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Arenaria norvegica *subsp.* norvegica *was re-discovered in Ireland in 2008 after an absence of 47 years. A detailed survey in 2009 revealed a small population restricted to skeletal soils on the edges of limestone pavement.* A. norvegica *subsp.* anglica *occurs in an almost identical habitat in Northern England. Irish plants also appear to flower at least a month earlier and produce more infloresences than in Britain. These differences warrant further investigation given the isolation of the Irish population. That it remained undetected for so long is remarkable and cautions against declaring a species as 'extinct' even in such a well botanized locality as the Burren.*

Keywords: arctic sandwort, limestone pavement, post-glacial history

Introduction

In Britain and Ireland *Arenaria norvegica* (Caryophyllaceae) is a very rare Arctic-montane sandwort recorded from nine disjunct localities in north and west Scotland, northern England and western Ireland (Fig. 1). All Scottish populations belong to subspecies *norvegica*, a widespread taxon of gravelly 'fellfield' and screes in Iceland and scattered localities in the mountains of Norway, northern Sweden and one small area of Finnish Lapland (Enontekiön Lappi) (Halliday 1960a, see map in Jonsell 2001).

The largest British population of subsp. *norvegica* occurs on the island of Unst, Shetland, where it was first recorded by Thomas Edmonston in 1837 (Edmonston 1841, Scott and Palmer 1987). Here up to 15 000 plants have been recorded on shallow soils derived from ultrabasic (serpentine) rocks on the Keen of Hamar and a few adjacent hills (Slingsby 1981, Carter *et al.* 1987, Kay 1997, Slingsby *et al*. 2001, Kay and Proctor 2003). A second large population occurs on ultrabasic (peridotite) outcrops and the gravelly shore of a loch on the Island of Rum in the Inner Hebrides (Clark 1939, Heslop Harrison *et al*. 1941, Pearman *et al*. 2008). Smaller colonies occur on eroding basalts on the adjacent island of Eigg and on a single mountain in Morvern (MacLeay 1953, Coker 1969) and on Cambrian (Durness) limestone outcrops in Argyll (Slack and Dickson 1959, Slack 1965) and Inchnadamph, West Sutherland, where it also occurs sporadically on the gravelly shores of the River Loanan (Gray 1886/7, Evans *et al.* 2002).

The English subspecies, *A. norvegica* subsp. *anglica*, appears to be endemic to Upper Ribblesdale, Mid-west Yorkshire (v.c.64), where it was first discovered by Lister Rotheray in 1889 (Rotheray 1889a). Although initially thought to be an altered form of *Arenaria norvegica* (Baker 1889, Rotheray 1889b) it was described as *Arenara gothica* Fries (Rotheray 1989b, Bennett 1891), a species now known to only occur in Sweden, as var. *fugax* (J. Gray ex Gren.) M. B. Wyse-Jacks. and J. Parn., and the Jura mountains in southern Europe as var. *moehringioides* (Murr.) M. B. Wyse-Jacks. and J. Parn. (Wyse-Jackson and Parnell 1987, Jonsell 2001). However, Halliday (1958, 1960a,b) showed that Yorkshire plants were closer to *Arenaria norvegica* than either Swedish or Jura *Arenaria gothica*.

The English plant differs from subsp. *norvegica* in being a winter annual (rarely biennial) with few sterile shoots, larger flowers, narrower, more lanceolate leaves, and greater ciliation especially on the margins of the outer sepals (Halliday 1960b). The total population, which fluctuates between a few hundred and a few thousand plants depending on spring rainfall, is restricted to Carboniferous limestone outcrops on the eastern slopes of Ingleborough where habitats include shallow, gravelly soils in solution hollows on limestone pavement, flushes, and on tracks

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Figure 1. The hectad distribution of Arenaria norvegica in Ireland, Scotland (subsp. *norvegica*) and England (subsp. *anglica*).

and the floor of an abandoned limestone quarry (Walker 2000).

In Ireland, *A. norvegica* was recorded in 1961 by John [Jack] Heslop Harrison during a University field trip to the Burren, Co. Clare (Heslop Harrison *et al.* 1961). The identity of the plant was confirmed by Geoffrey Halliday who counted the chromosomes on a plant cultivated from seed sent to him ($2n$ = 80; G. Halliday 2008, pers. comm.). In an account published in this journal, Heslop Harrison *et al.* (1961) described the habitat as "shallow crevices and solutions hollows on an area of limestone pavement" at *c.*800 feet [244 m] on "the south slope of Gleninagh Mountain overlooking Caher Lower". The precise locality has always been unclear as Gleninagh Mountain does not have a southern slope, but extends southwards in a long ridge to the east of Caher Lower. Webb and Scannell (1983) suggested a more likely location on the adjacent mountain of Carnsefin at M164092 "or not far away" but there is very little suitable habitat at 250 m in this area (K.J. Walker 2009, pers. obs.) and it has not been refound despite repeated searches. Irish botanists therefore considered it to be extinct or possibly based on an erroneous determination (*e.g.* Webb and Scannell 1983, Curtis and McGough 1988), though this clearly contradicts the findings of Halliday. Possibly the association with the name Heslop Harrison influenced their views, as his father, John W. Heslop Harrison, is now known to have claimed a series of discoveries in the Hebrides during the 1930s and 1940s that are not accepted by others (Pearman and Walker 2004). Coincidentally, both father and son were in the party that first discovered *A. norvegica* on the Island of Rum in 1938 (Clarke 1939, Pearman *et al.* 2008).

During a visit to the Burren in 2008, KJW made a chance discovery of two small populations of *A. norvegica* subsp. *norvegica* a few kilometres to the south-west of Caher Lower on the lower slopes of Carnsefin Mountain (Walker *et al.* 2009). Here the plant was confined to shallow, gravelly soils in the middle of a 'green road' linking Murroogh to Black Head, between and on limestone exposures close by. The author returned in early June 2009 to carry out a more detailed survey and to collect information on the ecology of the species as part of a wider study. This paper describes the results of the 2009 survey and compares the habitats, vegetation, and morphology of Irish plants with populations of subsp. *anglica* in England and subsp. *norvegica* in Scotland. Nomenclature for vascular plants follows Stace (2010) and Rodwell (1993, 2000) for British National Vegetation Classification (NVC) communities. Throughout this paper *Arenaria norvegica* refers to *Arenaria norvegica* subsp. *norvegica*.

Methods

In early June 2009, KJW carried out a detailed survey of suitable habitats in the 1 km × 1 km grid square M1510 where the plant was re-discovered in 2008, and the adjacent squares M1509, M1609 and M1610 which includes the area suggested by Webb and Scannell (1983). The position and number of plants were recorded within 100 m^2 (10 × 10 m) grid cells using a hand-held GPS (Garmin Etrex).

To characterize the vegetation in which *Arenaria norvegica* occurred the percentage cover of all species (excluding bryophytes) were recorded in large (1 m^2) quadrats placed in representative stands of vegetation (n = 12). These were assigned to British National Vegetation Classification (NVC) communities using the computer programme Tablefit (Hill 1996) and compared to British sites using multivariate ordination (Detrended Correspondence Analysis in Canoco for Windows version 4.5; Ter Braak and Šmilauer 1988). Percentage cover values were square-root transformed to achieve normality of residuals as required.

Because these larger quadrats included pockets of adjacent grass-heath, a series of smaller quadrats was also recorded to identify 'close associates' growing on skeletal soils. These included all species (excluding bryophytes) growing within 10 cm of 112 randomly selected individuals of *A. norvegica*. The performance of these 112 individuals was compared to plants from three British populations of subsp. *norvegica* (Rum, Inchnadamph, Beinn Iadain) and subsp. *anglica* (Yorkshire) by measuring the number of flowers (including buds, open/senesced/failed flowers and capsules) and maximum horizontal extent. Measurements at British sites were carried out in 1995 (Yorkshire), 2001 (Rum, Beinn Iadain) and 2003 (Inchnadamph).

Results

Distribution and abundance

In 2009, 249 individuals of *Arenaria norvegica* were recorded in 60 10 × 10 m grid cells all within OS 1 km grid square M1510 (Fig. 2). No plants were found outside this restricted area despite the presence of suitable habitat in all the monads visited. In M1510 plants were scattered at very low density (mean 4.1 ±0.6 plants per 100 m^2) over 300 × 700 m of limestone pavement with a single outlier approximately 200 m to the east. Sixty-three per cent of grid cells held less than 3 plants and only 10 per cent exceeded 10 plants; the maximum found in any one 10 × 10 m cell

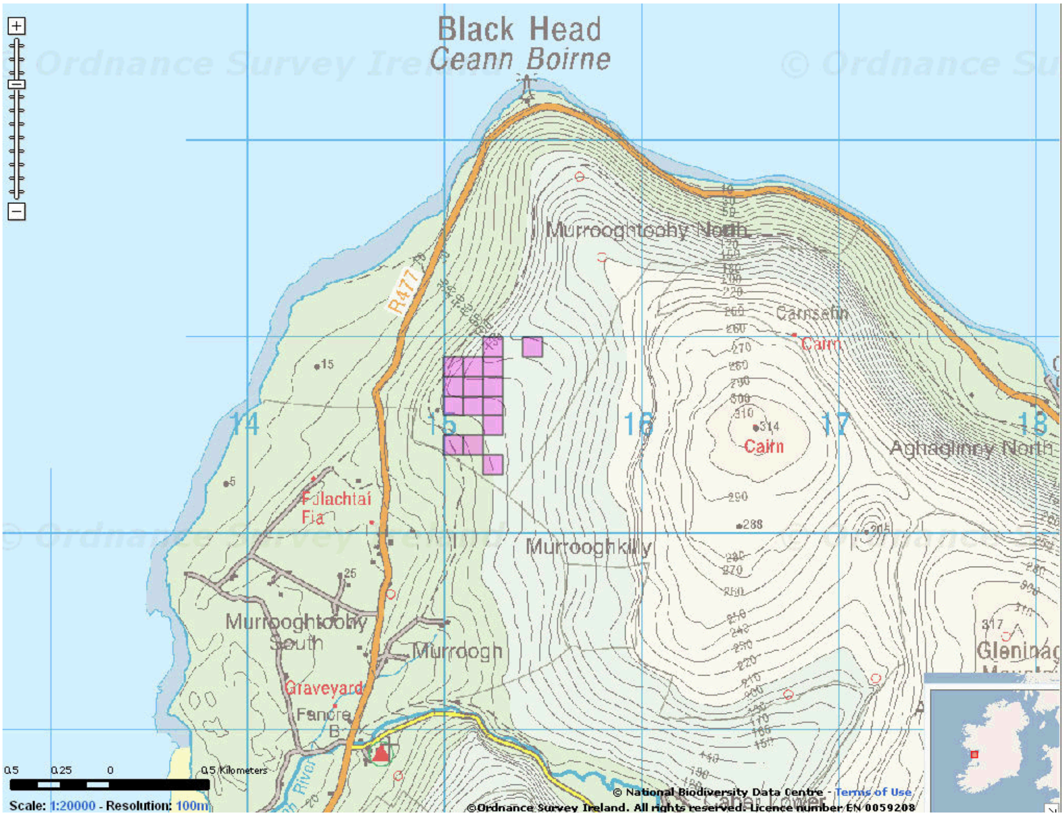


Figure 2. The distribution of *Arenaria norvegica* subsp. *norvegica* in the Burren, Co. Clare. Symbols represent presence within 100 × 100 m grid cells. The map was produced by Una Fitzpatrick and is reproduced with permission of the Irish Biodiversity Data Centre.

was 22. Most colonies were usually confined to just a few square centimetres of gravely soil and consequently total cover of *A. norvegica* never exceeded 1 % m^{-2} (Table 1). The altitude of the entire population occurred between 80 to 140 m with the bulk of the population occurring between 100 to 130 m above sea-level.

Habitat

The bulk of the population was confined to shallow depressions containing soil and limestone gravel on flat or very gently sloping (< 5°) limestone exposures (Fig. 3). These included solution hollows on natural exposures, the 'ruts' of a rough track, small rock crevices and more rarely flat limestone slabs where flushing had created temporary pools (these were dry at the time of the survey). These habitats were typically, but not exclusively, confined to the edges of limestone pavements that had been laterally deformed to create a series of gently sloping terraces. The accumulation of fine gravel and soil on these terraces had produced a shallow skeletal soil, often along the rear edge of limestone exposures where they graded, often abruptly, into adjacent grass-heath (Fig. 3). In most cases this habitat was inter-mixed with pockets of deeper soil supporting grass-heath and bare limestone pavement. In the larger quadrats the cover of bare soil and gravel comprised around 40 per cent and vegetation around 20 per cent whereas on the skeletal soils vegetation cover alone rarely exceeded 5 per cent (Table 1). Typically this habitat was very limited in extent often comprising just a few square centimetres within a matrix of bare limestone and grass-heath. In this habitat *A. norvegica* was usually rooted amongst fine gravel or larger stones where the microhabitat was more sheltered than on the surrounding pavement surface.

Associated species

Of the 53 species recorded with *Arenaria norvegica*, only 34 (including *A. norvegica*) were recorded as 'close associates' on skeletal soils (*i.e.* growing within 10 cm; Table 1). Of these the most frequent were *Festuca ovina* (77%), *A. norvegica* itself (58%), *Agrostis capillaris* (45%), *Minuartia verna* (29%), *Plantago maritima* (25%), *Thymus polytrichus* and *Sesleria caerulea* (both 12%). All other species were very rare on

Table 1. Associates of *Arenaria norvegica* in the Burren in (a) small (10 cm radius) quadrats (*n* = 112) and (b) large (1m^2) quadrats (*n* = 12). '+' equals <1%. Species in more than 50% of larger quadrats are highlighted in bold.

Species	Small freq.	Large freq.	Large %
Arenaria norvegica	58	100	+
Festuca ovina	**77**	**100**	**8**
Agrostis capillaris	**45**	**58**	**5**
Minuartia verna	29	17	1
Plantago maritima	**25**	**75**	**1**
Thymus polytrichus	**12**	**100**	**1**
Sesleria caerulea	12	42	1
Gentiana verna	7	42	+
Bellis perennis	7	8	+
Plantago lanceolata	5	17	+
Taraxacum officinale	5	17	+
Anagallis arvensis	5	8	+
Carex flacca	**4**	**75**	**2**
Succisa pratensis	**4**	**50**	**+**
Geranium robertianum	4	42	+
Anthyllis vulneraria	4	25	1
Sedum acre	4	0	–
Lotus corniculatus	3	42	+
Erophila verna	3	0	–
Campanula rotundifolia	2	25	+
Carlina vulgaris	2	17	+
Geranium sanguineum	2	17	+
Senecio jacobaea	2	17	+
Leontodon hispidus	2	8	+
Teucrium scorodonia	2	8	+
Viola riviniana	1	42	+
Asperula cynanchica	1	25	+
Helianthemum oelandicum	1	25	1
Polygala serpyllifolia	1	25	+
Pilosella officinarum	1	8	+
Saxifraga tridactylites	1	8	+
Hypochaeris radicata	1	0	–
Koeleria macrantha	1	0	–
Rhinanthus minor	1	0	–
Prunella vulgaris	0	42	+
Achillea millefolium	0	25	+
Blackstonia perfoliata	0	25	+
Carex pulicaris	0	25	1
Centaurium erythraea	0	25	+
Dryas octopetala	0	25	+
Potentilla erecta	0	25	+
Solidago virgaurea	0	25	+
Antennaria dioica	0	17	1
Asplenium ruta-muraria	0	17	+
Calluna vulgaris	0	17	2
Carex caryophyllea	0	17	+
Scorzoneroides autumnalis	0	17	+
Armeria maritima	0	8	+
Briza media	0	8	1
Carex panicea	0	8	4
Deschampsia cespitosa	0	8	+
Juncus articulatus	0	8	+
Linum catharticum	0	8	+
Sonchus oleraceus	0	8	+
Higher plants	–	100	18
Bryophytes	–	100	3
Bare limestone	–	100	41
Bare soil/gravel	–	100	38

skeletal soils but abundant on the surrounding limestone grassland (e.g. *Carex flacca*, *Succisa pratensis*, *Gentiana verna*, etc.). Only a handful of associates were entirely restricted to skeletal soils (*Anagallis arvensis*, *Erophila verna*, *Minuartia verna*, *Saxifraga tridactylites*, *Sedum acre*). Ecologically the majority of associates were small hemi-cryptophytes (*n* = 23) with smaller numbers of chamaephytes (*n* = 7 including *A. norvegica*) and therophytes (*n* = 4). These comprised 59 per cent (±3), 37 per cent (±3) and 2 per cent (±1) of the total species present in the smaller quadrats respectively.

Forty-nine species were recorded in the larger (1m^2) quadrats. The average number of associates (14 ±1) was higher than for both Scottish sites for subsp. *norvegica* (12 ±0.8) and English sites for subsp. *anglica* (11.5 ±0.6) though not significantly so (ANOVA F = 1.68, P = 0.193). The most frequent were also common associates within the smaller quadrats (*Agrostis capillaris*, *Festuca ovina*, *Plantago maritima*, *Thymus polytrichus*) with the exception of a few species that were more typical of the adjacent grass-heath (*e.g. Carex flacca*, *Lotus corniculatus*, *Succisa pratensis*, *Viola riviniana*). The larger quadrats also contained many species absent from skeletal

Figure 3a

Figure 3b

Figure 3c

Figure 3d

Figure 3a-d. Habitats of *Arenaria norvegica* subsp. *norvegica* in the Burren: (a) close-up of plant amongst bare soil, limestone gravel and *Thymus polytrichus;* (b) gravelly soils on flat limestone exposure; (c) gravelly soils in shallow solution hollows to the rear of limestone pavement (centre of photograph); (d) limestone exposures on the 'green' road where *A. norvegica* was re-discovered in 2008.

soils (*e.g. Achillea millefolium*, *Calluna vulgaris*, *Dryas octopetala*; Table 1). The most abundant species were *A. capillaris* and *F. ovina* whereas only three other species exceeded 1 per cent cover (*Carex flacca*, *C. panicea*, *Calluna vulgaris*).

Vegetation communities

The majority of plants of *Arenaria norvegica* occurred on bare gravely soil within a matrix limestone grassland and bare limestone. This grassland bears closest similarity to the *Antennaria dioica-Hieracium pilosella* nodum of the Bromion erecti previously described for the Burren by Ivimey-Cook and Proctor (1966). This is one of the richest grasslands in the Burren and differentiated from the closely related *Dryas octopetala-Hypericum pulchrum* association by the presence of five species, four of which were recorded growing with *A. norvegica* (*Anthyllis vulneraria*, *Bellis perennis*, *Centaurium erythraea*, *Hieracium pilosella*), and the abundance of *Helianthemum oelandicum*, that was recorded in a quarter of the samples (Table 2). The open therophyte community on bare gravels to which *A. norvegica* was confined has not been described for the Burren but most closely resembled OV37 *Festuca ovina-Minuartia verna* metalophyte and OV39 *Asplenium trichomanes-A. ruta-muraria* crevice communities of the British National Vegetation Community (Fig. 4). The weaker association with acid and calcareous grassland types (i.e. U1, CG1, 8, 9 & 10) clearly reflected the abundance of *Festuca ovina* on bare gravels and the inclusion of 'islands' of the adjacent grass-heath in the larger quadrats.

The similarity between the vegetation of British and Irish sites for both subspecies is shown in Figure 5. On the first axis quadrats were clearly grouped in relation to geology with Irish quadrats being closest to those of subsp. *anglica* in Yorkshire. In comparison all Scottish sites had similar scores of the first axis but were clearly differentiated on the basis of geology on the second. Quadrats on basalts (Eigg, Beinn

Figure 4 (right). The British National Vegetation Classification (NVC) communities in which *Arenaria norvegica* occurs in the Burren, Co. Clare. For each community the '% goodness-of-fit' was calculated by taking the average of the top 5 'best-fits' produced for each quadrat (*n* = 12). The total number of 'best fits' was therefore 60. Four communities with only one best fit are excluded (% best-fit in parentheses): U4c (26), U5c (12), CG 4 (26), OV34 (15). Codes for NVC communities are as follows: CG1 – *Festuca ovina-Carlina vulgaris* grassland; CG4 – *Brachypodium pinnatum* grassland; CG8 – *Sesleria albicans-Scabiosa columbaria* grassland; CG9 - *Sesleria albicans-Galium sterneri* grassland; CG10 – *Festuca ovina-Agrostis capillaris-Thymus praecox* grassland; OV34 – *Allium schoenoprasum-Plantago maritima* community; OV37 – *Festuca ovina-Minuartia verna* community; OV39 – *Asplenium trichomanes-A. ruta-muraria* community; U1 – *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland; U4 – *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland; U5 – *Nardus stricta-Galium saxatile* grassland.

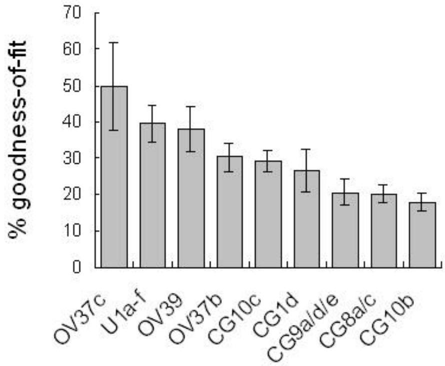
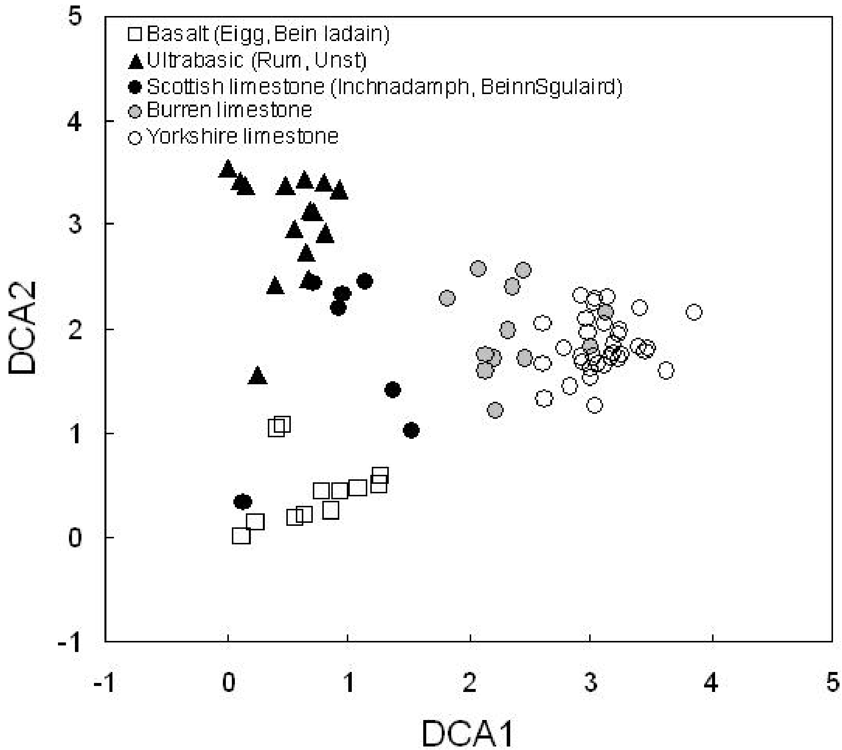


Figure 5 (below). Ordination plot (Detrended Correspondence Analysis) of British and Irish *Arenaria norvegica* quadrats in relation to geology (*n* = 80). Sites are grouped by geology (number of quadrats in parentheses): *basalt* – Eigg (2), Beinn Iadain (10); *ultrabasic* – Rum (12), Unst (3); *Durness limestone* – Inchnadamph (6), Beinn Sgulaird (1); *Carboniferous limestone* – Burren (12), Yorkshire (34). Eigenvalues for the first two axes (shown) were 0.68 and 0.43 respectively. Species-cover data were square-root transformed prior to analyses.



Iadain) and ultrabasic rocks (Rum, Unst) formed the most distinct clusters whereas vegetation on the Durness Limestone (Inchnadamph) was more variable with similarities to all three groups. A single quadrat recorded on limestone on Beinn Sgulaird was rather surprisingly grouped with the basalts of Beinn Iadain.

The mean Ellenberg scores (Hill, Preston and Roy 2004) for the smaller quadrats were high for light (7.6 ± 0.06) and reaction (5.9 ± 0.08) and low for both moisture (4.5 ± 0.06) and nitrogen (2.5 ± 0.05) indicating a open, xerophytic conditions with high pH and low fertility. The mean values for the larger quadrats were significantly lower for light (L = 7.3 ± 0.04; t = -1.29, P = 0.004, *d.f.* = 65) and significantly higher for moisture (F = 4.9 ± 0.1; t = -3.55, P = 0.002, *d.f.* = 22) presumably because they included species more typical of the adjacent grass-heath (*e.g. Achillea millefolium, Prunella vulgaris*). Values for R (5.9 ± 0.07) and N (2.7 ± 0.08) were not significantly different from the smaller quadrats.

Morphology and ecology

Irish plants resembled Scottish subsp. *norvegica* in having small flowers (<10 mm) with 4 styles and obovate leaves (the flowers of subsp. *anglica* are >11 mm across, with 3 styles and the leaves are narrowly ovate; Stace 2010). The leaves were characteristically succulent, glossy-green with an indistinct midrib and a few basal cilia (those of Ben Bulben *Arenaria ciliata* subsp. *hibernica* have a distinct mid-rib and hairs that extend for greater than a third of the length of the leaf). The average width of Irish plants was also well within the range of Scottish subsp. *norvegica* (Fig. 6a) being most similar to plants on limestone in Inchnadamph but significantly larger than those in Argyll and Yorkshire and significantly smaller than those on Rum (Fig. 6b).

However, there were notable differences between Irish and Scottish subsp. *norvegica*. Irish plants appear to flower about a month earlier than in Scotland (by June most had dehisced capsules containing seed). The flowers were also noticeably smaller although the total number of inflorescences produced was the highest of all populations surveyed (7.8 ±1) though not significantly more so than plants on Rum (Fig. 6b). Although Irish plants displayed the characteristic trailing habit of Scottish *norvegica* the leaves were noticeably smaller (2.5-4 mm) and more obovate. The reasons for these differences in morphology and performance would warrant further investigation given the highly disjunct position of the Irish population.

Discussion

Although the Irish population is much removed from the nearest stations in Britain, the generally scattered distribution of *Arenaria norvegica* is not unusual for a European Arctic-alpine or Arctic-montane plant species and fits a pattern seen in many other members of this ecogeographic group. Widespread contiguous populations in either Arctic or Alpine regions, or both, are often supplemented by smaller outlying populations, most often in isolated mountain ranges or on exposed islands in the northern seas. This distribution pattern appears to be relatively recent in origin, however. Many Arctic-alpine/montane

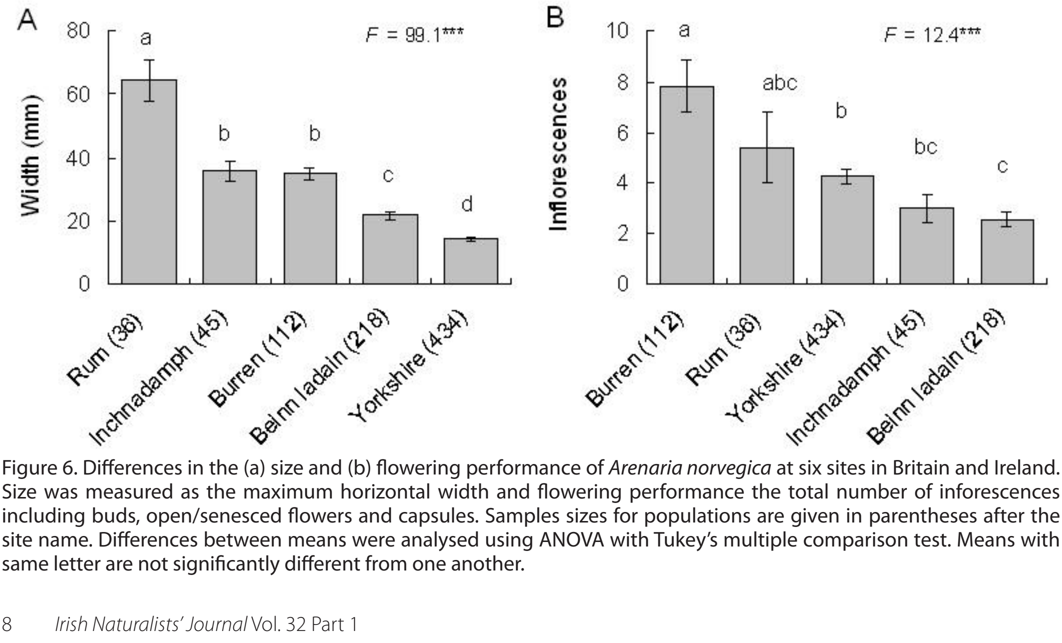


Figure 6. Differences in the (a) size and (b) flowering performance of *Arenaria norvegica* at six sites in Britain and Ireland. Size was measured as the maximum horizontal width and flowering performance the total number of inforescences including buds, open/senesced flowers and capsules. Samples sizes for populations are given in parentheses after the site name. Differences between means were analysed using ANOVA with Tukey's multiple comparison test. Means with same letter are not significantly different from one another.

taxa appear to have had wide distributions across the north European Plain until at least 18 000 years ago (Huntley and Birks 1993, Birks and Willis 2008), when the region was covered mostly by permafrost and tundra-like vegetation (Hewitt 1999). Paleoecological data indicates that when the regional climate began to moderate about this time (Dansgaard *et al*. 1993) the Arctic-alpine group of plants expanded northwards in the wake of retreating glaciers into present day Ireland, Britain and Fennoscandia, while populations in the more temperate southern lowlands either became extinct or underwent significant contraction and spatial fragmentation, eventually retreating to cold-climate 'islands' above the treeline in Alpine mountain ranges (Huntley and Birks 1983, Birks and Willis 2008).

This contraction in southern areas can be attributed to a number of climate-mediated environmental changes occurring through the period, including a regional increase in temperature and precipitation (Dansgaard *et al*. 1993, Mitchell and Ryan 1997), gradual increases in the structural complexity and biological activity of the soil substrate (Dimbleby and Mitchell 1965, Preece *et al*. 1986), and the parallel negative selective pressures arising from continuous northward immigration of temperate species from Mediterranean refugia in Iberia, Italy and the Balkans (Taberlet *et al*. 1998, Petit *et al*. 2002, Mitchell 2006).

In northern Europe the shallow free-draining sediments exposed in the wake of deglaciation initially presented ideal colonizing habitat for Arctic-alpines with exceptional tolerances for both cold temperatures and poor soil substrate (Dahl 1951). However, in time the successional pattern seen in southern areas was repeated in northern Europe also, and temperate species eventually came to dominate most lowland areas to the near total exclusion of the Arctic-alpine element.

In Ireland and Britain, aside from a temporary climate reversal during the Younger Dryas cold period from *c*.11-10 000 years ago, this progressive change in vegetation cover continued up to *c*.6000 years BP, by which time soils and plant communities had largely assumed their present day composition (Preece *et al*. 1986, Mitchell and Ryan 1997, Hewitt 1999, Mitchell 2006). It has only been in colder montane areas of the two islands, particularly in Scotland, that any vestige of a cold Pleistocene-like environment has persisted, and it is in these areas where the remnant Arctic-alpine or Arctic-montane elements are most common (Webb 1983, Preston *et al*. 2002, Birks and Willis 2008). Outside these montane areas, there are a small number of disjunct, mostly cliff-side locations where Arctic-alpines also persist, often at or near the sea coast (Preston *et al*. 2002, Birks and Willis 2008).

It is likely that following initial post-glacial immigration from the south, most of these populations have survived *in situ* since the late post-glacial period, where local conditions of extreme weather exposure and rudimentary soil development inhibited the development of more typical Holocene-era vegetation. Less probable, but not impossible, are more recent long-distance dispersal events from small sister populations many hundreds (or thousands) of kilometres distant (Webb 1983). A final possibility is that the *A. norvegica* population in the Burren (along with for example *Arenaria ciliata* in Ben Bulben and *Minuartia recurva* in Waterford and the south-west) predates the Pleistocene Glacial Maximum altogether, having survived *in situ* on ice-free mountain slopes since the Midlandian warm period *c*.35 000 years ago. Significantly, Colhoun *et al*. (1972) found fossil evidence for a diverse Arctic-Apline element in Co. Fermanagh dated to this period, including *A. ciliata*, *Dryas octopetala* and *Silene acaulis*, among others.

The re-discovery of *Arenaria norvegica* subsp. *norvegica* in the Burren, after an absence of 47 years, confirms the presence of this rare Arctic-montane sandwort in Ireland at its most southerly station in the world (53°N). The fact it has eluded botanists for so long is remarkable. The site is described in Charles Nelson's (1999) botanical guidebook of the area and so scores of very competent botanists must have missed it. An alternative explanation, given its presence on a track, is that this colony originated more recently. This could have arisen from seed transported by walkers or livestock from the original colony in a more remote location and that it then dispersed onto natural exposures on the surrounding limestone pavement. This is known to have occurred in at least two sites in Yorkshire where subsp. *anglica* colonised man-made habitats from natural populations within the vicinity (Walker 2000).

Even if further populations are discovered in the future, we will probably never know if this is the same site as the original locality. Heslop Harrison only realized the significance of his find on returning from a long day in the field and so the possibility that he or one of his students confused the locality details cannot be discounted. Unfortunately none of the group returned to confirm the locality or showed it to others in subsequent years. Another possible source of confusion might have been the poor quality of maps which were notoriously vague on place names in the 1960s. Furthermore, Webb and Scannell's (1983) rather pessimistic assessment that it "would take a dozen botanists…a week's hard work to demonstrate conclusively that the plant was absent" is unlikely to have inspired many botanists to go and search for it (although a few did). All these factors probably delayed its rediscovery and provide a salutary warning against declaring a species as 'extinct', even in such a well botanized area as the Burren, where one might have assumed it would have been relocated sooner.

The similarities between the Irish and Yorkshire habitats are striking and first alerted KJW to the plant's possible presence moments before its discovery. This similarity was confirmed by the vegetation analysis presented here (Fig. 5) and highlights the importance of the Irish population which is currently the only population of subsp. *norvegica* on Carboniferous limestone. Like the Yorkshire plant it occurs on tracks where it is likely to be dispersed by walkers. The differences in the morphology and flowering behaviour of Scottish and Irish populations warrants further investigation to assess whether they have a genetic base or are environmentally induced. Analyses of the genetic relationships between British, Irish and European populations are currently being undertaken by some of us (EH-W and CM) and will hopefully help to elucidate the post-glacial history of this species, in particular whether it arrived in Ireland by direct overland migration from Northern Europe or survived *in situ* in areas free from ice.

The rediscovery of *A. norvegica* in Ireland adds further weight to the outstanding phytogeographical importance of the Burren. This is recognized internationally by its designation as a Special Area for Conservation mainly for its limestone pavement, itself a priority habitat under the EU Habitats and Species Directive. The ecological findings for *A. norvegica* in the Burren presented here are timely, as the ongoing decline in seasonal grazing on winterages is encouraging the spread both of hazel scrub and deeper soils on the margins of bare limestone pavement. Given the soil habitat preference of *A. norvegica* and its associates, this could present a significant conservation challenge in the future.

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