not in north-west France or Portugal and rare in the Mediterranean. Extends eastwards to Caucasus and Siberia.
3. Ancient broad-leaved woodlands on moderately acid to calcareous damp clays.
4. –
5. –

Rhinanthus angustifolius
1. Only in one of the selected areas, Anglesey, where it was recorded by Druce but has not been seen since. Otherwise absent from the whole of Britain west of a line from the Outer Hebrides to the Isle of Wight.
2. Most of Europe (W) but absent from the Mediterranean region, the south-west and most of the islands.
3. Cornfields, meadows and sand dunes.
4. –
5. –

Scabiosa columbaria
1. Mainly absent from Devon, Cornwall, Scotland and Wales but extending westwards on limestone of North and South Wales and occurring in one 10-km square on east side of St David's.
2. Continental (Perring 1985). Scattered in Scandinavia to 60°N and southwards to the Mediterranean but absent from most of the islands and from north-west France.
3. Base rich grassland, open scrub and rocks.
4. Quaternary deposits show that it was present during the Cromerian, Hoxnian, Ipswichian and Weichselian interglacials and in the post-glacial in Kirkudbrightshire about 9,000 BP. No doubt persisted in Britain throughout the period (Godwin 1975).
5. –

Sedum telephium subsp. *fabaria*
1. One of only two taxa to occur in five of the eight areas. Commoner in the west of Britain than the east and only absent from north-west Scotland. (Fig. 11, but not native in Arran, see (5) below).

TABLE 3. *continued*

2. Though the species occurs throughout Europe, North America and temperate Asia this subspecies appears to be Continental. It occurs throughout western and central Europe including western France, Spain and Portugal but is absent from most Mediterranean islands and is only in southern Scandinavia.
3. Shady roadsides, open woods and scrub on moderately acid to basic soils.
4. –
5. Successful introduction in several parts of Ireland, e.g. "naturalised in the woods by L Neagh nr Shane's castle . . . – first reported here c. 1878" (Hackney 1992). Also reported as naturalised in all other three selected areas in which it is not native (Allen 1984; Church & Smith 1991; Ogilvie 1995).

Valeriana dioica

1. Throughout England, Wales and southern Scotland but absent or not recorded since 1930 from any of the western peninsulas. Occurred in two of the selected areas but now extinct in both. Two 19th century records in Anglesey (Roberts 1982) and one in the Isle of Man where it was last seen about 1909 (Allen 1984).
2. Continental (Perring 1985). From south-east Norway and Sweden east to Macedonia and the western borders of Russia. Absent from western France and most Mediterranean islands but in Spain and Portugal.
3. Fens, marshes and flushes on moderately acid to base rich soils.
4. Quaternary records throughout the period from Hoxnian, Ipswichian and Weichselian interglacials to post-glacial (Godwin 1975) all point to the long persistence of this species in Britain and its presence before the land bridges were severed.
5. –

woodland site in Anglesey (Fig. 10) apart from which there is no other record within 30-km of a former land bridge. *P. quadrifolia* is a species confined to ancient woodlands, usually on base-rich soils which, even today, has not penetrated far west in Britain and may never have reached a bridge-head.

There are, however, three woodland and woodland margin species which have a strong claim to be considered as candidates: *Campanula latifolia*, *Hieracium vagum* and *Sedum telephium*.

Sedum telephium is outstanding in being one of the only two species which occurs in five of the eight areas (Fig. 11). It is also an established introduction in the other three areas – the islands of Arran, Islay and Man – as well as being naturalised in several parts of Ireland. It occurs widely along the western seaboard of Britain and, of all the species considered, is probably the strongest candidate for inclusion in a list of species which would be in Ireland as a native today if there were a land bridge.

Campanula latifolia and *Hieracium vagum* both occur in two areas and, unlike most other species considered, but like *Sedum telephium*, are very abundant on the west coast, *C. latifolia* in south-west Scotland and the Lake District, *H. vagum* in North Wales. Both species have become established further west: *C. latifolia* in numerous localities in north-east Ireland as well as in Anglesey, Islay and Man, whilst *H. vagum* has been established for about 100 years in Man. Both species would surely have been in Ireland, especially the north, if there had been an opportunity to cross when they reached the coast.

Two other species of more open habitats including grassland near the sea, are also strong candidates for species which reached the coast too late – *Genista tinctoria* and *Helictotrichon pratense*. *G. tinctoria* including the subsp. *littoralis* has occurred or occurs in four of the eight areas and it reaches the coast in many places around the northern half of the Irish Sea. It is also common in a small area of the Isle of Man and, though there is some doubt about its status, it has long survived there and is clearly a species well adapted to growing in that area which could have colonised Ireland had a land bridge been available. *H. pratense* has been referred to above: it is in four of the eight areas and with its wide range of grassland habitats, especially in Scotland, and altitude range, could surely have found a niche in Ireland had the way been open for it to cross the gap.

It is interesting to compare these species with two species which do occur in Ireland as natives, one of woodland and the other of grassland. *Adoxa moschatellina*, which is native to Ireland, still occurs in a single locality in Co. Antrim though lost from another over a century ago. However *A. moschatellina* occurs in six of the eight selected areas (Fig. 12), more than any of the candidate species, being absent only from the Isle of Man and Islay, though it is on Jura (Ogilvie 1995). Like *Sedum telephium* it is also frequent throughout the west of Britain. It is a Europe-wide but

TABLE 4. CONTINENTAL SOUTHERN SPECIES

1 = distribution inside Britain; 2 = distribution outside Britain; 3 = habitat; 4 = glacial/post-glacial records; and 5 = behaviour if introduced into Ireland or other part of the selected areas. W = widespread taxa placed in the element which most conforms with their distribution in Europe.

Acer campestre
1. Throughout lowland England and Wales north to Northumberland and the Lake District; probably not native in Scotland. Rarer in the west reaching the coast in St David's and north Cornwall but not native in Anglesey (Roberts 1982) and west Cornwall (Margetts & David 1981). (See Fig. 14).
2. Southern Continental (Matthews 1955). Denmark and southern tip of Sweden south to the Mediterranean but absent from north-west France and Portugal.
3. Woods, hedge and scrub on well-drained moderately acid to base-rich soils.
4. First Quaternary records from the Neolithic about 4,500 BP (Godwin 1975).
5. Widely established as an introduction outside its native area in the British Isles. "Occasionally run wild" in Ireland (Webb 1977).

Clematis vitalba
1. Lowland England and Wales northwards to the Humber and North Wales and reaching the west coast in Cornwall and two of the selected areas, St David's and Anglesey.
2. Continental Southern (Matthews 1955). From southern Denmark southwards to the Mediterranean, including many of the islands, and south-eastwards to Greece and the Balkans. (See Fig. 13, upper map).
3. Woods, hedges and scrub on well-drained, moderately acid to base-rich soils.
4. First Quaternary records from warm periods in interglacials but then a long gap until wood and pollen dated c. 6,300 BP was found in Hampshire (Godwin 1975).
5. Widely naturalised outside its native area. "Hedges and thickets, mainly in S. half" [of Ireland] (Webb 1977), and in Man (Allen 1984).

Cruciata laevipes
1. Somewhat eastern and not on west coast of Wales, but reaching the west coast of Scotland on the Mulls of Galloway and Kintyre, and recently from Jura (Ogilvie 1995). (See Fig. 16). The Isle of Man record in Perring & Walters (1982) was an error (Allen 1984).
2. Continental Southern (W) (Perring 1985). Absent from Scandinavia but in Spain and Portugal and several Mediterranean islands and extending eastwards to Poland and Russia and western Asia.
3. In rough grassland, hedge bottoms and woodland margins on moderately acid to base rich soils.
4. –
5. Established at one locality at Downpatrick, Co. Down (v.c. H38) since at least 1744 (Hackney 1992).

Cyperus longus
1. Only found as a native near the coast in the south and west north to Lleyn. Extinct near St David's for over 100 years (Davis 1970).
2. Continental Southern (W) (Matthews 1955). Widespread throughout west, central and southern Europe east to central Asia, north and east Africa; at its northern limit in Britain.
3. Wet pastures near the coast and base-rich flushes on cliffs.
4. One doubtful record from the Anglian interstadial of the glacial period (Godwin 1975).
5. Introduced in many sites in England, especially in the south, and also in a few places in Wales. Not reported as an introduction to Ireland.

Daphne laureola
1. Throughout lowland England and Wales north to the Lake District and Durham and west to Devon and Cornwall though thought to be mainly bird-sown in the former (Margetts & David 1981). Occurs in all three Welsh selected areas.
2. Continental Southern (Matthews 1955). South, south central and western Europe: at its northern limit in England and Hungary.
3. Woodland margins and clearings on dry, neutral to calcareous soils.
4. –
5. Recently established in Cos Down (v.c. H38) and Antrim (v.c. H39) in N. Ireland (Hackney 1992). Also widely naturalised in the Isle of Man where "Solitary bird-sown bushes are usual, but on the steep bank of the Ballaglass stream near Rhenab it occurs in profusion." (Allen 1984).

Hornungia petraea
1. Scattered in west and central England and Wales from sea level in South Wales to c. 490 m in North Yorkshire. (See Fig. 20).

TABLE 4. *continued*

2. Continental Southern (Matthews 1955). Although placed in this element by Matthews it is a more continental species than others reaching southern Scandinavia and the Baltic as well as occurring in western, central and southern Europe. It has a very disjunct distribution suggesting a species in retreat: absence from west Brittany and north-west Spain may be significant.
3. "South and south-west facing slopes on carboniferous limestone and calcareous sand dunes . . . . . open vegetation on bare soil which is dry in summer but moist in winter." (Stewart *et al.* 1994).
4. –
5. –

Inula conyzae

1. Throughout lowland England and Wales north to the Lake District and Durham; widespread in Devon and Cornwall and in all three Welsh selected areas.
2. Continental. Although placed in this element by Matthews (1955) and accepted by Perring (1985) its distribution in Europe fits more closely with members of the Continental Southern element. It only just reaches Sweden, is absent from the northern quarter of Germany and reaches north-west Ukraine but is mainly in western, central and southern Europe including many of the Mediterranean islands.
3. Open scrub and grassy banks, old pastures and rock ledges on moderately acid to calcareous soils.
4. –
5. –

Lathyrus sylvestris

1. Scattered through the southern half of lowland England and along the coasts of Wales and south-west Scotland. More frequent in the selected areas than shown by Perring & Walters (1982) and occurring now in three: St David's, Lleyn and Galloway, and in the past in Anglesey and Arran. There is also a recent (1959) record from Jura (Ogilvie 1995).
2. Continental Southern (W). Throughout most of Europe from southern Scandinavia southwards to the Mediterranean including Spain and Portugal and some of the islands. Also in the Caucasus and north-west Africa.
3. Scrubby vegetation, overgrown hedgerows and damp places on sea cliffs.
4. No authenticated Quaternary records (Godwin 1975).
5. –

Ranunculus sardous

1. Scattered through lowland England, most frequent near the east coast, but also on the south and west coasts of Wales, the Lake District and Scotland north to the Outer Hebrides where a single record dates from 1949 (see Fig. 19). Only present now in one selected area, St David's, but there is a pre-1930 record from Galloway. Often only a casual on the western fringe (Wade *et al.* 1994).
2. Continental Southern. Although not placed in this, or any other, element by Matthews (1955) or Perring (1985) the recently published map of its distribution in Europe (see Fig. 13, lower map, from Jalas & Suominen 1989) is so similar to that of *Clematis vitalba* (Fig. 13, upper map) that it clearly belongs to this element, though it does extend slightly out of Europe into North Africa and western Asia.
3. Damp meadows, salt meadows by the sea and cornfields.
4. Quaternary records from the Early and Middle Weichselian interglacials, 20,000–70,000 BP and then not again until Roman times, 2,000 BP, when found as a weed of four Romano-British occupation sites in England and South Wales (Godwin 1975).
5. Only once recorded in Ireland, as a probable casual in Belfast Docks in 1986 (Hackney 1992).

Ruscus aculeatus

1. Native only in the southern third of England and on the limestones of North and South Wales where it occurs within the St David's area but just outside the West Anglesey area.
2. Continental Southern (Matthews 1955). From France eastwards to central Hungary and the Balkans, and southwards to the Mediterranean, where it is widespread and on most of the islands.
3. Dry woodland and rocky cliffs on moderately acid to base-rich soils.
4. –
5. ". . . extremely rare as a 'wild' plant" [in Cos Down (v.c. H38) and Antrim (v.c. H39)] (Hackney 1992) and first recorded about 1974. In the Isle of Man "naturalised in old plantations and in one or two hedgebanks." (Allen 1984).

Tamus communis

1. Almost throughout lowland England and Wales north to Northumberland and the Lake District (see Fig. 15). In all three of the selected areas in Wales.

TABLE 4. *continued*

2. Continental Southern (Matthews 1955). From Belgium and west Germany south to Spain and Portugal and the Mediterranean including all the larger islands.
3. Hedgerows and woodland margins on moderately acid to calcareous soils.
4. –
5. Listed in Scannell & Synnott (1987) as an introduction in Co. Clare (v.c. H9), Co. Sligo (v.c. H28), Co. Leitrim (v.c. H29), Tyrone (v.c. H36) and Co. Armagh (v.c. H37) and recorded in Webb & Scannell (1983) as "from 1971 to 1979 in a hedge 4 km S.S.W. of Ballyvaughan, and, as it is a difficult weed to eradicate from gardens, it is likely to remain there for some time."

Vicia tetrasperma

1. Lowland England and Wales northwards to Northumberland and the Lake District and reaching the west coast there, in Cornwall and in two of the selected areas in Wales, St David's and Lleyn, and formerly in east Anglesey (see Fig. 17).
2. Continental Southern (W). Throughout Europe north to southern Scandinavia and south to the Mediterranean including most of the larger islands and N. Africa. Extending eastwards to W. Asia and Japan and westwards to Macaronesia.
3. Coarse grassland, hedgebanks on dry to damp moderately acid to calcareous soils.
4. First recorded from the late Bronze Age in Sussex about 2,500 BP (Godwin 1975).
5. Webb (1977) did not include it in the flora of Ireland but it is included, as probably introduced, in Scannell & Synnott (1987) for W. & Mid Cork (v.cc. H3 & H4), Co. Dublin (v.c. H21), Meath (v.c. H22), West Meath (v.c. H23), Co. Down (v.c. H38), Co. Antrim (v.c. H39) and Co. Londonderry (v.c. H40) and as a native in *Flora Europaea*. Recorded in 1967 as a native or colonist in the Isle of Man (Allen 1984).

somewhat continental species absent from N.W. France, Spain and Portugal. It grows in open woodland and shady hedgebanks on moderately acid to neutral soils. There are no glacial or post-glacial records.

The other grassland species which has a similar distribution to *A. moschatellina* and to others in this group and which, like *A. moschatellina*, just gets into the northern half of Ireland, is *Helianthemum chamaecistus*. It is absent from the south-west of England and Wales but it does occur in Anglesey and Arran and is extremely abundant on the coast of Galloway – clearly 'population pressure' may have been important in determining its success in crossing the water.

It is surely not without significance that both these species are found in the north of Ireland, in the part of the country which has the most continental climate.

CONTINENTAL SOUTHERN ELEMENT

Details of the twelve members of the Continental Southern element which occur in the selected areas are given in Table 4. They all have similar distributions in Britain and Europe. The distribution in Europe of two of the species, *Clematis vitalba* and *Ranunculus sardous*, which are typical, are shown in Fig. 13. Taxa in this element only just reach Scandinavia but go southwards to the Mediterranean where they occur in most of the larger islands and occasionally reach N. Africa.

In Britain they are essentially southern in distribution, occurring throughout the lowlands of England and Wales and extending northwards to a more or less horizontal limit in Durham/Northumberland across to the Lake District. They are more frequent on the west coast than species of the Continental Element and are often widespread in Devon and Cornwall and in Wales. *Acer campestre* (Fig. 14) and *Tamus communis* (Fig. 15) are good examples.

The northern limits of these species correlate with the July average means of daily mean temperature isotherm of 15–15·5°C (Fig. 8) and are characteristic of those which require warm summer temperatures to complete their life cycles. Even *Cyperus longus* and *Ruscus aculeatus*, which reach their northern limit in North Wales, are there in an area on the coast where the July mean is the same as that inland further north.

The warmest part of Ireland, with a July mean of over 15·5°C falls south and east of a line from Kerry to Dublin, and provides a summer climate which should be suitable for all the species in this group.

Nine of the twelve species in this group are either trees or shrubs or woodland or woodland margin species and all have a strong claim to be considered as candidates. The four trees/shrubs plants are *Acer campestre*, *Clematis vitalba*, *Daphne laureola* and *Ruscus aculeatus*. All reach the

TABLE 5. OCEANIC WEST EUROPEAN AND OCEANIC SOUTHERN SPECIES

1 = distribution inside Britain; 2 = distribution outside Britain; 3 = habitat; 4 = glacial/post-glacial records; and 5 = behaviour if introduced into Ireland or other part of the selected areas.

Dactylorhiza praetermissa

1. Throughout most of lowland England and Wales as far north as Northumberland in the east but absent from the Lake District. Very rare in north-west Wales but is recorded from one 10-km square in Lleyn: extremely abundant in St David's and in every 10-km square there (Ellis 1983).
2. Oceanic West European (Matthews 1955). Britain is at the centre of its distribution. Known elsewhere from Denmark, Holland, Belgium and northern France.
3. Meadows, wet hollows, flushes, valley mires and quarry floors on moderately acid to calcareous soils.
4. –
5. –

Genista anglica

1. Throughout Britain north to Ross but absent from all of western Scotland and the north though reaching 700 m in Atholl (Wilson 1956). Occurs abundantly in all three selected areas in Wales.
2. Oceanic West European (Matthews 1955). Western Europe extending north east to the southern tip of Sweden and north-east Germany and south to Spain and Portugal and south-west Italy.
3. Heaths, dry mosses and infertile pastures on moist to dry often peaty soils.
4. –
5. –

Hypericum linariifolium

1. Restricted to one locality in Cornwall, two in Devon and one in Lleyn. Formerly in the selected area of Anglesey, but not seen there for 80 years (Roberts 1982), and apparently no longer in Radnor or Merioneth where it has not been seen for over 50 years (Ellis 1983).
2. Oceanic West European (Matthews 1955). Western Britain, western France southwards to Spain and Portugal.
3. Steep, dry rocky acid banks in open vegetation on acid soils.
4. –
5. –

Hypericum undulatum

1. Confined to Devon and Cornwall and west Wales where it is abundant in the St David's area occurring in eight post-1970 and one pre-1970 10-km squares and 17 tetrads (Stewart *et al.* 1994).
2. Oceanic West European (Matthews 1955). From Wales southwards through western France to Spain, Portugal and the Azores.
3. Rushy pastures and damp heaths on acid soils which are seasonally or permanently waterlogged with lateral movements.
4. –
5. –

Iris foetidissima

1. Britain north to a line joining the Humber to the Dee estuaries but much commoner south of the River Thames. In two 10-km squares in both St David's and Anglesey (Ellis 1983).
2. Oceanic Southern (Matthews 1955). South and west Europe from Britain southwards through France to north-east Italy and the western Mediterranean including the larger islands.
3. Open woodland and scrub, roadside banks and field margins on dry, moderately acid to calcareous soils.
4. –
5. Although through most of Ireland considered only to be a garden escape (Webb 1977; Webb & Scannell 1983; Hackney 1992). Praeger (1934) suggests that, on Ireland's Eye, an islet, and on Lambay Island, both to the north of Howth in Co. Dublin (v.c. H21), it might be native as it is well established on sands and cliffs remote from houses or former cultivation. Naturalised on the Isle of Man (Allen 1984).

Limonium vulgare

1. Coasts of Britain north to the Firths of Forth and Solway. Abundant on the east coast, less common on the west. Though it occurs in Anglesey of the selected areas, and to the east of Lleyn, it is replaced in St David's by *L. humile*.
2. Oceanic Southern (Matthews 1955). From southern Sweden along the coasts of western and southern Europe as far east as Turkey and on most of the larger Mediterranean islands. N. Africa.
3. Muddy salt-marshes.
4. Tentatively recorded from the post-glacial about 2,500 BP in south Devon.
5. Thought to be extinct in the Isle of Man but found in two new localities in 1971 and 1972 (Allen 1984).

TABLE 5. *continued*

Mibora minima
1. One of Britain's rarest plants known only from Wales as a native: on the coasts of Glamorgan and Anglesey where it occurs in three 10-km squares in the selected area.
2. Oceanic Southern (Matthews 1955). From western Germany, Holland, Belgium and France southwards through Spain and Portugal to north-west Africa; Greece.
3. Sandy and other light soils, damp in winter.
4. –
5. Not recorded as an introduction in Ireland but has spread and become established in sand dunes in East Lothian, where it has been introduced and re-introduced since 1800 (Silverside & Jackson 1988). Also established in Dorset, Suffolk and Bedfordshire and as a casual elsewhere.

Moenchia erecta
1. Scattered throughout England and Wales north almost to the Scottish border in the east but now only to North Wales in the west where it occurs in Anglesey; also recorded from St David's of the selected areas. (See Fig. 23).
2. Oceanic Southern. Although placed by Perring (1985) in the Continental Southern element the map published by Jalas & Suominen (1983) (Fig. 21, upper map) shows that the main centre of distribution lies to the south of Britain conforming very closely to the criteria for the Oceanic Southern element as defined by Matthews (1955). Matthews, curiously, did not include *Moenchia* in his list of Continental Southern species even though its distribution is very similar to that of *Ranunculus parviflorus* (Fig. 21, lower map) which he does include.
3. Bare patches in dry open grassland, rock outcrops, cliff-tops, path-sides and dunes.
4. –
5. –

Ononis reclinata
1. Confined in Britain to the coasts of Devon and Glamorgan, and to two of the selected areas, St David's where it occurs in one locality, and the Mull of Galloway in a recently rediscovered site where it had not been seen since 1835.
2. Oceanic Southern (Matthews 1955). West coast of Europe from Galloway southwards and then throughout the Mediterranean east to Iran including all the larger islands.
3. Coastal cliffs.
4. –
5. –

Petroselinum segetum
1. Almost entirely confined to the area of England south and east of a line joining the Humber and Severn estuaries but with a Western extension along the coast of South Wales to St David's where it is recorded from four 10-km squares.
2. Oceanic West European (Matthews 1955). From Holland and western France southwards to Spain and Portugal and east to central Italy.
3. Dry hedgebanks and rocky places in the west, perhaps more often arable fields in the east.
4. Recorded from at least three interglacials, Hoxnian, Ipswichian and Late Weichselian and from the post-glacial about 2,000 BP in Cumbria
5. –

Puccinellia rupestris
1. Coasts of Britain; formerly as far north as Northumberland in the east and to the Solway Firth in the west but now only to south Durham in the east and to St David's in the west. Now in two 10-km squares in the selected area of St David's; formerly in four. Appears to be retreating southwards (Stewart *et al.* 1994).
2. Oceanic West European (Matthews 1955). Western Europe from Holland and Britain southwards to Spain. Mainly coastal but inland on damp sands in central Spain.
3. Edges of brackish pools and ditches and in open, ephemeral vegetation behind sea-walls; also on muddy shingle and in rock crevices.
4. –
5. Found in Larne and Belfast in Northern Ireland in 19th century and persisted for several years in Belfast until site was paved (Hackney 1992).

Rubus bertramii
1. England and Wales north to the Lake District but much commoner in the west than the east. Widespread in central and west Wales extending to St David's where it is recorded from one 10-km square (Edees & Newton 1988). A small patch in the Isle of Man may have been this but only inadequate panicles present (Allen 1984).

TABLE 5. *continued*

2. Oceanic West European. Widespread in north-western Europe from Denmark to France and east to Germany.
3. Damp woods and heath margins.
4. –
5. –

Rubus lindebergii
1. Almost absent from south and east England, west Wales and Scotland north of Perthshire. Occurs in two of the selected areas, Man and Galloway, and on the eastern edge of Lleyn (Edees & Newton 1988).
2. Oceanic West European. From southern Sweden, Norway and Denmark as well as Britain.
3. "Wood and moor margins particularly in upland areas" (Edees & Newton 1988).
4. –
5. –

Sison amomum
1. Almost entirely confined to the south and east of a line joining the Humber and Severn estuaries with a small concentration in North Wales where it formerly occurred in Anglesey but has not been seen for over 100 years. The record in Perring & Walters (1982) requires confirmation.
2. Oceanic Southern (Matthews 1955). From Britain southwards through France and Spain to the Mediterranean east to Turkey, including most of the larger islands. W. Asia; N. Africa.
3. Hedge-bottoms and roadsides.
4. –
5. Not reported from Ireland; a rare casual in northern England.

Trifolium strictum
1. Recorded since 1970 in Cornwall, Radnorshire and the Channel Isles. The only record from a selected area, Anglesey, dates from 1837.
2. Oceanic Southern (Matthews 1955). Britain southwards through western France to Spain and Portugal and the Mediterranean east to Turkey, including some of the larger islands; also in Hungary and other parts of south-central Europe.
3. Short, dry grassland.
4. –
5. Not reported from Ireland; a rare casual in Sussex and Midlothian.

TABLE 6. ENDEMIC SPECIES

1 = distribution inside Britain; 2 = distribution outside Britain; 3 = habitat; 4 = glacial/post-glacial records; and 5 = behaviour if introduced into Ireland or other part of the selected areas.

Coincya monensis
1. Centred on the coast of north-west England and south-west Scotland and extending to both Arran and the Isle of Man and in four 10-km squares in each. Also in South Wales.
2. Endemic.
3. Sand dunes, sandy ground and sometimes on cliffs by or near the sea.
4. –
5. Not recorded as an introduction in Ireland but has occurred recently in ruderal communities in central Scotland (Stewart *et al.* 1994).

Rubus silurum
1. Widespread throughout central Wales and recorded from single 10-km squares in St David's, Lleyn and Anglesey. Also in North Devon.
2. Endemic.
3. "Hedgebanks, thickets and margins of woods and moors to 1000ft" (Edees & Newton 1988).
4. –
5. –

TABLE 7. SPECIES LISTED BY PRAEGER (1934) AS EXCLUDED FROM IRELAND WHICH ARE NOT IN THE SELECTED AREAS IN BRITAIN

1 = distribution inside Britain; 2 = distribution outside Britain; 3 = habitat; 4 = glacial/post-glacial records; and 5 = behaviour if introduced into Ireland or other part of the selected areas. W = widespread taxa placed in the element which most conforms with their distribution in Europe.

Chrysosplenium alternifolium
1. Scattered through England, east Wales and Scotland north to the Moray Firth. Almost absent from Devon and Cornwall and only reaching the west coast of Britain in a few localities and some distance from the selected areas (Fig. 2).
2. Continental Northern (Matthews 1955). From 65° N in Scandinavia southwards through continental Europe and absent from western France, Spain and Portugal and the whole of the Mediterranean including Greece.
3. Stream banks and valley woods on basic to acid soils.
4. Seed was found in a Hoxnian interglacial site near Birmingham (Godwin 1975).
5. –

Convallaria majalis
1. Distribution similar to that of *Chrysosplenium alternifolium* hardly reaching the west coast. Also doubtfully native and not known today in Cornwall (Margetts & David 1981) and not regarded as a native in Devon (Ivimey-Cook 1984) or Anglesey (Roberts 1982).
2. Continental (W). Most of Europe from the Arctic Circle in Scandinavia to the mountains of the Mediterranean but absent from the islands, and also absent from Brittany and Portugal.
3. Open patches in old woodland on damp to dry acid to basic soils.
4. –
5. Not included in the Irish flora as an introduction by Webb (1977) or by Scannell & Synnott (1987) but recorded from four scattered localities in Perring & Walters (1982) and as "established in the Umbra woodland [Derry] from at least 1953, still there 1989" by Hackney (1992).

Ononis spinosa
1. Predominantly a species of lowland England which is much more abundant in the east than the west. Not known as a native in Devon and Cornwall except in the extreme east of Devon (Ivimey-Cook 1984). Although reported from one of the selected areas, St David's, the record is unsubstantiated by specimens and was not included by Davis (1970). It is frequently mistaken for *O. repens*.
2. Continental (W). From southern Norway and north-west Ukraine southwards and westwards to southern Italy and north-east Portugal but absent from Brittany.
3. Roadsides and rough pastures especially on heavy, basic clays.
4. There is a Late Weichselian record, about 10,000 BP, from Cornwall (Godwin 1975).
5. –

west coast of Wales. *A. campestre* and *C. vitalba* are particularly abundant there and both have become extensively naturalised in Ireland, especially in the south and east; *A. campestre* is described by Webb (1977) as "occasionally running wild". *D. laureola* and *R. aculeatus* are also established introductions in Ireland though in the north in Down and Antrim, where they have appeared in the last 25 years (Hackney 1992). However both these species also have a longer history of introduction in the Isle of Man; in one locality *Daphne laureola* "occurs in profusion" (Allen 1984).

A. campestre and *C. vitalba* have been recorded in Quaternary deposits but *A. campestre* not until the Neolithic about 4,500 BP, whilst *C. vitalba*, although reported from warm periods in interglacials, has not been reported from the post-glacial until c. 6,300 BP suggesting that it died out before returning after the last glaciation. There are no Quaternary records for *D. laureola* or *R. aculeatus*.

The five woodland or woodland margin species are *Cruciata laevipes*, *Inula conyzae*, *Lathyrus sylvestris*, *Tamus communis* and *Vicia tetrasperma*. Of these *C. laevipes* has an anomalous distribution in Britain (Fig. 16). Although it is absent from Scandinavia and reaches the Mediterranean, so that it occurs in similar area to that covered by *Clematis vitalba* (Fig. 13, upper map), its distribution in Britain is much closer to that of Continental species such as *Helictotrichon pratense* (Fig. 1) than to a Continental Southern species such as *Tamus communis* (Fig. 15). It therefore occurs on the west coast, in the selected areas, in Scotland rather than in Wales and it is

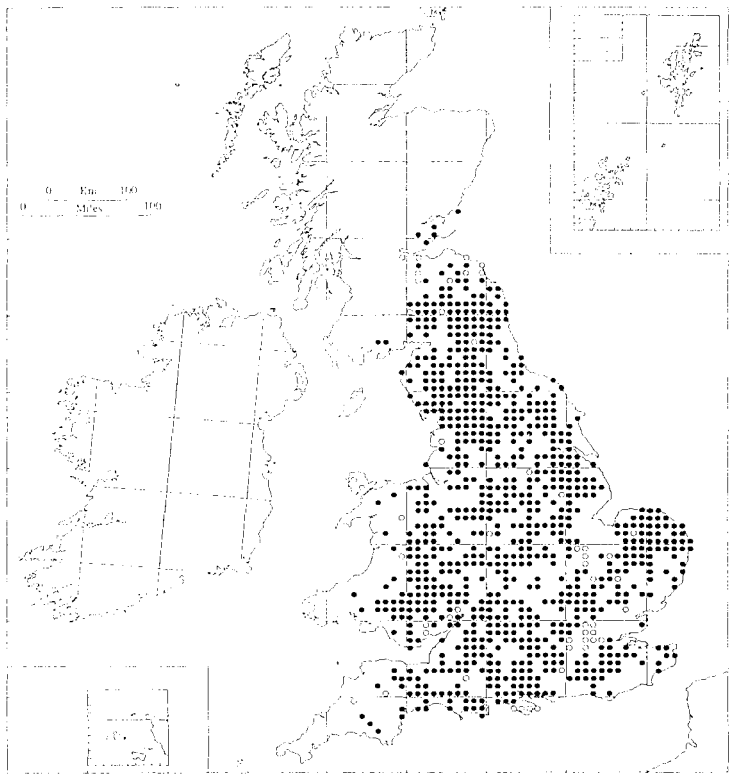

FIGURE 7. The distribution of *Valeriana dioica* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

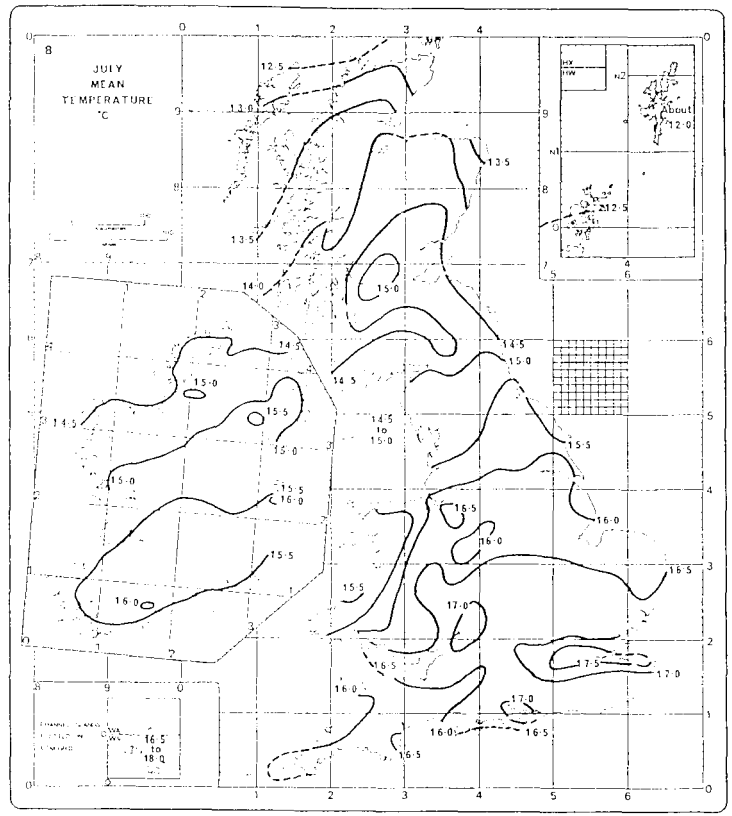

FIGURE 8. July mean temperature. Isotherms show the mean temperatures in °C based on 1941–70 average for Britain and the 1931–60 average for Ireland. From Institute of Terrestrial Ecology (1978).

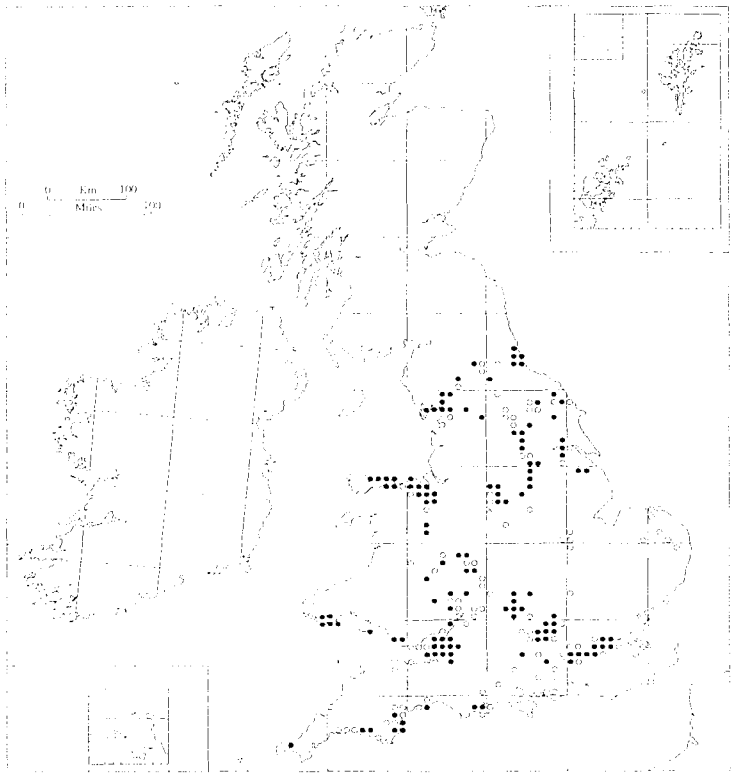

FIGURE 9. The distribution of *Hypericum montanum* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1970 onwards record, ○ = pre-1970 record, × = introduction. Based on Stewart, Pearman & Preston (1994) and prepared by the Biological Records Centre, Institute of Terrestrial Ecology.

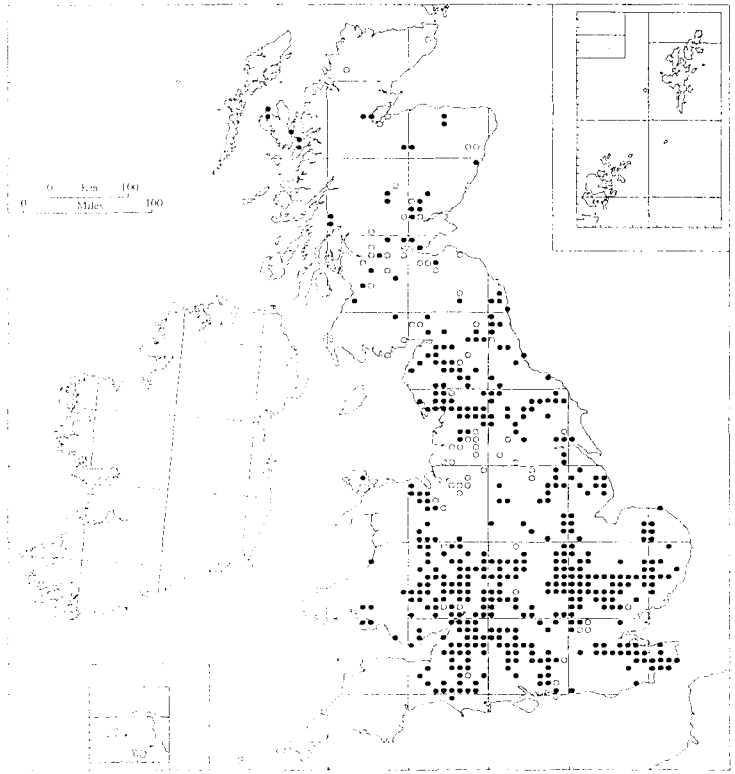

FIGURE 10. The distribution of *Paris quadrifolia* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

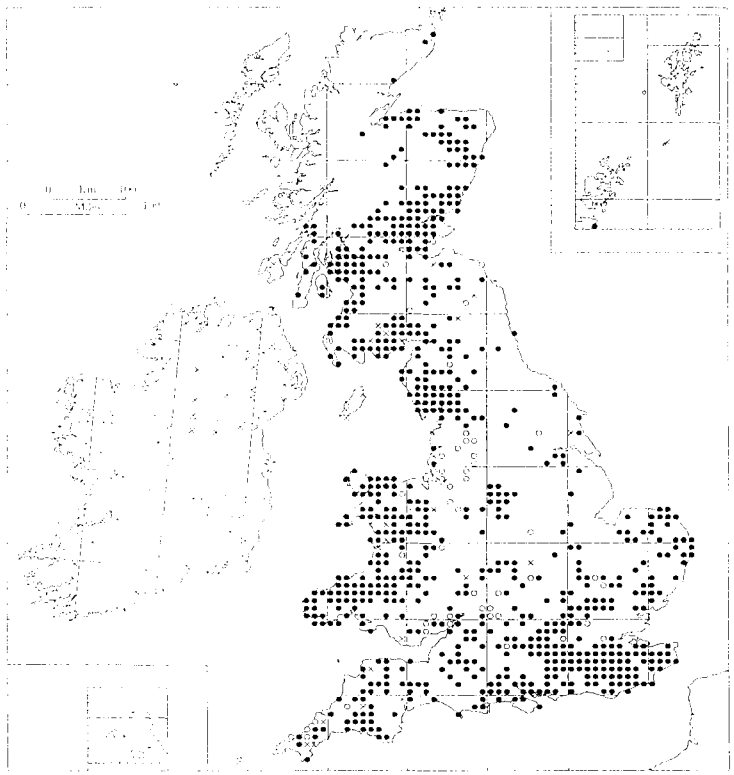

FIGURE 11. The distribution of *Sedum telephium* subsp. *fabaria* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record, × = introduction. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

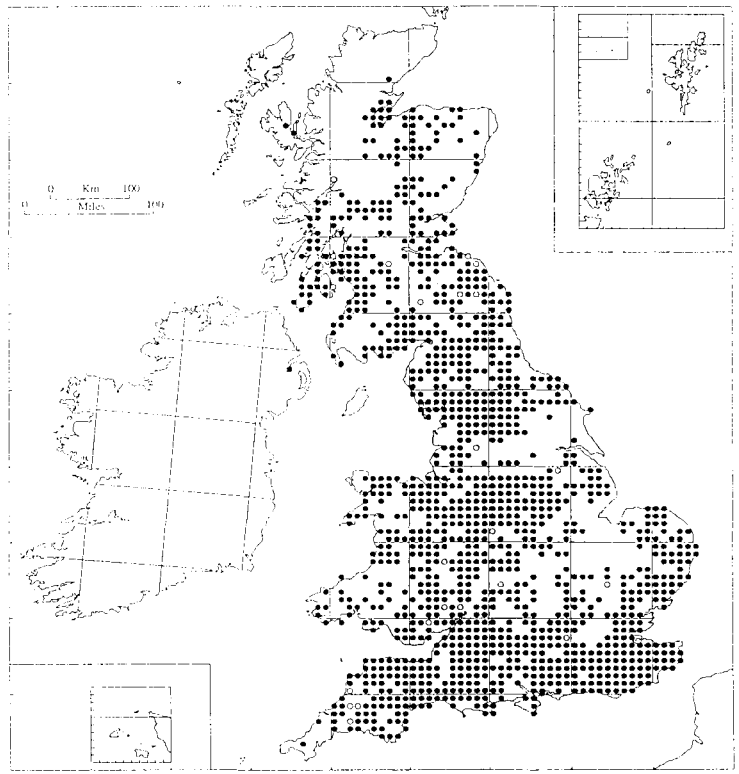

FIGURE 12. The distribution of *Adoxa moschatellina* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

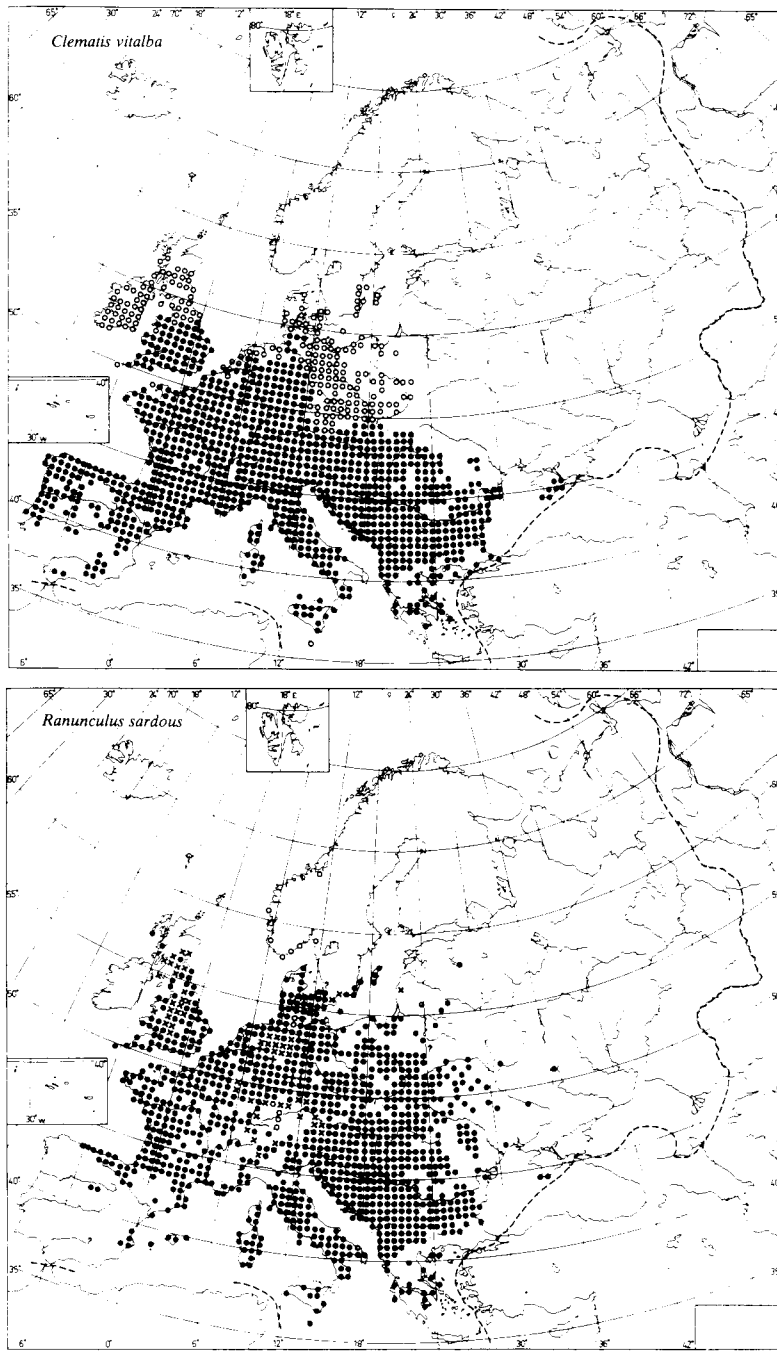

FIGURE 13. European distribution maps. Each dot represents at least one record in a 50-km square of the U.T.M. grid. ● = native occurrence, × = probably extinct or not recorded since 1930, ○ = introduction. Upper map *Clematis vitalba*; lower map *Ranunculus sardous*. From Jalas & Suominen (1989).

FIGURE 14. The distribution of *Acer campestre* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record, × = introduction. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

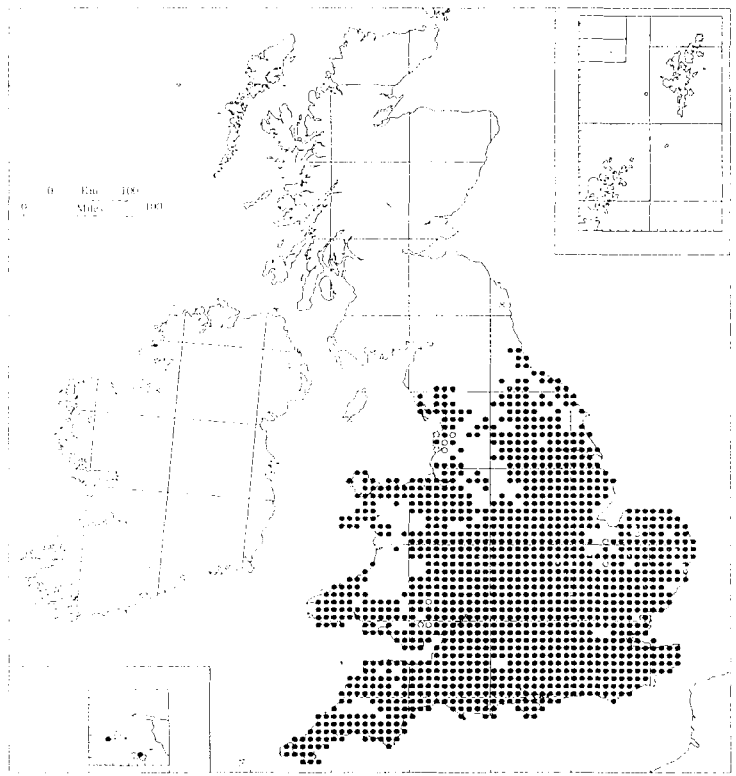

FIGURE 15. The distribution of *Tamus communis* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record, × = introduction. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

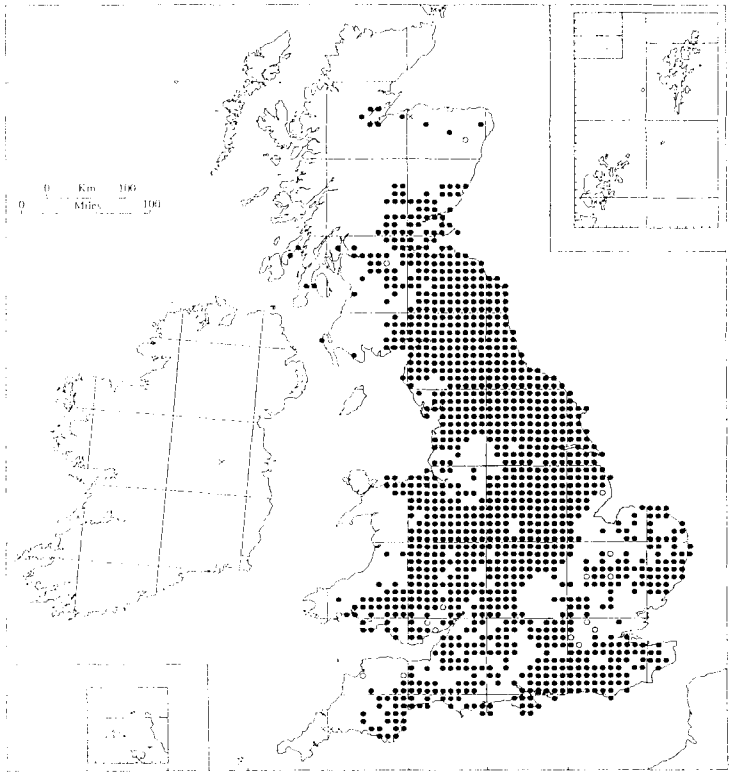

FIGURE 16. The distribution of *Cruciata laevipes* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record, × = introduction. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

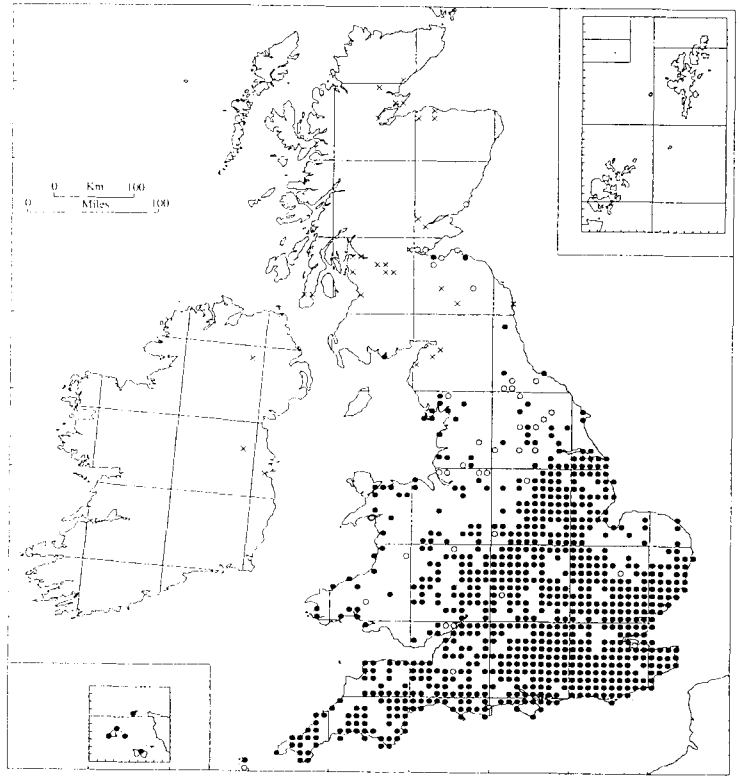

FIGURE 17. The distribution of *Vicia tetrasperma* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record, × = introduction. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

not surprising that, as an established introduction in Ireland, it occurs in north-east Ireland, where it has been known for over 250 years, rather than in the south-east.

The other four woodland species have much more intelligible British distributions. *Tamus communis* (Fig. 15) is perhaps the most outstanding candidate of the species in this group. Not only is it extremely abundant on the west coast of England and Wales but it has recently demonstrated its ability to persist for a decade as an introduction in the west of Ireland, though a similar introduction to the Isle of Man did not persist (Allen 1984). *Vicia tetrasperma* (Fig. 17) has also been reported as an introduction in Ireland though the reports are confused and it is not clear whether it has ever become established there. A record from the Isle of Man in 1967 is also enigmatic: "native or colonist" (Allen 1984).

Lathyrus sylvestris is also a strong candidate, being one of only two species, along with *Sedum telephium*, to have been recorded from five of the selected areas as well as from Jura, so close to a sixth, Islay.

Vicia tetrasperma is the only one of these five species to have been found in Quaternary deposits, but these were not until the Bronze Age c. 2,500 BP.

It is evident that within this Continental Southern element there is a group of woodland species including small trees, shrubs or lianes, or herbs of shade and woodland margins for which there are either no glacial or post-glacial records or which, as in the cases of *Acer campestre*, *Clematis vitalba* and *Vicia tetrasperma*, are of dates after the land bridge was broken. They are all thermophilous species which arrived in Britain from the south across the land bridge to the Continent which was broken later there (about 7,500 BP) and despite some such as *Acer campestre*, *Clematis vitalba* and *Inula conyzae* having wind dispersed seeds and *Daphne laureola* being distributed by birds, could not reach the west coast in time. However most of them, *Acer campestre*, *Clematis vitalba*, *Cruciata laevipes*, *Daphne laureola*, *Ruscus aculeatus*, *Tamus communis* and possibly *Vicia tetrasperma*, are successfully established in the wild in Ireland today.

Chance no doubt plays a significant part in determining whether or not a species has crossed the gap. A woodland species with similar distribution in Britain (although it only just reached east Anglesey outside the selected area) which did reach Ireland is *Campanula trachelium* (Fig. 18). It is a somewhat more continental species than some of the eight discussed above though similar to *Acer campestre*, *Inula conyzae* and *Lathyrus sylvestris* but it has the same clear horizontal northern limit in Britain and, significantly, occurs in the area of Ireland with the highest summer temperatures.

Two of the remaining three species, *Cyperus longus* and *Ranunculus sardous*, occur in wet habitats near the sea. *C. longus* is at its northern limit in Britain and, though widely established as a deliberate introduction or as an escape from cultivation, there is a suggestion that it does not produce ripe seed in Britain (Stewart *et al.* 1994). It has not escaped from cultivation in Ireland, so the climate may be even less suitable for it there.

Ranunculus sardous is present now only in one selected area, St David's (Fig. 19), and often appears to be only a casual at the western fringe of its distribution in Britain (Wade, Kay & Ellis 1994) whilst it has only been recorded once from Ireland, and then as a casual. Though it has a considerable fossil record during the last glacial period and there is a possibility that it was in the British Isles throughout, the long gap between its Late and Middle Weichselian records and its records as a weed from Romano-British occupation sites, suggests that it is likely that this thermophilous Continental Southern species died out and only returned long after the land bridge had gone.

There is no evidence which suggests that *C. longus* or *R. sardous* are species which would have become established in Ireland had there been a bridge in the later stages of the post-glacial period.

The last species of this group, *Hornungia petraea*, has an unusual, mainly western distribution in Britain (Fig. 20). It is a species of dry habitats which thrives best in areas with mild, damp winters (Ratcliffe 1959).This suggests that the climate of south-east Ireland would have been as suitable as west Wales and that a species of sand dunes, like so many other coastal species, would have had no difficulty in spreading, even without a land bridge. *H. petraea* perhaps remains as a candidate, though a doubtful one.

OCEANIC WEST EUROPEAN AND OCEANIC SOUTHERN ELEMENTS

It is convenient to consider these two biogeographical elements together because species in both

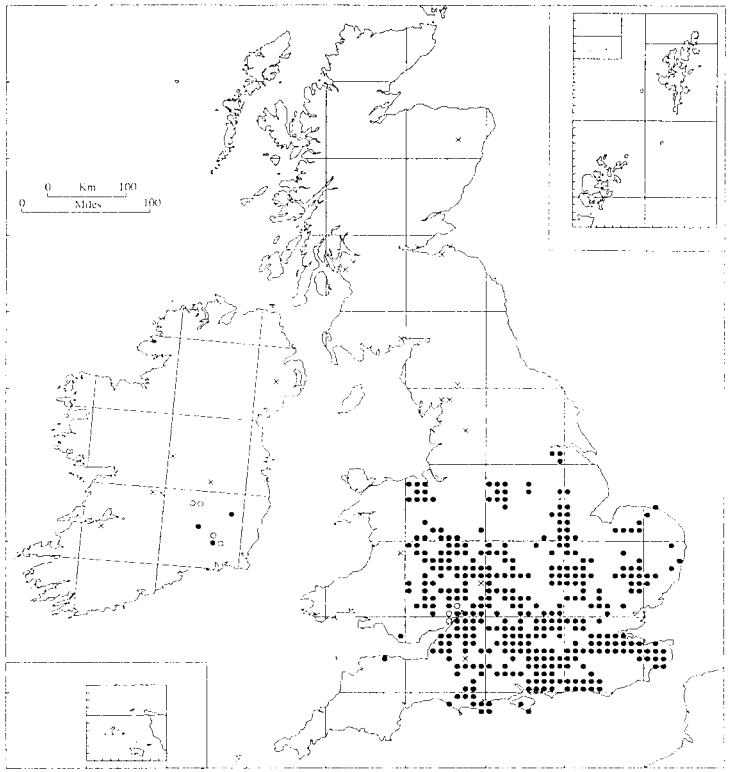

FIGURE 18. The distribution of *Campanula trachelium* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record, × = introduction. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

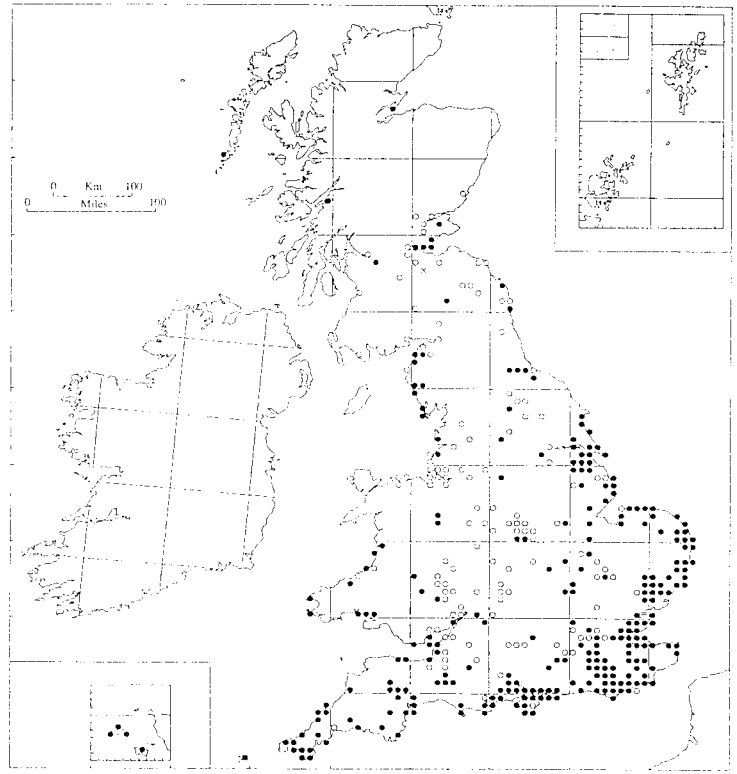

FIGURE 19. The distribution of *Ranunculus sardous* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1930 onwards record, ○ = pre-1930 record, × = introduction. Based on Perring & Walters (1982) and updated by the Biological Records Centre, Institute of Terrestrial Ecology.

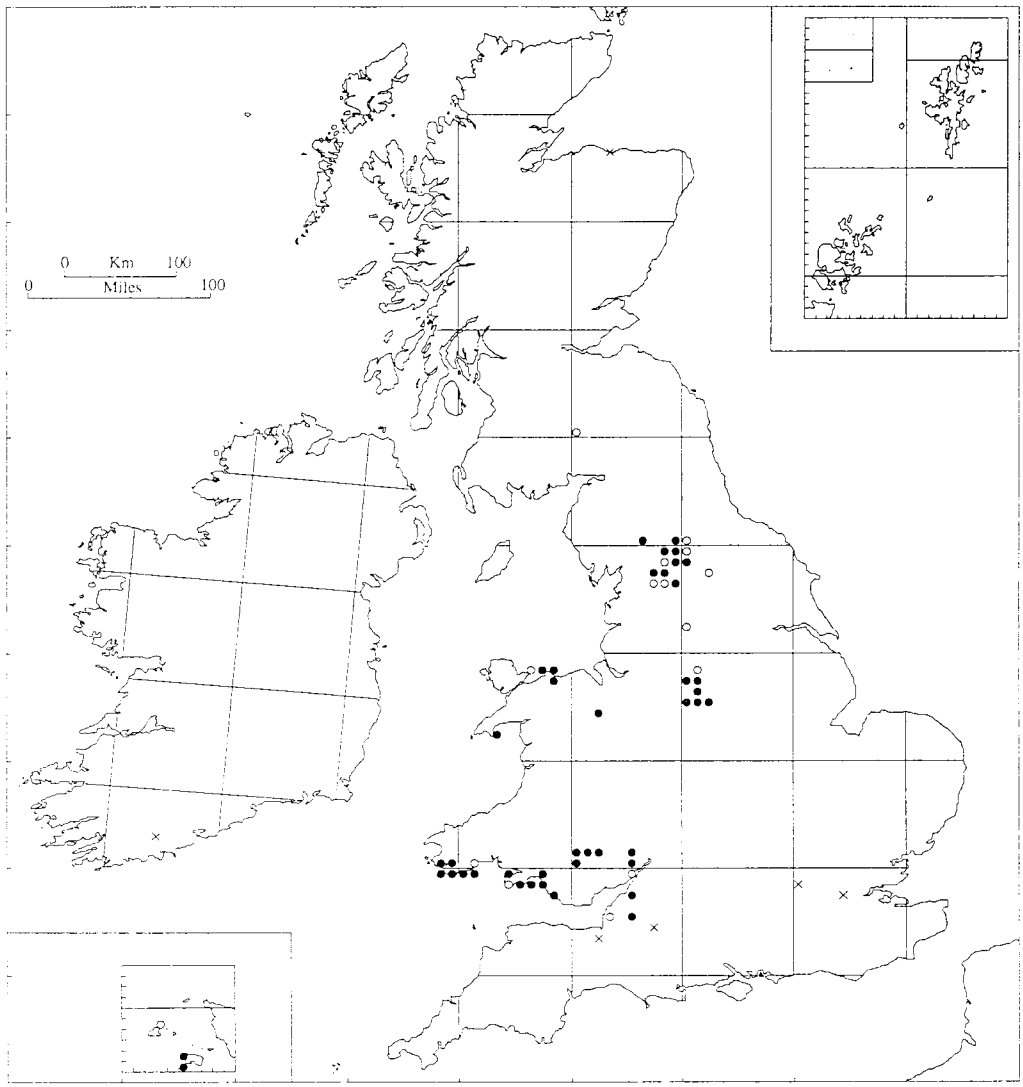

FIGURE 20. The distribution of *Hornungia petraea* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1970 onwards record, ○ = pre-1970 record, × = introduction. Based on Stewart, Pearman & Preston (1994) and prepared by the Biological Records Centre, Institute of Terrestrial Ecology.

have broadly similar distributions in Britain and north-west Europe, which is the main area of interest. They have been allocated as follows:

a. Oceanic West European. *Dactylorhiza praetermissa*, *Genista anglica*, *Hypericum linarifolium*, *H. undulatum*, *Petroselinum segetum*, *Puccinellia rupestris*, *Rubus bertramii*, *R. lindebergii*.

b. Oceanic Southern. *Iris foetidissima*, *Limonium vulgare*, *Mibora minima*, *Moenchia erecta*, *Ononis reclinata*, *Sison amomum*, *Trifolium strictum*.

The difference between these two elements is that whereas Oceanic West European species are restricted to an area from southern Sweden or Denmark through north-west Germany, Holland,

Belgium and western France to Spain and Portugal, Oceanic Southern species 'add on' the Mediterranean and often extend eastwards and southwards to south-west Asia and North Africa. There is also an overlap between the two elements, the decision as to which a particular species belongs to depending on how far they penetrate the Mediterranean. *Moenchia erecta* (Fig. 21, upper map) is a good example. The main part of its range is characteristic of an Oceanic West European species, but the thin scatter of records eastwards to Greece places it into the Oceanic Southern.

Details of the 15 members of these two elements which occur in the selected areas are given in Table 5. Whilst they do form a group of species which are not found in 'Continental' Europe their distribution in Britain does not have the same degree of uniformity of pattern which was discernible with the Continental and the Continental Southern elements where winter and summer temperatures seemed to be the dominant factors. They vary from rare species confined to a few localities in the west, e.g. *Hypericum undulatum* (Fig. 22), to species which are widespread in the south and east with a few relict localities in the west, e.g. *Petroselinum segetum*. Two are littoral species: one, *Limonium vulgare* reaching well into Scotland, the other, *Puccinellia rupestris* almost confined to the southern half of England and Wales. History and habitat appear to have been more important in determining the present distribution in Britain of species in these elements than isotherms. They are therefore considered in the following habitat groupings:

a. Dry, often open, habitats. *Hypericum linarifolium*, *Moenchia erecta*, *Petroselinum segetum*, *Trifolium strictum*.
b. Wetland habitats. *Dactylorhiza praetermissa*, *Genista anglica*, *Hypericum undulatum*.
c. Woodland margins. *Iris foetidissima*, *Rubus bertramii*, *R. lindebergii*, *Sison amomum*.
d. Coastal habitats. *Limonium vulgare*, *Mibora minima*, *Ononis reclinata*, *Puccinellia rupestris*.

a. *Dry habitats.*

Hypericum linarifolium is at its northern limit in Europe in Britain. It has a very restricted distribution here and appears to have been lost from three of its four Welsh localities this century. It is a species of steep, open, dry acid rocks and this coupled with its decline, suggests a retreating species, a relict of a warmer period of the post-glacial maximum, which could have been included with the relict species discussed on p. 20 had it not been an Oceanic West European species rather than a 'Continental' one.

Moenchia erecta in contrast is widely distributed along the western seaboard of Wales, is frequent in Cornwall and Devon and is probably still under-recorded (Fig. 23). It has a distribution in Britain and Europe (Fig. 21, upper map) which is remarkably similar to that of *Ranunculus parviflorus* (Fig. 21, lower map). The latter, however, is a species which does occur in Ireland – in the south-east which, as we have seen, is where the highest summer temperatures are enjoyed and is just the area in which *M. erecta* might have been expected to have grown had it been able to cross the gap on dry land.

Petroselinum segetum has a very long glacial and post-glacial history and was recorded from the Flandrian c. 2,000 BP in Cumbria. So perhaps it was more widespread during the post-glacial climatic optimum about 7,000 BP, when it could have been in Ireland, but has retreated since and is now only a relict in dry, open habitats on the Welsh coast. It has a typical 'Continental' distribution in Britain today.

Trifolium strictum is included on the slender basis of one record from Anglesey where it has not been seen for over 150 years. It is another rare, relict, species which, like *Hypericum linarifolium*, is at its northern limit in Britain and hangs on in a small number of dry, short grassland localities.

b. *Wetland habitats.*

Dactylorhiza praetermissa has a distribution in Britain which would suggest it ought to occur in south-eastern Ireland. However it appears to have general difficulty in spreading and, despite its abundance in Britain and in the St David's area, it is otherwise very restricted and only occurs in northern France, northern Denmark, Belgium and Holland. Perhaps it is a 'young' taxon with very special mycorrhizal requirements which, like other light-seeded orchids, will become established in Ireland when the conditions are right there; lack of a bridge has not been its problem.

Genista anglica was one of the species listed both by Praeger (1934) and by Webb (Meenan & Webb 1957) as being excluded from Ireland because of the absence of land bridges to Britain. It has already been discussed (p. 15) and is clearly a very strong candidate: one of only nine species in three or more selected areas (all three Welsh ones); a species of moist to dry peaty habitats which are

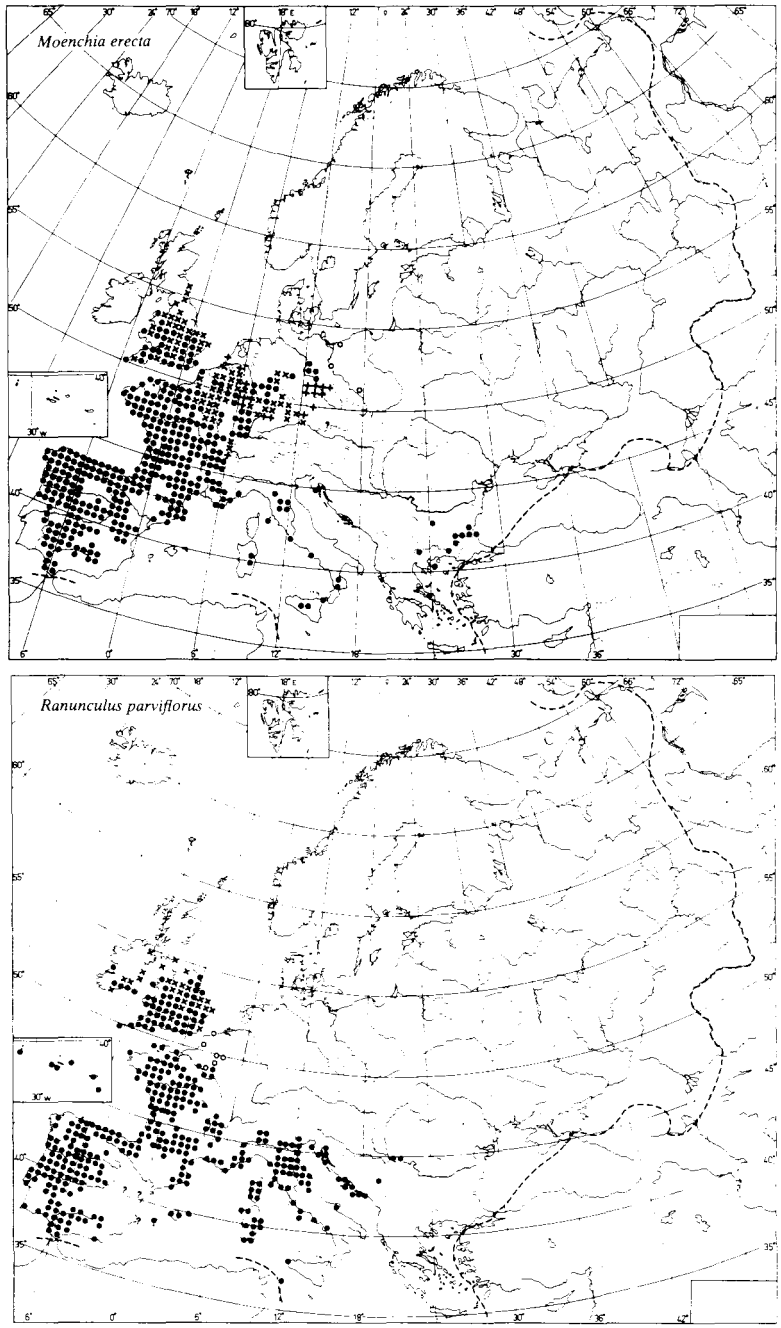

FIGURE 21. European distribution maps. Each dot represents at least one record in a 50-km square of the U.T.M. grid. ● = native occurrence, × = probably extinct or not recorded since 1930, ○ = introduction. Upper map *Moenchia erecta* from Jalas & Suominen (1983); lower map *Ranunculus parviflorus* from Jalas & Suominen (1989).

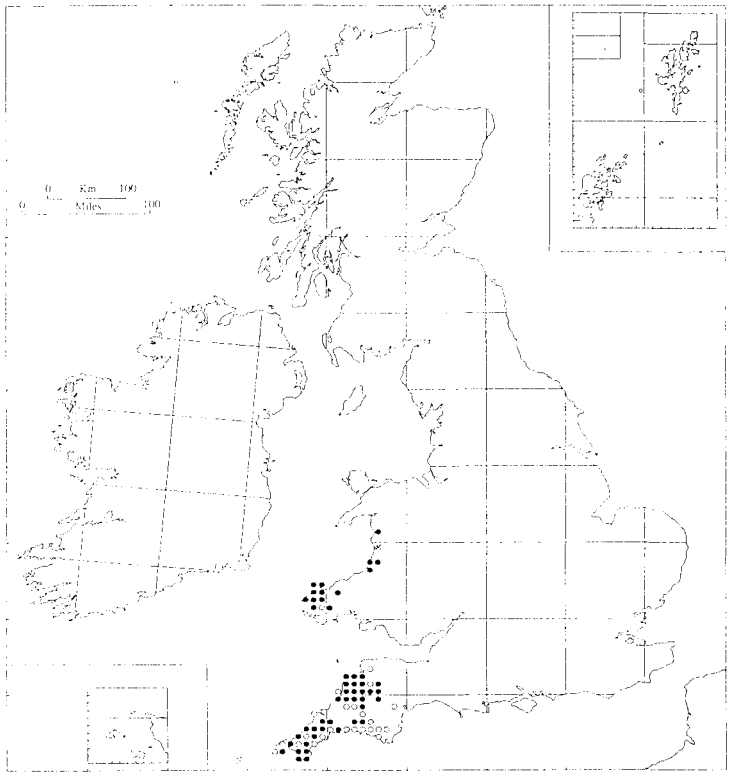

FIGURE 22. The distribution of *Hypericum undulatum* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1970 onwards record, ○ = pre-1970 record, × = introduction. Based on Stewart, Pearman & Preston (1994) and prepared by the Biological Records Centre, Institute of Terrestrial Ecology.

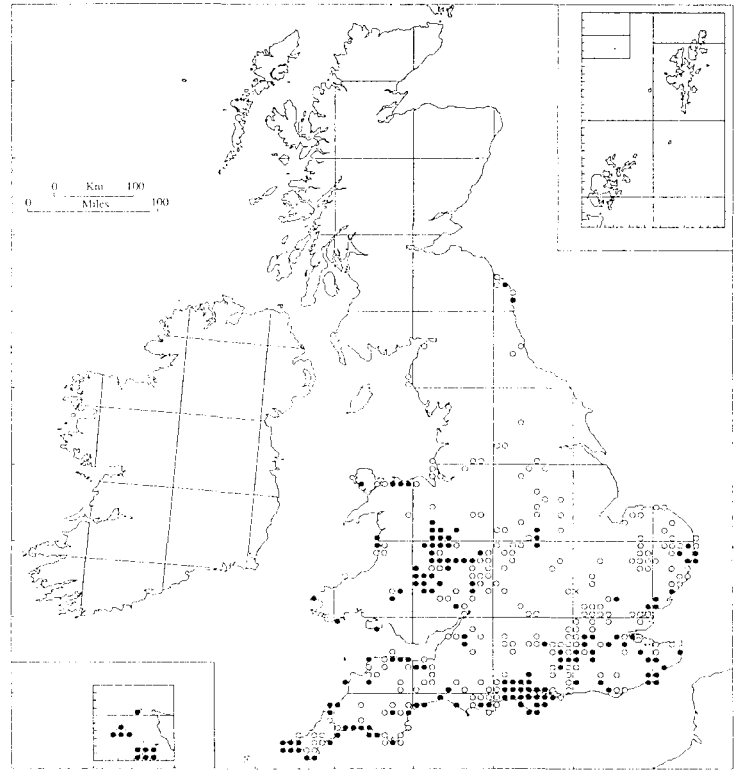

FIGURE 23. The distribution of *Moenchia erecta* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. ● = 1970 onwards record, ○ = pre-1970 record, × = introduction. Based on Stewart, Pearman & Preston (1994) and prepared by the Biological Records Centre, Institute of Terrestrial Ecology.

abundant in Ireland and, despite this habitat, where Quaternary remains might have been expected to be preserved if it had been in Britain during that period, there are none.

Hypericum undulatum is a species requiring warm summers and a higher water-table throughout the year. Though the summers in south-east Ireland across the sea from St David's, where it is abundant (Fig. 22), are as warm (Fig. 8). The rainfall is lower on this more sheltered side of the Irish Sea (Fig. 24) and it may have been excluded by absence of suitable climate/habitat conditions when this

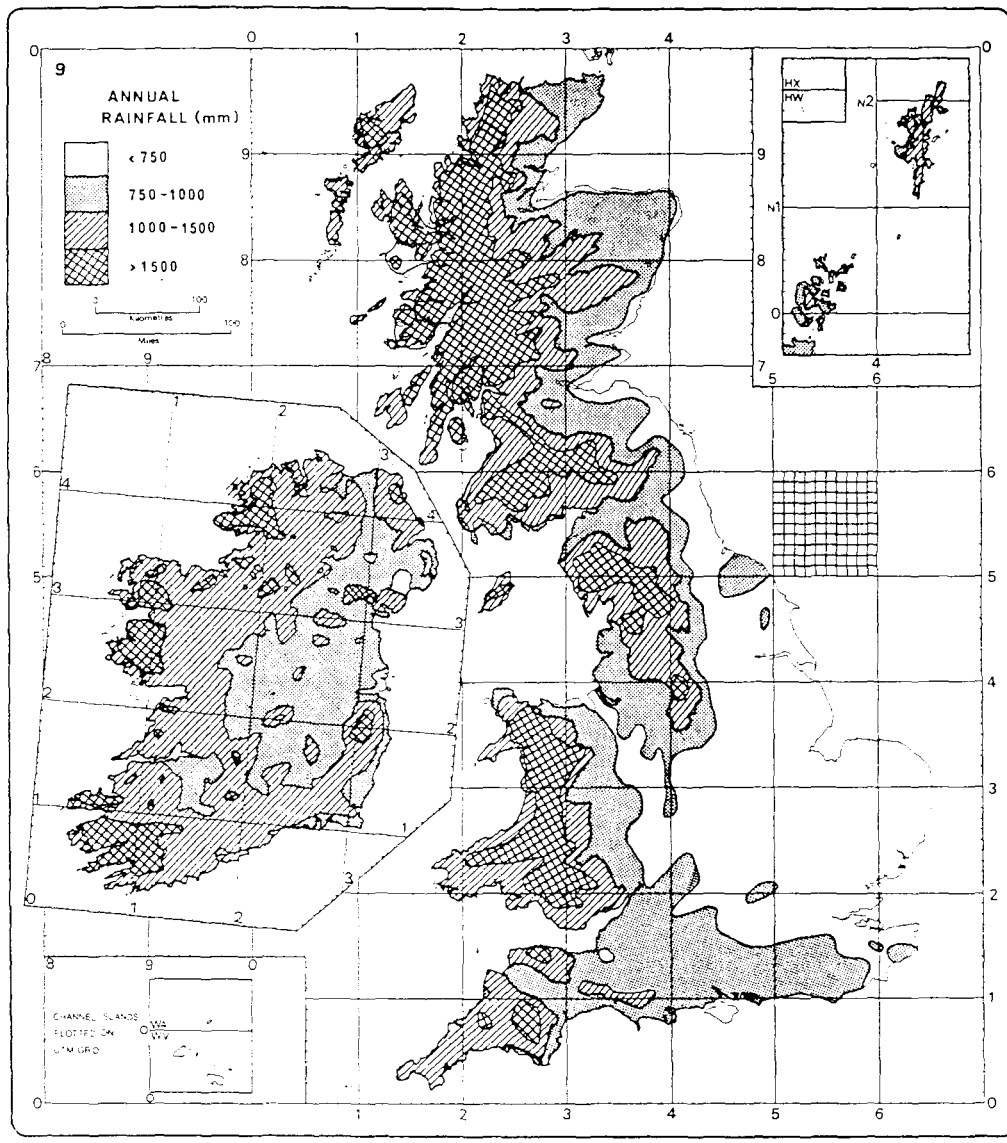

FIGURE 24. Annual rainfall. Isohyets show the rainfall in mm based on the 1941–70 average for Britain and the 1931–60 average for Ireland. From Institute of Terrestrial Ecology (1978).

thermophilous species was spreading during the post-glacial. However it is a possible, though not a very strong, candidate for inclusion in the list.

c. *Woodland margins.*
Iris foetidissima is a thermophilous species, well-established as a native on the west coast of Wales and behaving as if it were a native on islands off the Irish coast just across the sea. If it is not native in Ireland it has clearly demonstrated its ability to become established in natural habitats there, and in the Isle of Man, and must consequently be a prime candidate for inclusion. Absence of Quaternary records supports the view that it was a late arrival in Britain.
Rubus bertramii and *R. lindebergii* are both woodland margin species with distributions centred on north-west Europe and Britain. They are both conspicuously western in Britain: *R. bertramii* is more southern with the greatest number of records in Wales and the west Midlands but stretching from Devon and Cornwall to Cumbria; *R. lindebergii* is more northern extending from South Wales to Perthshire but with the greatest concentration in northern England. Perhaps significantly there are records for both species from the Isle of Man (though there is some doubt about that for *R. bertramii*). This demonstrates an ability to spread westwards to Man whilst the bridge remained but that the arrival was too late for the next step. They join other woodland margin species as strong candidates for the final list.

d. *Coastal habitats.*
Limonium vulgare is a curious absentee from Ireland. The similar *L. humile* does occur there even though it is the less frequent of the two in Europe, not reaching Spain or Portugal, going slightly further north in Scandinavia and getting into Norway. When they grow together in the north-west of Britain *L. humile* seems more successful (Stewart *et al.* 1994) so the absence of *L. vulgare* from Ireland may be due to competition from a closely related species which grows in almost the same habitat. *L. vulgare* has recently been found in two new localities in the Isle of Man after being thought extinct there. Though this may only demonstrate "the usual floristic fluctuation to which tide dispersed communities are subject" (Allen 1984), it could also indicate that this species could cross the Irish Sea without a bridge if the conditions (e.g. lack of competition) were suitable.
Mibora minima grows in sand dunes at the north of its range in Anglesey and on the Dutch coast: it appears to be a relict like *Trifolium strictum* discussed above (p. 43). It does however have the ability to spread and has persisted, with assistance, for nearly 200 years in East Lothian, 350 km north of its natural northern limit in Anglesey.
Ononis reclinata has an extremely disjunct distribution. It is an annual found throughout the Mediterranean which could have been in the British Isles (including Ireland?) for a very long time, being more widespread when the climate was warmer but now retreating.
Puccinellia rupestris also appears to be a species retreating and the St David's records may be relicts of a period in the post-glacial climatic maximum when this southern species (which reaches Syria) was more widespread and may even have been in Ireland. It is self compatible and reproduces by seed which can germinate after many years in the ground (Stewart *et al.* 1994) so it might reappear in some of its former northern localities after a particularly hot summer (1995). It was once found in Northern Ireland and persisted for several years until the site was paved.

On this evidence it is difficult to conclude with confidence that any of these four species would be native in Ireland today if there were a land bridge. *Limonium vulgare* may be kept out by competition whilst the other three are in retreat. Moreover coastal species, especially those of salt marshes and sand dunes are usually mobile with ability to spread across the sea to new areas or return to old ones e.g. *Atriplex pedunculata* to eastern England or *Limonium vulgare* to the Isle of Man cited above.

ENDEMIC ELEMENT
There are only two endemic species which occur in the selected areas but are absent from Ireland: *Coincya monensis* and *Rubus silurum*. Details are given in Table 6. Both are species of western Britain with distributions overlapping in Lancashire.

It is surprising that *Coincya monensis*, which is of recent origin and is a coastal species which has demonstrated its ability to cross water by reaching Arran and the Isle of Man or has spread from an island origin to the mainland, should not have reached the north of Ireland. Perhaps it will, given more time.

Rubus silurum is one of only nine species which occur in three or more of the selected areas – St David's, Lleyn and Anglesey. It is another woodland margin species and fits well with those other woodland margin species which have already been accepted as strong candidates such as *Sedum telephium* and *Hieracium vagum*. It may be significant that the closely related endemic, *Rubus robii*, which is widespread in hedgebanks and wood borders on the west side of the Pennines and along the coast of Lancashire and the southern Lake District, does occur, in a single locality, in Armagh in Northern Ireland (Edees & Newton 1988).

OTHER EXCLUDED SPECIES

As indicated earlier (p. 18) three species included by Praeger (1934) in the list of species which failed to reach Ireland, do not occur in any of the selected areas. However it would be unreasonable not to give them the same analysis as has been afforded to the 58 taxa which do occur in these areas. The details of these three species, *Chrysosplenium alternifolium*, *Convallaria majalis* and *Ononis spinosa* are given in Table 7.

The last named is perhaps the easiest to dismiss. It is predominantly eastern in Britain today with scattered localities in the west, with the suspicion that some at least are errors through confusion with *O. repens* (Margetts & David 1981). As well as being absent from Cornwall and Devon except the extreme east, and most of Wales, it does not occur in Brittany. Moreover there is a pollen record from Cornwall in the early post-glacial c.10,000 BP suggesting that this Continental species was more widespread at that time and could have spread to Ireland over a land bridge and become established there had soil and climate been suitable.

A stronger case might be made for *Chrysosplenium alternifolium* (Fig. 2) and *Convallaria majalis* because of the similarity of their distributions to that of *Helictotrichon pratense* (Fig. 1). However closer analysis discloses that they hardly reach the west coast, and seem to have their western limit to the east of Ireland similar to *Paris quadrifolia* (Fig. 10), already rejected as a candidate, and in no way comparable with another woodland species *Sedum telephium* (Fig. 11), a strong candidate. Both are also distinctly eastern in Europe. *C. alternifolium* is absent from W. France, Spain and Portugal whilst *C. majalis* is absent from Brittany and Portugal.

Of the two only *C. majalis* has been reported as an established introduction in Ireland, though only in one place (H40, Co. Londonderry). Whilst this is in the north, where a Continental species would be most likely to become established, the rarity of such establishment for such an attractive species so commonly grown in gardens suggests it is not well adapted to Irish soils and climate. It may be significant that there are no reports of establishment from the Isle of Man.

The record of *C. alternifolium* from the Hoxnian interglacial is an indication that this species was in Britain and could have crossed the Irish Sea long before the land bridge was broken.

DISCUSSION

The taxa which have been identified as candidates are listed in Table 8 according to their biogeographical elements and with their habitats.

It is noteworthy that the majority (15 out of 22) are in the Continental or Continental Southern elements which, as a whole, have an eastern tendency in Britain. Equally noteworthy is the absence of any species from any of the Northern elements in our flora i.e. Continental Northern, Oceanic Northern or Northern Montane (sensu Matthews 1955), the first two of which include species which embrace all the selected areas within their overall distribution patterns whilst the third embraces the non-Welsh ones. Matthews pointed out, and this is substantiated by Godwin (1975), that many of these 'northern' species "have been identified from plant material of full-glacial and late-glacial age in Britain and Ireland. It seems probable, therefore, that a large proportion if not all the species having a northern facies, survived the last glaciation . . .". This contrasts vividly with the candidate species in Table 8. 19 out of the 22 have no full-glacial or post-glacial records and two of the other three for which material has been found have their first records in the late post-glacial after any land bridges had been severed: *Acer campestre* in the Neolithic, 4,500 BP, and *Vicia tetrasperma* in the Bronze Age, 2,500 BP. Only the third, *Clematis vitalba*, has a considerable Quaternary history having been reported from one or two warm periods before 70,000 BP but then not again until c.

TABLE 8. CANDIDATE SPECIES (NATIVE BRITISH VASCULAR PLANTS ABSENT FROM IRELAND – SEE TEXT) BY BIOGEOGRAPHICAL ELEMENTS WITH HABITATS

Continental	
Campanula latifolia	woodland
Genista tinctoria	open scrub and rough grassland
Helictotrichon pratense	grassland and cliff-tops
Hieracium vagum	woodland margins
Sedum telephium subsp. *fabaria*	woodland margins
Continental Southern	
Acer campestre	woodland
Clematis vitalba	woodland
Cruciata laevipes	woodland margins and rough grassland
Daphne laureola	woodland margins
Hornungia petraea?	sand dunes and rocks
Lathyrus sylvestris	scrub and cliffs
Ruscus aculeatus	woodland and cliffs
Tamus communis	woodland margins
Vicia tetrasperma	hedgebanks and rough grassland
Oceanic West European and Oceanic Southern	
Genista anglica	heaths and dry mosses
Iris foetidissima	woodland, scrub and field margins
Moenchia erecta	dry open grassland and cliff-tops
Rubus bertramii	damp woods and heath margins
R. lindebergii	wood and moor margins
Endemics	
Coincya monensis	sand dunes and cliffs
Rubus silurum	wood margins and moors

6,300 BP suggesting that it died out after one warm glacial period ended and returned after another had begun, though still too late to cross to Ireland.

Another noteworthy feature of the list is perhaps its small size – far smaller than the 186 suggested by Webb (1983). This small number is however supported by the analysis made by Rose (1972) who examined the floristic connections between south-east England and northern France and found only about twelve native species in the coastal zone of northern France which are absent from the British flora and wrote "that the Channel has not proved an important barrier to plant migration in the post-glacial period. In addition some of the species may well have formerly existed in S.E. England and become extinct before recording began". This view is reflected by Allen (1984) when considering the Manx and Irish floras and the fact that there are only four vascular plants in the former not in the latter (the present analysis has six but he omitted *Limonium vulgare* and the microspecies *Rubus lindebergii*): ". . . it is odd that there are not more higher plants among this non-Irish element. Maybe there were some which died out before modern records began".

Whereas Praeger (1934) believed the reduction of the Irish flora was largely due to its insularity, Webb (Meenan & Webb 1957) agreed that lack of certain habitats and a smaller climatic range in Ireland compared with Great Britain accounted for a large number of species that are absent from Ireland. What this analysis, outlined in Table 8, suggests is that we should not be surprised at the small number or that it is very much smaller than Webb's final figure of 186. It discloses that there is a group of species, mainly of Continental and Continental Southern distribution, which could be in the Irish flora and that 17 out of the 22 are either woody species or are herbs of woodland, woodland margin or hedgebanks. This is part of a group of warmth demanding woodland species which did not begin to arrive in Britain until the climatic amelioration of the Boreal period of the Flandrian post-glacial about 9,000 BP.

The other five species in the group in Table 8 are all species which include cliff-tops or sand dunes amongst their habitats today. They are species of open habitats suited to the sea-cliffs and sandy shores which had no doubt already been formed by the time they arrived at the points where the land bridges had been. Because they do form a distinctive, though smaller group, than the woodland

species it seems to add weight to the case for including *Hornungia petraea*, which appears in Table 8 with a question mark, and leaving the final number of candidate species at 22.

The fact that, whilst the 22 species are mainly woodland, there are five others of more open habitats would support the view of Synge (1985) that the land bridge was broken in the Allerød when both woodland and open habitat species would have been prevented from crossing rather than in the Boreal proposed by Godwin (1975) when only some woodland species might have been prevented from so doing.

This may still be a minimal list: perhaps there are others, which do not occur in the selected areas today, which were in them once and have since retreated or for which no suitable habitat existed (though St David's, Anglesey and Man between them, for example, exhibit a considerable range) but it is unlikely to result in a final list anywhere near as large as the 186 postulated by Webb (1983) and any additions should be looked for amongst thermophilous species of woodland and woodland margins or of dry, open grassland and cliffs.

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REFERENCES

ALLEN, D. A. (1984). *Flora of the Isle of Man*. The Manx Museum, Douglas, Isle of Man.

CHURCH, T. & SMITH, T. (1991). *Arran's Flora*, revised ed. Arran Natural History Society, Arran.

CLAPHAM, A. R., TUTIN, T. G. & MOORE, D. M., eds. (1987). *Flora of the British Isles*, 3rd ed. Cambridge University Press, Cambridge.

CUNNINGHAM, M. H. & KENNETH, A. G. (1979). *The flora of Kintyre*. E. P. Publishing Ltd, Wakefield.

DAVIS, T. A. W. (1970). *Plants of Pembrokeshire*. West Wales Naturalists' Trust, Haverfordwest.

EDEES, E. S. & NEWTON, A. (1988). *Brambles of the British Isles*. The Ray Society, London.

ELLIS, R. G. (1983). *Flowering plants of Wales*. National Museum of Wales, Cardiff.

GODWIN, H. (1975). *The history of the British flora*, 2nd ed. Cambridge University Press, Cambridge.

HACKNEY, P., ed. (1992). *Stewart & Corry's Flora of north-east Ireland*, 3rd ed. Institute of Irish Studies, The Queen's University, Belfast.

INSTITUTE OF TERRESTRIAL ECOLOGY (1978). *Overlays of environmental and other factors for use with Biological Records Centre Distribution Maps*. Institute of Terrestrial Ecology, Cambridge.

IVIMEY-COOK, R. B. (1984). *Atlas of the Devon flora*. Devonshire Association, Exeter.

JALAS, J. & SUOMINEN, J. *Atlas Florae Europaeae*. Part 6 (1983); Part 8 (1989). Societas Biologica Fennica Vanamo, Helsinki.

KENNETH, A. G. (1985). Additions to the flora of Kintyre. *Glasgow naturalist* **21**: 1–12.

KENT, D. H. (1992). *List of vascular plants of the British Isles*. Botanical Society of the British Isles, London.

MARGETTS, L. J. & DAVID, R. W. (1981). *A review of the Cornish flora 1980*. Institute of Cornish Studies, Redruth.

MATTHEWS, J. R. (1955). *Origins and distribution of the British flora*. Hutchinson, London.

MEENAN, J. & WEBB, D. A., eds. (1957). *A view of Ireland*, pp. 40–61. British Association for the Advancement of Science, Dublin.

OGILVIE, M. (1995). *The wild flowers of Islay*. Lochindaal Press, Isle of Islay.

PENNINGTON, W. (1969). *The history of British vegetation*. English Universities Press Ltd, London.

PERRING, F. H. (1985).Biogeographical elements, in SINKER, C. S. *et al.*, eds. *Ecological Flora of the Shropshire region*, pp. 69–76. Shropshire Wildlife Trust, Shrewsbury.

PERRING, F. H. & FARRELL, L. (1983). *British red data books*: 1 – *Vascular plants*, 2nd ed. Royal Society for Nature Conservation, Lincoln.

PERRING, F. H. & SELL, P. D., eds. (1968). *Critical supplement to the atlas of the British flora*. T. Nelson & Sons, Ltd, London.

PERRING, F. H. & WALTERS, S. M., eds. (1962). *Atlas of the British flora*, 1st ed. T. Nelson & Sons, Ltd, London.

PERRING, F. H. & WALTERS, S. M., eds. (1982). *Atlas of the British flora*, 3rd ed. E. P. Publishing Ltd, Wakefield.

PIGOTT, C. D. & WALTERS, S. M. (1954). On the interpretation of the discontinuous distributions shown by certain British species of open habitats. *Journal of ecology* **42**: 95–116.

PRAEGER, R. L. (1934). *The botanist in Ireland*. Hodges, Figgis & Co., Dublin.

RATCLIFFE, D. (1959). *Hornungia petraea* (L.) Rchb. Biological Flora of the British Isles. *Journal of ecology* **47:** 241–247.

RICHARDS, A. J. (1989). Some problematic *Epipactis* in northern Britain. *B.S.B.I. news* **51**: 51.

RICHARDS, A. J. & SWAN, G. A. (1976). *Epipactis leptochila* (Godfery) Godfery and *E. phyllanthes* G.E.Sm. occurring in South Northumberland on lead and zinc soils. *Watsonia* **11**: 1–5.

ROBERTS, R. H. (1982). *The flowering plants and ferns of Anglesey*. National Museum of Wales, Cardiff.

ROSE, F. (1972). Floristic connections between southeast England and North France, in VALENTINE, D. H., ed., *Taxonomy, phytogeography and evolution*, pp. 361–379. Academic Press, London.

SCANNELL, M. J. P. & SYNNOTT, D. M. (1987). *Census catalogue of the flora of Ireland*, 2nd ed. Stationery Office, Dublin.

SILVERSIDE, A. J. & JACKSON, E. H. (1988). *A check-list of the flowering plants and ferns of East Lothian*. Botanical Society of Edinburgh, Edinburgh.

STEWART, A., PEARMAN, D. A. & PRESTON, C. D., eds. (1994). *Scarce plants in Britain*. Joint Nature Conservation Committee, Peterborough.

SYNGE, F. M. (1985). Coastal evolution, in EDWARDS, K. J. & WARREN, W. P., eds. *The quaternary history of Ireland*, pp. 115–131. Academic Press, London.

WADE, A. E., KAY, Q. O. N. & ELLIS, R. G. (1994). *Flora of Glamorgan*. H.M.S.O., London.

WEBB, D. A. (1977). *An Irish Flora*, 6th ed. Dundalgan Press, Dundalk.

WEBB, D. A. (1983). The flora of Ireland in its European context. *Journal of life sciences of the Royal Dublin Society* **4**: 143–160.

WEBB, D. A. & SCANNELL, M. J. P. (1983). *Flora of Connemara and the Burren*. Cambridge University Press, Cambridge.

WILSON, A. (1956). *The altitudinal range of British plants*. T. Buncle & Co. Ltd, Arbroath.

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