Orobanche reticulata Wallr. populations in Yorkshire (north-east England)

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ABSTRACT

In the British Isles, *Orobanche reticulata* Wallr. (Orobanchaceae) has only been recorded with certainty from Yorkshire. Its distribution and abundance within this area are reviewed, and the circumstances surrounding its original discovery and those of other early records are described. The plant, a protected species, has been recorded from at least 68 separate populations in ten 10-km squares, and 52 of these populations are extant, although many are very small; it is particularly frequent in two separate but limited riverside areas.

INTRODUCTION

Orobanche reticulata Wallr. (Orobanchaceae) occurs in the British Isles as a root parasite of thistles, especially Cirsium species (Asteraceae). All confirmed records are from Yorkshire (v.cc. 61, 62, 64, 65) where it occurs mainly, but not exclusively, on the magnesian limestone. In Europe its principal area of distribution is in the alpine region but there are also many outlying, isolated localities in northern Europe, including Scandinavia, the Baltic states, Holland, and north Germany (Hegi 1965; Chater & Webb 1972; Meusel et al. 1978). The plant also occurs in Russia, the Balkans, North Africa, and extends eastwards into western Asia.

Its restriction to such areas of Yorkshire is unique amongst British native plants, and perhaps because of this, doubts have been raised about its status (e.g. Pugsley 1926). Roman roads and settlements occur near some of the earliest known localities and so an early introduction is a possibility. However, when its British distribution is considered in the context of its overall European pattern, where similar fragmented occurrences are frequent, especially near the limits of its range, it seems most likely that the plant is genuinely native in Britain. Variability witnessed in some populations (Foley 1992) supports this view, whilst an apparent reliance on a limited host range suggests a persistent, isolated group of native populations.

O. reticulata is confirmed from 68 separate populations in ten 10-km squares, mainly in central Yorkshire (v.c. 64) where there are two principal areas of distribution: between Leeds and Wetherby and near Ripon. It also occurs at an isolated locality in v.c. 61, as well as on the extreme south-western borders of v.c. 62 and v.c. 65, but has not been recorded from v.c. 63. In the few large populations, the number of plants varies from one year to the next, but many populations are very small, often with less than ten flowering plants annually. Owing to its rarity and very limited distribution, it is a scheduled species protected under the Wildlife and Countryside Act, 1981 and has been given a Red Data Book rating of 11E – Endangered (Perring & Farrell 1983). Unfortunately, the host species are a great nuisance to farmers and landowners, and consequently are frequently destroyed. O. reticulata therefore comes under an additional threat to that from which other plants suffer.

In the field, confusion with other *Orobanche* species is unlikely although this may occur with robust *O. minor* Sm. which occasionally shares the same host. Nevertheless, *O. reticulata* is quite distinctive, being tall (up to c. 70 cm) and robust, with a fairly dense inflorescence, especially in the upper part, and with cream-coloured corollas marked distally with blue-purple glands. The corolla is cylindrical-campanulate and has a curved dorsal line which is especially characteristic amongst British broomrapes. The stigma lobes are mauve-purple and the filaments glabrous to sparsely hairy proximally, but can be somewhat glandular above. Even as a herbarium specimen, the plant is still

distinctive, particularly with regard to its corolla shape, and in this state confusion is really only likely to occur with O. rapum-genistae Thuill., or with O. elatior Sutton.

Many infraspecific taxa have been described from populations in continental Europe, and these are summarised by Beck-Mannagetta (1930) and Gilli (1966), although none was recognised by Chater & Webb (1972). British plants have been referred to O. reticulata var. procera (Koch) Beck, which was differentiated from other varieties by its shorter, curved (not nearly straight) corollas. However, further work may reveal that var. procera cannot be maintained even at varietal level. Colour variants and forms of O. reticulata are much less frequent in Yorkshire than in Europe, but some records have been noted recently (Jones 1989; Foley 1992).

In Britain, typical habitats are those of its hosts, rough pastures, road verges, and especially river banks, river flood plains and associated light scrub. Cirsium arvense (L.) Scop. appears to be the most frequent host, but C. vulgare (Savi) Ten., C. eriophorum (L.) Scop., C. heterophyllum (L.) Hill and Carduus nutans L. are recorded, and also occasionally Cirsium palustre (L.) Scop. (e.g. 1932, Vachell, NMW). Scabiosa, Knautia (Dipsacaceae) and Cistus (Cistaceae) species are also said to be parasitised in Europe. As with other Orobanche species, some claims for host can be erroneous, since actual attachment to the roots is difficult to establish in the field. O. reticulata seems to be at least partially perennial in Britain, flowering in early July, with the dead flower spikes persisting for several months afterwards.

The account given below is based upon field work carried out over several years during which all extant populations were visited by the author, many on several occasions. Estimates of plant numbers were made and the various habitats assessed. Many herbarium specimens have also been examined and if necessary re-determined by the author or by F. J. Rumsey. Relevant archival records have also been consulted.

THE ORIGINAL DISCOVERY AS A BRITISH PLANT

In August 1907 H. E. Craven, a pharmaceutical chemist of Roundhay, Leeds, found an Orobanche at Hetchell Crags, south-west of Wetherby, which he was unable to name. It appeared to be parasitic on Cirsium eriophorum and was closest to O. minor. The following year, on seeing a letter from G. C. Druce in the Pharmaceutical Journal in which he referred to the Botanical Exchange Club, Craven wrote to Druce, asking for further details and enquiring whether membership of the Club would enable him to get doubtful plants named as he had a few puzzling plants, one of which was an Orobanche. Craven offered to send Druce some fresh specimens and this he did on 31 July 1908, having kept two plants in water, which had apparently become rather shrivelled. He also offered to send a spike pickled in formalin, as well as duplicates from his previous year's (1907) collection, for Druce to forward to Beck-Mannagetta of Prague, the authority on European Orobanche. A detailed description of the fresh plant and some duplicates were sent to Druce in August 1908, and Druce exhibited the *Orobanche* at the Linnean Society that autumn, convinced that it was not a known British species. During the summer of 1908, Craven also sent plants to E. M. Holmes for naming. Holmes agreed that it was not previously known in Britain but suggested it might be a hybrid; he also showed a specimen to the herbarium curator at Kew who was unable to identify the plant. However, some months later, apologising for the delay due to illness, Beck-Mannagetta replied to Druce (9 January 1909) naming the plant Orobanche reticulata f. procera (Koch) Beck (= O. procera Koch). An original specimen sent to Beck-Mannagetta is in his herbarium (PRC) and Beck-Mannagetta's letter is appended to a sheet in Druce's herbarium (OXF) on which the latter mounted a specimen described "First as British" - presumably one of Craven's original specimens. Other early collections by Craven are in BM and MANCH. During the summer following Beck-Mannagetta's determination of the Hetchell plants as O. reticulata, Craven (17 July 1909) despatched most of his remaining duplicates for Druce's retention, along with a map and a detailed sketch of the habitat at Hetchell stating that the Orobanche grew there and nowhere else. He also remarked that the tenant farmer had mown down all the thistles during the previous summer (1908) and that he was concerned for the future of the plant. (This point is also made in subsequent annotations to another sheet (1909, Lees & Pickard, YRK).)

Another Yorkshire botanist involved in the early recognition of the plant in Britain was F. A. Lees. On receiving Beck-Mannagetta's determination from Druce, Craven informed Lees and

presumably sent him a specimen, since one is preserved in Lees' herbarium (July 1908, Craven, BM); on the label, in Lees' handwriting is the comment "Orobanche procera, Koch (teste Dr Beck, per Druce ad Craven 12.1.09)". Also attached to the sheet are three photographs of the plant at Hetchell Crags taken by J. H. Gough on 19 July 1913. On 29 July 1909, Lees, with J. F. Pickard, went to see the plant at Hetchell, and one of the three specimens which they collected is preserved (29 July 1909, Lees & Pickard, YRK). Writing to Druce on the following day, Lees commented that the parasitised Cirsium eriophorum appeared to be very unhealthy, and that he had established the connection from the *Orobanche* to the roots of the thistle. In this same letter Lees asked Druce to publish a description of the plant which he subsequently did (Druce 1909a), and also offered to send him specimens. Despite this, and Craven's offer of a map on 17 July, Druce, along with A. H. Evans, had already visited the site the previous month since a specimen exists which he collected at the time (30 June 1909, Druce, OXF). This is added to a sheet of material collected by Craven in 1908, although Druce (1909a) stated that his visit was in July. From his correspondence with Druce, it appears that Lees was the first person to raise the suggestion that the plant could be a Roman introduction. He was aware that close to Hetchell Crags is the Pompocali, where the Romans had their summer camp, and that there were also Roman roads and earthworks nearby,

Whilst the credit for the discovery of O. reticulata in Britain (and at Hetchell Crags) goes to Craven, this is perhaps not strictly correct. The plant was first found there on 16 August 1902 by J. F. Pickard (Lees' companion in July 1909) but the specimen which he collected was erroneously identified as O. elatior by Pickard and Lees (see notes on herbarium sheets: 1909, Pickard, BM; 1909, Lees & Pickard, YRK; 1910, Pickard, BM), and considered to be "O. major" by Lees (quoted by Cheetham & Sledge (1941)). Shortly afterwards, Pickard was away on business for two years (see annotation, 1909, Lees & Pickard, YRK) and presumably did not question this identification further. Craven subsequently re-found the plant at Hetchell, and not satisfied with these diagnoses (Lees 1909), had it re-determined as described above. Pickard's 1902 specimen has so far not been traced. Although evidence points to the contrary, Druce appears to have indicated that the first correct determination of the plant was his own, given directly on receipt of Craven's original specimens (Druce 1909a, 1911). However, in another statement, Druce (1909b) stated only that he was convinced it was not a British plant, and had therefore sent a specimen to Beck-Mannagetta for identification (see also Druce's letter in herb. Beck (PRC)). Beck-Mannagetta's reply to Druce (9 January 1909) reads as a determination rather than a confirmation, and that is probably the case.

Shortly after Craven's letter to Druce on 17 July 1909, it was thought that the *Orobanche* had been exterminated at Hetchell. This resulted from a report in the *Yorkshire Weekly Post* of an address given by J. G. Wilkinson, who was blind, to a Leeds Naturalist Club meeting. To disprove this, on 25 August 1909, Pickard and Wilkinson went to the place where Pickard saw the plant in 1902 (and also in July 1909 with Lees) and found two in flower and eleven in fruit. Pickard stated that Wilkinson considered that this locality was a different one "higher up on the slope and further on than Craven's", and Pickard was of the opinion that Craven's population had been exterminated. Even though Wilkinson was blind, he was considered reliable, and it is likely that there had been two separate populations, with Craven's being lost shortly after discovery. Examination of the general area around the present site at Hetchell, together with the sketch which Craven sent to Druce, contemporary notes on the flora, and Druce's description (1909a) of Craven's site – "a grassy slope with bushes" – all support this view. Ironically, immediately after his visit in 1909, Druce had received assurances from the landlord at Hetchell, that the thistles would be preserved.

OTHER EARLY RECORDS

Although the acceptance of *O. reticulata* as a British plant dates from the Pickard/Craven find, specimens exist from other localities well before this date. These were, however, erroneously referred to other *Orobanche* species. In the Leeds/Wetherby area a specimen was collected in 1868 from Roundhay Lime Hills (*Lees & Abbott*, CMM); it was identified as *O. major* (= *O. rapumgenistae*) and thought to be growing on whin (*Ulex europaeus*), but is undoubtedly *O. reticulata*. Roundhay is only a few kms from Hetchell Crags. Shortly after the Hetchell discovery, the plant was also recognised from the large and already known broomrape colony at Hook Moor, Aberford (a few kms south-east of Hetchell) whence it had variously been recorded as *O. major* and *O. minor*.

Several specimens exist from here which are thus mistakenly labelled, with one collected as O. major as early as 1878 (Webster, CMM). Despite assertions about the host for this specimen – "One root especially was only one or two inches from the gnarled stem of Ulex being far advanced to ripeness. I did not trace any actually to the root of Ulex, altho' I have no doubt" – and another identified as O. minor "on Trifolium" (1883, Williamson, YRK), both are nevertheless O. reticulata. This illustrates the difficulty in being positive about which plant is actually parasitised. The first contemporarily confirmed record at Hook Moor may be that of F. Ashwell (1916, LES) and there is also a specimen from the previous year (1915, Cockerline, LES), but which may not have had contemporary confirmation.

Another early record for O. reticulata is from Linton Common (again quite near Hetchell Crags) where it was described by the finder as O.major. The date on the sheet (Pickard, CMM) is unclear, being either 1901 or 1907. By 1907, Pickard might have been wary of this plant, following his involvement at Hitchell in 1902 with what he thought was O.elatior, and so 1901 is perhaps the more likely date. There is also a later annotation to a herbarium sheet (1909, Lees & Pickard, YRK) stating that Pickard had also found and pressed the plant at Linton Common, where it was rare, but that it was still there in 1936.

A second main centre of distribution is in the Ripon area of v.c. 64. In contrast to the Leeds/ Wetherby localities for which many early records can be confirmed by herbarium specimens, there is little similar from here. The only specimen of O. reticulata so far traced which approximates to the date of the Pickard/Craven find at Hetchell is one described as O. major "on gorse?", collected by C. A. Cheetham on 18 July 1903 (C.A.C., BM). Unfortunately the label simply states "Ripon" with no further details of the locality. This specimen is erroneously referred to O. rapum-genistae by Lees (Cheetham & Sledge 1941). It was not until 1939 that a localised Ripon area specimen was preserved - from Bridge Hewick (Rob, YKN), although possible evidence for the plant's early presence in the area can be gained from the old Floras. In the Ripon area, nearly all modern records for O, reticulata have been from riverside habitats, and the plant is now especially frequent there along an 8 km stretch of the Ure, where at least 38 separate populations are extant. This lends credence to the suspicion that some of the nineteenth century riverside Flora localities for other Orobanche species in this area were misidentifications for O. reticulata. Those given for O. minor near Nunwick, at Sleningford, Howe-upon-Swale, Ure Banks, Burnistone, and Bishopton (Baker & Nowell 1854; Baker 1863; Slater 1883/4; Lees 1888), and for O. rapum-genistae below Tanfield (Cheetham & Sledge 1941) are mostly close to extant O. reticulata populations, and may well have been mistaken for that plant. Misidentifications for O. reticulata have already been shown to occur for some nineteenth century specimens collected elsewhere as O. major and O. minor. Flora records from Roundhay and from Lotherton Moor (Hook Moor) both given by Lees (1888) must, in fact, have been O. reticulata, and it is very likely that the same applied near Ripon.

Unfortunately it is rare for specimens of *Orobanche* to have been preserved from localities near Ripon; ironically one of the few traced is undated (but prior to 1922) and was collected close to the Ure between Ripon and Hutton Conyers (*Lees*, CMM). Lees finally determined this specimen as O. reticulata but it is in fact O. elatior. An isolated occurrence lying to the east of the main area of distribution was at Backhouse's Nurseries, York (1886, Backhouse, K) where it was found in a garden on Cirsium heterophyllum, presumably a casual occurrence. This is probably the first correct identification of the host plant in Britain.

The first record from south-east Yorkshire (v.c. 61) was made in 1953 at North Grimston (Sledge 1954), at which site the plant is extant. In the same year it was also found at a nearby quarry (W. A. Sledge, pers. comm.), but was not seen there again until 1992 during this survey; it is not known elsewhere in v.c. 61. There are apparently only three instances of the plant being definitely recorded from v.c. 62, and two of these are rather obscure. The first is an 1852 specimen (the earliest so far traced from Yorkshire) of atypical O. reticulata collected from near Thirsk as O. elatior (Fowler, OXF). Interestingly, there is also a collection (two sheets as O. minor) made in the previous year from Sowerby, also near Thirsk (Baker, 1851, herb. Boswell-Syme, BM); the specimens are intermediate between O. reticulata and O. minor and may possibly represent the hybrid. This record deserves further investigation since natural hybrids of O. reticulata are not recorded in Britain although they have recently been deliberately cultivated (Jones 1989). Whilst Fowler's 1852 plant is distinct from those collected by Baker, it is quite possible that they could be from the same population. (Dead flower spikes, similar to the Sowerby plants, and again possibly of hybrid origin,

were seen near the Ure in 1992.) The second vice-county collection of O. reticulata is slightly more recent and is typical, although labelled O. minor (1881, Webster, BM) but is unfortunately unlocalised simply as "N.E. Yorkshire" (see also Bennett 1917). Thereafter, it was not until 1984 that the plant was found in a riverside habitat in the extreme south-west of the vice-county, where a flourishing colony survives. Before about 1980 there were apparently no records from v.c. 65, but nine populations are now known, all on river margins, where only the past vagaries of the river channel have resulted in their inclusion within that vice-county.

Outside Yorkshire, there are several dubious or erroneous records for O. reticulata. One which may be significant is that given as O. major from Nottinghamshire (1835, Cooper, in herb. H. C. Watson, K). The magnesian limestone does extend southwards into that county, but some of Cooper's specimens are considered to be of dubious provenance (Rumsey & Jury 1991) and this one would benefit from independent verification. A record from Cheshire (v.c. 58) (Druce 1918; Perring & Walters 1962; Perring & Farrell 1983) is erroneous since the specimen is O. minor (1918, Dallman, OXF), as is an earlier one from Guildford (v.c. 17) quoted by Druce (1918) (1916, Kennedy, OXF). Another error is that for Falmouth Dock (v.c. 1) in 1917 which again was O. minor (F. J. Rumsey, pers. comm.). A record for var. pallidiflora (Wimm. & Grab.) Beck based on a specimen collected from Brecon (v.c. 42) in 1905 (Knight, BM) has also been shown to be an error (Pugsley 1940; Graham 1957; Rumsey & Jury 1991); a duplicate from this collection is in PRC. Reports from E. Norfolk (v.c. 27) (Jones 1989) including one of an Orobanche parasitising Cirsium vulgare are thought to be errors for other species (A. L. Bull, pers. comm.).

DISTRIBUTION AND HABITAT

The magnesian limestone formation occurs as a narrow band running north-south from Durham to Nottinghamshire. In the area of distribution of *O. reticulata* it is rarely more than 10 km wide, and is crossed in a roughly eastwards direction by the rivers Swale, Ure, Nidd, Wharfe and Aire. Magnesian limestone is well-known for its species-rich flora.

10-km squares and tetrads (2 × 2-km squares) for which there are confirmed records for O. reticulata are mapped in Fig. 1 and Fig. 2 respectively, and fall within an area approximately 50 km square. The two principal centres of distribution in the vicinity of Leeds/Wetherby and Ripon, the disposition of the magnesian limestone formation and the principal rivers of the area, can all be clearly seen.

Following the recognition of *O. reticulata* as a British plant there was a lull in the discovery of new localities until the 1930s find by the river at Bridge Hewick, Ripon. Since then, other riverside ones have been found some distance upstream from this site, many of which survive, and the plant is particularly frequent in that area. Downstream also, new localities have occasionally come to light, including one on the Ouse (formed by the confluence of the Ure and the Swale) found in 1984, the first confirmed modern record for v.c. 62; there are, however, no definite records near the Swale itself. Apart from a small population just south of Ripon and away from the Ure, all other post-1930 colonies in this northern (Ripon) area are on river banks or flood plains, and it seems clear that rivers play an important role in dispersing seed. Also, plants often occur close to river banks and eventually may be dislodged by water erosion. It is quite possible that these together with their host will sometimes become established elsewhere. Favoured habitats for *O. reticulata* are near the upper flood limit by the river bank, and especially the flat pasture borders nearby; occasionally they grow some distance from the river but in places where winter flooding occurs. These are also the areas where the host species are plentiful.

In the southern (Leeds/Wetherby) area most newly-found localities are again in similar habitats on the banks of the Wharfe, where propagation or dispersal has presumably occurred in a similar manner. Population sizes can vary, but some appear to persist for many years with just a few plants annually. The Linton Common locality is such an example. Here, even at the beginning of this century only a few plants were recorded, and the same is the case today. Similarly at Hetchell Crags where the plants occur on the magnesian overlay of the gritstone substrate and well away from the river, numbers have apparently never been high. Cheetham & Sledge (1941) quoted a contemporary account of F. A. Lees in which he stated that an increase in thistles had been observed at Hetchell Crags between 1870 and 1879 but that he was certain that the broomrape was not present

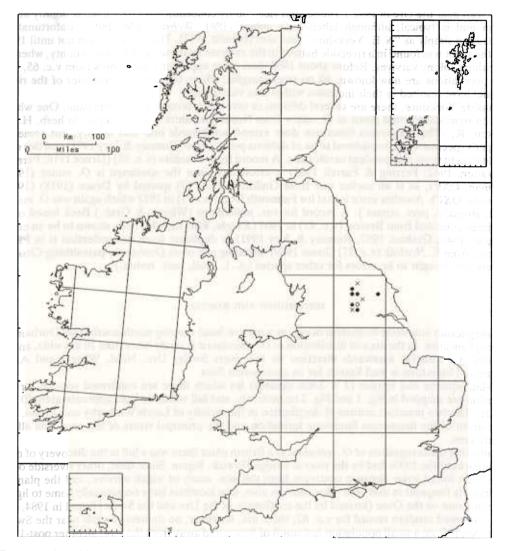


FIGURE 1. The British distribution of *O. reticulata* shown on a 10-km square basis for which there are confirmed records: ● 1991 onwards; ○ 1901–1990; × up to 1900.

during that time; this suggests a relatively recent colonisation just prior to its discovery there in 1902. During the 1920s about 20 plants were known at Langwith Scrub (W. A. Sledge, pers. comm.) and today similarly small numbers still persist close by.

At Hook Moor, the classic site was unfortunately ploughed out about 1940, but surprisingly, and despite reservations expressed at the time (Sledge 1942), what is still the largest British population occurs on road embankments within the vicinity. Earth from the former site may have been removed and used in construction of the present embankments and thus led to the plant's presence there, although natural recolonisation cannot be ruled out. Being on steep slopes, this is very well drained and is also multi-aspect. It is rather different from the moister riverside localities favoured elsewhere, and as the plant thrives here, it suggests that it may be a preferred habitat to the more opportunistic riverside ones. Close to this re-colonised area, there is at least one, more natural, yet very small population on an arable field border, probably a remnant of the former pre-1940 colony.

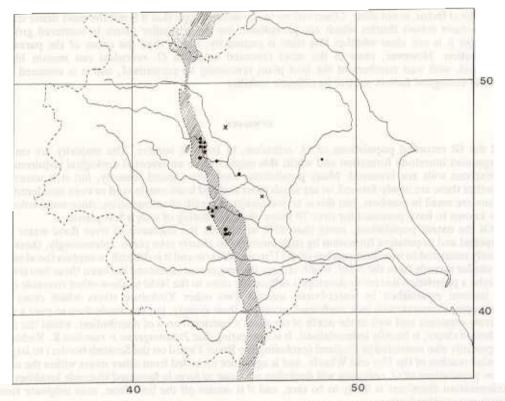


FIGURE 2. The British distribution of O. reticulata showing tetrads from which there are confirmed records:
1991 onwards;
1901–1990; × up to 1900; the major river pattern and the disposition of the magnesian limestone (hatched) are also indicated.

Roundhay limehills are mainly commercially developed nowadays and the plant is presumably long extinct. Craven, the original discoverer in Britain, lived at Roundhay at the turn of the century and would presumably have recorded it if he had known it there, and so it had perhaps gone even in his day. Nothing is known of the plant's habitat or frequency there, but Roundhay and Hook Moor are both well away from major rivers, and could be remnants of an earlier area of distribution, from which it has subsequently expanded.

All the localities mentioned occur on, or just eastwards of, the magnesian limestone formation. Those to the east of it are usually close to major rivers and their occurrence there is likely to be a result of downstream dispersal by water into habitats rich in alluvial deposits. No records for O. reticulata have been traced to the west (upstream) of the magnesian limestone, and this reinforces the argument for the downstream river dispersal through and away from this formation. However, a magnesian limestone soil is not an essential requirement as shown by the plant's occurrence in v.c. 61 on the chalk at North Grimston, where it formerly thrived (W. A. Sledge, pers. comm.) but is now much less abundant. This locality is separated from all others and distant from any rivers, and its presence there could possibly be from accidental introduction, since it has only been known since 1953.

Within the last 60 years or so, O. reticulata appears to have become more widely distributed in Yorkshire than formerly, but whether this is due to a genuine expansion of range or results from being previously overlooked, is uncertain. Some populations are highly stable, appearing on the same area of thistle year after year, but others are more dynamic. These latter may change in size and spatial distribution, apparently dying out (at least temporarily) in one part of the population, only to appear a short distance away. Whether this depends on the vigour of the host or on some

other local factor, is not clear. Observations in the field indicate that it is not the most dense stands or the most robust thistles which are parasitised, but often smaller plants in scattered groups, although it is not clear whether this state is caused by, rather than the cause of the parasite's distribution. However, even in the most favoured localities O. reticulata can remain highly localised, with vast numbers of the host plant remaining un-parasitised, and it is assumed that critical ecological factors control its ultimate viability.

SUMMARY

Of the 68 recorded populations of *O. reticulata*, at least 52 survive. The majority are on the magnesian limestone formation and whilst this might not be an essential ecological requirement, calcareous soils are favoured. Many populations have been found recently, but it is uncertain whether these are newly-formed, or are much older and had been overlooked or even misidentified. Many are small in numbers, but this is no indication of length of colonisation, since some colonies are known to have persisted for over 70 years whilst consisting of only a few plants.

Of the extant populations, more than 85% are within the influence of river flood water and dispersal and population formation by such means must clearly take place. Interestingly, these are mostly restricted to two short reaches of the Ure and Wharfe and it is difficult to explain the absence of similar records from the Nidd, which crosses the magnesian limestone between these two rivers. Maybe a population has never developed sufficiently close to the Nidd to allow other riverside ones to become established by water-borne means? Two other Yorkshire rivers which cross the magnesian limestone also lack confirmed records in their vicinity, but the Swale does so over a very narrow exposure and well to the north of the plant's restricted area of distribution, whilst the Aire although closer, is heavily industrialised. It is interesting that *Potamogeton* × suecicus K. Richter is apparently also restricted in England (excluding the River Tweed on the Scottish border) to largely similar reaches of the Ure and Wharfe, and is again not recorded from other rivers within the area. New populations of O. reticulata will doubtless continue to form in favoured riverside localities but colonisation elsewhere is likely to be rare, and if it occurs off the limestone, may originate from inadvertent introduction.

The main threats to its survival result from the deliberate destruction of its hosts, from adverse agricultural practices, and through engineering operations such as road construction. Some populations may be lost when river banks are eroded, whilst gravel extraction is yet another threat. Nevertheless it appears to be relatively resilient, occasionally reappearing at sites from which it was thought to be extinct. There is much scope for investigation of the autecology and population dynamics of *O. reticulata*.

RECORDED LOCALITIES AND RELEVANT HERBARIUM SPECIMENS

Whilst it is recognised that the number of flowering spikes can fluctuate annually and that two or more may sometimes represent just a single plant, an attempt has been made to estimate a typical size for each population. This is indicated using the following notation: A = 1-10 plants; B = 11-50; C = 51-200; D = 201-1000; E = 1000+; X = PODD = 201-1000; E = 1000+; E = 1000+;

Localities which are *not* on the magnesian limestone formation are indicated by (*); those well away from the influence of river flood water by (#).

Being a protected species, precise details of the populations are not given here, but have been deposited at English Nature, York, and the Biological Records Centre, Monks Wood.

Herbarium specimens quoted earlier in the text are not usually repeated here, but their existence is indicated by the code (Hb) inserted after the locality name. Others of relevance are listed after each locality entry and although not exhaustive, they represent the majority of the more interesting, historical specimens held in major national, or locally important herbaria. The fact that O. reticulata is a Red Data Book plant is stressed and therefore further collections should not be made, but the

specimens quoted used for reference or examination. Where specimens have been redetermined these are shown in this section as follows: (i) by F. J. Rumsey, (ii) by M. J. Y. Foley.

Notts., v.c. 56:

Based upon the single unlocalised (Hb) record of a specimen of doubtful provenance.

S.E. Yorks., v.c. 61:

SE/8.6, North Grimston (* #), found in 1953 (Sledge 1954) on chalk, well away from magnesian limestone and river influence. Recently decreased, but still survives (B); herbarium specimens: 1953, Sledge (CMM, RNG). In 1953 also recorded at a nearby quarry but not seen again until 1992 (B). It is possible that there has been a recent introduction nearby at Wharram.

N.E. Yorks., v.c. 62:

SE/4.6, Linton-on-Ouse (*), first found in 1984, probably formed from a population further upstream (B). There is also an unlocalised herbarium specimen from north-east Yorkshire (Hb) collected as O. minor. (ii).

SE/4.8, near Thirsk (* #) in 1852, based upon atypical specimens (Fowler, OXF). Two other sets of specimens collected near here (at Sowerby) in 1851 (Baker, BM) may be of hybrid origin and are possibly from the same population. Apparently not recorded since (X).

Mid-W. Yorks., v.c. 64:

SE/3.3 Roundhay Lime Hills (#), the early specimen as O. major (ii), (1868, Lees & Abbott, CMM) is the only record traced. The site is now mostly developed and industrialised (X).

SE/3.4, East Keswick A, first noted in 1990 in a rough pasture (C). The following year several interesting variants were observed (Foley 1992); East Keswick B, overgrown scrub, known since about 1985 (B); Hetchell Crags (Hb), calcareous grassland above the gritstone escarpment, the locality from which the first identified British O. reticulata specimens were collected by Craven in 1907 (B). It is probable that two populations formerly existed here, one becoming extinct in 1909 (X); herbarium specimens from Hetchell include: 1907, Craven (MANCH); 1908, Craven (OXF); 1908, Druce ex Craven (PRC); 1908, Craven (BM, CGE); 1908, Craven (OXF); 1909, Lees & Pickard (CMM); 1909, Pickard (LES, CGE); 1910, Palmer (BM); 1913, Horrell (LES); 1919, Cockerline (LES); 1951, Boniface (NMW); 1966, Hodgson (LANC); Whitwell, north bank of river, first found in 1991 by P. P. Abbott (A); Langwith Scrub, known from this riverside locality since the 1920s (W. A. Sledge, pers. comm.) and thought extinct, but a few plants were found close by in 1991 (A). Lees' (1888) record for O. major at Langwith Woods is very likely an error for O. reticulata and there are also herbarium specimens probably from here: 1917, Horrell (OXF, LES); Linton Common (Hb), recorded just after the beginning of this century, and still present in small numbers (A).

SE/3.6, South Ripon (#), an area of limestone grassland, where occasional plants have been found since 1989 including a single plant in 1992 (A); Roecliffe (*), a rough riverside pasture, first recorded in 1969 in small numbers. Thought to be extinct, but four plants were found close by in 1992 (A).

SE/3.7, near Queen Mary's Dubbs, five populations found in 1992, but a further one lost to ploughing some years earlier (A, A, A, A, B, X); Ripon Parks, formerly several populations with five still remaining on the flood plain of the Ure on Ministry of Defence land. Two others were lost when the ground was ploughed in the early 1980s. Fasciated plants have been recorded from this locality (A, A, A, A, C, X, X); Norton Conyers A, east bank of the Ure, ten populations mostly found in 1992, one of which possibly contained hybrid plants (× O. minor) (A, A, A, A, A, A, B, B, B, B); near Nunwick, four populations found recently (A, A, B, B); north of Ure Bank found in 1992 (A); Bridge Hewick (Hb) where two separate populations flourished about 1940-1950 on opposite banks of the Ure. Rob (1953) commented that the plant had decreased here, but there were about 70 plants at one population in 1954 (H. J. M. Bowen, pers. comm.). Apparently extinct at one of the old localities but four populations were found near the other in 1992 (A, A, A. B. X). Herbarium specimens from Bridge Hewick include: 1952, Bangerter (BM); 1954, Rob (YKN); 1954, Bowen (RNG). Other specimens only partially localised and probably from near here are: Ripon, as O. major (i), 1903, C.A.C. (BM); near Ripon, 1956, Branson (E, RNG). SE/4.3: Hook Moor (#) (Hb), one of the classic sites from which specimens can be found in most major herbaria (often under the alternative locality names of Micklefield or Lotherton Moor), one such early specimen dating from 1878. Formerly widespread prior to the site being ploughed in about 1940. Since then good populations have developed on road embankments within the vicinity, plants or seed possibly having been brought in with the soil during road construction, or even formed by natural re-colonisation. Probably the strongest British population (D, possibly E); there are two other nearby localities: a probable relict population on an arable field border. (A), and another on a road embankment to the north (A). Three other records in the period 1952–1972 from other areas of Hook Moor (#) have not been recently confirmed (X, X, X). Herbarium specimens include: as O. eu-minor (ii), 1881, Webster (BM); as O. minor (i), 1881, Webster (E); 1892, Foggitt (BM); 1919, Sledge (CMM); 1922, Barnett (LES); 1922, Roper (LDS); 1929, Jones (LDS); 1930, Foggitt (BM); 1932, Vachell (NMW); 1932, Vachell & Knowling (NMW); 1936, Sledge (LIV, RNG); 1936, Jackson (K); 1937, Lousley (LIV, RNG, K); 1937, Woodhead (LANC); 1938, Chapple (OXF); 1939, Lousley (NMW); 1946, Lousley (E, RNG); 1946, Libbey (LTR); 1949, Raven (LTR); 1953, Frankland (three sheets) (LIV); 1988 (photographs only), Rumsey (RNG). There is an unlocalised specimen probably from here: near Leeds, as O. rubra (i), 1922, Rogers (CGE).

SE/4.4, near Tadcaster, the sole record is based upon a semi-localised herbarium specimen collected in 1935 (W.R.W., K) and now presumed extinct (X); near the Dunsforths, rumoured to have been found here in the mid-1980s, but no definite records traced.

SE/5.5: The Nurseries near York (* #), based on Backhouse's 1886 specimen (K). At this date, Backhouse's nurseries were in what are now the south-western suburbs of the city. Presumably a casual introduction with no records since (X).

N. W. Yorks., v.c. 65:

SE/3.7, Badger Bank, five separate populations on the east bank of the Ure (A, A, A, A, B); Norton Conyers B, east bank of the Ure, first found in 1988, including one broken, fasciated plant, *Norris & Lloyd-Evans* (LES) (A); North Stainley, on a nature reserve on the west side of the Ure. Recorded here in 1984, this population has apparently died out, but a second one appeared close by in 1992 (A). There is a further population a short way downstream (A); Low Batts, discovered here about 1980 (B).

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