The distribution, ecology and conservation of *Arenaria norvegica* subsp. *anglica* Halliday (Caryophyllaceae)

K. J. WALKER

I.T.E., Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire, PE17 2LS

ABSTRACT

Arenaria norvegica subsp. *anglica* is endemic to the Craven area of Mid-west Yorkshire (v.c. 64) where it grows exclusively amongst limestone fragments (clitter) and in shallow solution hollows with a thin covering of soil on level or slightly inclined limestone exposures. Since its discovery at Ribblehead in 1889 over 20 populations have been found, all but one of which occurs on the eastern slopes of Ingleborough. Over 70% of the entire population, of around 2000–3000 plants, occurs within two adjacent pastures where numbers are apparently stable. However, subsp. *anglica* has declined on tracks and bridleways where it was first recorded over 100 years ago. Although colonies within pastures appear to have fared better, their frequent small size (less than 50 plants) makes populations susceptible to drought and disturbance. The current rarity of subsp. *anglica* owes more to climate change (contraction of habitat) and aspects of its autecology (limited seed production and dispersal) rather than human activities. However, grazing and recreational disturbance still threaten some populations. As a result conservation measures are being introduced in order to reduce grazing levels and protect sensitive trackside populations. In addition, the creation of "safesites" and collection of seeds for genebanking will ensure its ultimate survival.

KEYWORDS: taxonomy, population size, rarity, habitat management, Yorkshire.

INTRODUCTION

Arenaria norvegica Gunn., Arctic Sandwort (Caryophyllaceae, Subfamily Alsinoideae), is an arctic-montane therophyte which occurs in Iceland, Norway, Sweden, Finland, Shetland and north-west Scotland. Two subspecies occur in the British Isles (Fig. 1): *A. norvegica* subsp. *norvegica*[1] is a plant of base-rich screes, river shingle and fell-field, confined to a small number of sites in Scotland (Beinn Iadain, v.c. 97; Beinn Sgulaird, v.c. 98; Rum and Eigg, v.c. 104; Inchnadamph, v. c. 108; Unst, v.c. 112) and one somewhat problematical site in the west of Ireland (Gleninagh Mountain, v.c. H9), where it may be extinct (Webb & Scannell 1983). *A. norvegica* subsp. *anglica* Halliday, English Sandwort, (*Arenaria gothica* auct., non Fries hereafter referred to as subsp. *anglica*) appears to be endemic to England occurring in only two 10 km squares in the Craven region of Mid-west Yorkshire (v.c. 64). This subspecies can be distinguished from subsp. *norvegica* by its often annual (rarely biennial) habit, somewhat larger flowers, laxer habit, greater ciliation (especially on the base of the sepals) and narrower, more lanceolate leaves (Halliday 1960b).

Subsp. *anglica* is an undoubted Yorkshire speciality which has attracted many generations of botanists to the area, not least because it shares its habitat with a number of other rarities (e.g. *Minuartia verna* and *Sedum villosum*). The population in Craven, which is in the order of (1000–) 2000–3000(–4000) plants, is confined to the Carboniferous limestone outcrops on the eastern slopes of Ingleborough (Walker 1995). Remarkably there is only one very small population outside a restricted (5 km square) area, despite the occurrence of suitable habitat elsehwere. As a result it is now recognised as "endangered" (Hodgetts *et al.* 1996) and afforded full protection under Schedule 8 of the *Wildlife and Countryside Act* (1981).

This paper describes the history of the plant in Britain, in terms of its taxonomy, distribution and status. Information on aspects of its ecology are also presented, and are discussed in relation to rarity as well as conservation measures proposed within a recent action plan (Walker & Corkhill 1996).

[1] Nomenclature follows Kent (1992) for vascular plants and Smith (1978) for bryophytes.

TAXONOMY

Arenaria norvegica is included within the *Arenaria ciliata* L. complex, a polymorphic taxon incorporating a number of closely related montane plants with highly disjunct distributions stretching some 40° from northern Spain to 82° north in the Arctic. The taxonomic history of this complex is very confused, with up to four species and seven geographically distinct subspecies being recognised (Chater & Halliday 1993).

Subsp. *anglica*, in particular, formerly posed a number of taxonomic problems for British botanists. On discovery in July of 1889 it was initially thought to be a form of *A. ciliata*, although it was later confirmed by F. A. Lees and Professor C. C. Babington as *A. norvegica* Gunnerus (Rotheray 1889b). At the time this species was known from only two sites in the British Isles; on Unst where it had been known of since 1837 and in West Sutherland on the Scottish mainland where it had been recently discovered (Scott & Palmer 1987). However, a number of botanists who were familiar with the Scottish plants, including J. Gilbert Baker of Kew, commented on the laxer habit, narrower leaves and differing shoot structure of the "Yorkshire sandwort" (Baker 1889). After visiting the Ribblehead populations in September of 1889 both Baker and Lees began to doubt these earlier determinations, particularly Lees who suggested that the Yorkshire plants may represent an "altered form" of *A. norvegica* (Rotheray 1889b). As a result he sent specimens to William Whitwell and Arthur Bennett who had a small collection of European *Arenaria* material sent to him by Nilsson in 1882.

After comparing these with Lees' plants and Fries' original descriptions Bennett concluded that the Ingleborough plant was in fact *A. gothica* Fries (Rotheray 1889b; Bennett 1891), a very rare plant of dry limestone habitats and lake shores in southern Sweden (Västergötland), Gotland and the Swiss Jura (Lac de Joux) (Williams 1898; Albertson 1946). The Ribblehead population represented a notable extension of its curiously disjunct European distribution although both Bennett and Baker thought that its true place was with *A. norvegica* either as a subspecies of *A. ciliata* or as a variety (Baker 1889; Bennett 1891).

Despite these misgivings botanists remained faithful to Bennett's determination until Halliday's study of the *A. ciliata* complex in the late 1950s (Halliday 1960a). Using a variety of techniques Halliday showed the Yorkshire plants to have a greater affinities to *A. norvegica* than either the Swedish or Jura *A. gothica* and remarked that "apart from differences in habit, the British plant is closer to *A. norvegica* in most other respects, in particular in leaf shape, colour, ciliation and inflorescence size" (Halliday 1960a). Furthermore, British plants were diploid ($2n = 80$; Swedish plants $2n = 100$), could interbreed freely and produce fertile seeds whereas seed production declined in Swedish × English hybrids (Halliday 1958, 1960a, b). On this basis Halliday concluded that the English plant was better placed under *A. norvegica* and proposed two geographical subspecies: *A. norvegica* subsp. *norvegica* and *A. norvegica* subsp. *anglica*, "taxa sufficiently distinct morphologically and geographically separated but capable of interbreeding freely and with a common origin" (Halliday 1960a). Subsequent taxonomic work on the *A. ciliata* complex has supported this division (Wyse-Jackson & Parnell 1987). In this study the two subspecies were shown to be closely related and distinct from all the other European members of the complex, including both *A. ciliata* s.s. and *A. gothica*.

DISTRIBUTION

HISTORICAL RECORDS: 1889–1980

Subsp. *anglica* was originally discovered by Lister Rotheray at Ribblehead Station, near Ingleborough, on 12 July 1889 where it was growing "in some profusion" amongst limestone "staging" on a recently constructed track (Rotheray undated, 1889a, b; Whitwell 1889). F. A. Lees who visited the site soon after located hundreds of plants, including a new population growing "300 and 400 yards [350 m] away" from the original colony on the opposite side of the railway line (Whitwell 1889). Its occurrence on a man-made track initially raised doubts as to whether the plant was native (Baker 1889; Whitwell 1889; Bennett 1892). However, the use of local stone for track-building led Lees and J. G. Baker to predict its presence on "the neighbouring hills" (Baker 1889; Whitwell 1889). Indeed a small population was discovered on a track at Selside in the

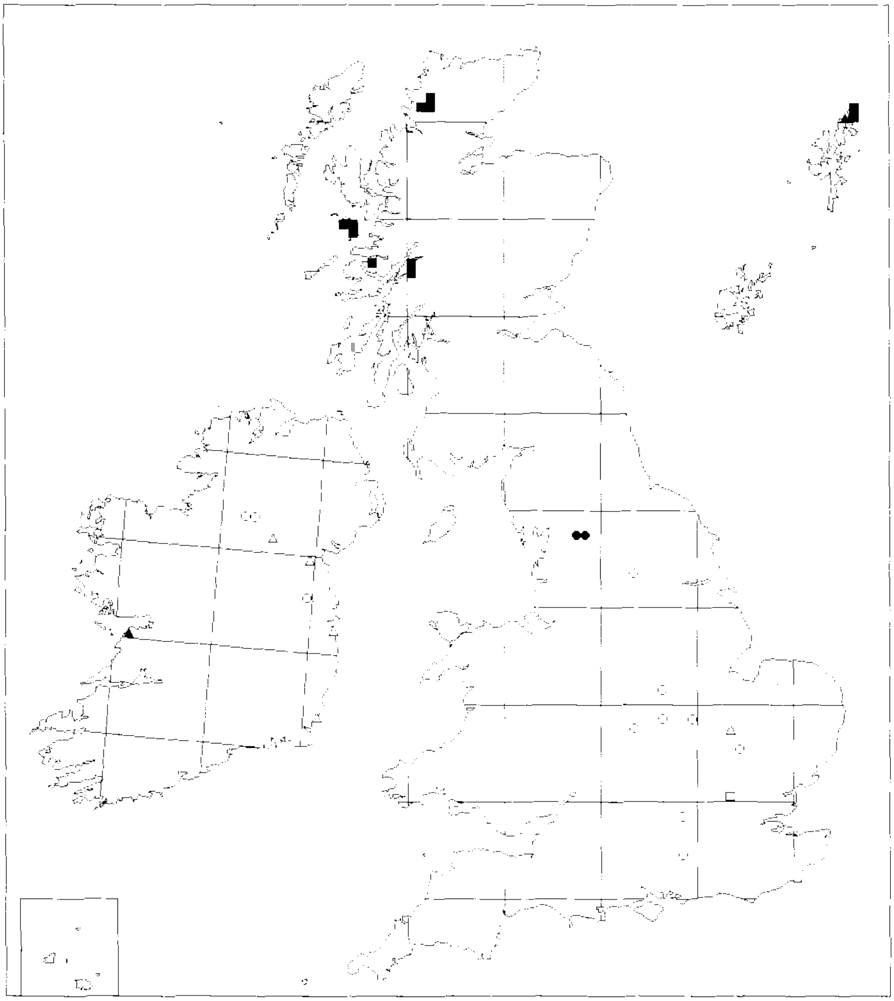

FIGURE 1. The past and present distribution of *Arenaria norvegica* subsp. *norvegica* (■ 1970 onwards; ▲ pre-1970) and subsp. *anglica* (● 1970 onwards) in the British Isles. Sites where undetermined fossil seeds of *A. ciliata* agg. have been found are indicated as follows: △ late Devensian/Flandrian, □ mid Devensian, ○ early Devensian.

following August and as a result botanists began to search more widely (Whitwell 1890). Then in September of 1894 Reginald J. Farrer, the famous plant-collector of Ingleborough Hall, reported its presence at "Sulber Nook" [Nick], in a spot so remote as to confirm its native status (Farrer 1894; Rotheray 1895). Several more populations were found by him in the following year, all of which occurred on or adjacent to the Clapham Lane, a popular bridleway connecting Selside and Crummack Dale (Whitwell 1890, 1895; Rotheray 1895). Farrer communicated these new finds to Rotheray who promptly visited the following August. His account of this trip gives a good indication of the numbers and location of plants as well as describing a number of populations which were undoubtedly new to Farrer (Rotheray undated).

An intriguing record was the discovery by Farrer of a small population within the grounds of his own residence, Ingleborough Hall, some 9 km from Ribblehead (Whitwell 1895). Given the numbers of alien plants which have been found in the vicinity in recent years (Abbott 1996) one wonders whether such a keen plant-collector could have moved it there?

Although Rotheray and Farrer undertook extensive searches of the Craven limestones over subsequent decades no new populations were found until the 1950s when Halliday discovered a small colony close to Farrer's original Sulber Nick site (Halliday 1960a). A number of other populations were discovered by Bartley & Clark (1978) who were the first to describe the extensive flush population within Sulber pasture (refound in 1993), and the two outlying colonies to the south-east; at Foredale, in a disused quarry, and close by on pavement at Juniper Gill.

To date the only verified record away from the eastern slopes of Ingleborough is the small trackside colony at Dawson Close which was discovered by Ruth Kilby during a Yorkshire Naturalists' Union field excursion in 1952 (Sledge 1952). This site on the northern slopes of Fountains Fell was a notable extension in range, some 6 km to the east of the nearest Ingleborough population. Further afield Lees' (1937) unconfirmed report of having "picked up two or three specimens from a limestone-metalled road near Healuagh" (Swaledale) in 1906 is conceivable given the transport of Ingleborough limestone for track-building, although this population has never been relocated. Most unlikely is Arthur Bennett's claim of having found a fragment of *A. gothica* whilst collecting *Potamogeton obtusifolius* from Grasmere (Cumbria) given the absence of suitable habitat within the vicinity (Halliday 1960a).

CURRENT DISTRIBUTION AND STATUS

Since 1981 staff of the Nature Conservancy Council (and latterly English Nature) have carried out a number of detailed population censuses of all extant populations (Table 1). In 1995 all these sites were visited by the author and extensive searches made of the neighbouring limestone pastures (Foley 1995; Walker 1995). The results of these surveys have given a much clearer indication of the plant's distribution and abundance. However, given the discovery of at least eight new populations over the last half century, one of which is situated some 6 km to the east of Sulber, it is not inconceivable that subsp. *anglica* may well await discovery elsewhere in Craven.

In 1995 over 2700 plants were recorded in approximately 20 colonies within eleven 1 km squares. Over 70% of the total population (Table 1; populations 2–7 & 8–14) occurred within two adjacent pastures at Sulber on the eastern slopes of the Ingleborough massif (Walker 1995). Here a series of loosely connected populations are confined to shallow soils on limestone exposures, flushes and rough tracks all of which occur on or within 500 m of the Claphman Lane. Elsewhere small populations occur by tracks, at Dawson Close and Selside, in a disused quarry at Foredale and on limestone exposures at Juniper Gill and Thieves' Moss.

Although overall populations sizes are small (mean 143 ±43; n = 18) these vary consistently by habitat. Trackside populations are by far the smallest (mean 16 ±4; n = 6) and only account for 3% of the total population. As a result these populations are vulnerable to trampling and drought which presumably caused the localised extinction of subsp. *anglica* at Selside and Sulber Nick in 1992. Populations on gently inclining pavement, which account for 53% of the entire population, are much larger (mean 161 ±54; n = 9) and apparently less prone to fluctuations in overall numbers (Table 1). In contrast the two flush colonies at Sulber, which alone account for over 40% of the entire population, show marked fluctuations in numbers from year to year presumably due to the ephemeral water-supply within spring-fed flushes.

CHANGE SINCE 1889

The distribution of subsp. *anglica* has changed little since it was discovered in 1889 and it can still be found in the localities described by Rotheray and Farrer over a hundred years ago. Extinction has occurred in only two sites; in Spring Valley at Ingleborough Hall (where it may have been introduced) and at Ribblehead, where over-collecting led to its demise within two years of discovery (Whitwell 1890). Rotheray's accounts and the results of recent surveys suggest that it has also been lost, or declined, from numerous sections of the Clapham Lane, particularly those which traverse Sulber and the adjacent Borrin's pasture (Rotheray undated; Whitwell 1895).

The most likely cause of decline is presumably the increased recreational usage of tracks within the Sulber area over the past century. Since the opening of the National Park in 1953 visitor numbers have increased dramatically, particularly at Ingleborough where there are now around 250,000 visitors annually (S. Rogers, pers. comm., 1995). This is undoubtedly due to the increasing popularity of the Three Peaks footpath which passes directly through Sulber Nick (and a number of populations of subsp. *anglica*). This figure is likely to increase further when the Clapham Lane is incorporated into the "Pennine Bridleway", a new long-distance routeway designed to cater for walkers, horse-riders and cycling enthusiasts.

TABLE 1. HISTORICAL AND CENSUS RECORDS FOR EXTANT *ARENARIA NORVEGICA* SUBSP. *ANGLICA* POPULATIONS.

No.	Site name	Habitat	1890s	1950s	1978[6]	1981[7]†	1985[8]	1990[9]	1992[10]	1993[11]	1994[12]	1995[13]
1	Selside (Font Green)	Track	"abundant"[1]			c.30	7	0	0	2	8	8
2	Sulber pasture (below flush)	Flush										23
3a	Sulber pasture	Pavement			P	c.50	170	89	5	158	146	214
3b-g	Sulber pasture ("valley")	Flush			P					1392	nv	611
4	Sulber Nick (Halliday's)	Pavement		24[4]					5	85	nv	13
5	Sulber Nick (sheep-track)	Pavement										59
6	Sulber Nick (west)	Pavement								50-60	nv	187
7	Sulber Pot	Pavement	"plentifully"[1]			100s	148	316	91	138	380	151
8	Thieves' Moss	Pavement							1	41	8‡	3
9a	Sulber Nick-Clapham Lane	Track	"twos & threes"[2]			c30	?	9	0	0	?	15
9b-d	Sulber Nick (flush)	Flush	"scanty nos"[3]			300+	112	481	184	1238	920	452
10	Clapham Lane (gate)	Track	"small nos"[2]			100s	172	41	5	10	nv	33
11	Clapham Lane (cross-road)	Track				5	3	3	1	0	11‡	12
12	Clapham Lane (Long Scar)	Track	"few plants"[2]			35	55	39	18	30	nv	21
13	Crummack Dale	Pavement				c.200	190	65	69	98	nv	455
14	Clapham Bottoms	Pavement				500+	51	156	17	431	418	356
15	Foredale Quarry	Quarry floor			P	c.335	46	nv	0	286	nv	88
16	Dawson Close	Track		P[5]		c.25	30	nv	5	14	3‡	8
17	Juniper Gill	Pavement			P							8§
18	Scar Close (introduction)	Pavement								12	nv	0

NOTES: † Figures based on estimates of plant numbers. Surveyed by; § P. Corkhill & N. Asbey, ‡ M. J. Y. Foley (1995). "nv" not visited. "P" present.
SOURCES: 1. Whitwell (1895), 2. Rotheray (undated), 3. Rotheray (1895), 4. Halliday (1960a), 5. Sledge (1952), 6. Bartley & Clark (1978), 7. Blakemore (1981), 8. Wilson (1986), 9. Taylor (1990), 10. Morley (1992), 11. Daniels (1993), 12. Daniels (1994), 13. Walker (1995).

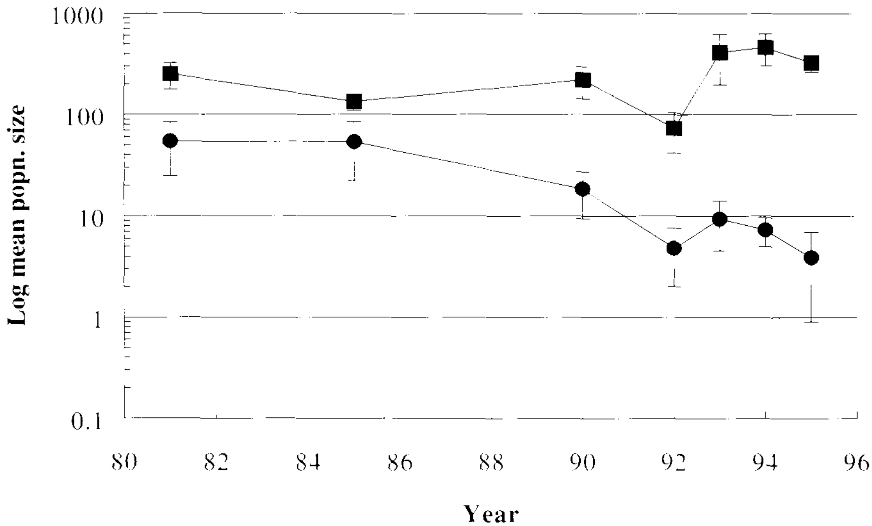

FIGURE 2. Changes in the mean numbers of plants of *Arenaria norvegica* subsp. *anglica* on: a. tracksides (●) (populations 1, 9a, 10, 11, 12 & 16) and b. limestone pavement/flush habitats (■) (populations 3a, 7, 9b–d, 13 & 14).

In contrast, populations on "primary" habitats, such as limestone pavements and flushes appear to be steadily increasing (Fig. 2). The extent to which this is a result of more information or relaxation in grazing pressure is unclear. In the past overgrazing has presumably reduced plant numbers, particularly in the Sulber pastures where census returns have shown a tripling in sheep numbers this century (from around 13,000 to just over 35,000 in 1989; P. Corkhill, pers. comm., 1995). Although stock are important in maintaining open conditions and transporting seed, excessive defoliation and trampling by stock has been observed to cause some mortality, especially around the edge of flushes where grazing is particularly intense (Walker 1995).

ECOLOGY

HABITAT, SOILS AND CLIMATE

Subsp. *anglica* is a plant of shallow skeletal soils (lithomorphic protorendzinas) on sparsely-vegetated level or slightly inclined limestone exposures. Here plants grow amongst limestone fragments (clitter) and in shallow solution hollows with a thin covering of soil. At one site it also grows directly on tufaceous "crusts" (hydromorphic gleys) which have developed on flat or gently sloping limestone slabs around the edge of flushes and seepage lines. In addition, it has been long established within "ruts" of trackways and amongst shattered limestone on a quarry floor. Recently it has also been observed on disturbed rabbit scrapes (Walker 1995).

In all of these habitats soils are shallow (usually <7 cm), circumneutral (mean pH of 7·59 ± 0·06 n = 37), with both high levels of calcium (>30 mg Ca 100 g^{-1}) and organic material (mean 67% ± 2). In most habitats moisture supply is limited and unpredictable and as a result populations are small and sparsely distributed. In contrast, where water-supply is more predictable, i.e. around the edges of flushes and springs, populations are larger and numbers less variable from year to year.

The altitudinal range of populations is between 310–390 m (see Appendix). Here the climate is distinctly oceanic with rainfall being uniformly high (average of 1590 mm yr^{-1}; 1981–95) tending towards a spring minimum and autumn maximum. At this altitude the growing season (accumulated temperatures >6°C) lasts for 5–6 months (April to September) and the distribution of the plant appears to be limited to areas where the oceanic influence ensures that the summer temperatures do not exceed 23°C (Dahl 1951).

TABLE 2. SPECIES ASSOCIATED WITH *ARENARIA NORVEGICA* SUBSP. *ANGLICA* IN NON-FLUSHED, FLUSHED AND DISTURBED SITES.

Species	Frequency (n = 43)	Mean abundance	Non-flushed‡ (n = 21)	Flushed (n = 19)	Disturbed (n = 3)
Arenaria norvegica subsp. *anglica*	43	2·2	V(1–3)	V(1–4)	V(1–3)
Festuca ovina agg.	42	5·1	V(3–7)	V(2–8)	V(5–7)
Linum catharticum	42	1·3	IV(1–3)	V(1–3)	IV(2)
Sesleria caerulea	34	2·5	V(1–5)	V(1–7)	II(3)
Minuartia verna	33	1·8	V(1–4)	IV(1–3)	II(2)
Ctenidium molluscum	27	1·4	IV(1–5)	III(1–4)	IV(1)
Thymus polytrichus subsp. *britannicus*	26	1·3	IV(1–4)	III(1–4)	V(5)
Carex panicea	25	1·7	II(1–2)	V(1–5)	V(4–6)
Briza media	22	1·0	III(1–3)	III(1–3)	V(1–4)
Tortella tortuosa	22	1·7	IV(1–7)	II(1–4)	II(1)
Agrostis capillaris	16	1·1	III (1–4)	II(1–4)	II(4)
Koeleria macrantha	15	1·0	II(1–4)	II(3–5)	
Euphrasia officinalis s.l.	14	<1·0	I(1–3)	II(1)	IV(1–2)
Carex caryophyllea	10	<1·0	III (1–4)		II(6)
Plantago lanceolata	10	<1·0	I(1)	II(1–2)	V(2–4)
Cerastium fontanum	9	<1·0	II(1–3)	I(1–2)	II(1)
Schistidium apocarpum	9	<1·0	II(1–4)	III(1–4)	
Juncus articulatus	9	<1·0	I(3)	II(1–2)	
Prunella vulgaris	8	<1·0	I(1)	I(1)	V(2–3)
Taraxacum officinale s.l.	8	<1·0		II(1)	IV(1)
Hypnum cupressiforme	7	<1·0		I(1)	
Sedum villosum	7	<1·0	I(1)	I(1–2)	II(1)
Potentilla erecta	6	<1·0	II(1–3)	I(1)	II(5)
Sagina nodosa	6	<1·0	I(1–3)	I(1)	II(2)
Viola riviniana	6	<1·0	I(1)	I(1)	II(1)
Bellis perennis	5	<1·0	I(1)	I(1)	V(1–2)
Carex viridula subsp. *oedocarpa*	5	<1·0		II(2–5)	
Carex flacca	5	<1·0	I(1–3)	I(5)	IV(3)
Carex pulicaris	4	<1·0	I(1–2)	I(1)	II(1)
Cratoneuron commutatum	4	<1·0	II(1–7)		
Ranunculus bulbosus	4	<1·0		I(1)	V(1–2)
Agrostis canina	3	<1·0		I(2–3)	
Poa annua	3	<1·0	I(1)	I(3)	IV(1–2)
Bare soil	39	5·6	V(1–8)	V(4–9)	V(5)
Bare limestone	36	4·9	V(1–9)	IV(1–8)	II(5)
Limestone gravel (<10cm)	33	3·0	IV(3–8)	IV(1–5)	IV(1)
Limestone gravel (>10cm)	24	2·4	IV(1–7)	IV(1–9)	
Faeces (rabbit/sheep)	11	0·3	II(1–3)	I(1)	IV(1)

Notes: ‡ Frequency classes: I = 0–20%; II = 20–40%; III = 40–60%; IV = 60–80%, V = 80–100%. Additional species in <2 quadrats: Non-flushed: *Antennaria dioica*, *Cirsium* sp., *Dicranum scoparium*, *Drepanocladus revolvens*, *Erophila verna*, *Galium sterneri*, *Lotus corniculatus*, *Polytrichum juniperinum*, *Pseudoscleropodium purum*, *Vulpia bromoides*. Flushed: *Bryum argenteum*, *Plantago media*, *Primula farinosa*, *Racomitrium lanuginosum*. Disturbed: *Achillea millefolium*, *Ajuga reptans*, *Cardamine pratensis*, *Hypericum montanum*, *Polygala vulgaris*.

However, drought can have a devastating effect on plant numbers as in 1992 where low spring rainfall (83 mm for May and June as opposed to an average of 163·5 ± 16·6 mm between 1981–1995) caused a number of localised extinctions (Fig 2.). As a result subsp. *anglica* is most frequently found within sheltered microtopographichal niches (e.g. rock fissures, moss cushions, solution cups etc.) where water-loss and exposure to extreme temperatures are reduced (Halliday 1960a).

VEGETATION

The habitat of subsp. *anglica* typically occurs as scattered "islands" of open ground, usually only a few metres in extent, within upland limestone pastures dominated by *Sesleria caerulea* (CG9; Rodwell 1992). Within this localised habitat subsp. *anglica* occurs within three closely related assemblages with differing microtopographic, edaphic and disturbance regimes (Table 2).

On non-flushed soils overlying gently inclining limestone exposures subsp. *anglica* occurs with a number of other diminutive species (e.g. *Minuartia verna*, *Sagina nodosa* and *Erophila verna*) on bare patches of soil/gravel amongst scattered clumps of *Festuca ovina* and *Sesleria caerulea*. Here vegetative cover rarely exceeds 30% and is characterised by the presence of stress-tolerants such as *Thymus polytrichus* and *Carex caryophyllea*.

On flushed soils and gravels vegetative cover is less fragmentary and more species-rich. Here the constants, *Sesleria caerulea*, *Festuca ovina*, *Minuartia verna* and *Linum catharticum* are joined by a number of species of moister soils most notably *Primula farinosa*, *Carex viridula* subsp. *oedocarpa* and *C. panicea*. Presumably this is the *Arenaria norvegica* subsp. *anglica* – *Sedum villosum* heath described by Bartley & Clark (1978) which they considered a transitional variant between the more species-rich flushes and the surrounding calcareous grasslands.

Subsp. *anglica* also occurs within a species-poor "disturbance" assemblage on tracks and rabbit scrapes. Here it is associated with ruderals of bare soils, such as *Prunella vulgaris* and *Poa annua*, and rosette-forming hemicryptophytes such as *Bellis perennis*, *Plantago lanceolata*, *Taraxacum officinale* and *Ranunculus bulbosus* which can tolerate heavy trampling pressure.

LIFE-CYCLE

Classified as an annual or biennial (e.g. Clapham *et al.* 1987), the majority of plants germinate in the autumn, over-winter as leafy shoots and flower and set-seed in the following spring or summer (winter annual) (Halliday 1960a; Walker 1995). Under exceptional circumstances plants have also been observed to flower and set seed within one season (summer annual) (Walker 1995), or survive two winters (biennial) (Halliday 1960a).

Throughout its life subsp. *anglica* is exposed to extreme variations in both temperature and moisture supply; as a consequence there is no general relationship between the time of flowering and season. This is achieved by the production of polycarpic shoots (cymes) which enable the plant to flower continuously (indeterminately) over an extended period. Thus although flowering typically takes place between early May and September, it is not uncommon to find plants flowering as late as December if conditions are favourable (Whitwell 1895). This trait (sometimes termed uniseasonal iteroparity) allows annuals such as subsp. *anglica* to avoid the potential dangers of synchronous flowering within an unpredictable habitat, and ensure that some seed is dispersed under favourable conditions (Harper 1977; Symonides 1988).

On average plants produce 2–3 hermaphrodite white flowers. As with many other members of the Alsinoideae, reproduction may be entirely autogamous (i.e. within the same flower) due to the automatic transfer of pollen between the homogamous reproductive surfaces. On maturity both the inner and outer whorl of anthers are forced into contact with the maturing stigmas ensuring that if they have not already been pollinated any remaining pollen grains are picked up (G. Halliday, pers. comm., 1998). In addition, plants which are artificially self-pollinated, and isolated from insect visitors with a fine muslin, are able to reproduce and set seed (Walker 1995). However, the production of obvious signals (simple white receptive flower, sweet scent) and rewards (nectaries) suggest that insects do visit the plant and that cross-pollination may take place.

Subsp. *anglica* produces relatively large seeds (0.8 × 0.9 mm), the tough black testa having numerous raised tubercles which presumably serve to reduce desiccation. The viability of fresh seed is usually very high, with over 90% germinating readily when placed on moist filter paper (S. Terry, pers. comm., 1995; Halliday 1960a). However, experimental studies carried out by the author have shown that germination declines with increased illumination and temperature, and at low moisture levels (Walker 1995). This suggests that optimal conditions for germination are in sheltered micro-sites where moisture supply is not limiting.

Capsules contain on average 3–4 seeds (mean 3·59 per capsule, n = 291) although under cultivation this can be much higher (Walker 1995; G. Halliday, pers. comm., 1998). After fertilisation it can take up to three weeks for the pericarp to split and reveal the seeds inside. Although some seeds are released at this stage the majority remain firmly attached by placentae to the capsule until detachment and decomposition of the pericarp on the surrounding soils. As a result dispersal is extremely limited and usually not more than a few centimetres from the parent plant. However, the presence of subsp. *anglica* on tracks, in particular the Clapham Lane and the outlying colony at Dawson Close, suggests that seed may be transported over greater distances, presumably within soil attached to humans, vehicles or sheep which are often "away-wintered" from the Sulber pastures (P. Corkhill, pers. comm., 1995; Sledge 1952). In addition, like *Thlaspi perfoliatum* it may have been widely dispersed within limestone ballast used in the construction of road and railways in the past (Rich *et al.* 1989). However, although both species are now well established on artificial sites (such as quarry floors, tracks and railway embankments) the lack of any specialised seed dispersal mechanisms means there is little tendency for further spread to occur.

Although experiments suggest that relatively few seeds are incorporated into the seed-bank, the sporadic reappearance of the plant within a number of trackside sites suggest that some seed may persist for short periods.

CONSERVATION

It seems likely that subsp. *anglica* may well have evolved, through isolation, from a more widely distributed and variable population (Pigott & Walters 1954; Raven & Walters 1956). The occurrence of fossil seeds of *Arenaria* cf. *ciliata*, to which subsp. *anglica* undoubtedly belongs, within Mid- and Late Devensian deposits in the south and east of England and the east of Ireland suggests a much wider glacial distribution (Fig. 1). These species presumably survived the height of glaciation within periglacial refuges free of ice (i.e. unglaciated massifs, coastal areas) or on the periglacial "park-tundra" to the south of the ice limits (Godwin 1975). However, as a result of climatic changes during the post-glacial this once continuous lowland distribution has been restricted to a number of disjunct montane and coastal refugia where immature soils still persist (Godwin 1953; Rose 1957; West 1988).

Today the rarity of these habitats, as well as poor dispersal ability has presumably compounded this restriction in range. As such subsp. *anglica* is likely to remain extremely rare being restricted by biological and ecological factors rather than as a direct result of human activities.

CURRENT THREATS

Although there is no evidence for an overall decline in numbers this century many trackside populations have been lost or severely degraded as a result of the increased usage by walkers, "off-road" vehicles, scramble and mountain bikers. This has led to severe soil erosion and a decline in plant numbers at numerous sites along the Clapham Lane. In particular track-widening and shortcuts created by walkers threaten large colonies at Sulber Gate and Crummack Dale. At Selside, where the plant grows on the edge of a popular track leading to Alum Pot, car-parking has reduced numbers to the verge of extinction.

Many of the pastures in which the plant occurs were formerly overgrazed (sheep numbers tripled between 1940 and 1980). As a result sheep numbers have been reduced through management agreements since designation as a S.S.S.I. in 1986. However, many populations are still highly susceptible to disturbance caused by off-road vehicles.

There are no 20th Century reports of collecting of subsp. *anglica* and disturbance caused by visiting botanists is unlikely to pose a threat to many of the larger populations. However, smaller, more accessible colonies (some with less than ten plants) are extremely vulnerable to trampling, particularly at Selside which is frequently visited by botanists.

CONSERVATION MANAGEMENT

Subsp. *anglica* has been included within English Nature's Recovery Programme as a species considered to be in danger of extinction and requiring special conservation measures (Whitten 1990). As a result an action plan has recently been proposed in order to ensure its long term self-sustained survival in the wild (Walker & Corkhill 1996).

By the early 1990s all the sites in which subsp. *anglica* occurred received statutory protection either as part of the Ingleborough National Nature Reserve (N.N.R.) or as Sites of Special Scientific Interest (S.S.S.I.) (Ingleborough, Pen-y-Gent and Foredale Quarry). As a consequence grazing levels are now agreed with farmers (in some cases voluntarily under the Wildlife Enhancement Scheme), and ensure that sheep numbers do not exceed two ewes (and followers) per hectare throughout the year. In addition, one pavement on which the plant occurs (Juniper Gill) has been recently stock-proofed (P. Corkhill, pers. comm., 1995). The steady increase in plant numbers recorded within these pastures (Fig. 2) suggests that these measures are having favourable results.

In order to arrest the decline of subsp. *anglica* on vulnerable track-side localities a number of measures have been proposed. At Sulber Gate on the Clapham Lane a diversion of the Pennine Bridleway has been agreed with the Countryside Commission in order to protect a large colony. In addition, better way-marking of routes will reduce the numbers of "unofficial" paths which have appeared in recent years. At Selside limestone boulders have been placed around sensitive areas in order to discourage car-parking.

In the long term ex-situ measures, such as seed-banking and the establishment of populations in "safe-sites", will safeguard the plant from ultimate extinction as well as providing material for further research and public viewing. In 1992, 500 seeds were collected from two extant populations and are now held at the Royal Botanic Gardens Kew Seed Bank at Wakehurst Place. In the same year seed was also artificially introduced to Scar Close N.N.R. where it has apparently failed to establish. Introduction into further "safe-sites" is currently being discussed with a view to creating a public viewing facility in order to reduce pressures on extant populations (P. Corkhill, pers. comm., 1995).

In order to assess the success (or otherwise) of these management activities a sample of populations are being monitored every three years. The results of recent surveys suggest that the efforts of conservationists and landowners have ensured the survival of this endemic plant for many years to come.

ACKNOWLEDGMENTS

I am especially grateful to Peter Corkhill at Ingleborough without whose support and invaluable assistance this project would not have been possible. I would also like to thank Mike Foley, Barrie Goldsmith, Adrian Soames, Janet Terry and Peter Welsh for information and advice on various aspects of this work. Chris Preston, Geoffrey Halliday and Owen Mountford all made valuable comments on an earlier draft of this paper and Dave Roy at Monks Wood produced Fig. 1. Fieldwork was supported by grants from English Nature as part of the C-E-L Scheme and Species Recovery Programme.

REFERENCES

ABBOTT, P. (1996). Alien plants from Yorkshire. *BSBI news* **73**: 47.

ALBERTSON, N. (1946). Österplana hed. *Acta phytogeographica Suecica* **20**: 156.

BAKER, J. G. (1889). On the varieties of *Arenaria (gothica) ciliata*. *The naturalist* **14**: 337–339.

BARTLEY, D. D. & CLARK, S. C. (1978). *A vegetation survey of Ingleborough Site of Special Scientific Interest*. Unpublished report by the University of Leeds for the Nature Conservancy Council.

BENNETT, A. (1891). Notice of the occurrence of *Arenaria gothica*, Fries, in Great Britain. *Botanical Society of Edinburgh* **18**: 252–254.

BENNETT, A. (1892). *Arenaria gothica*. *Journal of botany* **30**: 86.

BLAKEMORE, J. (1981). *Survey of* Arenaria norvegica *subsp.* anglica. Unpublished report for English Nature.

CHATER, A. O. & HALLIDAY, G. (1993). *Arenaria* in TUTIN, T. G. *et al.*, eds. *Flora Europaea* **1**: 140–148, 2nd ed. Cambridge University Press, Cambridge.

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

DAHL, E. (1951). On the relation between summer temperature and the distribution of Alpine vascular plants in the lowlands of Scandinavia. *Oikos* **3**: 22–52.

DANIELS, A. C. (1993). *A survey of* Arenaria norvegica *subsp.* anglica *in the Ingleborough area in 1993*. Unpublished report for English Nature.

DANIELS, A. C. (1994). *A sample survey of* Arenaria norvegica *subsp.* anglica *in the Ingleborough area in 1994*. Unpublished report for English Nature.

FARRER, R. T. (1894). *Arenaria gothica*. *Journal of botany* **32**: 344.

FOLEY, M. J. Y. (1995). *Survey for* Arenaria norvegica *subsp.* anglica *Halliday (Caryophyllaceae) in the Ingleborough area, North Yorkshire*. Unpublished report for English Nature.

GODWIN, H. (1953). British vegetation in the full and late glacial periods, in LOUSLEY, J. E., ed. *The changing flora of Britain*, pp. 54–74. Botanical Society of the British Isles, Oxford.

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

HALLIDAY, G. (1958). The northern species of *Arenaria ciliata* complex and some interspecific hybrids. *Proceedings of the Botanical Society of the British Isles* **3**: 90.

HALLIDAY, G. (1960a) *Taxonomic and ecological studies in the* Arenaria ciliata *and* Minuartia verna *complexes*. Ph.D. thesis, University of Cambridge.

HALLIDAY, G. (1960b) The identity of *Arenaria gothica* auct. angl. *Watsonia* **4**: 207–209.

HARPER, J. L. (1977). *The population biology of plants*. Academic Press, London.

HODGETTS, N., PALMER, M. & WIGGINTON, M. (1996). *The pink book of plants. Lists of vascular and non-vascular plant species which are nationally threatened, localised or protected in Great Britain*. J.N.C.C., Peterborough.

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

LEES, F. A. (1937). The vegetation of Yorkshire and supplement to the floras of the County. *The naturalist* **62**: 233.

MORLEY, J. (1992). *Rare plant survey of* Arenaria norvegica *subsp.* anglica *in the Craven District of North Yorkshire*. Unpublished report for English Nature.

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.

RAVEN, J. & WALTERS, S. M. (1956). *Mountain flowers*. Collins New Naturalists Series, London.

RICH, T. C. G., KITCHEN, M. A. R. & KITCHEN, C. (1989). *Thlaspi perfoliatum* L. (Cruciferae) in the British Isles: distribution. *Watsonia* **17**: 401–407.

RODWELL, J. S. (1992). *British plant communities. Vol. 3. Grasslands and montane communities*. Cambridge University Press, Cambridge.

ROSE, F. (1957). The importance of the study of disjunct distributions to progress in understanding the British flora, in LOUSLEY, J. E., ed. *Progress in the study of the British flora*, pp. 61–78. Botanical Society of the British Isles, London.

ROTHERAY, L. (1889a). *Arenaria gothica* Fries, a plant new to West Yorkshire. *The naturalist* **14**: 314.

ROTHERAY, L. (1889b). The discovery of *Arenaria gothica* in West Yorkshire. *The naturalist* **14**: 335–339.

ROTHERAY, L. (1895). Further discoveries of *Arenaria gothica*. *The naturalist* **21**: 303–306.

ROTHERAY, L. (undated). *Botanical rambles: 1888–1900*. Photocopied manuscript held by the author.

SCOTT, W. & PALMER, R. (1987). *The flowering plants and ferns of the Shetland Islands*. The Shetland Times, Lerwick.

SLEDGE, P. (1952). Litton v.c. 64, June 14th: flowering plants. *The naturalist* **72**: 179.

SMITH, A. J. E. (1978). *The moss flora of Britain and Ireland*. 1st ed. Cambridge University Press, Cambridge.

SYMONIDES, E. (1988). Population dynamics of annual Plants, in DAVEY, A. J., HUTCHINGS, M. J. & WATKINSON, A. R., eds. *Plant population ecology*, pp. 221–264. Blackwell, Oxford.

TAYLOR, I. (1990) *A survey of* Arenaria norvegica *subsp.* anglica. Unpublished report for English Nature.

WALKER, K. J. (1995). *The ecology and conservation of* Arenaria norvegica *subsp.* anglica *Halliday*), *Caryophyllaceae*. M.Sc. thesis, University College London.

WALKER, K. J. & CORKHILL, P. (1996). *Species Action Plan: English Sandwort* (Arenaria norvegica *subsp.* anglica *Halliday*) [draft version]. English Nature, Peterborough.

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

WEST, R. G. (1988). A commentary on Quaternary cold stage floras in Britain. *Journal of biogeography* **15**: 523–528.

WHITTEN, A. (1990). *Recovery: a proposed programme for Britain's protected species*. English Nature, Peterborough.

WHITWELL, W. (1889). *Arenaria gothica* Fries in Britain. *Journal of botany* **27**: 374–378.

WHITWELL, W. (1890). An additional station for *Arenaria gothica* in West Yorkshire. *The naturalist* **15**: 257.

WHITWELL, W. (1895). More about *Arenaria gothica*. *The naturalist* **20**: 257–260.

WILLIAMS, F. N. (1898) A revision of the genus *Arenaria*. *Botanical journal of the Linnean Society* **33**: 326–437.

WILSON, P. (1986). *Arenaria norvegica* subsp. *anglica*. Unpublished manuscript for the quinquennial review of rare species. Nature Conservancy Council, Peterborough.

WYSE-JACKSON, M. B. & PARNELL, J. A. N. (1987). A biometric study of the *Arenaria ciliata* L. complex (Caryophyllaceae). *Watsonia* **16**: 373–382.

(Accepted March 1999)

APPENDIX. EXTANT, EXTINCT AND UNVERIFIED RECORDS FOR *ARENARIA NORVEGICA* SUBSP. *ANGLICA*.

Population	Recorder/year	Altitude	Status	Position
Extant				
Selside (Font Green)	S. & R. F. Thompson (1890)	295	-	Small population by popular bridleway. Once abundant but has declined in recent years.
Sulber pasture (below flush)	K. Walker (1995)	360	N.N.R.	Small population by the edge of a small flush.
Sulber pasture	D. D. Bartley & S. C. Clark (1978)	355	N.N.R.	Medium sized population on edge of *Eleocharis* flush and on pavement surface.
Sulber pasture ("valley")	D. D. Bartley & S. C. Clark (1978)	345-55	N.N.R.	Largest population scattered over extensive area (c. 1ha) within "shallow valley". Most abundant on moist ground around, and within, large tufaceous flush/mire. Small numbers also on pavement and rabbit scrapes.
Sulber pasture (Halliday's)	G. Halliday (1956)	355	N.N.R.	Very small population growing on broken pavement clitter.
Sulber Nick (sheep-track)	K. Walker (1995)	360	N.N.R.	Small population on exposures along sheep-track between the "Nick" and "shallow valley".
Sulber Nick (west)	K. Walker (1994)	385	N.N.R.	Large population on flat limestone terraces below wall.
Sulber Pot	R. Farrer (1895)	390	N.N.R.	Large population on flat pavement. Presumably the one discovered by Farrer in 1890s.
Thieves' Moss	P. Corkhill (1992)	355	S.S.S.I.	Very small population on limestone exposures adjacent to large mire.
Sulber Nick-Clapham Lane	L. Rotheray / R. Farrer (1895)	370	S.S.S.I.	Small population within ruts of track. Recorded in 1890s, now virtually extinct.
Sulber Nick (flush)	L. Rotheray / R. Farrer (1895)	360	N.N.R.	Large population on flat limestone exposures within tufaceous flush/mire system. Recorded in abundance in the 1890s (Rotheray 1895). A diversion of the Pennine Bridleway away around this population has been proposed.
Clapham Lane (gate)	L. Rotheray / R. Farrer (1895)	360	S.S.S.I.	Small population within "ruts" of track. Recorded over extensive area in the 1890s.
Clapham Lane (cross-road)	J. Blakemore (1981)	385	S.S.S.I.	Very small population in "embayment" next to the track. Threatened by recreational use.
Clapham Lane (Long-Scar)	D. D. Bartley & S. C. Clark (1978)	380	S.S.S.I.	Large population on limestone exposures next to the track. Threatened by recreational use.
Crummack Dale	J. Blakemore (1981)	360	S.S.S.I.	Large population on small area of limestone within a hill track (now disused).
Clapham Bottoms	D. D. Bartley & S. C. Clark (1978)	310	S.S.S.I.	Large population on terraces in "dry" valley. Threatened by use of short-cut by walkers.
Foredale Quarry	J. Blakemore (1981)	350	S.S.S.I.	Four populations amongst clitter on quarry floor. Threatened by dumping of quarry waste.
Dawson Close	R. Kilby (1952)	410	S.S.S.I.	Small population on flat limestone adjacent to a track. Threatened by recreational use.
Juniper Gill	D. D. Bartley & S. C. Clark (1978)	400	S.S.S.I.	Small population within a "dry" valley. Recently relocated and stock-fenced.
Scar Close (introduction)	P. Corkhill (1992)	340	N.N.R.	Seed translocated onto flat pavement. Recent surveys suggest it has failed to establish.
Extinct				
Ribblehead Station	L. Rotheray (1889)	315	-	Original discovery site on track close to the railway station. Extinction due to over-collecting.
SpringValley	R. Farrer (1895)	200	-	On pavement close to the lake (Whitwell 1895). Possibly introduced.
Borrins Pasture (Sulber)	L. Rotheray / R. Farrer (1889)	350	-	Within "ruts" of the track. Probably became extinct due to grazing and recreational use.
Unverified				
Grasmere, Cumbria	A. Bennett (1889)	c.100	-	Fragment of an undetermined plant material collected from Grasmere (Whitwell 1889).
Healaugh, Swaledale	F. A. Lees (1937)	?	-	Single record for a "small number of plants on metalled limestone track". Never relocated.