

Small Cow-wheat *Melampyrum sylvaticum* L.; Scrophulariaceae in England

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ABSTRACT

Small Cow-wheat (*Melampyrum sylvaticum* L.); Scrophulariaceae occurs in Britain as a rare plant in Scotland and in Northern Ireland. It formerly occurred in North Wales and more recently in northern England (Durham, v.c. 66 and Yorkshire, v.cc. 64, 65). The English distribution and ecology of *M. sylvaticum* are given together with its taxonomy, and the reasons for its decline are discussed.

KEYWORDS: ecology, extinction, hemiparasitism, plant records, rare species, taxonomy.

INTRODUCTION

Small Cow-wheat (*Melampyrum sylvaticum* L.), Scrophulariaceae (or Orobanchaceae, as redefined by Olmstead *et al.* 2001), is an annual, hemiparasitic herbaceous plant of open woodland which has very special ecological requirements. It is a Nationally Scarce Species in Britain (Rumsey 1994) and is classed as Vulnerable in the *Vascular Plant Red Data List* (Cheffings & Farrell 2005). It occurs very locally in submontane habitats throughout most of the Scottish Highlands and in the Scottish lowlands from where it has now largely disappeared. It still occurs very locally in Northern Ireland and quite recently it was found that it had formerly occurred in North Wales (Rich, 1997). It has also been known since the beginning of the 19th Century from northern England, in Durham (v.c. 66) and in Mid-west and North-west Yorkshire (v.cc. 64 and 65), where it is now on the verge of extinction or extinct. A record for Staffordshire (v.c. 39) exists, based on an authentic, but probably mis-labelled, specimen. In spite of the distinctive appearance of *M. sylvaticum*, its characters have been widely misunderstood until comparatively recent times, often by otherwise experienced botanists. This has resulted in *M. sylvaticum* being included in the published records of very many counties throughout England, whereas in nearly all of these cases a form of the commoner *M. pratense* L. was intended. The English

distribution and records are therefore updated here, details of the ecology of *M. sylvaticum* in its former English habitats are given and its past taxonomic treatment briefly considered; the reasons for its decline are also discussed.

Outside Britain, *M. sylvaticum* occurs in Europe from Iceland and Scandinavia to the former U.S.S.R., the Alps, the Pyrenees and extends to central Italy, Bulgaria and the Balkans; it is endemic to this area of distribution.

TAXONOMY

Melampyrum sylvaticum is quite distinctive in its characters, yet surprisingly has previously been widely confused with *M. pratense* in Britain, particularly in English localities. Smith (1961) summarised and illustrated the main character differences between the two species. A further, more extensive list of the important characters of *M. sylvaticum* (Table 1) with illustrations (Fig. 1), which has been compiled from the characters of fresh plants growing in situ in its last known English locality, and a comparison with *M. pratense*, is therefore given below. However, there appear to be no significant differences between plants in this English population and those seen by me in two separate populations in Mid Perthshire (v.c. 88) in the Central Highlands of Scotland. A single gathering of *M. sylvaticum* from a different locality in Upper Teesdale (v.c. 66) made in 1874 (**BM**) however, does appear to differ from the plants described in Table 1 and from those collected elsewhere in the north of England, and this is discussed below.

Most Scottish and English examples of *M. sylvaticum* have uniformly rather deep yellow flowers which deepen to orange when withering, although a pale-flowered variant was described locally from Scotland, var. *pallidiflora* White, and more variation occurs in mainland Europe (Britton 1943). *Melampyrum pratense* is more variable in this respect, although the majority of variant forms are often somewhat paler yellow, the colour varying

TABLE 1. CHARACTERS SEPARATING *MELAMPYRUM SYLVATICUM* FROM *M. PRATENSE*. BASED ON OBSERVATIONS OF *M. SYLVATICUM* IN SITU IN UPPER TEESDALE, NORTH-WEST YORKSHIRE (V.C. 65), DJT 1975–1980, WITH AMENDMENTS FROM BRITTON (1943), SMITH (1961)

Character	<i>M. sylvaticum</i>	<i>M. pratense</i>
Longest upper bracts	Almost as long as mid-stem leaves, entire except in largest plants	Usually distinctly shorter than mid-stem leaves, dentate except in some small plants
Flowers	Suberect	Spreading to semi-erect
Calyx lobes	Lax to spreading, linear-lanceolate, straight, equal in size and shape, sharply acute; remaining lax and markedly widening in fruit, \pm equal to or exceeding mature capsule	More appressed to corolla, linear-subulate or triangular, upturned, unequal, upper pair usually wider, sharply to very finely acute; remaining \pm appressed, not enlarging in fruit, shorter than mature capsule
Corolla	Typically 8–10 mm long, tapering abruptly to a narrow tube at base, with a pronounced, often bulbous, helmet and wide gape at the mouth; lower lip strongly deflexed with 3 equal, oblong-ovate, obtuse or subacute lobes with distinct, usually rounded basal sinuses	11–20 mm long, tapering gradually to a broader tube at base, helmet less pronounced and gape at mouth narrower; lower lip projecting forward or sometimes deflexed, with 3, often unequal, usually triangular, \pm acute teeth with narrowly acute basal sinuses
Fruit	Ovoid, rather abruptly tapering to a sharp apical point or beak, somewhat flattened (broadly elliptic in cross-section); 2-seeded, dehiscing by dorsal and ventral suture	Ovoid-obpyriform, more gradually tapering to an apical beak, distinctly flattened (narrowly elliptic in cross-section); 2–4-seeded, dehiscing by dorsal suture†

†Smith (1961) stated that the fruits of *M. pratense* contain four seeds, however the capsules examined in this study of the variety *hians* (Druce) contained only two large, unequal seeds (5.0–7.0 × 2.0–3.0 mm), so this character is variable.

from rather deep yellow in var. *hians* (Druce 1885) to pale yellow or bicoloured with a pale yellow or white tube and deeper yellow or occasionally crimson lip.

Although the Upper Teesdale plants described above from v.c. 65 appear to match Scottish examples of *M. sylvaticum* with no significant differences, one specimen collected in Upper Teesdale (v.c. 66) by F. A. Lees (BM) (undated, but collected with others in 1874 from the same locality, ½ mile above Middleton Bridge) differs considerably from others collected in Upper Teesdale or elsewhere in England. This specimen is robust, up to 30 cm tall, with broad leaves up to 12 mm wide (described as “succulent”, and clearly fleshy) and with large flowers. This BM specimen had also been noted by C. E. Britton (1939: 96) who linked it with similar specimens which had been collected in Northern Ireland (County Antrim, v.c. H39 and County Londonderry, v.c. H40) and he referred these to *M. silvaticum* subsp. *aestivale* Ronn. (*M. aestivale* Ronn. & Schinz) (Britton 1943:

378), but there is no clear inference that Britton ascribed other Teesdale examples of *M. sylvaticum* to subsp. *aestivale*, as stated by Rich *et al.* (1998). C. E. Salmon (1929) sent British material of *M. sylvaticum*, which had been collected by J. Beanland at Colt Park Wood, Mid-west Yorkshire (v.c. 64) (confirmed in Bradford Naturalists report, December 1930), and other specimens from Upper Teesdale, Durham (v.c. 66) to R. V. Soó, who determined all of the plants as *M. silvaticum* var. *subsylvaticum* (*M. silvaticum* subsp. *subsylvaticum* (Schinz & Ronn.) Soó, thus linked English material (except the 1874 Lees specimen mentioned above) with Scottish plants (Salmon 1929), and not with the subsp. *aestivale*.

G. C. Druce suggested that *M. pratense* var. *hians* Druce, which occurs in northern and western Britain was often confused with *M. sylvaticum* (Backhouse 1884), and this statement has been repeated by later authors, most recently Rich *et al.* (1998), however the former is quite unlike *M. sylvaticum* and could

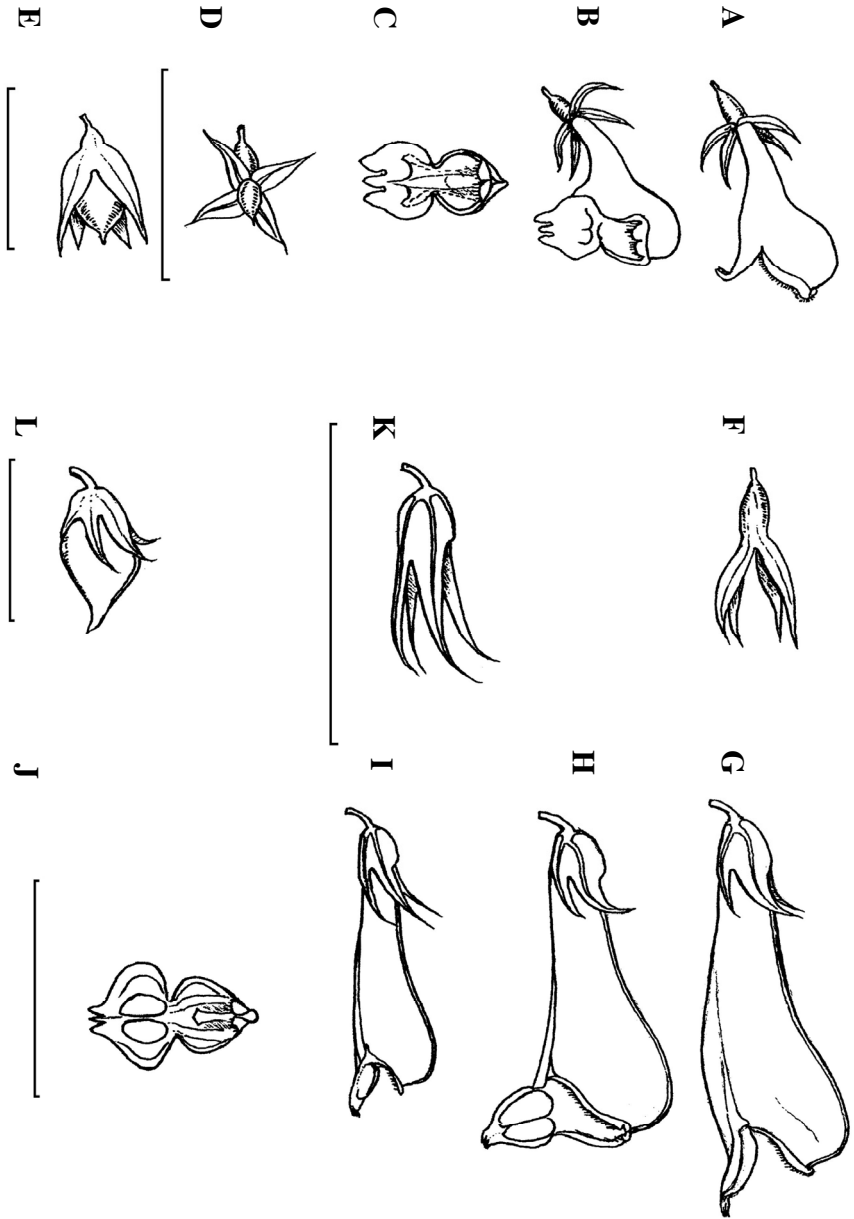


FIGURE 1. *Melampyrum sylvaticum* and *M. pratense*: Flowers, calyx and fruit. A-F. *M. sylvaticum*, Upper Teesdale (v.c. 65); A-C. flower; D. Developing fruit; E. Mature fruit; F. Calyx. G-K. *M. pratense*; G, H, J, L. Var. *hians*; G, H. Typical flower with projecting lip, Ullswater, Cumbria (v.c. 70) and Londonderry; (v.c. H40); H. Flower with deflexed lip, Upper Teesdale (v. c. 65); J. Flower showing typical lip; L. Mature fruit; I, K. Smaller form, Aberfeldy, Perthshire (v.c. 88); I. Flower; K. Calyx (scale bars 1 cm).

not be confused with it by anyone familiar with these two plants. The floral morphology in var. *hians* is typical of that found in other *M. pratense* variants and its flowers are much larger (13)15–20 mm long) than those found in *M. sylvaticum*. The only connection between the two is the deepish yellow flower colour and the deflexed lower lip which can sometimes occur in var. *hians*, as well as the fact that the two taxa have frequently occurred together in northern England. *Melampyrum sylvaticum* is much more likely to be confused with small-flowered variants of *M. pratense*, but the characters of the calyx, widely gaping flower and the capsule will readily separate such plants. Down-turned corolla lips also occur in some Scottish montane variant populations of *M. pratense*, notably small plants from parts of the Cairngorm Mountains and sometimes in a wider-spread Scottish montane variant with a crimson lip, referred to as forma *purpureum* by Smith (1963: 366), and possibly in other variants of *M. pratense*.

DISTRIBUTION IN ENGLAND

The authentic English records of *M. sylvaticum* which are supported by a confirmed specimen seen by me, or based on a reliable source of information are listed below by vice-county. Rich *et al.* (1998: Fig. 1, p.37) showed no post 1969 English records, although the species persisted here until c. 1990.

MID-WEST YORKSHIRE (V.C. 64):

Moors above Middlesmoor, June 1886, R. M. Norman (**BM**) (Rich 1998). Location uncertain, either near Keasden (SD7063), Kettlewell (SD9571) or Nidderdale Head (SE0974), however “moors” a highly unlikely habitat. Specimen confirmed(?). Near Ribblesdale, scars under Park Fell at 1000 ft (305 m), 18 July 1891, J. Beanland (Annotation in G. A. Shaw’s copy of Lees (1888) flora (G.A.S. pers. comm.)).

Horton in Ribblesdale, July 1891, J. Beanland (Specimen exhibited at B.N.C. meeting, 20 July 1981 (Anon 1891) Ribblesdale at 1500 ft (457 m), August 1891, J. Beanland, herb. C. E. Salmon (**BM**)).

Ribblesdale District. “Still there 1 July 1905” (J. Beanland, B.N.C. card index, July 1905 (Anon 1905)).

Colt Park Wood (Ribblesdale). Specimen sent to C. E. Salmon by J. Beanland in 1907, from this locality. B.N.C. report Dec. 1930 (Anon 1930). West of north slope of Pen-y-ghent, J. Beanland. (F. A. Lees 1939).

Park Scar Scrub (=Colt Park Wood), 1891, J. Beanland (F. A. Lees 1941).

All of the Ribblesdale records in 1891 and 1905 probably refer to Colt Park Wood, SD7777 at 340–350 m, although Lees’ 1939 description of the locality is vague, and the altitudes given in G. A. Shaw’s annotated flora and on the sheet in C. E. Salmon’s herbarium (**BM**) may be errors in the annotations. The B.N.C. report by J. Beanland dated 15 December 1930 confirms that the site was Colt Park Wood and there is no evidence that there was any other site in the area.

Oughtershaw (=Oughtershaw, Langstrothdale), 30 July 1904, H. Foster, in herb. J. Cryer (**LDS**).

Oughtershaw Wood, 30 July 1904, W. Ingham (**NMW**). Conf. DJT.

Buckden, 30 July 1904, J. Beanland (with F. A. Lees). Yorkshire Naturalists field meeting (*Naturalist* 1904: 279: B.N.C. report November 1904 (Anon 1904)).

Oughtershaw Wood, 1905, R. Butterfield (Annotation in G. A. Shaw’s copy of Lees (1888) flora).

Woods about Buckden. (F. A. Lees 1939).

Oughtershaw Hall, 1904, J. Beanland (F. A. Lees 1941).

These records all refer to Oughtershaw Hall Wood, SD8781, at c. 345 m, and the initial discovery is credited to J. Beanland, although no specimen collected by him here has been traced, nor any further records post 1905 from Mid-West Yorkshire (v.c. 64).

NORTH-WEST YORKSHIRE (V.C. 65):

(A) UPPER TEESDALE RECORDS:

Winch Bridge (near Bowlees, NY9027, at c. 270 m) (Winch 1805; **HAMU**: Baker 1906).

Winch Bridge, 1844, J. Backhouse junior (**BM**); 1850, G. S. Gibson (2 sheets **BM**); Just above Winch Bridge, 1852, A. W. Bennett (**BM**); Winch Bridge, 1884, J. E. Griffith (**NMW**); 1923, A. J. Wilmott (**BM**); Teesbank at Winch Bridge 1968, J. M. Mullin, sighting of single plant (J.M.M. in pers. comm., and not 1969 as hitherto reported. A later visit by DJT & J.M.M. showed that J.M.M.’s exact site, a steep rocky bank immediately above the river by the bridge had been searched carefully by me in the years preceding and following this record, and later, without success, suggesting that this was a stray seedling. Although this record was never officially accepted in the absence of a specimen (A. J. E. Smith and J. Gaman in pers. comm.) it is likely that JMM would have known the true plant.

Holwick, 1853, J. G. Baker (**BM**): Below Holwick (Baker 1906).

Park End Wood, Holwick, NY9225–26, 1888, Yorkshire Naturalists field meeting (*Naturalist* 1888: 279; 1889: 284); F. A. Lees (undated, period 1871–1883) (**LDS**).

Teesbanks near High Force, NY8828, 1934, herb. H. Stanley Redgrave (**BM**).

Between Middleton and High Force, rocky bank above river at 285 m, NY82, 17 June 1975–c.1990, D. J. Tennant, conf. A. J. E. Smith, herb **DJT** (*Naturalist* **104**: 70 (1979)).

(B.) OTHER VICE-COUNTY 65 RECORDS:

West bank of Whitfell (=Whitfield) Gill above the main force, Wensleydale, SD9292, at 400 yards (365 m), 1884, J. Percival, herb. F. A. Lees (**KGY**). Yorkshire Naturalists field visit to Hawes area, 28 June 1884 (*Naturalist* **10**, 1884–1885: 18; December 1890: 368; Baker (1906).

Mill (=Whitfield) Gill, 1892 (?), J. Wheldon (Anon 1892); Baker (1906) Not found here during the Yorkshire Naturalists field meeting in 1934 (*Naturalist* 1934: 161).

Cantley (=Cautley), near Sedburgh (=Sedbergh), 1909, F. Booth (Specimen exhibited at B.N.C. meeting November 1909 (Anon 1909). F. Booth (Vice-president of Bradford Natural History Society at the time) apparently collected the specimen on the Yorkshire side of the vice-county boundary with Westmorland (v.c. 69) near Cautley Spout, SD6897, but the specimen has not been traced and there are no other records from this well visited area, creating slight doubt about the record. However, J. Beanland, as president and recorder for B.N.C. at the time knew the species well and “spared no pains to check the correctness of a record” (*Naturalist*, June 1933: 125). J. Beanland published the record (Beanland 1910) and there was no later suggestion by him that this record was incorrect.

UPPER TEESDALE RECORDS, VICE-COUNTY (65 OR 66)

UNSPECIFIED:

The records from various sources all refer to Winch Bridge NY9027, or near Winch Bridge on the boundary of these two vice-counties, but which one is not specified (Records which specifically refer to the island in the River Tees immediately above the bridge, NY9027, have been included in Durham (v.c. 66) records.

1871, F. A. Lees (**BM**); 1873, F. A. Lees (**KGY**); 1886, W. C. Barton (**BM**); 1887, C. A.

Wright (**BM**); E. Backhouse (1810, **E**; **BM**); 1888, H. E. Fox (**BM**); 1889, J. A. Wheldon (**NMW**); 1892, Miss Hazlehurst (**BM**); 1895, F. J. Hanbury (**BM**); 1895, Hanbury (**NMW**).

DURHAM (V.C. 66)

All certain Durham records are from Upper Teesdale, either from the north bank of the River Tees or from the island in the river immediately above Winch Bridge, NY9027. The classic site was the south tip of this island (G. G. Graham in pers. comm.) and E. Vachell noted in her diaries (held at **NMW**) c.1930 that *M. sylvaticum* was fairly abundant there. There was a sighting here in 1927 by G. W. Temperley (Graham 1988) and a final sighting in 1947 (A. J. E. Smith in pers. comm.). An extensive search in the area in 1959 by A. J. E. Smith, D. H. Valentine and party failed to find it here. Other records are:

Winch Bridge. (Winch, 1805; **HAMU**); 1839, R. B. Bowman (?**HAMU**); 1871, J. E. Leefe (**BM**); 1892, H. E. Fox (**E**).

North bank of the Tees below Middleton, c. NY9524, 1874, F. A. Lees (**BM**).

Tees-side at Breckholm, ½mile above Middleton Bridge, NY9325, 1874, F. A. Lees (2 sheets **BM**: **LDS**); Above Middleton Bridge, 1874, F. A. Lees (**BM**); Near Dent Bank Cliff by the Tees above Middleton, NY9325, 1874, F. A. Lees (**BM**); Tees-side 1 mile above Middleton Bridge, NY9325, 1874, F. A. Lees (**KGY**; **LDS**).

Two miles above Middleton, NY9226, 1883, R. P. Murray (**BM**).

The island, Winch Bridge, 1883, H. T. Mennell (**BM**); 1883, F. J. Hanbury (**BM**); 1907, J. F. Pickard (**LDS**); 1913, Mrs Wedgwood (**BM**); 1927, herb. J. E. Lousley (**BM**).

Wood by Tees immediately above High Force (Durham) (Record source mislaid, but seen in 1934 nearby on the opposite river bank, so likely to be correct, NY8728 (c. 315 m).

ERRONEOUS, DUBIOUS OR UNCONFIRMED ENGLISH RECORDS OF *M. SYLVATICUM*

The majority of these records are almost certainly errors for *M. pratense* (other records which certainly refer to *M. pratense* are omitted). In all cases a specimen has not been traced.

MID-WEST YORKSHIRE (V.C. 64):

Grass Woods, Grassington, SD9865, 1881. (Yorkshire Naturalists field meeting 1881; B.N.C. records, per Malins Smith (Anon 1881; 1895), R. Dewhirst, B.N.C. records (Anon

1895); 1905, W. West & C. A. Cheetham, B.N.C. records (Anon 1905); 1905, J. Beanland (Annotation in G. A. Shaw's copy of Lees (1888) flora).

Several correct records for *M. pratense* are known from this locality, e.g. 1902, J. F. Pickard (**KGY**), and a specimen which is named as *M. sylvaticum* collected here in 1882 by P. F. Lee (**NMW**, det. D.J.T.) is *M. pratense*, making all of these records doubtful. However, if the annotation in G. A. Shaw's flora is correct and J. Beanland really did see it in Grass Woods in 1905, then this record could almost certainly have been correct, but the record was never published. (*M. pratense* var. *hians*, which often occurred with *M. sylvaticum* in v.c.c. 64, 65, 66, was known in Grass Woods).

Helks Wood, Ingleton, SD6974 (Baines 1840), and repeated in later Yorkshire Floras.

In this former locality for *Cypripedium* both *M. pratense* var. *montanum* Johnston and var. *hians* were recorded by F. A. Lees, so it must remain a doubtful site for *M. sylvaticum*.

Kettlewell, Upper Wharfedale, SD9772, 1864, W. Horsfield (J. Windsor 1873). Very probably an error for *M. pratense*, but neither species appears to be at the described site now.

Feizor Wood, Austwick, SD7668, R. Clapham (undated) (J. Windsor 1873).

M. pratense, which I have seen in this area, has other records here Clapham's record is no doubt an error for this species; about Buckden (F. A. Lees 1939) refers to the correct records at Oughtershaw (v.c. 64).

NORTH-WEST YORKSHIRE (V.C. 65):

Muker Woods, Swaledale, SD9198. (*Naturalist*, **181**, 1890: 254). W. Whitewell (*Naturalist* 183, 1890:305 suggested that this record probably referred to *M. pratense*, which was well known here).

DURHAM (V. C. 66):

Egleston (=Eggleston), near Barnard Castle, NZ0023; Shipley Wood, NZ0120 (Winch 1805: **HAMU**), specimen confirmed?

Drydale (Near Hamsterley, NZ0833), Graham *et al.*, (1972). Specimen (DHM) requires confirmation.

Barnard Castle Woods, NZ01, (E. Robson 1794). Specimen not traced.

Traced specimens require confirmation, but Shipley Wood would have been a likely locality at this early date.

NORTHUMBERLAND (V.C.C. 67, 68):

V.c. 67: Woods near Hexham, F. Scott (Winch 1831); Newbiggin Scar, NY9449, ? Vachell, 1930 in Swan (1993).

V.c. 68: Lesbury NU2411, 1892 (Luckley 1893); Cheviot, NT9120, H. Thomas (in Swan 1993).

Swan (1993) suggested that all Northumberland records were likely to be errors (for *M. pratense*).

CUMBRIA (WESTMORLAND, CUMBERLAND,

V.C.C. 69, 70):

All records from these two vice-counties were regarded as errors by Halliday (1997), as no authentic specimens have been traced. Records from widespread localities throughout v.c.c. 69, 70 are now regarded as errors for forms of *M. pratense*. This is perhaps surprising as there appear to be numerous favourable habitats and some of the records for *M. sylvaticum* here were made by very experienced botanists, such as W. Hodgson, W. H. Pearsall, D. A. Ratcliffe and T. G. Tutin, although none of these records are supported by a specimen and more recent searches have revealed only *M. pratense* at the recorded localities. It is suggested below that the more acidic nature of numerous otherwise suitable habitats in Cumbria is the main reason for the absence of *M. sylvaticum* there.

STAFFORDSHIRE (V.C. 39):

Lark (=Park?) Edge, North Staffords., ?G.R., July 1891, J. W. White, in herb Ida M. Roper (**LDS**). The specimen is correctly named (det. DJT), however, assuming the collector was James Walter White there is some discrepancy. White (1912) stated in his *Flora of Bristol* that *M. sylvaticum* "was apparently unknown south of Yorkshire", so he had either forgotten about his 1891 record or the specimen is from some other locality and mislabelled. It is very unlikely that White would have given his only specimen to I. M. Roper, but there are no specimens of *M. sylvaticum* in White's herbarium at Bristol.

Although dismissed as errors for *M. pratense*, records for *M. sylvaticum* appeared in floras of nearby English counties (Gloucestershire (1948) and Shropshire (1841)), but there are no records in the *Flora of Staffordshire* (1972).

Finally, although many older records of *M. sylvaticum* clearly referred to *M. pratense* it is perhaps dangerous to reject all the old records

of the former simply because a more recent visit to the locality concerned only revealed the presence of *M. pratense*. The two species have nearly always occurred together in Britain, and *M. sylvaticum* appears to be the earlier of the two to have declined or disappeared from its confirmed localities. The above records suggest that other small herbarium collections might be worth examination.

ECOLOGY

HABITATS

Melampyrum sylvaticum in Britain has several different specific ecological needs, which explain its local occurrence and its rarity; a change in any one of these requirements may have led to its rapid decline. Its major ecological requirements can be summarised as:

1. Sensitivity to the level of light.
2. High atmospheric humidity.
3. Soil conditions
4. As an obligate hemiparasitic plant, the presence of suitable host species

In Britain, light tree cover, as provided in natural open woodland, at woodland fringes, tree-lined streams in rocky ravines, or tree-lined riverbanks provide the ideal light conditions, and *M. sylvaticum* has disappeared where the tree canopy has increased to give higher levels of shade. The only British records where it has been found in the absence of trees are very few and in Northern Scotland, where it is recorded on rock ledges at fairly high altitude. In Britain it has always been found under deciduous trees, although elsewhere it also occurs in coniferous forests, and I have seen it in such habitats in several places in the Central Alps. In its last known English locality it occurred under *Betula pubescens*, *Corylus avellana* and *Sorbus aucuparia*.

The high level of atmospheric humidity which appears to be necessary for *M. sylvaticum* seems clear from its chosen habitats in partial shade, but especially on sheltered banks or in rocky ravines close to rapidly flowing streams, and it is almost certainly no coincidence that many known sites are close to a substantial waterfall, where the aerosol effect from spray increases the atmospheric humidity very locally, enhanced by shelter from wind in the narrow gorge carved out at the base of a waterfall. In the absence of streams or rivers other English habitats are known to have nearby flushes from

natural springs and are very rich in mosses and hepatics, indicating a significant level of humidity.

Soil conditions where *M. sylvaticum* has been recorded are somewhat acidic but in English localities this invariably appears to be where rather shallow acidic soils have accumulated over more mineral-rich or base-rich rock formations, such as basalt and/or carboniferous limestone, and particularly where the soil is thinner or bare rocks are exposed, this has led to a herb-rich community in the adjacent area. Where the habitat is close to a river there is no doubt that some of these sites are flushed during times of spate by river sand and grit whereas other sites above the flood zone must only be enriched by seepage from the underlying rock. Soils on woodland slopes are probably enriched by flushing from nearby springs. *M. sylvaticum* has not been found on more acidic, herb-poor and mineral-poor soils, habitats in which at least some variants of *M. pratense* often occur, and *M. sylvaticum* never occurs on open moorland soils amongst *Calluna* or *Vaccinium myrtillus* in the absence of trees, where *M. pratense* is often found. There appear to be numerous suitable habitats for *M. sylvaticum* in montane parts of the Lake District in Cumbria (v.cc. 69, 70), and *M. pratense* var. *hians*, which often accompanies it, is still to be found here, but the more acidic, hard, nutrient-poor underlying rocks may be the main reason why *M. sylvaticum* has not been found there. There appear to be at least three differing habitats where *M. sylvaticum* has been recorded in England, although there is some overlap between these.

The first of these is ancient upland open woodland, dominated by *Betula pubescens*, which occurs in England now only as small, isolated relics of former extensive native forest, and it might be speculated that *M. sylvaticum* once occurred throughout this habitat, but as such woodland has declined to small remnants or the shade from tree canopy has increased, it has had nowhere to go and largely become extinct there. The best example of such ancient woodland in England where *M. sylvaticum* formerly occurred is probably Park End Wood (v.c. 65), which J. Backhouse (1896) described as a remnant of the ancient Forest of Teesdale. This small wood occurs on a slightly raised pavement of basalt, and in places carboniferous limestone rock, with scattered tree coverage. *Geranium sylvaticum* and *Paris quadrifolia* were recorded here, showing the presence of

basic habitats, with *M. sylvaticum* (*Naturalist*, Sept.–Oct. 1888:279). Rumsey (1994) noted the similarity of some Scottish sites to montane *Geranium sylvaticum*-rich Birch woodlands found in Norway. In more recent times Park End Wood has been heavily grazed and trampled by cattle and many of its former plant species are no longer present. A second example of such woodland is Colt Park Wood (v.c. 64), a rather unique remnant of woodland situated on a highly raised limestone pavement, the wood being bordered by carboniferous limestone pillars some 3 m high. Many other less common plants have been recorded here, mainly on very shallow limestone soils, including species which are rare in England, such as *Actaea spicata*, *Carex muricata* subsp. *muricata*, *Cardamine impatiens*, *Crepis mollis*, *Polypodium* × *font-queri*, *Potentilla crantzii*, and close by, *Pseudorchis albida* and *Pyrola rotundifolia*. *M. sylvaticum* must formerly have occurred here where slightly deeper, more acidic soils had accumulated over the limestone in places where *Vaccinium myrtillus* and other acid-loving plants can be seen today. There is little doubt that the barrier of vertical limestone rocks surrounding this wood largely prevented access and grazing by sheep, which is responsible for the survival of this woodland and most of its plants. Another remnant of ancient woodland where *M. sylvaticum* formerly occurred is Oughtershaw Hall Wood (v.c. 64), although a small river runs through it and the exact site where *M. sylvaticum* occurred here is not known. *Pyrola rotundifolia*, a rare plant in Yorkshire, occurred here at the time *M. sylvaticum* was discovered in 1891. A major reason for the decline of *M. sylvaticum* here was increasing shade from the tree canopy, probably increased by the introduction of additional tree species, the site being much more open at the beginning of the 20th Century as photographs show (W. A. Sledge in pers. comm.).

Whitfield Gill in Wensleydale (v.c. 65) is another locality which may represent ancient woodland, but is closer to many of the habitats which are found in Scotland where *M. sylvaticum* occurs. The site where *M. sylvaticum* occurred here was well described and is a small area of steeply sloping open woodland over limestone with several wet flushes and a small river below, not far from a large waterfall. *Cypripedium calceolus* once grew here, and other scarce plants in this area,

Persicaria vivipara and *Pyrola minor* are still to be found. The site is especially rich in mosses and hepatics, with over 100 species recorded here, particularly *Eurhynchium striatum*, *Kindbergia praelonga*, *Rhytidiadelphus triquetrus* and many rarer species (*Naturalist*, 1934: 161). This wood is seemingly unchanged, so the reason for the decline of *M. sylvaticum* here is not obvious, but there are no records since 1892, so it must have been very scarce then and a slow decline though climatic factors is the most likely reason.

The second type of habitat for *M. sylvaticum* in England is also similar to many of the habitats known in Scotland: that is, a steep rocky bank above a fast flowing stream, often near a waterfall and fringed by light tree coverage. Examples of this habitat in England occur mainly in Upper Teesdale (v.cc. 65, 66) and, if the record was correct, at Cautley near Sedbergh (v.c. 65). The last known English locality in Upper Teesdale (v.c. 65) for *M. sylvaticum* has been examined in detail by me between 1975 and 1990. This was also found to be surprisingly species-rich, being a very steep bank near a small waterfall with areas of exposed rock, comprised here of Whin Sill (quartz-dolerite, a hard igneous rock) overlying or intruded horizontally into carboniferous (Yoredale) limestone. The small population (c. 20 plants) of *M. sylvaticum* occurred here on ledges in an area rich in both mosses and grass species. The relatively dry, rather acid soil was situated above the normal flood zone, so soil enrichment would be primarily by seepage of ground water from the underlying rock, although not far below the population there was evidence of deposition of river sand and grit left during spate conditions. A list of the species accompanying *M. sylvaticum* here is given in Table 2. The species normally occurring on acidic soils were in most cases close associates, whereas close by on shallower soils or on bare rock a richer flora was present, due to the higher level of nutrients there. It can be seen in Table 2 that almost 90% of the closely associated flowering plant species and many of the grasses at these two v.c. 65 sites alone are also recorded from localities of *M. sylvaticum* in Scotland, showing the close correlation between them in this respect, although no detailed list of bryophytes from Scottish sites has been seen.

There appears to be a third type of habitat in England, possibly confined to Upper Teesdale

(v.cc. 65, 66), which is very similar to that which is described above, being a river-bank site, but in this case very clearly well within the zone of frequent river spates, where a high level of river-deposited sand and grit can be seen in the soil. The upper part of the River Tees is especially prone to sudden and extraordinarily heavy spate floods, as several tragic incidents record, so it is possible that even the habitat described above where *M. sylvaticum* was last seen, although situated above the level of the frequent flood-zone may be flushed very occasionally at times of exceptional river spates. The former main site for *M. sylvaticum* on the island at Winch Bridge, the site where a single plant was seen by J. M. Mullin in 1968, and other sites where specimens were collected downstream from Winch Bridge on the Durham banks of the River Tees would all be subject to such conditions and be affected by flood-water on frequent occasions. F. A. Lees described the habitat of a specimen collected above Middleton (v.c. 66) in an annotation on the herbarium sheet in **BM** as "Tees-side amongst brushwood" and "in sand", both obviously deposited there by floodwater. It is highly unlikely that so many collections made here, so far downstream from Winch Bridge, merely arose from seeds washed down from that location, and therefore waterside locations amongst deposited silt appeared to be one favoured habitat. It is interesting that the unique Lees specimen in **BM** described above (under Taxonomy) and ascribed to *M. sylvaticum* subsp. *aestivale* Ronn. by C. E. Britton (1943) was collected at this site and presumably in this habitat. Few perennial plants could survive long in such a habitat, but the annual *M. sylvaticum* may have some advantage there, and the nutrients released by friction from deposited river grit might result in rapid growth.

The host plants associated with *M. sylvaticum* are discussed later in this paper under "parasitism".

The following species which are less common or rare in Yorkshire and Durham are recorded in more than half of the seven separate localities where *Melampyrum sylvaticum* occurred with certainty in the counties: *Actaea spicata*, *Cardamine impatiens*, *Cirsium heterophyllum*, *Cochlearia pyrenaica*, *Galium boreale*, *Geranium sylvaticum*, *Melampyrum pratense* var. *hians*, *Parnassia palustris*, *Poa nemoralis*, *Persicaria vivipara*, *Potentilla crantzii*, *Pseudorchis albida*, *Rubus saxatilis* and *Trollius europaeus*, and other rare species occur in some of the same localities.

POPULATION SIZES

Apart from the single Upper Teesdale site in v.c. 65 studied between 1975 and 1990 there are no other specific details of population sizes in England and Wales. However, it can be assumed that all Yorkshire populations (v.cc. 64, 65) apart from those in Upper Teesdale were extremely small and had probably declined there through natural factors by the time of their initial discovery. The three definite sites there, Colt Park Wood, Oughtershaw and Whitfield Gill yielded only single or few specimens in the short period from 1884 to 1905, with no later records, and probably represented relic populations in that period. The same applies to the two less certain records from v.c. 64, Middlesmoor and Cautley, being only single gatherings in 1886 and 1909 respectively. However, *M. sylvaticum* was clearly once widespread in Upper Teesdale, the records showing that it had occurred by the River Tees from above High Force downstream to below Middleton, and at the beginning of the 19th Century possibly further downstream to Eggleston or even as far as Barnard Castle. At least 12 separate collections or accepted sightings were made from four of the known Yorkshire (v.c. 65) sites in Upper Teesdale (Park End Wood, Winch Bridge (2) and DJT's locality) but there is no confirmation available from these localities on population sizes, other than the single plant recorded only once by J. M. Mullin in 1968 at Winch Bridge and DJT's locality described above, where over 20 plants in 1975 were reduced to less than 10 by 1982 and these had probably gone by 1990. In Durham (v.c. 66), where all the records are from the north bank of the River Tees or from an island in the same river at Winch Bridge, there appear to be seven distinct localities where at least 30 separate gatherings or sightings were made. Ten of these collections were from a 6 mile stretch of riverbank in the period 1874–1875 and in 1883, but not since, and although there are no details of population sizes it would seem that *M. sylvaticum* was not infrequent locally there. A detailed search of the north bank of the Tees and adjacent woodland here in 1974–1975 revealed nothing. The remaining 20 or more v.c. 66 collections or accepted sightings were all from Winch Bridge (nearly all from the island immediately above the bridge), where *M. sylvaticum* was known to have been abundant (e.g. E. Vachell diaries (**NMW**), but diminished rapidly at the end of the 19th Century. The last collection traced from here was in 1927 (**BM**) and the final sighting made there was in 1947 (A. J. E. Smith in pers. comm.).

TABLE 2. SPECIES ASSOCIATED WITH *MELAMPYRUM SYLVATICUM* IN UPPER TEESDALE (V.C. 65)
SPECIES NOTED BETWEEN 1975 AND 1990 BY DJT IN THE TWO MOST RECENTLY KNOWN SITES (NY9027–28)

(a) Close associates	
<i>Anemone nemorosa</i> *	<i>Dicranum majus</i> †*
<i>Betula pubescens</i> *	<i>Dicranum scoparium</i> †
<i>Campanula rotundifolia</i> *	<i>Diplophyllum albicans</i>
<i>Conopodium majus</i> *	<i>Eurhynchium striatum</i> †
<i>Corylus avellana</i> *	<i>Hylocomium splendens</i> *
<i>Dryopteris filix-mas</i> *	<i>Hypnum jutlandicum</i> †
<i>Galium saxatile</i> *	<i>Lophozia ventricosa</i>
<i>Hyacinthoides non-scripta</i> *	<i>Mnium hornum</i> †
<i>Hypericum pulchrum</i> *	<i>Plagiochila asplenoides</i>
<i>Lathyrus linifolius</i> *	<i>Plagiothecium undulatum</i>
<i>Luzula sylvatica</i> *	<i>Pleurozium schreberi</i> *
<i>Melampyrum pratense</i> (incl. var. <i>hians</i>) *	<i>Polytrichum formosum</i> *
<i>Mercurialis perennis</i> *	<i>Pseudoscleropodium purum</i>
<i>Oxalis acetosella</i> *	<i>Rhizomnium punctatum</i>
<i>Polygala serpyllifolia</i> *	<i>Rhytidiadelphus squarrosus</i>
<i>Succisa pratensis</i> *	<i>Rhytidiadelphus triquetrus</i> †*
<i>Teucrium scorodonia</i>	<i>Sphagnum quinquefarium</i>
<i>Viola riviniana</i> *	<i>Thuidium tamariscinum</i> †*
	<i>Tortella tortuosa</i>
	<i>Tritomaria quinquedentata</i>
Grasses	
<i>Agrostis canina</i> subsp. <i>capillaris</i> †	
<i>Agrostis canina</i> subsp. <i>montana</i> †	(b) Species close by
<i>Arrhenatherum elatius</i> *	<i>Allium ursinum</i> *
<i>Brachypodium sylvaticum</i>	<i>Cirsium heterophyllum</i>
<i>Briza media</i>	<i>Cruciata laevipes</i>
<i>Deschampsia caespitosa</i> *	<i>Equisetum pratense</i> *
<i>Deschampsia flexuosa</i> †*	<i>Galium boreale</i> *
<i>Elymus caninus</i>	<i>Geranium sylvaticum</i> *
<i>Festuca ovina</i> subsp. <i>tenuifolia</i> †*	<i>Primula vulgaris</i> *
<i>Festuca rubra</i>	<i>Rubus saxatilis</i> *
<i>Festuca vivipara</i> *	<i>Sanguisorba officinalis</i>
<i>Holcus mollis</i> *	<i>Sorbus aucuparia</i> *
	<i>Trollius europaeus</i> *
Bryophytes:	
<i>Bartramia pomiformis</i>	Grasses:
<i>Calypogeia muelleriana</i>	<i>Helictotrichon pratense</i>
<i>Campylium stellatum</i>	<i>Melica nutans</i>
<i>Dicranum bonjeanii</i>	<i>Poa nemoralis</i> *

Species marked † were abundant or dominant, and those marked * have also been reported from Scottish habitats of *M. sylvaticum* or recorded by DJT there.

ALTITUDE

In England the known altitudinal range of *Melampyrum sylvaticum* lies between c. 210 m and 365 m, the highest localities being at Colt Park Wood and Oughtershaw Wood in v.c. 64,

both 340–350 m, and Whitfield Gill in V.C. 65 at 365m.

In Scotland it has been recorded as high as 760 m (Rich *et al.* 1998).

FLOWERING PERIOD

In Upper Teesdale, flowering commenced in the second or third week in June according to season, at least a week or more earlier than *M. pratense* in the same area. There is one herbarium specimen collected in Yorkshire in advanced bud collected in late May, and several herbarium specimens collected in good flower are dated well into August.

PARASITISM

Melampyrum sylvaticum is an obligate hemiparasitic annual by means of root haustoria (Rumsey 1994) and obtains both nutrients and water from its host plant. Smith (1963) studied the related *M. pratense* and found that the host plants seemed to be either trees such as *Betula pubescens*, *Corylus avellana* and *Sorbus aucuparia*, or woody shrubs such as *Calluna vulgaris* and *Vaccinium myrtillus*, and although herbaceous plants occurred with *M. pratense* he concluded that they were unlikely to be involved as hosts, as *M. pratense* never occurred with these alone, but was always found near either trees or specific woody shrubs. However, Weber (1976) specifically studied *M. sylvaticum* in Europe and found that herbaceous plants including a grass species (*Briza media*) and *Melampyrum pratense* acted as host plants, in addition to the woody shrubs mentioned above. Although *M. sylvaticum* occurs on slightly more nutrient-rich soils than *M. pratense* in some of its habitats, the same tree species, the same woody shrubs, grasses and *M. pratense* are all usual associates of *M. sylvaticum*, and one or more of these probably acts as its host plant. Smith (1963) stated that it was not clear whether *M. pratense* is host-specific but that there was some indication that this might be the case although there is little evidence for this, but if so, this is also likely to apply to *M. sylvaticum*, which would be an additional reason for its localised occurrence. Smith (1963) also suggested that the reliance of a shallow-rooted plant like *M. pratense* on woody plants for water, as well as nutrients, was advantageous in times of drought, and it was noticed that associated herbaceous plants had wilted in such conditions whereas *M. pratense* appeared to be unaffected. The same would no doubt apply to *M. sylvaticum*, through attachment to one of the tree species or woody shrubs listed above.

REASONS FOR THE DECLINE OF *MELAMPYRUM SYLVATICUM*

It is clear the *Melampyrum sylvaticum* must have declined markedly by that time that the majority of the earliest English recordings were made in the relatively short period between 1871 and 1905, and that many of the localities then held only relic populations. The decline in this case is most likely to have been over a very long period through two main causes: gradual climate change and a slow reduction of ancient forests through early forestry and grazing by domestic animals. Many other species of open woodland habitats declined or were lost in northern England in the same period.

FORESTRY

The former extensive ancient upland forests have been reduced in England to small remnants and subsequent grazing has prevented their re-establishment. *Melampyrum sylvaticum* may have thrived in such woodland habitats, but once such woodland was reduced to small, discontinuous remnants there was nowhere for the species to go. There is also evidence in a few former English localities, as well as some in Scotland, that the introduction of non-locally indigenous trees, especially Beech (*Fagus sylvatica*), which cast a deeper level of shade, may have led to a more rapid decline of *M. sylvaticum*. The large-scale planting of coniferous forests which has reduced the number of suitable habitats in Scotland is hardly a factor in England.

GRAZING

The effects of grazing are still apparent in several former English localities of *M. sylvaticum*. In Park End Wood (v.c. 65) both grazing and trampling were very obvious through the access of cattle, and the general flora was adversely affected. Extensive sheep farming in the parts of northern England where *M. sylvaticum* once occurred has prevented the re-establishment of woodland through the grazing of saplings. It is probably no coincidence that *M. sylvaticum* survived longer in Colt Park Wood (v.c. 64) as this wood uniquely has a high perimeter barrier of vertical limestone blocks, largely preventing access by sheep. In the last known v.c. 65 site in Upper Teesdale of *M. sylvaticum* a major factor in its rapid decline there between 1975 and 1990 was undoubtedly an increase in the local rabbit

population. The immediate area was covered in excavations by rabbits and some plants of *M. sylvaticum* itself were seen to be damaged (the single specimen taken from this site and its identity confirmed by A. J. E. Smith had been chewed-off at the base by a rabbit). Little could be done at this site to prevent access by rabbits, such as special fencing, as entry was clearly being gained via the river bed in times of low water level. The same may have occurred in other former localities in Upper Teesdale, as there was ample evidence of rabbit damage even on islands in the river which were largely inaccessible at times when water levels were normal.

CLIMATE CHANGE

Melampyrum sylvaticum may have declined over a very long period through gradual climate change. It is found in Britain only in areas where relatively high rainfall occurs and appears to have a requirement for a high level of atmospheric humidity, so would therefore be vulnerable to a reduction in rainfall. Rainfall records for Yorkshire, kindly provided by William Foggitt, show that there was a more-or-less progressive decrease in precipitation there between 1892 and 1910 when compared with the earlier decade 1882–1891, particularly in summer months. This period coincides with the time that *M. sylvaticum* disappeared in Mid-West Yorkshire (v.c. 64), however, the reduction in rainfall then was not very dramatic (c. 12%), and no figures were available for a longer period, so this may be coincidental. Two successive, abnormally hot, dry summers occurred immediately after *M. sylvaticum* was found in Teesdale in 1975, and thereafter the population was noticeably reduced. Whereas hot dry summers have always occurred periodically, the very unusual effect of two consecutive ones may have played a part in adversely affecting germination of seed or establishment of seedling plants.

AIR POLLUTION

One suggestion for the apparent rapid decline of *M. sylvaticum* in its English localities in the late 19th Century is the effect of acid rain through industrial pollution, as several other rare species from similar upland woodland declined or were lost in the same period in northern England, but this theory must remain speculative.

OVER-COLLECTING

In the vast majority of its former English localities over-collection was not responsible

for the decline or loss of *M. sylvaticum*, as it was already an extremely scarce plant in most localities at the time of its initial discovery. However, in Upper Teesdale (v.cc. 65, 66) collecting may have played a part, as there are numerous specimens in many herbarium collections from localities there, as seen in this study.

REPRODUCTION

Melampyrum sylvaticum produces few large seeds with a coating which is attractive to ants, which transport the seeds (Gibson 1993a, 1993b). In the absence of water, such as in ancient woodland habitats, the large seeds are largely dependent on ants for their dispersal and may be continually moved to more favourable habitats in this manner, such as to woodland fringes or clearings as the level of shade from the tree canopy increases. Thus a decrease in the local ant population, perhaps through disturbance by animals such as rabbits, would have an adverse effect.

PARASITISM

Melampyrum sylvaticum, as an obligate hemiparasite, depends on its host plant for both nutrients and water. The loss of the required host plant or plants would result in immediate extinction. The presence of *Corylus avellana* in many sites where *M. sylvaticum* has occurred may be of significance, as the former is found on more nutrient-rich, less acidic soils than most other tree species under which *M. sylvaticum* usually occurs in Britain, namely *Betula pubescens*, *Quercus petraea* and *Sorbus aucuparia*. *M. sylvaticum* may occur on rather acidic, nutrient-poor soils, but the roots of trees such as *Corylus avellana* penetrate deeper into underlying mineral-rich strata and this would provide the parasitic *Melampyrum* with minerals unavailable at the shallow depth which its roots can reach.

Melampyrum pratense, which usually occurred with *M. sylvaticum* in England is still frequent in Cumbria in Northern England, but has declined or been lost in many of its Yorkshire and Durham localities, including those where *M. sylvaticum* formerly occurred. The reasons for the decline of *M. pratense* are very probably the same as those for *M. sylvaticum*, and where it still survives this was because of its relatively larger population sizes.

CONSERVATION

Finally, it is probably too late to consider conservation measures for *Melampyrum*

sylvaticum in its recorded English localities, as it has not been seen in any of these very recently, the last sighting being in 1990 at a single site in Mid-west Yorkshire (v.c. 65). However, there may be lessons to be learned that can be applied in Scotland and Northern Ireland, where controllable measures involving forestry activities, woodland management, restriction of grazing, research into the preservation of local ant populations and host-specificity of this species would prove to be beneficial. The remarkable assemblage of plant species which are uncommon or rare in northern England which are recorded in Yorkshire localities where *M. sylvaticum* formerly occurred is probably no coincidence, and although many of these species probably occurred in differing habitats there, it shows that these were all special places which would have merited conservation for their rich general botanical diversity.

HERBARIA

The following herbarium collections were examined during this study. **BM**, Natural History Museum, London; **E**, Royal Botanic Garden, Edinburgh; **KGy**, Cliffe Castle Art Gallery and Museum, Keighley, West Yorkshire (includes the herbaria of J. Beanland, J. W. Carter and F. A. Lees (part),

and Bradford Naturalists Club (B.N.C.) records and reports; most of which were formerly held at Cartwright Hall Museum (**CMM**), Bradford); **LDS**, Botany Department, University of Leeds.

The following were also consulted: **BRIST**, Herbarium of the University of Bristol; **DHM**, Botany Department, University of Durham; **HAMU**, Herbarium of the Hancock Museum, Newcastle-upon-Tyne; **NMW**, Herbarium, National Museum of Wales, Cardiff, and the *Naturalist* (Field Meeting reports, plant records and Transactions), Journal of the Yorkshire Naturalists' Union, Hull.

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