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INTRODUCTION TO THE PROCEEDINGS OF THE BROOMRAPE CONSERVATION WORKSHOP

compiled by
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On 17 October 1997 a group of 18 out of a total of 27 invited delegates attended a one-day workshop on the conservation of broomrapes at English Nature's offices in Wakefield. This is the lead office for *Orobanche reticulata* and the Southern Magnesian Limestone Natural Area in which this plants distribution is centred. An informal partnership of English Nature, David Knight of Leeds City Council, Phyl Abbott and myself was established as a consequence of being involved in the conservation of the thistle broomrape, *O. reticulata* Wallr. in Yorkshire This partnership has been working together to solve some of the knottier problems of managing and researching the ecological requirements of this protected species for over three years.

It became clear from discussing issues with other organisations and individuals that the same problems arose with other rare species of *Orobanche*. It was felt that the lessons learnt from working on *O. reticulata* were applicable to many of the other rare or conservationally important species of *Orobanche*. A workshop was organised in order to disseminate these findings to a broader group of people responsible, in part at least, for managing sites supporting these species. The intention of the workshop was not only to impart our knowledge of *O. reticulata*, but to learn from other people's experiences in managing *Orobanche* populations, and hopefully to examine ways in which the conservation and the understanding of the ecology of this neglected group of plants could be advanced.

Broomrapes, *Orobanche* L., are an unusual group of plants that are holoparasitic on the roots of other angiospermous plants. The extant understanding of the biology of these plants is largely derived from studies of pest species that parasitise crops, mainly in the Mediterranean region, Africa and the Middle East. The paper given by Headley and Rumsey (1998) gives a review of this extensive literature in so far as it is relevant to the ecology and management of conservationally important species of broomrape. The taxonomy of *Orobanche* is notoriously difficult. These problems, as well as a report on the changing abundance and distribution of the nine species of the genus native to the British Isles were outlined by Fred Rumsey (1998).

The workshop opened with an outline of the status of *O. reticulata* and background to the conservation work by David Knight (1998). The conservation of any organism is crucially dependent on the monitoring of its population size. The sterling monitoring work carried out by Phyl Abbott and Michael Foley (Headley *et al*., 1998a) has important implications for the conservation work described by Colin Newlands and Helen Smith (1998).

The conservation of any organism should be based on a sound knowledge of its autecology. The most pertinent results of autecological investigations carried out by Michael Hughes and Mary Jeavans are also given (Headley *et al*., 1998b). Clearly, much remains to be done before the ecological requirements of this plant are adequately understood, but there is the added complication that the ecology of the host plant has also to be considered; for a common weedy species this is not as comprehensive as one would wish.

Lunch was kindly provided by English Nature, during which discussions proceeded on the problems of monitoring other species of broomrape and the ways in which the conservation of this group of plants could be advanced (Headley *et al*., 1998c). In the afternoon, delegates visited two sites with contrasting habitats and management. The first was at Hook Moor where Kvaerner-Balfour Beatty kindly gave permission for the group to examine the population on the embankments of the A1 near Aberford and the effects of management on it. Here the major M1-A1 link road scheme is being carried out and the full co-operation of the constructors in avoiding any damage to the populations must be commended. The group then made its way to near Collingham where David Smith and Katy Botrell of the East Keswick Wildlife Group guided the party around Ox Close wood and described the different experimental management regimes at the site. After further discussion it was decided that the presentations from the meeting would be of value to others and the following seven papers hope to go some way towards filling gaps in our understanding of the ecology and conservation of British broomrapes.

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TAXONOMIC PROBLEMS IN THE *OROBANCHACEAE* – THE BRITISH PERSPECTIVE

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WHAT ARE THE PROBLEMS AND WHY?

The taxonomy of *Orobanchaceae* is controversial and still largely unresolved. At the outset the recognition of the *Orobanchaceae* as a distinct family is an issue. Also some would treat the *Orobanche* subgenera as currently recognised at a generic level. These issues apart, there are still some intractable problems at the specific level. However, relatively few of these difficulties relate to the small number of taxa present in the British flora. As the British Isles are at the north-western extremity of the distribution of this mainly Mediterranean and south-west Asian 'genus', the number of species present are few and the population sizes are also small (see below).

The widescale morphological reduction as a consequence of parasitism has limited the number of available characters for traditional taxonomic methods. This therefore poses many taxonomic problems in this genus, as it does for most parasitic groups. Plant stature, pigmentation and perhaps other morphological characters depend to an unknown degree on the host plant. This makes them unreliable as taxonomic characters. In order to test the level of plasticity of characters and to determine what is controlled by the host and the environment, it is necessary to carry out controlled experiments in cultivation. The parasite, however, is often difficult to cultivate under controlled conditions. Such experiments are also needed to establish the potential host ranges and reveal any host-preferential or host-specific 'races' in taxa thought to be generalist parasites.

Speciation may be host driven (Norton & Carpenter, 1998). It is possible to envisage a situation whereby a single seed may be dispersed over a long distance and may establish itself on a novel, but just acceptable host. Geographic isolation resulting in repeated selfing, along with strong selective pressures to grow on a particular host, novel habitats and host plants influencing phenology, may all act to reinforce reproductive isolation. This may eventually lead to local 'races' or 'strains' which could be considered good 'biological species', but unless some morphological change from the ancestral stock has also become fixed, they will not be recognised by traditional taxonomic methods. These are termed 'cryptic species'. Host specific, or at least host preferential races, have been demonstrated to exist in *O. minor* (Musselman & Parker, 1982).

Because of the lack of morphological characters and host driven plastic responses it is possible to overlook biologically distinct lineages and, conversely, where easily observed morphological characters are expressed, they may be given too much weighting. In the absence of breeding programmes and cultivation, it is difficult to be sure. The development of a range of molecular methods will undoubtedly provide additional characters and reveal much more about the underlying genetic diversity, breeding systems and gene flow of taxa, all of which may have a profound importance when conservation strategies are being considered.

TAXONOMIC PROBLEMS IN BRITISH *OROBANCHE*

1. *O. reticulata* Wallr.

The first problem, particularly pertinent given the main thrust of these proceedings, relates to *O. reticulata s. lato*. Several taxa have been recognized and treated as various ranks, from full species to varieties, including *O. pallidiflora* Wimm. & Grab and *O. procera* Koch. Yorkshire plants have been ascribed to different segregates by different authors. As a whole, this aggregate is morphologically quite distinct by virtue of its corolla shape and the presence of numerous dark glands on the corolla, a feature shared by very few species. All are parasites of the tribe *Cynarae* of the *Compositae*, perhaps also parasitising *Dipsacaceae* and others in the Balkan part of their range.

Some central European authors suggest that ecological, host and general distributional differences exist between these entities (e.g. Kreutz, 1995).

The following taxonomic questions therefore need to be addressed:

- do we have more than one taxon in the British Isles?
- to which of the recognized segregates do our plants belong?
- are these segregates good species, or what rank do they deserve?

Preliminary studies suggest that the few British populations are of a single taxon. Marked differences in the extent of the pigmentation and to a certain extent nomenclatural confusion may have led to the suggestion that several entities were present. British plants have the very characteristic corolla shape and general stature of the more lowland *O. procera*, which Foley (1998) suggests is best treated as a subspecies of *O. reticulata*. Further work is clearly desirable to clarify this situation. However, other taxonomic issues in the genus, particularly with the *O. minor* agg., should have a far higher priority.

What is of high priority with regard to *O. reticulata* is a survey of genetic diversity, comparing material from the British sites with each other, within sites, within areas and with continental material. This would make it possible to test the ideas of lower genetic variation in the smaller populations and the idea of metapopulations within river systems (Headley *et al.*, 1998). It is likely that genetic variation is low in the more isolated populations, such as Cow Cliff pasture, due to past genetic bottlenecks and inbreeding. Conversely, some apparently small populations may maintain considerable genetic variation due to the presence of seed banks and some outbreeding and gene flow. This has the potential to be an exciting, small, hence achievable and yet not an overly expensive project.

2. *O. minor* L.

The *O. minor* aggregate probably poses the most difficulties within the genus, both from a British and European viewpoint. Within Britain, four taxa have been accorded varietal rank under *O. minor s. stricto*, one almost restricted to the British Isles, and for many years treated as a species as *O. maritima* Pugsley. It was included in the last edition of the U.K. Red Data Book (Perring & Farrell, 1983) and its distribution, etc. is given in *Scarce Plants in Britain* (Stewart *et al.*, 1994). This has been much confused with forms of *O. minor s. stricto* growing in maritime habitats and to a lesser extent with *O. picridis* where they co-exist in Kent. Old records, and some new, must therefore be treated with caution. This exclusively maritime taxon predominantly parasitises the south-west coastal subspecies of *Daucus carota*, ssp. *gummifer*. This, like the parasite, is a rather weakly morphologically differentiated taxon, split from a widespread variable species, but with a distinct ecology and geographic circumscription. '*O. maritima*' undoubtedly grows elsewhere along the Atlantic seaboard of Europe as material referable to this taxon was seen growing on the Cape St. Vincent, Portugal by the author in April 1995. Its rank may need to be re-assessed following any molecular work. Its demotion to varietal rank was largely a pragmatic approach to the problems of trying to differentiate it on purely morphological grounds and the very poor herbarium specimens in most cases. Chater and Webb (1972) suggest that it may be intermediate between the '*minor*' and '*artemisiae-campestris*' aggregates. There is no evidence for this supposition.

The correct name for plants included in British floras under var. *flava* E. Regel requires further research. All *Orobanche* species produce plants that are lacking in the purple pigmentation which can mask any underlying paler pigmentations. Assuming this has a genetic cause, it is possible that this character could become fixed in certain populations, even if it is a recessive mutation, following selfing and no significant gene flow to the var. *flava* population from 'normal' populations. Confusion with albino plants must be avoided. The suggestions that albino plants are found growing on injured or inappropriate hosts are based on ignorance of the mechanisms involved in plant metabolism and biosynthesis of plant pigments.

Yellow *O. minor* plants have been recorded from East Anglia and scattered localities throughout the geographic range of the normal type, but populations of these plants rarely persist. The British *locus classicus* of var. *flava* is the St. Ouens area of Jersey. Material from here may not be identical with most British yellow plants and are perhaps a pigment-less form of var. *maritima*. Though widely collected last century, similar plants have not been seen at this locality for over 50 years. Superficially similar plants still grow in the Newport Docks, Gwent and this population warrants further investigation.

O. minor var. *compositarum* Pugsley is a rather poorly defined taxon, separated on weak morphological grounds. Its distribution is unclear, most particularly its extra-British range, as most continental authors have not recognised or accepted it. It appears that Pugsley (1940) described it to accommodate plants of *O. minor* that approached *O. picridis* in some characters, and could be found on similar composite hosts. The narrow sub-erect corollas which typical material of this variety shows can, however, be found on plants parasitising legumes. Changes in corolla attitude occur in most plants of *O. minor* after anthesis and during seed maturation, such that the corollas are eventually somewhat sub-erect. It is suspected that this taxon has become something of a nomenclatural dustbin for specimens that do not fit neatly into a clear taxon; it is doubtful that it is worthy of recognition at varietal rank, but again work is needed before such a conclusion can be reached.

The typical variety of *O. minor* is a very variable plant, and as populations tend to be ephemeral, it makes it difficult to re-examine the consistency of characters within a population from year to year, let alone in individuals. It is considered to be an introduction in Ireland and much of central Europe and may well be so in Britain. A more convincing case for native status could be argued for *O. minor* var. *maritima*. Many areas in southern Europe have morphologically distinct and often host preferential races, where this taxon *s. lato* is more or less uniform; for example, in Mallorca plants primarily parasitize *Galactites tomentosa* and have a distinctive appearance, approaching another poorly known segregate *O. calendulae* Pomel in appearance. In Britain it can be hypothesized that populations of *O. minor* are survivors of repeated introductions from diverse sources elsewhere in its range. Cleaner seed and greater pesticide use over the last 40 years or more have slowed this input. A limited range of the genetic diversity present in this species may have been imported, i.e. a few strains particularly associated with definite crop hosts, such as *Trifolium* spp. The source populations were probably geographically isolated prior to their introduction to Britain, and the subsequent hybridization would create new patterns of diversity in morphology and host range. The possibility of hybridization with other taxa should also be considered, and indeed specimens that suggest possible hybridization between *O. minor* and *O. picridis, O. reticulata* and *O. crenata* have been observed. The artificial hybrid *O. minor* x *O. reticulata* was made by Mike Jones, demonstrating the possibility of such a cross (Jones, 1989). Furthermore, chromosome counts of some Mediterranean taxa would indicate that polyploidization has played a role in broomrape speciation (Valdes *et al.*, 1987). Whether these tetraploids are of an auto- or allopolyploid nature remains to be determined.

3. *O. hederae* Duby

One other taxa in the *O. minor* aggregate of concern from a British perspective is *O. hederae* Duby. This is a widespread and predominantly western parasite of ivy, especially the tetraploid *Hedera hibernica. O. hederae* differs in small, but more or less constant morphological characters from *O. minor* and has only ever reliably been recorded parasitizing members of the *Araliaceae*, whereas *O. minor* has rarely been found on *Hedera*. It is still questionable whether *O. hederae* should be given specific or subspecific rank, given the small morphological differences between it and *O. minor*.

4. *O. artemisiae-campestris* Vaucher

O. artemisiae-campestris resembles *O. minor* in being an aggregate of closely related, morphologically poorly distinguished taxa. This has been compounded by nomenclatural wrangling as the laws of priority despatch well known names, adding to confusion. Vaucher's name should in any case be rejected as a polynomial as the hyphen does not appear in the original publication (Vaucher, 1827). This is not just a lapse as he consistently used polynomials derived from suspected hosts to name his taxa. The British *O. artemisiae-campestris* is of the taxon which most central European authors accept at species rank as *O. picridis* F. W. Schultz. This was the name used in earlier British floras, but was found to be pre-dated if the taxa were treated in an aggregate sense, first by *O. loricata*, then the atrocious *O. artemisiae-campestris*. This latter taxon, in its restricted sense, is a parasite of *Artemisia campestris* and is much more geographically and ecologically restricted than *O. picridis*, which finds its northern-most limit in Britain. The proximity of *O. minor s. lato* in the Kent sites may be cause for concern if indeed the two do hybridize. Further work is clearly needed here.

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THE STATUS OF *OROBANCHE RETICULATA* WALLR. IN THE U.K. AND THE BACKGROUND TO THE WORK CARRIED OUT UNDER THE SPECIES RECOVERY PROGRAMME

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Thistle broomrape (*Orobanche reticulata* Wallr.) is a rare plant of limited distribution within Britain and is classified as 'endangered' in the *British Red Data Book of Vascular Plants*. It is listed in schedule 8 of the Wildlife and Countryside Act 1981 and is accordingly afforded legal protection under section 13 of the same Act. A number of Sites of Special Scientific Interest have been designated either solely or partly because of the presence of this species.

In Britain, thistle broomrape is confined to Yorkshire, and is largely restricted to the narrow strip of magnesian limestone within it (Fig. 1). Such a distribution would seem to make it a suitable species for championing or adoption by Yorkshire natural history or nature conservation bodies. However, like other British broomrape species, the profile of thistle broomrape has, hitherto, not been commensurate with the species' conservation

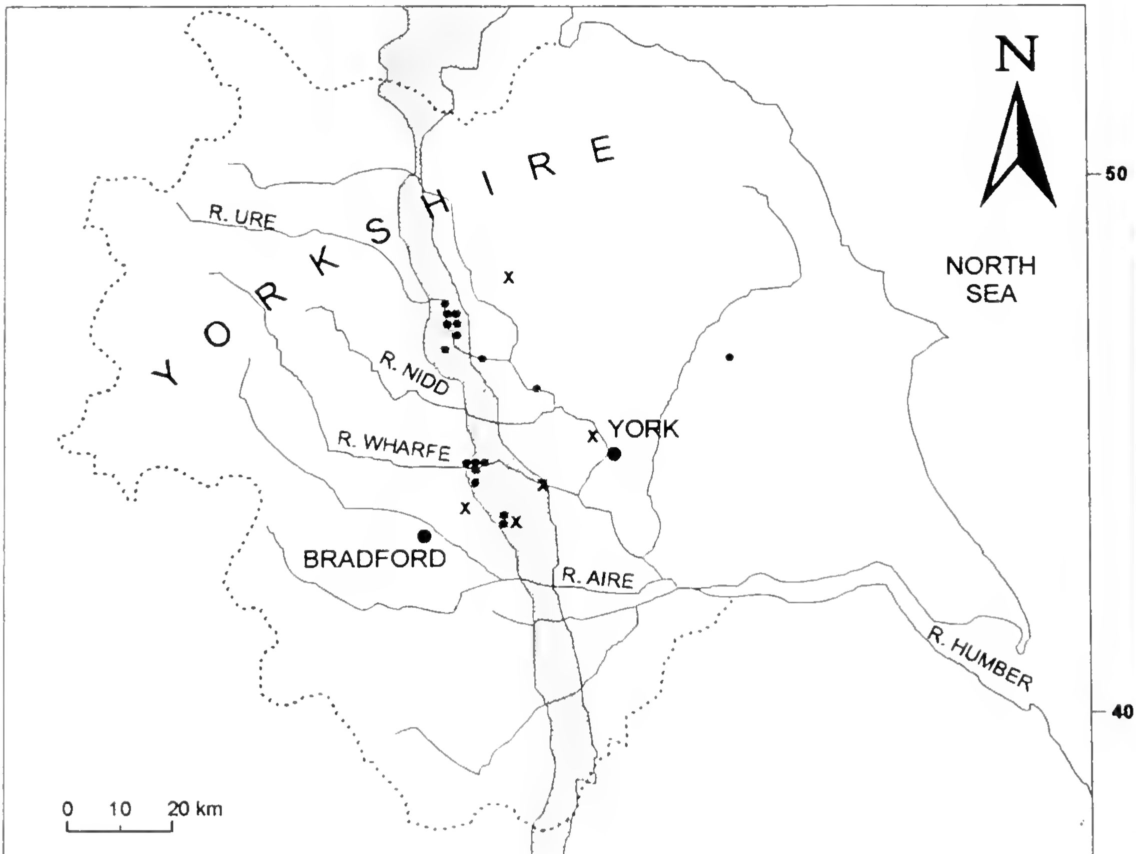

FIGURE 1
Map based on Foley (1993) showing the distribution of *Orobanche reticulata* in Yorkshire in relation to the major rivers and the band of magnesian limestone (shaded area). Solid circles represent extant localities in 2 km x 2 km squares and crosses represent colonies presumed extinct.

status. Although it is listed with proposed targets for its conservation in 'Biodiversity Challenge' (Anon., 1993), it is not listed in the sequel, 'Biodiversity Challenge (second edition)' (Anon., 1994), and within 'Biodiversity: The UK Steering Group Report, Volume 2: Action Plans' (Anon., 1995) it appears only on the 'long list' of 1,250 species, along with bluebell (*Hyacinthoides non-scripta*), great tit (*Parus major*) and roe deer (*Capreolus capreolus*).

There are a number of aspects of the species which make it 'difficult' and undoubtedly contribute to its apparent low ranking in terms of conservation concern. Firstly, *O. reticulata* was not discovered as a British species until 1907. This in itself reflects difficulties in the identification and taxonomy of the genus *Orobanche*, many of which still await clarification and resolution (Rumsey, 1998). It also means that there is no reliable body of historical records against which contemporary distributions can be compared.

Secondly, because of its parasitic nature, the plant appears only as a flowering spike during the summer months. Although the dead spikes frequently persist through the winter months, the living plant is ephemeral, and opportunities to see it in the field fully developed, in a reliably identifiable state, are limited.

As a parasite of thistles, and particularly creeping thistle (*Cirsium arvense*), thistle broomrape grows in greatest concentrations in the vicinity of thistle stands, making thorough surveying and monitoring an uncomfortable experience! These thistle stands are often within *Arrenatheretum elatioris* grassland (Hughes & Headley, 1996), a vegetation type of negligible interest to naturalists and conservationists alike. A further disincentive is provided at Hook Moor, a key site for the species, where thistle broomrape is found on steep road embankments at a junction on the A1.

A further problem arises from the wide fluctuations in numbers of plants to be found at sites from year to year and the sudden appearance of flowering spikes after years of apparent absence.

In view of the above difficulties, it is perhaps not surprising that, prior to the Species Recovery Project, very little was known about the ecology of thistle broomrape. It was this lack of information that prompted the establishment of the project, when in 1993 tree and scrub encroachment at Hook Moor seemed to pose a threat to the long-term viability of the broomrape population.

Although the project initially concentrated on monitoring population changes in response to site management, it also initiated the first comprehensive surveys for the species. It has subsequently expanded to include a programme of monitoring for key sites; the establishment of fixed experimental management plots; and a growing programme of research into many key areas of the species' ecology. A Species Action Plan has been produced and the partnership of organisations involved in the project publish an annual newsletter to raise awareness about the species and report on the progress of the project and the latest research findings. From the initial handful of enthusiasts, the conservation of thistle broomrape has grown to capture the interest of literally hundreds of people – the newsletter has a national distribution list and a print run of over 200.

The project partnership is grateful to English Nature for its financial assistance, and the commitment of a further three years' grant aid. Although ongoing resourcing of the project is still challenging, the project has achieved significant success in raising awareness and increasing understanding of thistle broomrape as well as achieving the management of key broomrape sites.

Perhaps the work of the partnership between English Nature, various landowners, Leeds City Council, Yorkshire Wildlife Trust, East Keswick Wildlife Trust and the University of Bradford could provide a model for dealing with issues concerning the genus *Orobanche* as a whole.

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MONITORING OF *OROBANCHE RETICULATA* WALLR. POPULATIONS IN YORKSHIRE

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History of Recording

The monitoring of *Orobanche reticulata* Wallr. populations is the most comprehensive for any of the species of broomrape in the British Isles. The site with the longest continuous period of recording and monitoring is that at Ripon Parks in North Yorkshire. The counting was carried out initially over many years by Mrs Janet Deane, a secretary to the Ministry of Defence establishment that owns the land at Ripon Parks and surrounding land. With the exception of 1989, all 14 years of recording have been covered since recording started in 1984. A complete survey of all the North Yorkshire sites was carried out in 1992 (Foley, 1992) and of all sites in West Yorkshire in 1994 and 1995 (Abbott, 1994, 1995). It was not until 1996 that all 27 extant sites were surveyed (Abbott, 1996). Some sites have had intermittent comprehensive or partial surveys of the number of flowering spikes in the 1980s and early 1990s (Abbott, 1991). This includes Quarry Moor, Hook Moor, Linton Common, Keswick Fitts, Carthick Wood and Hetchell Wood. Foley (1993) gives details of the distribution of the species, including the loss of *O. reticulata* from at least three sites in Yorkshire since it was first collected.

Methods

The surveying of populations by Abbott and Foley has been carried out using a 1:10,000 scale Ordnance Survey map for locating the colonies and a standard N.C.C. rare species recording sheet. These are used to help draw sketch maps of the position of individual spikes or groups of spikes at the sites, which are carefully walked up and down to ensure all the potential ground is covered. The time of year at which monitoring is carried out is important: if it is carried out too early, spikes which emerge late in the growing season will be missed and if carried out too late some or all spikes at a site may be destroyed or removed by flooding, ploughing or mowing. Since *O. reticulata* grows in tall herbaceous vegetation, Abbott carried out the monitoring in October when the tall *Arrhenatherum* and *Urtica* had largely died down. This reduced the likelihood of missing spikes in this type of vegetation. There is, however, the possibility of spikes at sites on the banks of the rivers Ure and Wharfe being washed away by autumn floods.

Results and Discussion

Broomrapes are notorious for showing large inter-annual fluctuations in population size, but are reasonably faithful to particular sites for most species. The results of the monitoring of the population size for four different *O. reticulata* sites with the longest periods of recording are shown in Figure 1. This clearly illustrates the large inter-annual variation in population size in all sites covered which are in some cases over three orders of magnitude. This results in arithmetic means of population size over-estimating the effective size of a population; for example, taking the average number of spikes recorded for all sites and years gives a mean value of 63, yet the actual median value is 12.5 spikes per population.

It is therefore recommended that the harmonic mean is calculated from the annual totals to give a realistic estimate of the effective population size of any particular population of broomrape (Caughley & Gunn, 1996). Table 1 shows the arithmetic and harmonic means for the sites with at least four years of data. The harmonic mean, N_{eg}, is calculated using the following formula, where is n is the number of years the population was censused and N_i is individuals recorded in the ith year.

$$N_{eg} \approx n \div \sum_{i=1}^{n} (1 \div N_i)$$

If there is a year without any individuals it is necessary to add one to each year's population size before taking the reciprocal. If this is carried out, one has to be subtracted from the the final value obtained at the end.

TABLE 1

The range, arithmetic and harmonic means of the number of flowering spikes of *Orobanche reticulata* at the largest and mostly frequently monitored sites in Yorkshire.

Site	number of years	range	arithmetic mean	harmonic mean
Nunwick meadow	3	35 – 113	71	57
Ox Close Wood	5	12 – 787	348	54
Hook Moor	9	12 – 555	232	53
Cow Cliff pasture	11	0 – >1000	153	23
Hetchell Wood	9	3 – 47	14	7
Ripon Parks	13	1 – 748	78	5
Keswick Fitts	8	6 – 74	25	5
Quarry Moor	8	0 – 81	19	2
Linton Common	8	0 – 34	9	2

The results of this analysis show that only three sites have effective population sizes of just over 50 spikes. According to the 50/500 minimum viable population rule (Frankel & Soulé, 1981), these populations stand a 95% probability of surviving for 100 years. The other sites are more likely to suffer significant inbreeding (>1%) and consequent loss of genetic variation. This principal, however, probably does not apply to a plant that relies on a persistent and probably large dormant seed bank for recruitment.

Figure 1 shows that there are no consistent patterns between years across sites; for example, 1995 was a hot, dry summer, but it did not result in peak numbers of flowering spikes across all sites. This suggests that climate is not a primary and over-riding factor controlling flowering in this species. Statistical tests were carried out to examine whether

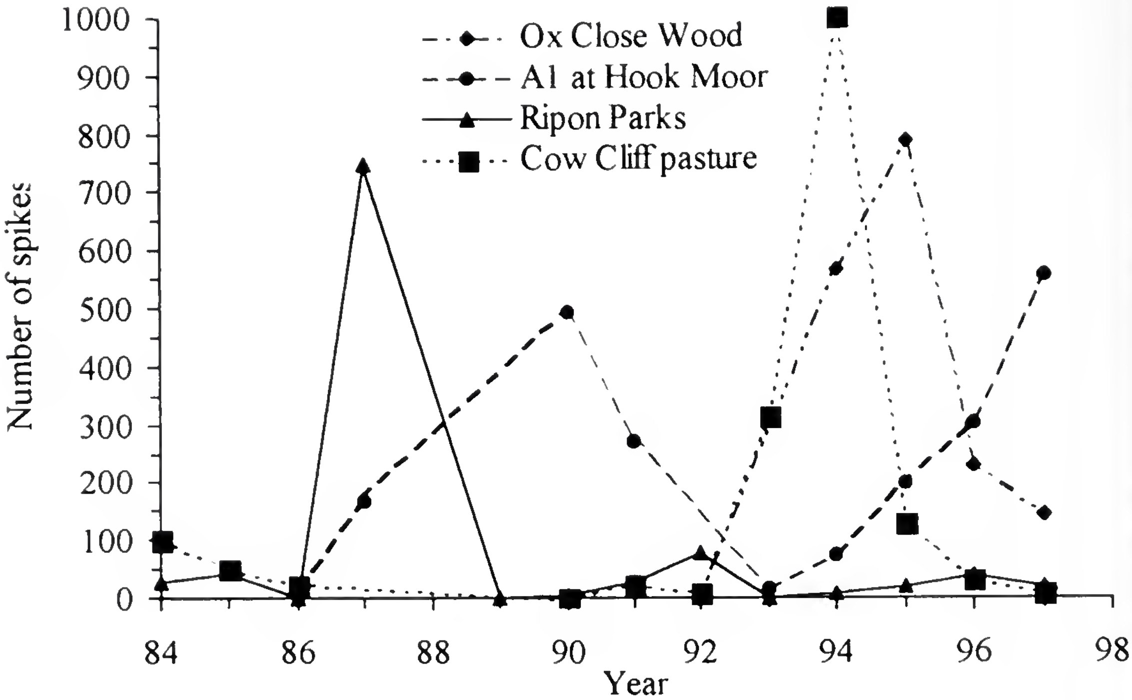

FIGURE 1
Changes in the flowering population size (number of spikes) of four populations of *Orobanche reticulata* in Yorkshire.

the number of flowering spikes at three *O. reticulata* sites (Hook Moor, Cow Cliff pasture and Ox Close Wood) were related to selected climatic variables (monthly mean minimum and maximum temperatures, monthly precipitation, monthly number of dry days and total monthly hours of sunshine) collated from the nearest meteorological station (Durham). The results of this analysis showed that none of the climatic variables in the summer had a significant effect on the population size. There are, however, significant positive correlations between increasing September precipitation and the size of the Cow Cliff pasture population, January precipitation and the Ox Close Wood population, and a significant negative correlation between April precipitation and the size of the Hook Moor population.

Given the distribution of sites of *O. reticulata* in Yorkshire along the banks of the rivers Ure and Wharfe and the small size of the seeds, it is likely that there is considerable input of seeds downstream along these notoriously 'flashy' watercourses. Thus one might suggest that the many small populations along the rivers are effectively two larger and more widely dispersed populations or metapopulations with occasional exchange of genetic information between the sub-populations along the banks of the river (Fig. 2). If this is the case then there are effectively between 6 and 8 populations in the whole of Yorkshire: Hook Moor, Cow Cliff pasture, Hetchell Wood, R.Wharfe, R.Ure and Quarry Moor. Ox Close Wood and Linton Common are well above the flood-plain of the river Wharfe, yet are very close to extant populations along the banks of the Wharfe and may therefore act as source populations.

Although it would be ideal to determine the number of tubers present at certain sites in order to ascertain the proportion of those that flower, such a procedure would be highly destructive. It might be argued that the number of flowering spikes is not a reliable means of determining population size as many tubers may not flower each year and perennate one or more years before flowering. However the number of flowering spikes and hence seed

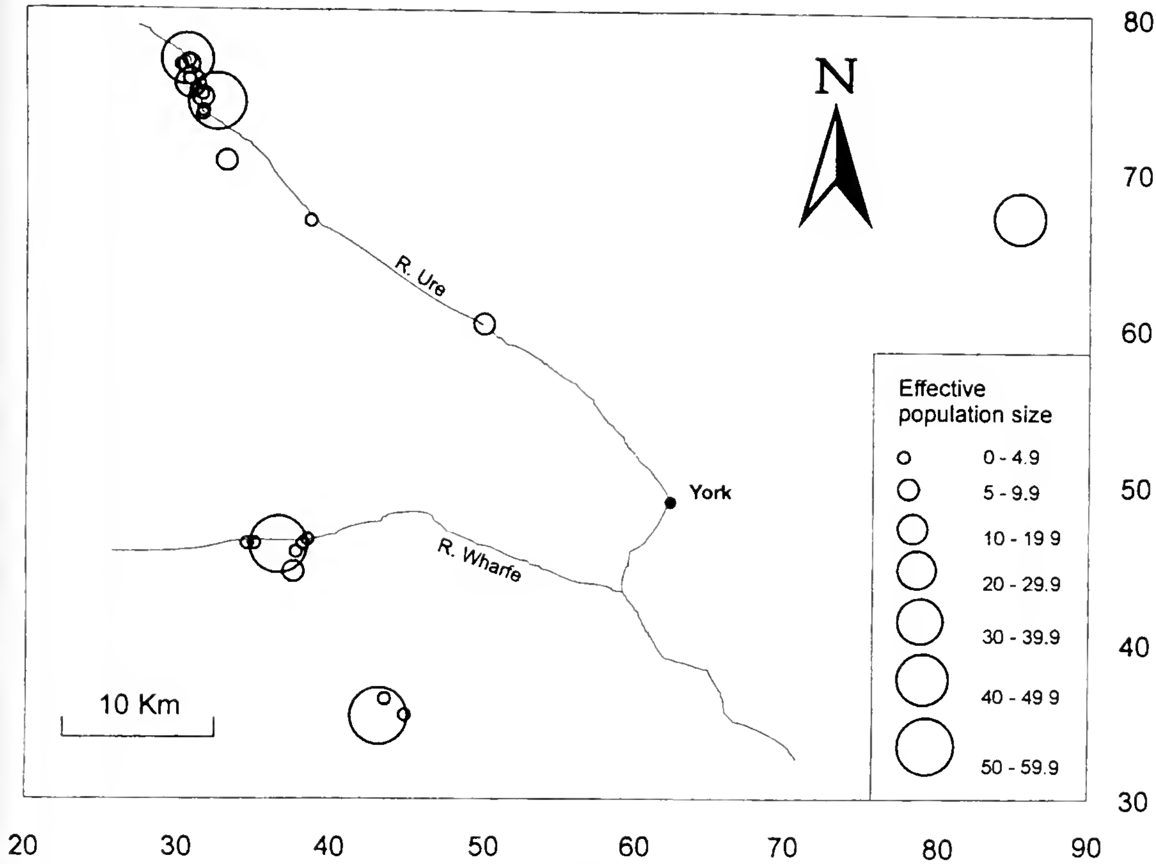

FIGURE 2

Map showing the location of populations of *Orobanche reticulata* in Yorkshire in relation to the rivers Wharfe and Ure and their effective size based on harmonic means of the number of flowering spikes.

output is the most important determinant in maintaining and replenishing the seed bank which is almost certainly the key factor in the persistence of any population.

Conclusions

- Counting flowering spikes is the only effective way of estimating population sizes of broomrapes.
- Monitoring of populations by counting flowering spikes infrequently may over- or under-estimate the size of a population due to the large inter-annual variation in flowering.
- Counting flowering spikes at the end of the flowering season is recommended to avoid missing flowering spikes that emerge late in the season.
- Calculating the average size of the flowering population of broomrapes using arithmetic means over-estimates the effective population size and the calculation of the harmonic mean is strongly recommended.
- The number of effective populations of *O. reticulata* could easily be much lower than the number of recorded sites due to metapopulation dynamics whereby much smaller sink populations are only maintained by significant dispersal of the minute seeds down rivers from larger source populations.

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SOME ASPECTS OF THE AUTECOLOGY OF *OROBANCHE RETICULATA* WALLR.

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INTRODUCTION

Our knowledge of the biology and ecology of broomrapes is heavily biased towards those which are serious crop pests in the Mediterranean, Africa and North America (Headley & Rumsey, 1998). This has meant the biology of infection of crop plants has been intensively studied and other aspects of the life-cycle, especially in non-pest species, is sadly lacking. An examination of certain aspects of the ecology of broomrapes was covered by Jones (1989), but again this is limited in its coverage of the ecology and biology of the rare broomrapes which is critical to their conservation. Michael Hughes initially examined the biogeography of *O. rapum-genistae* and *O. elatior* using GIS in an undergraduate dissertation in 1994/95 (Hughes, 1995a) and later carried out an autecological examination of *O. reticulata* with help from the College and Environment Link (CEL) scheme. It was clear from this work that factors governing germination of *O. reticulata* seeds and their infection of host plants was the critical stage governing population sizes of this plant. This was taken up by Mary Jeavans as an undergraduate project on the seed biology of *O. reticulata* in 1995/96 (Jeavans, 1996) which was extended into the late summer and autumn of 1996 with funding from the Species Recovery Programme.

The general biology and ecology of *Orobanche* is given by Headley and Rumsey (1998); broomrapes are, however, root holoparasites of a wide variety of mainly dicotyledonous plants (Kreutz, 1995). This means that their life-cycle is somewhat different to most angiosperms and it is summarised in Figure 1 with the critical processes and factors thought to be important in controlling population size indicated.

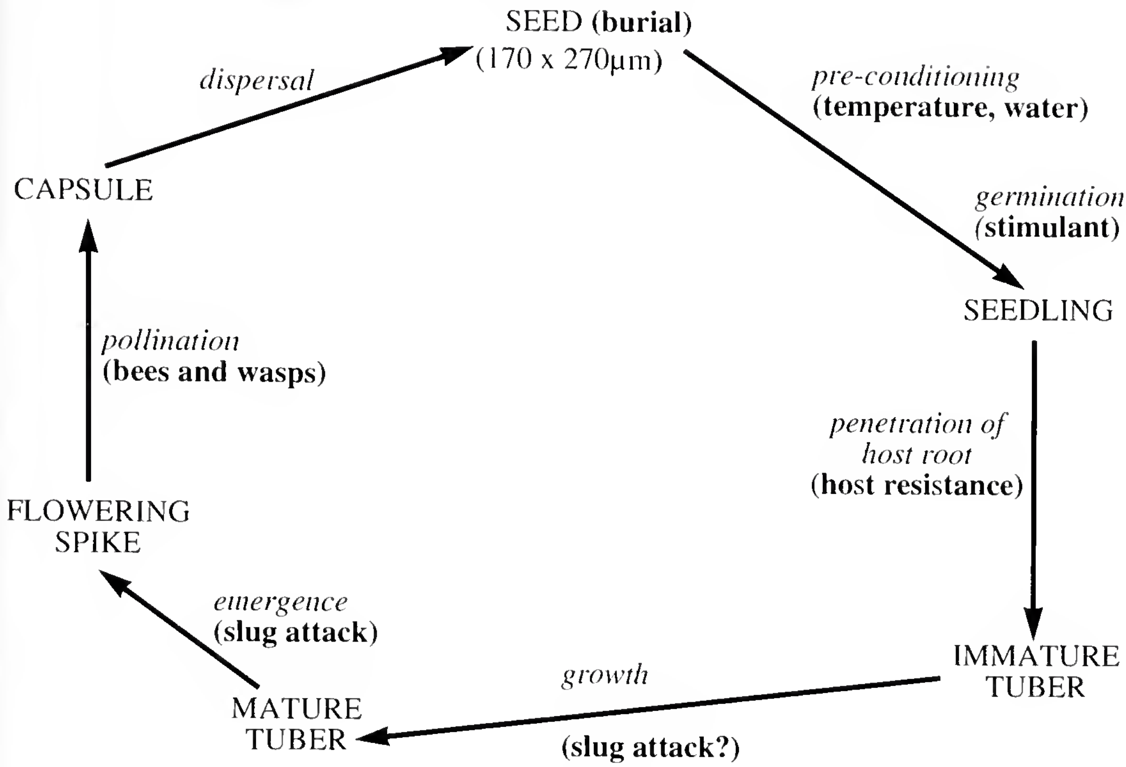

FIGURE 1
Generalised life-cycle of broomrapes with factors (bold) known to affect processes (italics) in the transition from various stages (capitals).

Results and Discussion

Geology and Soils

Although many sites for *O. reticulata* are found on magnesian limestone in Yorkshire, many of them are on deep layers of river or glacial alluvium in the flood-plains of rivers or other soil types (Table 1). The soils vary from undifferentiated alluviums to rendzinas and calcareous brown earths.

TABLE 1
The Total Number of Sites and their Conservation Status with different Lithologies and Soil types.

Lithology	Soil Type	Total No. of sites	No. of SSSIs	No. of Reserves
Magnesian limestone	calcareous brown earth	6	4	2
Magnesian limestone	rendzina	1	1	1
Chalk	rendzina	1	1	0
Fluvio-glacial deposit	alluvium	19	6	1

The texture of the soils where the plant is found today is typically a sandy loam or sandy soil. Despite being sandy the soils are calcareous with low to moderate amounts of total nitrogen and plant-available potassium and phosphate (Table 2). The restriction of the plant to particular soil characteristics might well be a reflection of the suitability with which a whole set of conditions make it possible for the parasite to infect its exceedingly common host plant, *Cirsium arvense*.

The restriction of *O. reticulata* largely to soils with a high pH (Table 2) is perplexing as the parasite is not dependent on the soil for any of its nutrients and its host plants are widespread on a wide range of soil types. It is possible to generate a number of hypotheses for such a relationship. These include (a) the higher pH soils may make the host thistles elicit the correct stimulus for germination of the *O. reticulata* seeds, or (b) it may make the host plant more susceptible to infection, or (c) these soils have factors, such as large populations of rabbits, which are correlated with calcareous sandy soils which then makes them suitable for establishment of this parasite on its host plant.

The concentrations of major plant nutrients in the soil are at the lower end of the range normally found in soils (Allen *et al.*, 1989). This is particularly the case for total nitrogen and exchangeable potassium. Not suprisingly, the concentrations of calcium are at the top of the range and are typical for soils derived from a calcareous bedrock. Low nutrient status soils and hence nutrient stressed plants are allegedly more susceptible to infection by parasitic plants in sub-tropical areas, but this has yet to be tested with any of the British species of broomrape.

TABLE 2

Some characteristics of 19 soil samples collected from 14 of the extant *Orobanche reticulata* sites in Yorkshire.

Soil Characteristic	Range	Mean ± S.E.
pH	4.9 – 8.0	7.4 ± 0.2
total nitrogen (% dry wt.)	0.04 – 0.79	0.30 ± 0.04
plant-available phosphate (ppm)	3.5 – 28.1	11.9 ± 1.6
exchangeable potassium (ppm)	3.74 – 45.5	13 ± 2.5
exchangeable-calcium (ppm)	750 – 7,500	3,200 ± 300

Vegetation Type

The plant is found in two main types of vegetation (Hughes & Headley, 1996). Most sites are grasslands of the *Arrhenatheretum elatioris* type (MG1 of the National Vegetation Classification or NVC). This very common grassland is the type of community in which *O. reticulata* occurs on the banks and flood-plains of the rivers Ure and Wharfe. It is, therefore, not suprising that the *Urtica dioica* sub-community (MG1b) is present at these sites due to the relatively high nutrient status of the soil. At Hook Moor, however, the community is more species-rich and can be placed in the *Centaurea nigra* sub-community (MG1e) of the *Arrhenatheretum*. The woodland sites at Hetchell and Ox Close woods are of the *Fraxinus excelsior-Acer campestre-Mercurialis perennis* woodland community (W8). However, *O. reticulata* is found in the clearings within the woodland sites where the understorey is typically dominated by *Mercurialis perennis* and it has a greater affinity to a *Rubus fruticosus-Holcus lanatus* understorey community (W24).

Seed Output

Spikes of *O. reticulata* have approximately 50 flowers per spike and there are about 1,000 to 2,000 seeds per capsule (Hughes & Headley, 1996). This means that the seed output of *O. reticulata*, like other broomrapes, is very large (Salisbury, 1942) and is in the order of 100,000 to 200,000 per flowering spike. The seeds are small (0.17 x 0.27 mm) and thus easily dispersed in air, water and mud or dust, by animals and humans. Thus, the distribution of broomrapes could represent the random dispersal of seeds over long distances by various agents, including humans, rather than a reflection of a set of specific abiotic and biotic factors which provide the correct niche for the species. The clear association of this species with the magnesian limestone area of Yorkshire counters this argument to a certain extent.

Seed Germination

Germination of the seeds of *O. reticulata* was achieved after pre-conditioning them for 6 days at 25°C on moist filter paper in the dark (Brown *et al.,* 1951; Sunderland, 1960; BarNun & Mayer, 1993). Extracts of fine roots of *C. arvense* stimulated germination at temperatures between 10 and 25°C, but the optimum temperature for germination was found to be 15°C (Headley & Jeavans, 1996). The seeds take between 14 and 45 days to reach maximum germination, depending on the temperature (Headley & Jeavans, 1996). Although all the experiments presented here were carried out in the dark, it was found that light did not inhibit germination in a few petri dishes that were accidentally left out on a bench.

Extracts from roots greater than 5 mm in diameter did not stimulate any germination, nor did gibberelic acid or a linseed root exudate which has been found to contain strigol by BarNun & Mayer (1993). There is a general decline in the germination of the seeds with increasing size of the *C. arvense* plant from which the fine root extract was taken (Fig. 2).

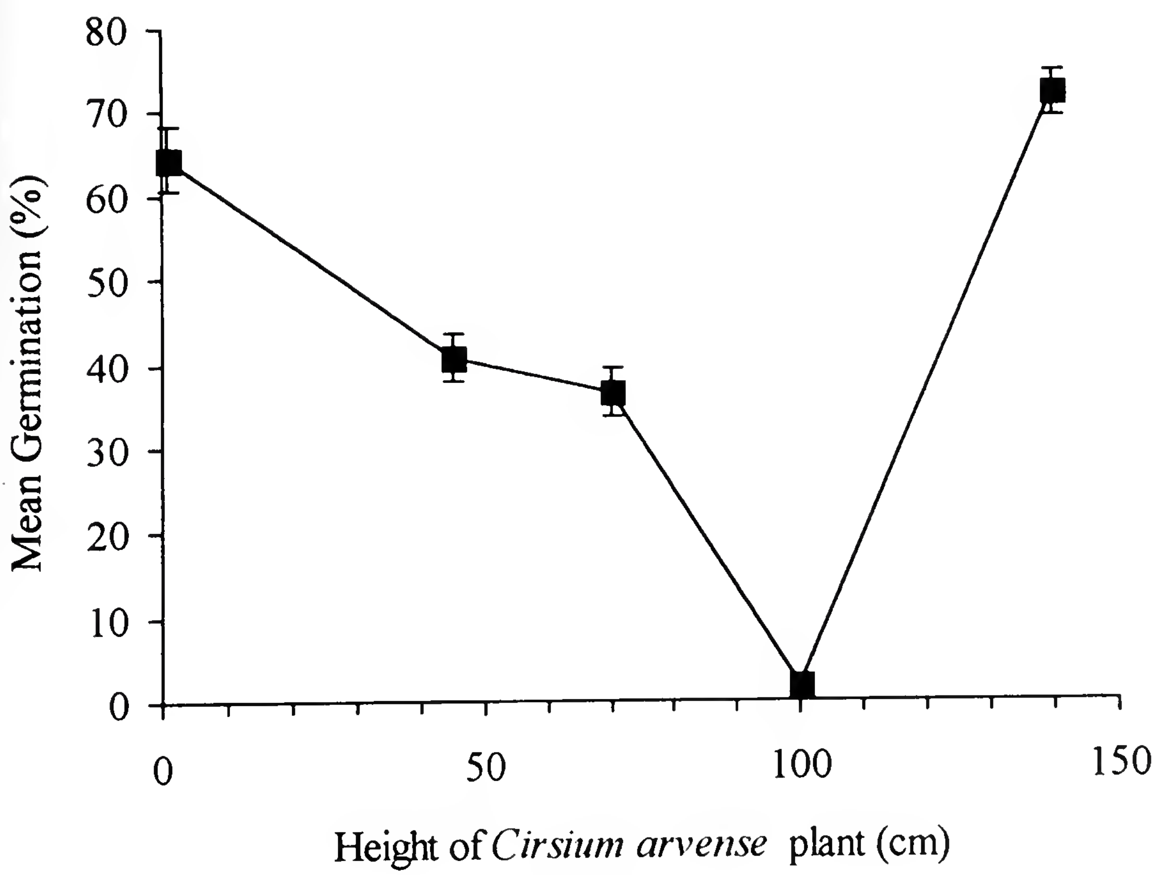

FIGURE 2

The mean germination (% of seeds with embryos) of *Orobanche reticulata* seeds treated with 1% aqueous extracts of fine roots (diameter < 0.5 mm) taken from *Cirsium arvense* plants of different heights (cm). Means of at least 150 seeds with embryos and bars represent standard errors.

Unfortunately, the trend is not significant due to the largest *C. arvense* plants stimulating the highest germination of *O. reticulata* seeds (Fig. 2). The field observations that *O. reticulata* is not found in the tallest and densest stands of *C. arvense* (Table 3) lends support to the hypothesis that it is young thistle plants that are more often parasitised. However a number of alternative explanations can be given for the observations in Table 3. It is possible that where there is disturbance, new roots are produced by existing thistles or that the opening out of the surface allows *Orobanche* seeds to reach the soil surface and thus be washed into the rooting zone, as opposed to being stuck on a mat of leaf litter. Whatever is the most appropriate explanation for this phenomenon, it appears that maintaining a relatively open sward with areas of bare soil is almost certainly beneficial for the establishment of thistle seedlings and roots for infection by *O. reticulata.*

TABLE 3

The density (m^{-2}) and mean height (cm) of all *Cirsium arvense* plants in 1 m^2 plots with or without the parasite *Orobanche reticulata. C. arvense* plants that were being parasitised by one or more spikes of *O. reticulata* were excluded from the observations. Parasitised *Cirsium arvense* plants have a mean height of 26 cm.

Cirsium arvense	*Orobanche reticulata*	n	range	mean ± S.E.	t-test
height (cm)	present	117	4 – 145	60 ± 3	16.15
	absent	173	9 – 165	116 ± 2	P<0.001
density (m^{-2})	present	13	4 – 20	9 ± 1.4	2.26
	absent	13	6 – 19	13.2 ± 1.2	P<0.05

There is a highly significant effect of the species of thistle from which the root extract is taken in affecting germination of *O. reticulata* seeds (Fig. 3). The two commonest species of thistle, *C. arvense* and *C. vulgare*, stimulated the greatest germination, with lower rates for other species of *Cirsium* and *Carduus*. This observation confirms field observations in 1995 that only 4 out of 414 *O. reiculata* appeared not to be parasitising *C. arvense*. With the exception of *C. vulgare*, this might in part reflect the relative abundance of the different host species. It does not however explain why the perennial *C. arvense* is parasitised more often than the equally common biennial *C. vulgare*. Although extracts of thistle roots does not necessarily mean that the intact plant will necessarily be susceptible to infection by the *O. reticulata* seedlings or that the correct stimulant is exuded from the roots in the correct quantity.

The presence of a significant correlation between the number of spikes at the Cow Cliff pasture site and the total rainfall for September of the previous year suggests that the life-cycle might in fact be annual (Fig. 4). This is supported by pot grown plants of other British *Orobanche* normally emerging within a year of being sown. The requirement for a relatively warm moist soil for satisfactory pre-conditioning of *O. reticulata* seeds provides a mechanistic explanation for the relationship shown in Figure 4. The satisfactory establishment of thistle seedlings and/or thistle root growth may also be a factor in this relationship.

The seeds of *O. reticulata* from the Hook Moor population germinated on a wider range of thistle root extracts than seeds taken from the Hetchell Wood population. This might imply that the seeds from the Hook Moor population have a greater potential genetic variation. This is likely to be the case given the much smaller effective population size and hence higher probability of selfing and consequent inbreeding of the Hetchell Wood population (Headley & Jeavans, 1996).

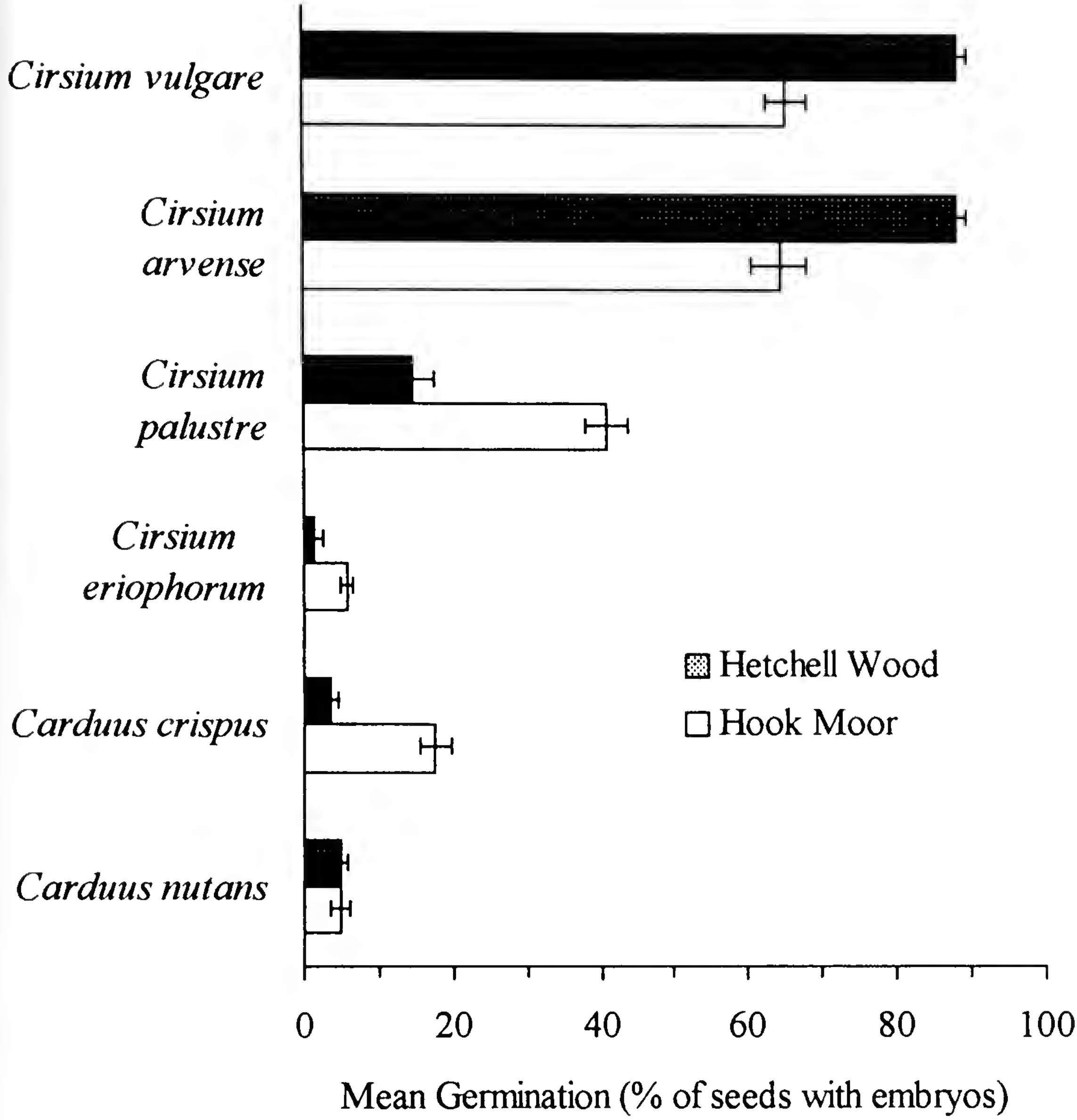

FIGURE 3
The mean germination (% of seeds with embryos) of *Orobanche reticulata* seeds from either Hetchell Wood (shaded bars) or Hook Moor (open bars) treated with 1% aqueous extracts of fine roots (diameter <0.5 mm) taken from 3 week old seedlings of different species of thistle. Means of at least 150 seeds with embryos and bars represent standard errors.

The radicles of *O. reticulata* died once they reached 2 mm in length, which is presumably due to exhaustion of the carbohydrate reserves in the seed. Thus seeds of broomrapes must germinate immediately next to the root of their potential host plant. The germinability of the seeds kept in a laboratory at room temperatures lost only 30% of their germinability over a 10 year period (Fig. 5). Seeds kept at the Millenium Seed Bank at Kew Royal Botanic Gardens had lost 35% of their potential germinability over only a 3 year period (Fig. 5).

Seeds collected from herbarium specimens that were between 42 and 118 years old did not germinate, but some seeds from an eight year old herbarium specimen did germinate (Fig. 5). Although the seeds from old specimens did not germinate, they still had viable

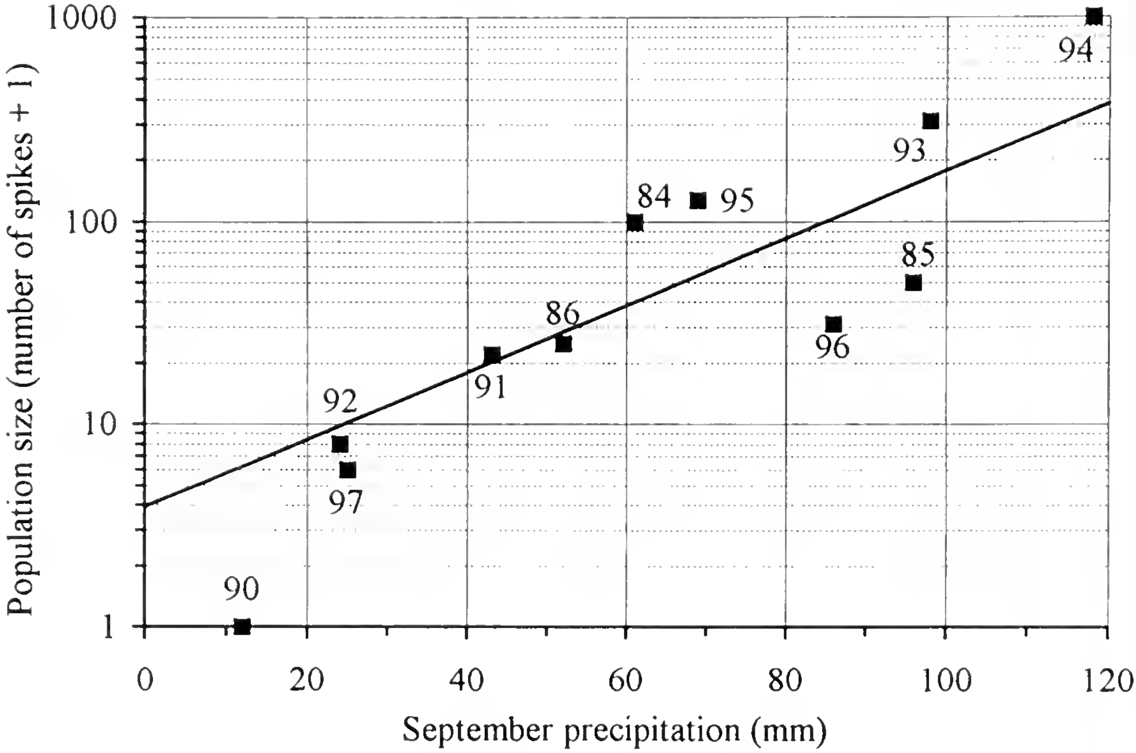

FIGURE 4
Scatter plot of logarithm of population size (number of flowering spikes +1) of *Orobanche reticulata* at Cow Cliff pasture and the total September precipitation (mm) recorded at the nearest available meteorological station (Durham) in the previous year. 90.2% of the variation in population size is accounted for by following equation:
Ln no. of spikes + 1 = 3.2025 + 0.0171*September ppt - 0.2013*October max. temp.
Numbers next to points indicate year in which census was undertaken.

embryos present, as detected using a fluorescein stain (Pritchard, 1985). There is every possibility such herbarium specimens require a longer pre-conditioning period before they will germinate. The implications of this are profound in suggesting that sites where broomrape spikes have not been seen for many years could be resurrected from a dormant seed bank being present in the soil. The seeds of other broomrapes have been estimated to have a longevity in the soil of up to 100 years. This may well have happened at the Ox Close Wood site (Newlands & Smith, 1997; Smith and Bottrell, *pers.comm.*). It may also be possible to resurrect plants with 'old genomes' with seeds from old herbarium specimens from extant or extinct sites.

Seed Bank

If the chances of an *Orobanche* seed coming into contact with its potential host root is the governing factor in determining the size of the flowering population of a broomrape, then it will be the density of broomrape seeds and host roots in the soil that will determine this chance event. For this reason an attempt was made to assess the size of the seed bank of *O. reticulata* at a number of its key sites. The man-power required for the comprehensive sampling, mechanical extraction and counting of the size of the seed bank at a large number of sites is not feasible. An indirect estimate of the presence of a seed bank may, however, be established by growing potential host plants in soils collected from extant or extinct sites.

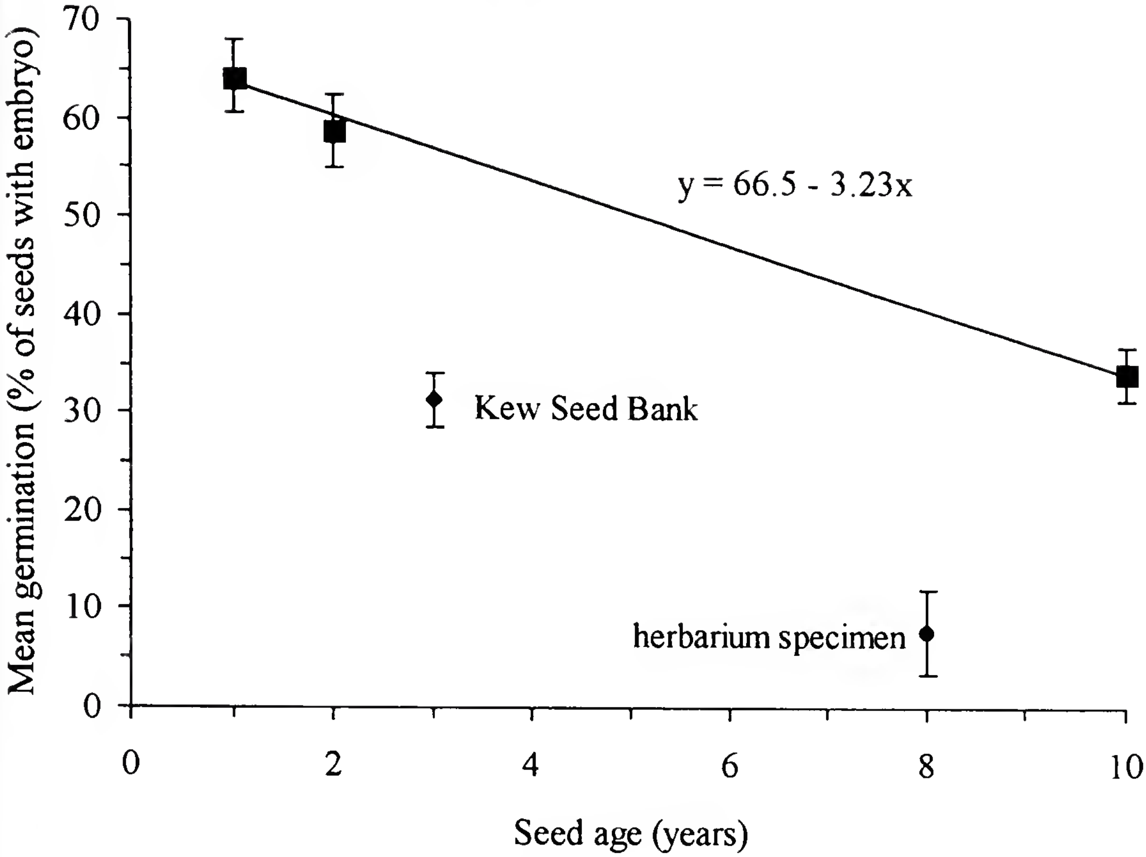

FIGURE 5
The effect of seed age (years) on mean germination (% of seeds with embryos) stored in either the laboratory at room temperature (squares) or at the Kew Millenium seed bank (–20°C and 10% humidity) or from a herbarium specimen kept at Leeds City Museum.

Seeds were extracted from 10 out of the 20 soil samples processed. The numbers varied from 1 to 313 with a median of 5 extracted for those samples where seeds were recovered. Considering the large spatial heterogeneity in seed numbers in the soil it was suprising to find that there is a reasonably close relationship between the mean number of seeds extracted out of a soil sample and the harmonic mean of the number of flowering spikes at the same site (Fig. 6). This relationship is not suprising as the size of the seed bank will depend on the number of flowering spikes that have been produced over many years as the seed bank is cumulative given the likely longevity of the seeds. The feedback loop between flowering and seed bank size indicated in Figure 1 also supports the supposition that the number of flowering spikes produced is dependent on the probability that *O. reticulata* seeds will encounter a thistle root. Therefore to increase the population at a site the number of thistle plants and/or the size of *O. reticulata* seed bank need to be maximised.

Flowering

Despite the circumstantial evidence it is not certain how long it takes for *O. reticulata* to complete its life-cycle *in situ*. Although it is monocarpic the vast majority of the time, a single herbarium specimen had clearly produced spikes in two different years (Rumsey *pers. comm.*). Also spikes that had been cut early in the summer in a strip of set-aside land produced replacement flowering spikes within three weeks of being mown (Hughes, 1995b).

The flowering shoots of broomrape emerge rapidly from the soil, primarily by the expansion of pre-formed cells. This is achieved by the accumulation of high concentrations

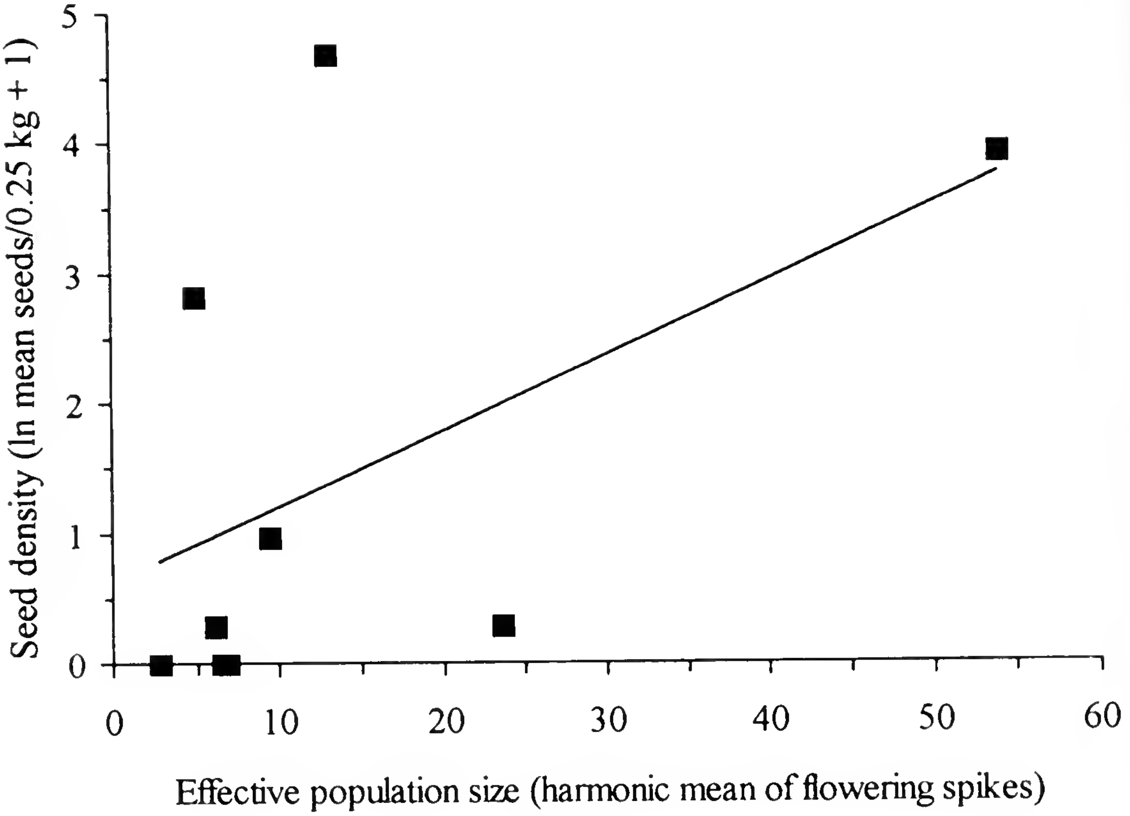

FIGURE 6
The size of the *Orobanche reticulata* seed bank (in mean number of seeds per 0.25 kg soil) and effective population size of *Orobanche reticulata* flowering spikes (harmonic mean) at 9 sites in Yorkshire. Spearmans rank correlation between the two variables ($r_S = 0.85$) is significant at the 1% level.

of sugars taken from the roots of the host plant. The flowering of *O. reticulata* starts in late June to early July. Spikes continue to emerge through July, but individual flowers and flowering spikes set seed within a few weeks. The majority of flowers have died by the end of July, but the occasional spike can emerge late in the season. It is not certain how long the capsules and seeds take to ripen but it is not until September that the majority of capsules are fully ripened.

Pollination

Although wasps and a wide variety of bees have been observed to visit the flowers of *O reticulata* (Jones, 1989) it is not certain whether any of these insects actually affect pollination (Ollerton, *pers. comm.*). The flowers are almost certainly self-compatible and it seems that the flowers affect self-pollination by mechanical means (Rumsey, *pers. comm.*).

Conclusions

Despite the amount of work carried out on this species of broomrape there are many aspects of the ecology of the plant that are not known. This is partly a reflection of the fact that a large part of their life-cycle is underground and therefore makes it difficult to study. The same is true for other parasitic and saprophytic plants which only produce their flowers above-ground, such as *Lathraea squamaria*, *Neottia nidus-avis*, *Corallorhiza trifida*, *Epipogium aphyllum*, *Monotropa hypopitys*, *Botrychium* and *Lycopodium* gametophytes and *Cryptothallus*.

The factors that may be limiting the population size of *O. reiculata* are considered to be the following:

- Size of the seed bank in the soil. (very variable from <1 to 313 per 250 g soil).
- The density of host roots in the soil, which will be affected mainly by the size of the host population and soil nutrient status.
- The presence of the correct stimuli for germination of the *Orobanche* seed and the susceptibility of the host's roots to infection. This in turn depends on the species of host plant, age of root, size of root, water availability, age of seed, temperature and possibly the nutritional status of the host plant.
- Damage to spikes by slugs, sheep and trampling as spikes emerge does occur, but this may not be significant. Some of the flood-plain populations of *O. reticulata* may lose a large proportion of the seed output in autumn floods.
- The burial of the seed in the soil at the correct depth for infection of the host plant is vitally important and disturbance by rabbits, moles, livestock, man and floods may all have an important role to play in this process. The presence of bare ground may be important in this respect. Whether this enables the seeds of broomrapes to enter the soil or whether it allows gaps for the establishment of young host plants or young roots of the host plant to grow into is not clear.

Further gaps in our knowledge of the autecology of broomrapes which may be of significance include the following:

- The species of pollinator and their distribution and abundance with respect to the parasite.
- The ecological requirements of some of the host plants.

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MANAGEMENT AND CONSERVATION STATUS OF SITES WITH *OROBANCHE RETICULATA* WALLR. POPULATIONS

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INTRODUCTION

English Nature's Species Action Plan for *Orobanche reticulata* Wallr. identifies the main threats to the British populations as (a) destruction of the host plant primarily creeping thistle (*Cirsium arvense*); (b) loss of habitat through scrub invasion; and (c) loss to competing land uses (Anon., 1996). The overall objective of the Action Plan is to encourage sympathetic management of sites on which it occurs to maintain and increase the population. The ecological requirements of *O. reticulata* are not yet fully understood, and as a result, site management to benefit the species remains somewhat experimental. The aim of the Plan so far has been to halt natural vegetation succession, for instance from rough grassland to scrub, and create disturbed open ground to maintain stands of *C. arvense*. Funding for some of this work has been through an English Nature Species Recovery Programme grant.

A substantial proportion of the 27 separate extant British populations of *O. reticulata* fall within the boundaries of various nature reserves or Sites of Special Scientific Interest (SSSI) notified under the 1981 Wildlife and Countryside Act, as amended (Table 1). Of these, only two, Cow Cliff pasture and quarry and Hook Moor, were notified specifically on account of the presence of large populations of *O. reticulata*. The other SSSIs were notified in order to conserve a range of habitats associated with the magnesian limestone or riverine habitats. Nevertheless, maintaining the populations of *O. reticulata* on these sites is a key consideration in site management. Additionally, the site at Ox Close Wood in West Yorkshire is a nature reserve owned and managed by the East Keswick Wildlife Trust, and identified as a Site of Ecological/Geological Interest in the Leeds City Council Unitary Development Plan. The remaining 15 sites have no formal conservation status, although in several cases the landowners take an interest in having *O. reticulata* on their land. Therefore, for the majority of the individual populations the opportunity exists to undertake positive management for the species, or influence broader site management to benefit *O. reticulata*.

TABLE 1

The number of sites and proportion of the British population of *O. reticulata* with different levels of conservation status. Effective population sizes are based on harmonic means of the available population census data for all sites.

Conservation Status	No. of sites	British Population Size	
		Effective Size	% of the total
Site of Special Scientific Interest and nature reserve	3	9.4	2.9
Site of Scientific Interest and private nature reserves	1	53.8	16.6
Site of Special Scientific Interest only	8	127.6	39.3
Without any conservation status	15	133.8	41.2

DEVELOPING MANAGEMENT TECHNIQUES

Developing management techniques to favour *O. reticulata* has focussed on six sites, Cow Cliff pasture and quarry, Quarry Moor and Ripon Parks in North Yorkshire, and Hook Moor, Hetchell Wood and Ox Close Wood in West Yorkshire. All provide important opportunities to study the effects of different techniques on *O. reticulata* populations. At Hook Moor and Cow Cliff pasture and quarry, where the only significant claim to conservation status is the presence of *O. reticulata*, this does not conflict with other site objectives. At the others, maintaining *O. reticulata* is only one of a number of nature conservation objectives. Given that the primary host of *O. reticulata* is *C. arvense*, a notifiable agricultural weed species, it is clear that there can be a conflict of interest with other grassland management and restoration objectives. Management practices carried out on the above six sites in recent years are listed in Table 2.

TABLE 2

Management on six sites with populations of *Orobanche reticulata*.

Site	Management
Cow Cliff pasture and quarry SSSI	Scrub removal/rotovation of ground
Quarry Moor SSSI	Scrub removal/cattle and sheep grazing/scraping off topsoil
Ripon Parks SSSI	Scrub removal/sheep and goat grazing
Hook Moor SSSI	Scrub removal/soil ripping
Hetchell Wood SSSI	Mowing/grazing
Ox Close Wood	Mowing/coppicing/clear cutting/grazing

A number of sites on which *O. reticulata* occurs have little or no management. Many are not grazed by domestic stock, and are prone to scrub encroachment. Succession from grassland to dense scrub results in the decline and eventual loss of the host plant. Scrub control was undertaken at Hook Moor, where hawthorn (*Crataegus monogyna*) and gorse (*Ulex europaeus*) had colonised the road embankments. At this site bramble (*Rubus fruticosus* agg.), dog rose (*Rosa canina*) and nettle (*Urtica dioica*) were also cut back, as monitoring of *O. reticulata* showed that these species, growing unchecked, formed dense stands which out-competed *C. arvense*. It has been noted, however, that *O. reticulata* does sometimes parasitise thistles growing under shrubs in rough grass (Hughes, 1996), and amongst scattered bushes of *Crataegus* where the plant tends to occur on thistles on the sheltered, sunny side of the shrub (Abbott, 1996). It has not been recorded growing where the shrub canopy is closed (Abbott, 1996). On this basis, scrub control need not necessarily aim at total eradication to benefit *O. reticulata.*

In managing sites with *O. reticulata* populations it has become evident that ground disturbance is a very important factor. At Ox Close Wood, dead flower spikes of the plant were first noticed in 1992. It is assumed that the species first appeared in 1991, two years after a section of the wood was clear-felled. It is likely that seed was already present in the soil, and the growth of the thistles which colonised the open, disturbed ground in the clear-fell provided the opportunity for it to germinate. The same happened at Hetchell Wood, where the plant appeared in an area coppiced by the Yorkshire Wildlife Trust two years previously. This new site was only a short distance south of the limestone grassland within the woodland where the species has been recorded for many years. Ground disturbance by soil ripping and light rotovation has taken place on some sites, most notably at Cow Cliff pasture where *O. reticulata* showed a large increase in numbers two years after rotovation and a consequent expansion of *C. arvense.*

Where populations of *O. reticulata* occur on sites grazed by domestic stock, such as Ripon Parks, there can be a conflict of interest as stated above. The species-rich grassland is a key reason for Ripon Parks being designated a SSSI and the extensive thistle encroachment is of concern from both a nature conservation and a stock management point of view. Observations from Ripon Parks and Hetchell Wood have confirmed that *O. reticulata* does not do well where the *C. arvense* stands become very dense (Hughes & Headley, 1996). On these grazed grassland sites, a compromise is reached by controlling the thistles to the extent of leaving only small groups or scattered individuals which will not adversely affect the broad management objectives of the site, yet will retain the *O. reticulata* population. It should be noted, however, that sheep at Ripon Parks, and livestock on other sites, have been reported to graze young spikes of *O. reticulata* (Hughes, 1996), although at current levels this is not felt to be a threat to the survival of the population within the SSSI.

In order to investigate the effects of different management techniques, in 1994 a project was set up under the Species Recovery Plan at Ox Close Wood. Five 25 x 25m plots were established in the felled area of the wood where *O. reticulata* had appeared three years previously. Each received a different type of management as follows: (a) mowing the field layer and leaving the woody regrowth, (b) coppicing all trees on a 5-year rotation, (c) grazing with goats, (d) clear-cutting of all vegetation and (e) a control plot with no management.

Response of *O. reticulata* to Management

Monitoring of the *O. reticulata* populations has shown that the number of flowering spikes present at each of the sites can be prone to dramatic annual fluctuations (Headley *et al.*, 1998a). However, the overall population across the suite of sites remains comparable (Abbott, 1996, 1997). Trying to equate management effects directly to population trends within a site is problematical, since no consistent pattern emerges over time. Hook Moor and Ox Close Wood serve as examples.

Table 3 shows the type of management that has taken place at Hook Moor, together with the numbers of *O. reticulata* spikes. In 1995 there was an increase in numbers in all four quadrants, although only one was managed. However, 1995 was a good year for the species, with annual monitoring showing increases at many sites. Continuously hot weather during the summer is likely to have been a contributing factor to this general increase in flowering. Scrub control and other work was carried out in October. The counts for 1996 showed a dramatic increase in *O. reticulata* numbers in two quadrants where management was undertaken. The area cleared of scrub had however suffered a reduction in numbers, as did the quadrant treated in 1994. In the north-west quadrant it was noted that rabbits were prolific on the road embankment. It is likely that rabbits play an important role at Hook Moor in maintaining open, disturbed ground after scrub clearance. This may well aid the burying of *O. reticulata* seed (Headley *et al.*, 1998b), and certainly creates suitable conditions for the establishment of *C. arvense.*

TABLE 3
Numbers of *Orobanche reticulata* flower spikes (numbers in bold) and management activities at Hook Moor Site of Special Scientific Interest in the years from 1991 to 1997.

Quadrant	1991		1994		1995		1996		1997
North-East	**16**	–	**10**	–	**31**	October: 15 x 15m area cleared of *Rubus, Crataegus, Rosa* and *Ulex.* Stumps treated with glyphosate to prevent regrowth.	**121**	Increased rabbit activity	**290**
North-West	**16**	–	**31**	–	**83**	October: 2 sycamores felled. Stumps treated with glyphosate. Removed fly-tipping from area 10 x 10m. Rabbits prolific.	**162**	Increased rabbit activity	**167**
South-East	**22**	–	**6**	–	**24**	October: 10 x 10m area cleared of *Crataegus.* Stumps treated with glyphosate.	**4**	–	**14**
South-West	**218**	Travellers' encampment on level area	**27**	Feb/March: scrub clearance on embarkment. Stumps treated with glyphosate. Soil stripped off to a depth of 20cm on level area to break up compaction.	**54**	–	**14**	–	**84**
Total	**272**		**74**		**192**		**301**		**555**

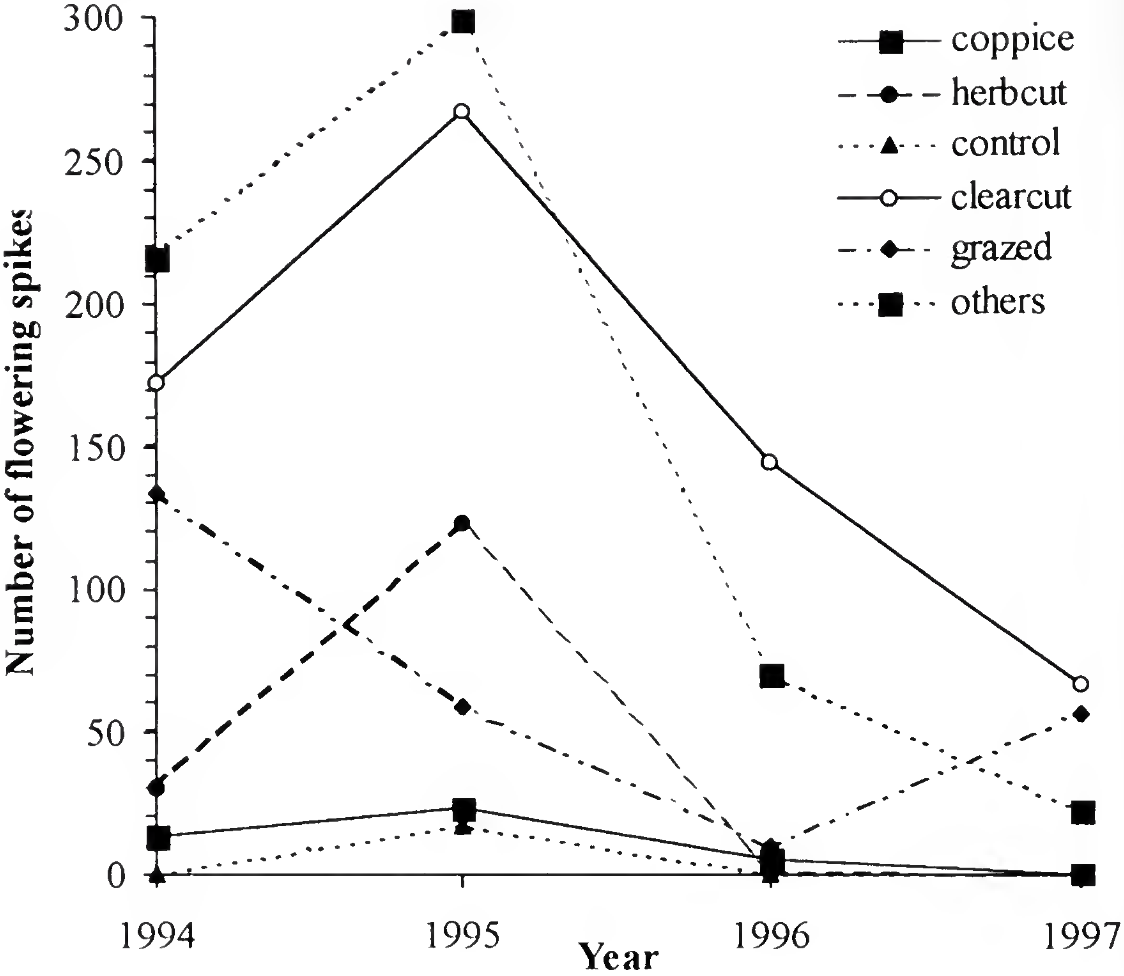

FIGURE 1
Changes in numbers of flowering spikes of *Orobanche reticulata* between 1994 and 1997 in separate plots treated in different ways at Ox Close Wood nature reserve.

The benefit of rabbit grazing and burrowing after management work can be shown by contrasting Hook Moor with Hetchell Wood. At Hetchell Wood numbers of *O. reticulata* in the coppice plot described above fell sharply between the counts of 1994 and 1995, probably due to the very dense regrowth of tall herbs, including *C. arvense*, as well as the coppice stools during 1995. With no control of the vegetation by large herbivores, there was little bare ground present for thistle seedling establishment.

After its first appearance in 1991, 1995 was a very productive year for *O. reticulata* at Ox Close Wood (Fig. 1). All but one plot showed an increase in flowering spikes. Large increases were noted in the plot mown in February with the woody growth left (herbcut), and in the plot clear-cut in February. Elsewhere in the wood, 59 spikes appeared where new steps had been created two years previously, and 67 spikes appeared for the first time in a new enclosure grazed by goats. By contrast, in 1996 there was a dramatic fall in numbers throughout the wood which has continued into 1997, including the experimental plots (Fig. 1). Even in the plot which had been clearcut in February and again in November 1995, the number of *O. reticulata* spikes has fallen markedly (Fig. 1). The reason for this decrease is almost certainly the unchecked rapid expansion of *Rubus* and bracken (*Pteridium aquilinum*) in the years following clear-felling, which had a suppressive effect upon *C. arvense* and reduced the area of bare soil available for seedlings of *C. arvense* to establish in. Even in the goat-grazed enclosures it would appear that the goats did not significantly affect the vigorous growth of *Rubus*. As at Hetchell Wood, the contribution of wild grazers to maintaining areas of open, disturbed ground was not significant.

Conclusions

The following conclusions are to be drawn from the management experience gained to date from those sites where *O. reticulata* has responded to habitat management, either planned or coincidental, and has been subject to population monitoring:

- Ground disturbance is beneficial for both the host plant and *O. reticulata*.
- *O. reticulata* appears in the second or third year following disturbance of the ground.

The following recommendations can also be made with regard to managing sites for *O. reticulata:*

- Moderate numbers of rabbits should be encouraged in order to create bare patches for thistles to colonise and aid burial of *O. reticulata* seed.
- An open sward should be maintained to provide opportunities for thistles to colonise.
- Ideally scrub control should be carried out mechanically rather than chemically as the disturbance of the ground after *O. reticulata* plants have set seed may be beneficial.
- Dense stands of *Rubus fruticosus* and other vigorous tall herbs and woody perennials, which invade open areas and out-compete thistles, need to be controlled.
- Vegetation management should not be undertaken between the very beginning of flowering (early June) and the completion of seed set (end of September/early October).

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ARE BRITISH *OROBANCHE* SPECIES IN DECLINE?

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Introduction

The necessity for monitoring rare and vulnerable species is now widely acknowledged. As conservation becomes pro-active, for example Plantlife's 'Back from the Brink' scheme and the developing suite of recovery programmes initiated under the Biodiversity Action Plan (Anon., 1995), it is becoming more important to audit what may be very costly proposed actions. Information on the autecology, reproductive biology and numbers is required to assess the suitability of such programmes and judgements on the risks involved. Many annual or monocarpic species show marked fluctuations in population size. *Orobanche* species, present at their northern extremes of range, are reliant on suitable, and perhaps exceptional climatic conditions to grow and reproduce successfully. They must also rely on the abundance and vigour of populations of their host plants.

It is therefore not surprising that this genus is well known for extreme annual variance in numbers. To what extent then do we need to study the distribution not just of one species, but two or more? The necessity for the close presence of a host to elicit germination would suggest that to some extent abundance of parasite and host must be linked. However, none of our broomrape species are uniformly distributed throughout the ranges of their host(s). The observations by Headley *et al.* (1998) and others also indicate that while it is a necessity that host plants are abundant for parasite numbers to be high, parasite numbers are not solely dictated by host abundance.

In addition to obvious climatic and edaphic conditions acting at the broad geographic level, many factors may be acting to limit parasite numbers within 'suitable' areas. These factors may include predation from other species; for example pre-emergence grazing by slugs, or perhaps more significantly, temporal changes in host susceptibility linked to the age structure of the host population. The latter might be expected to have a more profound effect on annual *Orobanche* species than perennial, as the latter can persist on/in a host root system and are not reliant on a suitable novel root presence for germination each year. It is unclear as to which British species of broomrape can perennate, although it is probable that only *O. rapum-genistae*, and to a lesser extent *O. elatior*, are perennial over several years. It is these species that occur in more stable communities, where disturbance and recruitment of new hosts is generally at a lower level than in the ruderal, cliff edge and dune communities favoured by the annual species. None of the species occur in climax communities and all will be reliant on disturbance, albeit less regular for perennials, to maintain flowering populations.

The apparent ability of *Orobanche* species to form a persistent seed bank enables them to exploit patchy environments that recur cyclically over time. Any species which is potentially highly dispersible and reliant on a patchy unstable environment might be expected to come and go. This means that they are apparently losing and gaining sites all the time due to the presence of a persistent seed bank, which therefore makes it difficult to prove extinction at a specific site. The fluctuation in population size, apparent absences and production of ephemeral populations pose problems when determining whether the species numbers overall are significantly changing over time. This is important for making decisions as to whether a species is in decline or not. Such information can only realistically be deduced if we have an accurate idea of the distribution and population sizes of the species over time.

Our knowledge of the true distribution of all taxa is reliant upon the level of recording activity and the expertise of those recording (Rich & Woodruff, 1992). 'Unusual' plants and those known to be rare, such as the broomrapes, attract attention and therefore might be expected to be more regularly noticed and recorded than many plant genera. However, the difficulty in accurately discriminating between taxa will result in a higher than average proportion of dubious records in this genus. This is a particular problem if spurious records inflate locality numbers and thereby influence decisions on legal protection, Action plant listing, etc.

Much of our knowledge of the distribution of British plants comes from national atlases of plant distribution as well as local floras (Perring *et al.*, 1962, 1976; Stewart *et al.*, 1994). The use of maps in national atlases recorded on a hectad basis (10km x 10km grid squares) or recent local floras at 5km or tetrad basis (2km) can be criticised, regardless of scale, if they are used alone in assessing abundance. They do not give a true picture of the dynamics of the species' occurrence; for instance, it is impossible to discriminate between a situation where a species may be constantly dominant over an area of several kilometres or present as single individuals at a few sites over a protracted period. The latter will give rise to a greater proportion of dots on a map for the same number of individuals of a species than the former. The *Orobanche* species tend to occur as small and sometimes ephemeral populations and therefore fit the latter category. They will always in a sense be over-represented by a dot mapping scheme. We must also consider that the number of records of such unpredictable species is likely to be more a function of the effort put into recording them than their absolute frequency.

Given these provisos we must start somewhere in identifying changing patterns in distribution and overall scarcity and the published hectad maps give us a snapshot of change over the last century. The numerous local and county floras provide an additional source of information with, in many cases, a subjective quantification. These publications vary greatly in style and content, making comparisons between and within areas and with earlier accounts difficult. They are thus of limited use, but provide supplementary information to mapped distribution data. From these it is possible to infer much as to the status and distribution of a species over time and thus determine those taxa needing further scrutiny.

Using the data in Perring *et al.* (1962), Rumsey and Jury (1991), Stewart *et al.* (1994) and subsequent records published in *Watsonia*, maps for a range of the rarer British species of *Orobanche* have been produced (Figs. 1, 2, 3, 5 and 6). New hectad records made after 1970 are indicated by arrows and give an impression of the flux. In all cases the frequency of occupied hectads has declined by 50% or more for those species examined here. In the case of *O. picridis* and *O. rapum-genistae* this decline is apparently 80% or more.

Orobanche caryophyllacea (Fig. 1)

In spite of an abundance of suitable hosts this species has apparently never expanded beyond its limited range on the Kent coast. Records from Argyll and N. Wales are considered to be errors through accidental or deliberate mixing of herbarium specimens (Rumsey, 1985). Records from Suffolk are supported by specimens and require confirmation. The limited British range cannot be ascribed solely to climatic factors as the species is thriving where introduced at Kew (Milne-Redhead, 1985). The most recent published account of the species' status is that in Philp's (1982) atlas and thus its current status is unclear. The loss of outlying populations following increased urbanization and agricultural change may have restricted it to two hectads. There is no regular monitoring and it appears the number of populations in Kent, let alone their size, is not known. However, in good years the population at Sandwich can be more than 100 spikes. The survey of past sites and monitoring of population size in the few remaining known sites should be considered a priority.

Orobanche picridis (Fig. 2)

In terms of currently occupied hectads versus past records this species has apparently shown the greatest proportional decline; however, several factors must be taken into consideration before concluding that this species is necessarily the most threatened. The past confusion of

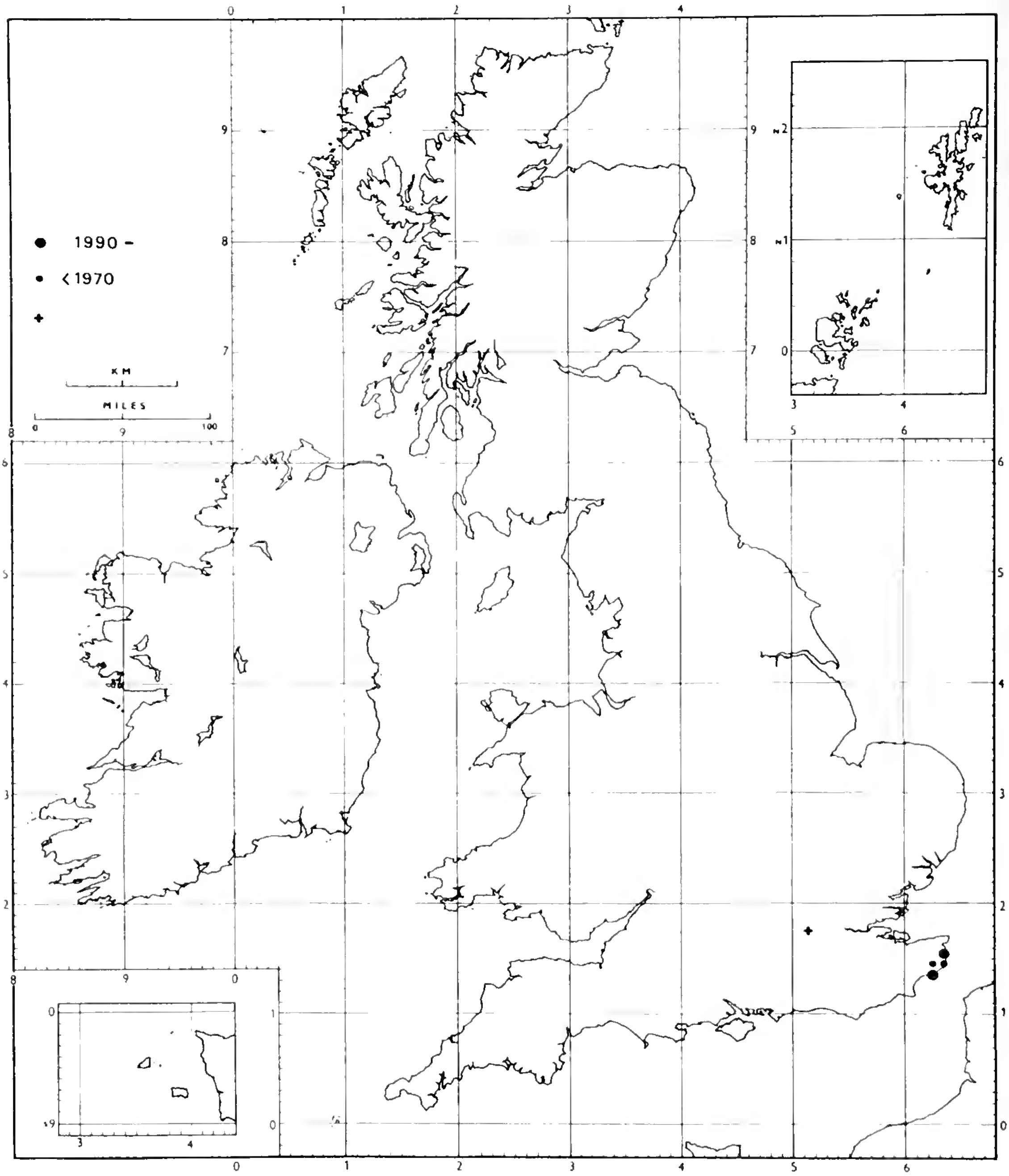

FIGURE 1
The distribution of *Orobanche caryophyllacea* records in Britain before 1970 (small circles) and from 1990 onwards (large circles). A cross represents an introduction.

this species with *O. minor* may have inflated the number of historical records, not all of which are supported by specimens. As with *O. minor*, it is probable that past introductions of *O. picridis* with crop seed may have produced additional, but ephemeral populations. Two post-1950 records relate to single or few individuals at sites in only one year. A better picture of the species' conservation status or 'health' can be gauged by studying its core populations. Of these, only that in the Haslingfield and Comberton area of Cambridgeshire has been lost. The fact that the three other known populations have persisted for over a century is encouraging. However, population sizes are regularly in single figures and the

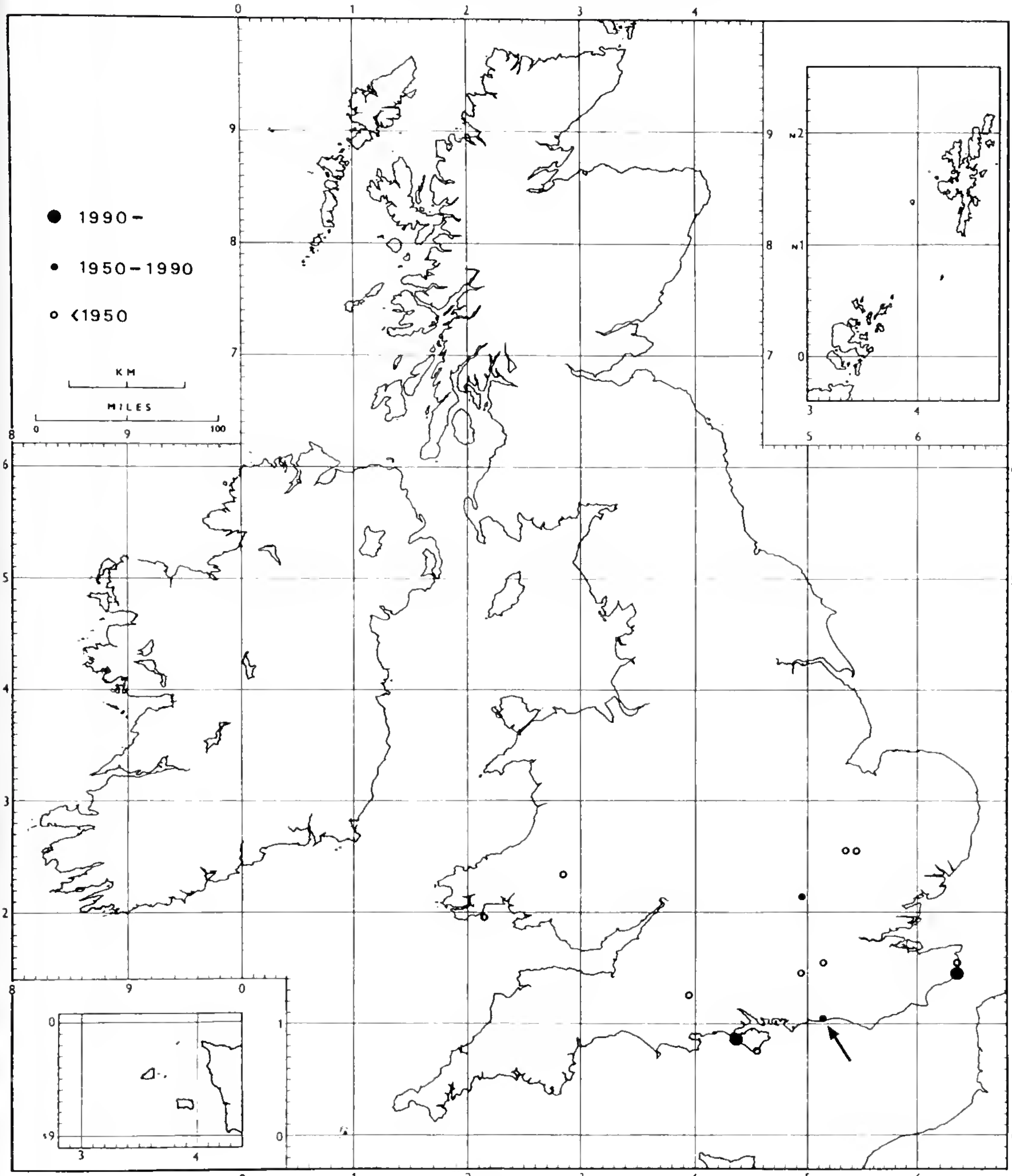

FIGURE 2
The distribution of *Orobanche picridis* (syn. *O. artemisiae-campestris*) records in Britain before 1950 (open circles), 1950 to 1990 (small filled circles) and from 1990 onwards (large filled circles). Arrows indicate new records after 1970.

species is reliant on a particular habitat on coastal chalk cliff ledges where the whole population and seed bank could potentially fall into the English Channel. A recent search of an area of chalk downland at the smaller of its two extant populations in Kent revealed a total of 36 spikes. This population has been small throughout the 1980s. There is no monitoring of the population on the Isle of Wight, due in part to being half-way up a 100m chalk cliff on a ledge. The presence of the plant on the cliff ledges is occasionally noted with the use of binoculars. Although an on-going programme of monitoring is desirable, there are clearly practical problems in carrying this out. Further action such as establishment of *ex situ* populations should be considered, given the precarious nature of the extant populations.

Orobanche rapum-genistae (Fig. 3)

Undoubtedly this species has declined the most in terms of the absolute number of sites and contraction in range. The most commonly encountered *Orobanche* in the early 19th century is now a considerable rarity. The bleak picture of progressive decline presented in Stewart *et al.* (1994) masks the true situation. If hectad records are treated as date classes, i.e. presence

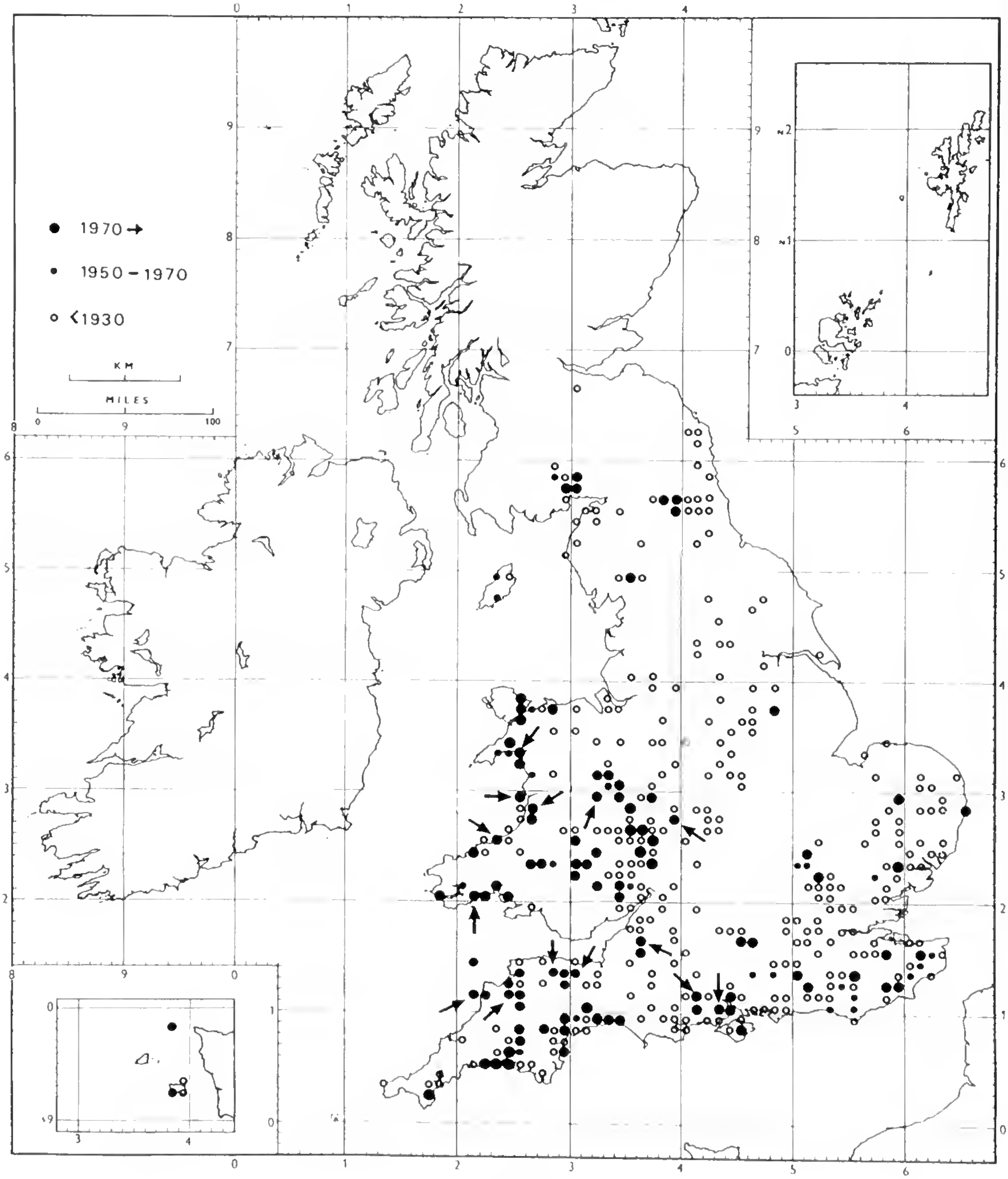

FIGURE 3

The distribution of *Orobanche rapum-genistae* records in Britain before 1930 (open circles), between 1950 and 1970 (small filled circles) and after 1970 (large filled circles). Arrows indicate new records after 1970.

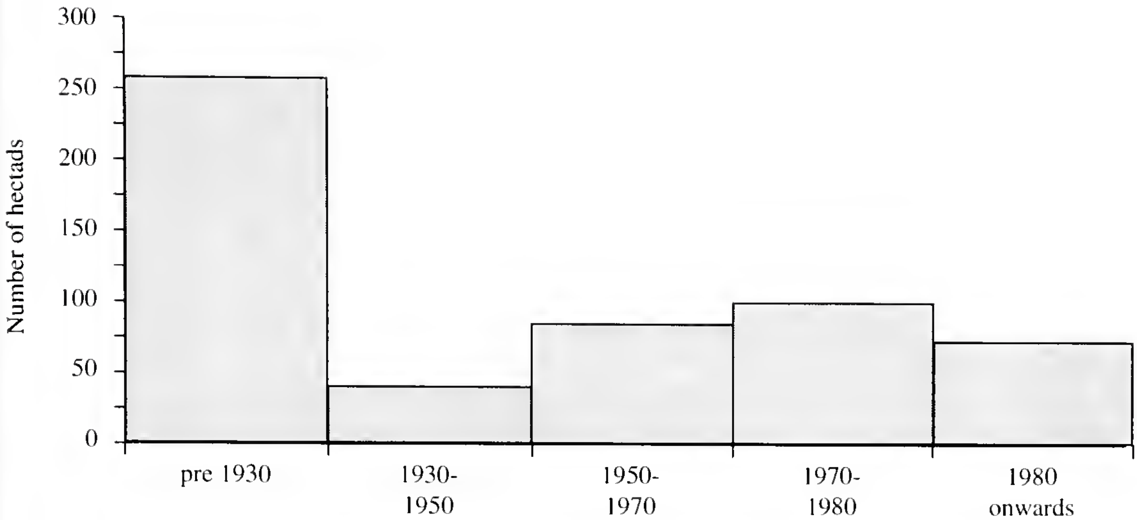

FIGURE 4
The number of hectads in which *Orobanche rapum-genistae* has occurred in Britain over different time intervals (taken from Hughes, 1995).

is not inflated by earlier or later records, we see that currently numbers appear to be higher than in the period 1930-1950 and they have remained at a similar level since concerted recording began in the 1950s (Fig. 4). The lower figure for 1930-1950, as taken from the 1962 atlas, may be a reflection of lower recording activity during this period. It is clear that the major decline in this species occurred much earlier with the wide-scale changes in land use during the last century and early part of this century. The creation of numerous and wide road verges, especially on the motorway system, has provided a novel and suitable habitat for large populations of its host plants, gorse and broom. This factor and the run of hot summers in the 1970s may be responsible for the small rise in records in the 1970s and 1980s.

Can we therefore afford to be complacent about the conservation of this species? In an attempt to assess the abundance of this species in the hectads from which it is reported and whether these populations are persisting, accounts from a range of county floras covering the past English distribution are briefly summarised in Table 1. Where possible the number of reported sites is given. Unfortunately, earlier accounts are often poorly localised, or single sites may be listed under many names depending on the individual recorder. Many recent floras give the number of tetrads/hectads, etc, but they give no indication of the number of populations or sites within them. The figures presented must therefore be treated with some caution. What is clear is that hectad numbers do not differ markedly from site numbers, i.e. each 'dot' on a distribution map represents a single population in most cases. Many of these records are of single individuals, with few populations producing larger numbers, i.e. >20 spikes or clumps. In those areas in which the species is most frequent, for example in south-west England and Wales, although the total number of populations has remained relatively constant, there is some flux in the populations. Population losses are therefore currently balanced by the appearance of new populations. The factors affecting the persistence of this species should be investigated. The potential to recover 'lost' sites from seed banks is evident from the return of the species when woodland stands reverted to heath scrub after the great storm of 1987.

Many potentially suitable areas of gorse and broom scrub now exist, but effective management to open these stands and encourage recruitment would undoubtedly be beneficial. This striking species may still be somewhat under-recorded as stands of its main hosts are unpleasant areas to investigate.

TABLE 1

Number of reported sites of *Orobanche rapum-genistae* in different counties of England and Wales.

County	Before 1950	1950-1980	After 1980
Bedfordshire	absent	absent	absent
Berkshire	4	absent	absent
Buckinghamshire	6	1	absent
Cambridgeshire	3	absent	absent
Cornwall	20	4	4
Cumbria	*c.* 14	4	2
Devon	34	11	?
Dorset	11	2?	?
Durham	7	absent	absent
Essex	15	1	absent
Glamorgan	10	absent	absent
Gloucestershire	14	absent	absent
Hampshire	29	10	6
Hertfordshire	*c.* 14	1	absent
Kent	*c.* 20	>8	?
Lincolnshire	1	1	1
Middlesex	2	absent	absent
Norfolk	11	absent	1?
Northumberland	>22	?	6
Oxfordshire	absent	absent	absent
Somerset	6	3	7
Suffolk	*c.* 15	?	1?
Surrey	9	1	1
Sussex	41	?	6?
Wiltshire	21	absent	absent

Orobanche minor var. *maritima* (Fig. 5)

Since this taxon has been the subject of considerable taxonomic and nomenclatural confusion, the map is therefore unlikely to be entirely accurate. As the habitat occupied by this species has not been significantly affected by land-use changes over the last century, it is probable that the decline of this species is apparent rather than real. Massive population fluctuations have been reported from various parts of its range, e.g. the Isle of Wight (Shepherd, 1983) and Jersey (Le Sueur, 1984). Although this taxon is not endemic, it is more frequent in the British Isles than elsewhere. This feature sets it apart from all the other species considered here, all of which must be considered not to be threatened on a global scale. Its true extent and in particular its continued survival in the somewhat isolated Kent populations, where it grows with *O. picridis*, requires investigation.

Orobanche purpurea (Fig. 6)

Like *O. minor* var. *maritima*, this is primarily a maritime species. However, it is not found exclusively in these areas, with recent finds almost as likely to come from inland pastures and churchyards than from coastal locations. Unlike the other species considered here, a high proportion of the hectad occurrences of this species refer to recent expansions in range. If this species becomes established in these new sites, as it seems to have done at Maryport in Cumbria, this may influence its conservation status. There has been some monitoring of the size of the population at Maryport and its only known extant population in Wales (Fig. 7). Again, this species of *Orobanche* shows marked fluctuations in population size. In 1994

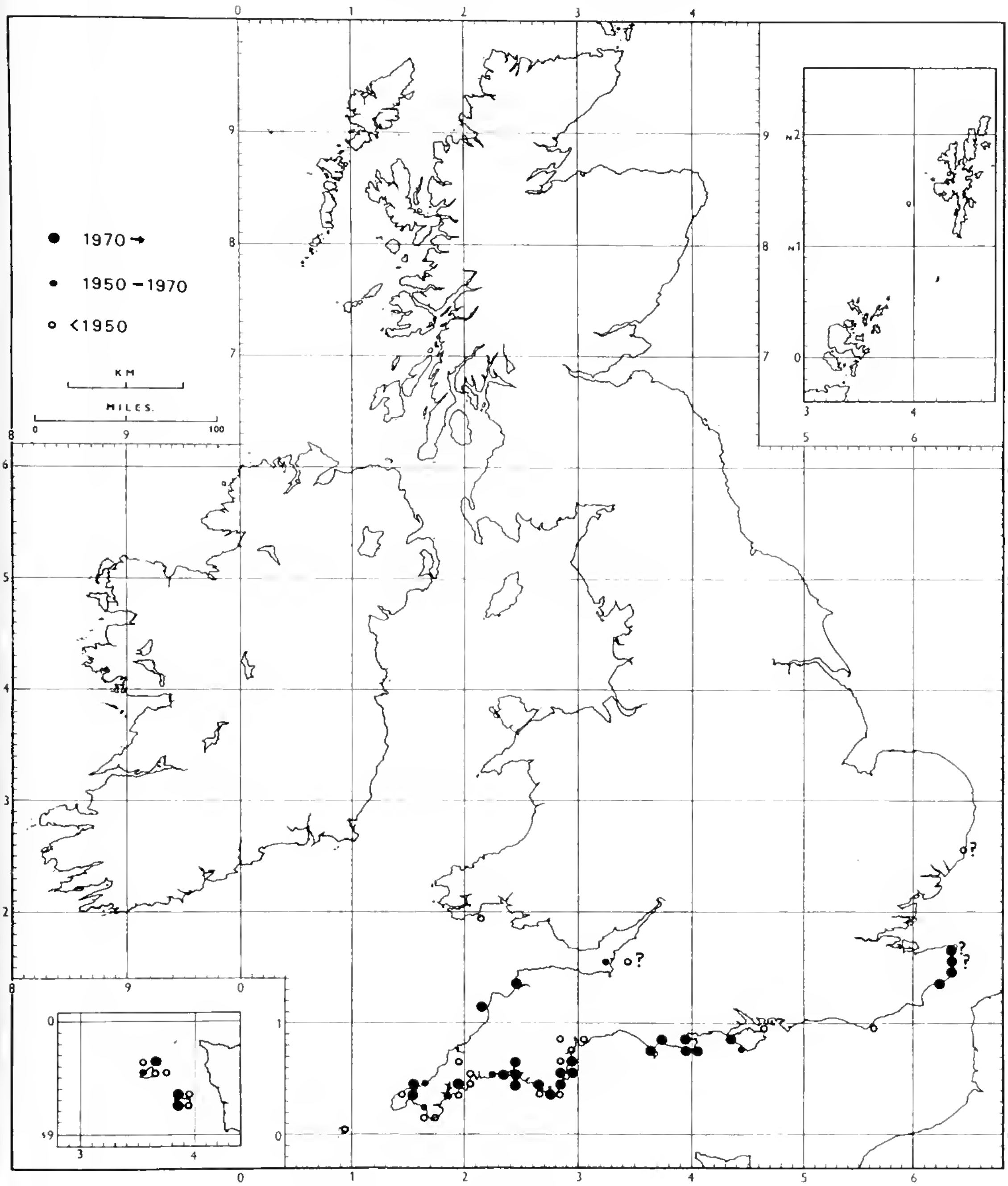

FIGURE 5
The distribution of *Orobanche minor* var. *maritima* (syn. *O. maritima*) records in Britain before 1950 (open circles), between 1950 and 1970 (small filled circles) and after 1970 (large filled circles). Question marks indicate doubtful records.

and 1995 spikes were reported to be present by the original discoverer of this population, but despite there being few spikes, they were not counted. A formalised programme of monitoring of these novel sites should be considered. The abundance of this species' host, *Achillea millefolium*, would indicate that either poor dispersal or particular climatic and edaphic factors are limiting the parasite's range. It could prove an interesting experimental organism upon which to study these questions.

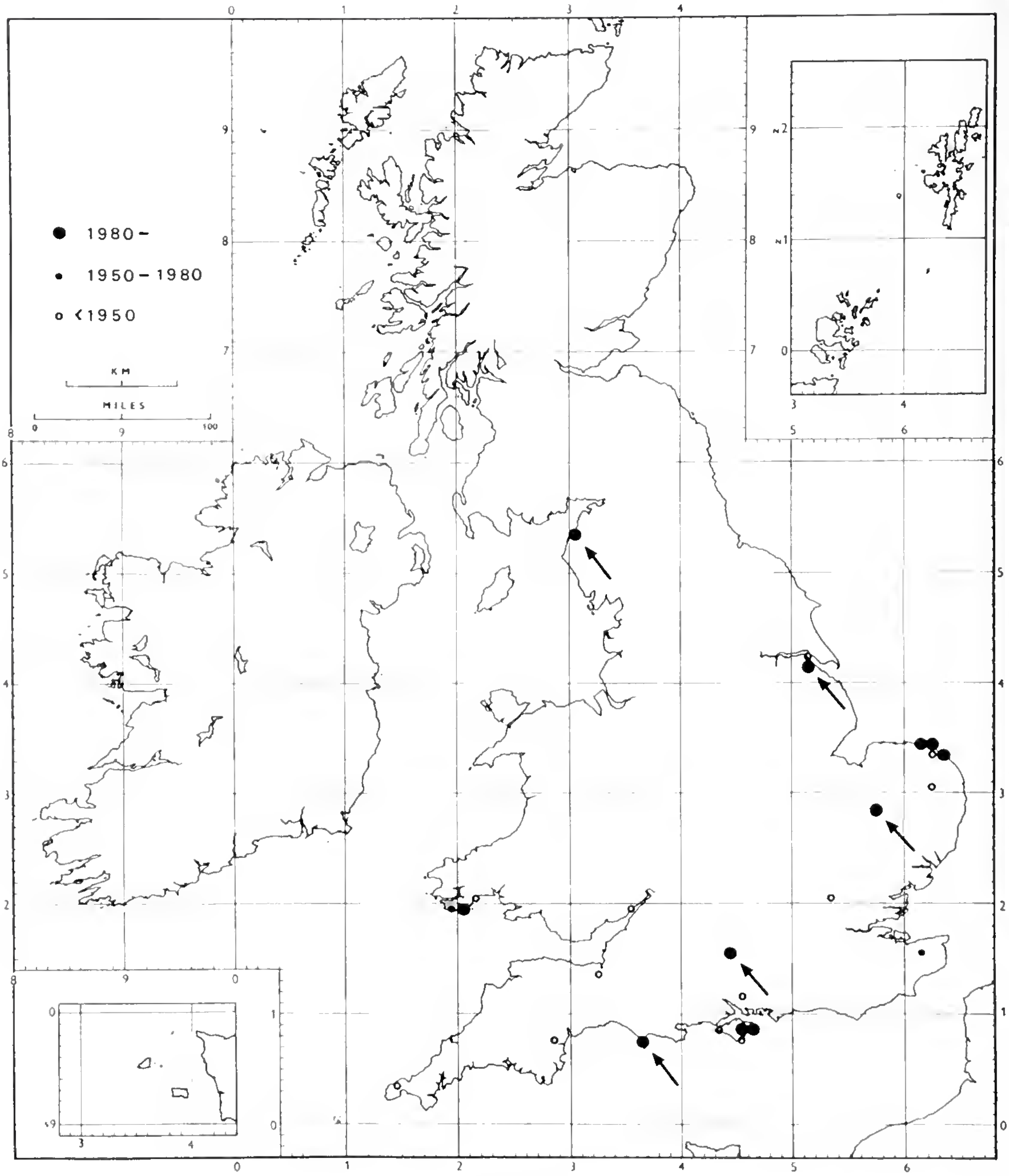

FIGURE 6
The distribution of *Orobanche purpurea* in Britain before 1950 (open circles), between 1950 and 1980 (small closed circles) and after 1980 (large closed circles).

WHY IS MONITORING NECESSARY?

As yet we have little understanding of many aspects of the ecology and biology of these unusual organisms. In the absence of extensive laboratory studies, an organised programme of field observation and recording will, over time, provide relevant information useful for determining conservation actions. To date, only *O. reticulata* can be said to have been the subject of any concerted censusing of population size. Even with this species we as yet have too little data to decide whether it is stable, or undergoing a protracted but inexorable decline.

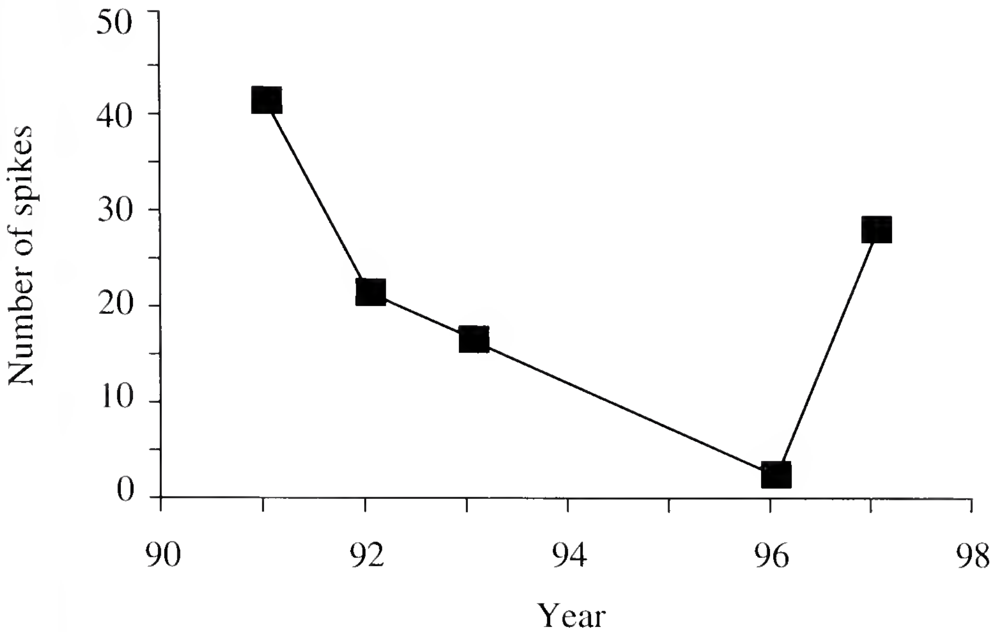

FIGURE 7
The inter-annual variations in the size (number of flowering spikes) of the *Orobanche purpurea* population in Pembrokeshire. Data kindly provided by A. Jones.

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THE WAY FORWARD FOR BROOMRAPE CONSERVATION IN BRITAIN

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Nearly all the rarer species of broomrape (*O. artemisiae-campestris, O. caryophyllacea, O. reticulata, O. purpurea* and *O. rapum-genistae*) present the same problems for their conservation. Firstly, most of them have very common host plants, such as *Achillea millefolium, Cirsium arvense, Cytisus scoparius, Thymus praecox, Galium mollugo, G. verum* and *Ulex europaeus*, or hosts that are at least locally abundant, such as *Picris hieracioides* (Rumsey & Jury, 1991). Secondly, they occur in relatively common, or at least not rare, habitats and often unattractive sites and are therefore not rated highly by conservation bodies. If anything, the broomrapes frequently occur in weedy and uninspiring grasslands or waste places, for example Maryport docks and the embankments of major roads. Some occur in inaccessible locations, such as chalk seacliffs, or in uncomfortable vegetation, such as gorse thickets and stands of thistles and nettles. If some of the sites had not been designated as SSSIs for the broomrapes themselves, it would have meant that the broomrapes would have largely slipped through the system of habitat protection or association with other rare organisms.

The large inter-annual fluctuations in numbers also count against them in terms of identifying controlling factors governing population size. The timing of flowering is also very variable between years for many species and therefore makes it more difficult to make a census of the populations. It is clear that there is very little systematic monitoring of populations for all species except *O. reticulata* (Rumsey & Headley, 1998a). The status and size of the British populations of *Orobanche* is therefore largely unknown (Rumsey & Headley, 1998a). There is consequently a very poor understanding of the factors that govern population size and the size of the host populations do not always appear to be the most important factor in determining the size of the parasite population.

Some understanding has been gained of the management requirements for *O. reticulata*, but different species of host will almost certainly have their own specific requirements. Despite this, the different species of *Orobanche* are likely to have some requirements in common as they possess the same parasitic life-cycle.

It is clear that most rare species of broomrape in Britain suffer from the same problems of (i) lack of monitoring of the number and size of populations, (ii) poor understanding of their ecology, (iii) a currently low profile in the Biodiversity Action Plans and (iv) a complex parasitic life-cycle. It is extraordinary that a genus which has such a large proportion of its species (7 out of a total of 9) in the Red Data, Near Threatened or Nationally Scarce categories has been largely overlooked in terms of its conservation.

Achievements to date

The workshop has certainly helped the conservation of broomrapes in the UK at least. A network of people working on the biology, conservation and management of sites with rare species of *Orobanche* has been established. This will enable conservationists and managers to obtain advice on management problems with greater ease. The workshop has passed on many of the lessons learnt from conserving and researching *O.reticulata* to those with responsibilities for conserving other rare species of *Orobanche*. The Thistle Broomrape Newsletter has succeeded in increasing awareness of this plant. Despite some inaccuracies in articles in the local and national press, the publicity surrounding this species can only be to the benefit of conservation organisations.

ISSUES

The following are issues raised at the workshop which are relevant and important in the conservation of *Orobanche* in general as well as being specific to *O. reticulata*.

- It is not clear which nomenclature should be followed with regard to *O.reticulata*. It may be either *O. reticulata* sensu stricta or *O. pallidiflora* or *O. reticulata* ssp. *procera*. This needs to be resolved by carrying out genetic studies of the British material alongside European material of the two species described by Kreutz (1995). This same issue also applies to the various subspecies of *O. minor*, some of which are regarded by some workers as worthy of specific rank (Rumsey, 1998). This has important implications for their status and conservation.
- The assertion that there may be significant inbreeding and consequent erosion and loss of genetic variation in the small populations of *O. reticulata*, as suggested by Headley *et al.* (1998b), needs to be checked. The population studies may also suggest that there are perhaps fewer effective populations of *O. reticulata* in Yorkshire than might be initially apparent due to seed dispersal along rivers from larger donor populations to smaller non-viable recipient populations (Headley *et al.*, 1998a).
- The monitoring of the number and size of the extant populations of the three most threatened species of *Orobanche* in Britain, O. *artemisiae-campestris*, *O. caryophyllacea* and *O. purpurea*, is lacking and needs remedying. This requires urgent attention to ascertain if populations are on the decline. A ten-year period of monitoring should give an indication of any significant trend in population size.

ACTIONS

- Establish working groups. An informal network of people working on the biology, conservation and management of sites with rare species of broomrape now exists and Dr Headley is willing to act as co-ordinator.

- Publicise and disseminate information. These proceedings are intended to disseminate the current state of knowledge to managers, conservation officers and researchers and will help others make better informed judgements in managing and conserving these species or sites where they exist. There is the intention to broaden the Thistle Broomrape Newsletter to cover the whole genus. This will increase the readership in number and geographical spread in the U.K.

- Establish effective monitoring. Monitoring of population sizes of priority species should be initiated as soon as possible. It is recommended that all extant populations of *O. artemisiae-campestris* and *O. caryophyllacea* be monitored and for *O. reticulata* that the largest sites and those with a history of recording of at least 4 previous years, be carried out. *O. purpurea* also appears to require some monitoring, preferably at all extant sites. The decline in *O. rapum-genistae* needs confirming by the monitoring of a number of sites with known management scattered throughout the U.K. The co-ordination of recording could be carried out by a single person or organisation, but the actual monitoring could be carried out by the local and most appropriate organisations with the populations of broomrape in their areas. The abundance and vigour of thc host plants in the sites where the species of *Orobanche* occur should also be monitored in some way.

- Species Action Plans. Ideally, these need to be prepared for *O. artemisiae-campestris, O. caryophyllacea* and *O. purpurea*. It was felt, however, that there was little to be gained from trying to press for raising *O. artemisiae campestris*, *O. caryophyllacea* and *O. reticulata* from the 'long' to the 'middle' list of the Biodiversity Action Plan, but their inclusion in local action plans should be encouraged. The local Biodiversity Action Plan for Kent has been produced, yet neither *O. caryophyllacea*, restricted to this county, or *O. artemisiae-campestris*, with two of its three extant populations, have been considered as species worthy of action!

- Old Sites. Former localities of broomrape should be surveyed for the presence of the host plant/s as well as the *Orobanche*, current land-use, vegetation and suitability for re-establishment of populations. If felt appropriate or worthwhile, soil samples could be collected to establish the continuing presence of a seed bank at those sites suitable for population re-establishment. Soil samples could be processed at one laboratory. All former sites of *O. artemisiae-campestris*, *O. caryophyllacea* and *O. purpurea* populations should be examined.

- Life span. There are many aspects of the autecology of *Orobanche* that are poorly understood. The length of the life-cycle in all the native *Orobanche* needs to be determined by cultivating plants on host plants in appropriate experimental conditions. The life-cycle in *O. reticulata* is likely to be monocarpic and usually completed within a year, but those of *O. rapum-genistae* and *O. elatior* may be polycarpic and perennial.

- Soil/host nutrient status. The influence of soil or host nutrient status on susceptibility to infection requires investigation. This is important in order to establish whether nutrient enrichment of the soil poses a significant rather than an imagined threat to any *Orobanche* population.

- Host-parasite relationships. A sound knowledge of the ecology and population dynamics of the host plants is also vital to the conservation of the *Orobanche* in question. Many of the host plants are very common, but our understanding of their autecology is not as complete as one would like.

- *Ex-situ* cultivation and propagation. Considering the precarious position and nature of the extant populations of *O. artemisiae-campestris* (Rumsey, 1998) they will require the re-establishment of extinct populations or establishment of a population in a suitably safe locality. *Ex-situ* cultivation will provide a safety net for those populations that may be lost due to natural catastrophic events such as collapse of cliff ledges (e.g. *O. artemisiae-campestris*) or floods (e.g. *O. reticulata*), or developments, such as road-widening and flood defences (e.g. *O. reticulata*). This can also form the basis for the re-establishment of extinct populations or to establish 'safe' populations elsewhere. The *ex-situ* cultivation and propagation of the rarer *Orobanche* will therefore be necessary to bulk-up seed for any re-establishment of extinct populations.

- Seed Viability. The development of effective means of *ex-situ* methods of propagation of plants from seed is also required by workers at the Millenium Seed Bank at Kew in order to replace collections of seed that have lost their germinability or viability. In this regard, the optimum storage conditions for seeds needs to be investigated and more rigorous checks on whether current storage conditions at Wakehurst Place are the best for these seeds. These matters will be raised with the newly appointed staff member responsible for microscopic seeded species. This applies to all of the rare and threatened species of broomrape.

- Systematics and breeding systems – a molecular approach. The taxonomic status of *O. reticulata*, *O. artemisiae-campestris* and subspecies of *O. minor* need to be elucidated with the latest molecular techniques. The British material of the rarer species of *Orobanche* may be genetically depauperate and/or genetically distinct from mainland European populations. Therefore the degree of genetic variation in the rare species of broomrape in Britain and its similarity to Continental European material requires urgent investigation. This will also help to shed light on whether the low population densities and vigour of some of the populations or species is due to inbreeding depression.

Despite the rapid progress in understanding the ecology of *O. reticulata*, there is still much that is not known about the ecology and conservation of nearly all of the species of *Orobanche* in Britain. If nothing is done to rectify this situation we may see at least one species of *Orobanche* become extinct in the British Isles soon, or more become even rarer.

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THE BIOLOGY AND ECOLOGY OF *OROBANCHE:* A BIBLIOGRAPHIC REVIEW

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Although it is not possible in a limited space to give a comprehensive review of the biology and ecology of species of broomrape other than *O. reticulata*, it is hoped that this paper will give a fair reflection of knowledge on the genus as a whole. It does serve to highlight the paucity of information relating to most non-crop weed species, which includes those species of *Orobanche* found in the British Isles.

The broomrapes are root holoparasites of a wide variety of mainly dicotyledonous plants (Kreutz, 1995). Members of the *Fabaceae* and *Asteraceae* are frequent host plants for European broomrapes. Few species of *Orobanche* are parasites of a single host species. *O. hederae* and *O. elatior* are notable exceptions to this general rule, in Britain at least, in parasitising almost exclusively *Hedera helix* and *Centaurea scabiosa*, respectively. Many though are restricted to a particular genus or closely related genera, the generalist parasites being very few.

Most work on the biology and ecology of broomrapes has concentrated on the pest species which parasitise crop plants, mainly in the Mediterranean, North Africa and Middle East (Weber & Fortstreuter, 1987; Parker & Riches, 1993; Press & Graves, 1995). Those that have received the greatest attention are *O. crenata*, *O. cernua*, *O. ramosa* and *O. aegyptiaca*, and to a lesser extent *O. minor*. There are various methods of controlling broomrapes and they include the use of herbicides, germination stimulants, catch or trap crops, cropping regimes, soil solarization (Abu Irmaileh, 1991), development of resistant genotypes of crop and diseases of the *Orobanche* themselves. A review of methods of controlling pest species of *Orobanche* is given by Dhanapal *et al.* (1996) and they conclude that integrated management systems are the only effective means of controlling them.

One of the aspects of the biology of *Orobanche* that has received the greatest attention concerns the conditions and requirements for seed germination. The results of this work has shown that seeds of *Orobanche* require a period of pre-conditioning under moist conditions for as long as 18 days in some cases (Sauerborn, 1989). The optimum temperature is between 15 and 20°C and depends on the provenance of the seeds. The requirement for a pre-conditioning of *Orobanche* seeds is largely reported from species found in semi-arid environments (Abu-Shakra, Miah & Saghir, 1970; van Hezewijk *et al.*, 1993; BarNun & Mayer, 1993).

The seeds require a stimulant after this pre-conditioning in order to germinate, which is present in exudates or extracts of the roots of its host plant (Brown, 1946; Brown *et al.*, 1951; Sunderland, 1960a, 1960b; Elghamrawy *et al.*, 1990). Because of the potential for controlling the pest species of *Orobanche* by applying these stimulants, a great deal of work has gone into identifying the chemical stimulant released by the host roots and examining how effective it is in stimulating germination of their seeds. The stimulant for germination varies between studies as much as between the different species of *Orobanche* tested, but strigol is a ubiquitous stimulant (Spelce & Musselman, 1981). Other chemicals that appear to be effective in germinating *Orobanche* seeds are various gibberellic acids, brassinolide, brassinosteroids, sorgolactone and various strigol analogues (Spelce & Musselman, 1981; Bergmann *et al.*, 1993; Takeuchi *et al.*, 1995; Thuring *et al.*, 1997a, 1997b, 1997c, 1997d, 1997e). Gibberellic acid appears to stimulate germination if applied in the pre-conditioning period as well as acting as a replacement for other chemicals that stimulate germination (Sahai & Shivanna, 1982; Dhanapal & Struik, 1997).

Seeds can remain viable without germinating after the pre-conditioning period (BarNun & Mayer, 1993; Thuring *et al.*, 1997a and 1997b). Other treatments, including scarification and treatment with sulphuric acid, have been reported to stimulate germination through softening the seed coat (Goldwasser *et al.*, 1995; López-Granados and Garcia-Torres, 1996; Mori *et al.*, 1997). Seeds can go into a secondary dormancy phase if they do not receive a stimulant after the pre-conditioning period.

The most active region of the host root in stimulating germination of *Orobanche* seeds appears to be close to the root-tip (Sunderland, 1960b). Increasing concentrations of nitrogen in the soil have been reported to reduce the infection rate of crops by *Orobanche* (Abu Irmaileh, 1981, 1994; Jain, & Foy, 1992), but recent work with *O. minor* grown on clover showed an increase in the number of spikes per host plant with increasing nitrogen levels added to the soil (Dale, *pers. comm.*). This is probably more related to the root density in the soil increasing the frequency with which host roots come into contact with *Orobanche* seeds, rather than any effects on germination. High concentrations of ammonium-nitrogen rather than nitrate or urea *per se* appear to be responsible for the inhibition of seed germination when applied during the conditioning and germination phases (van Hezewijk & Verkleij, 1996).

Once germinated, the seeds produce a corkscrew-like radicle that penetrates the host root by dissolving the walls of its root cells (Shomerilan, 1993; Singh & Singh, 1993), subsequently forming a haustorium (Sahai & Shivanna, 1981; Joel & Losnergoshen, 1994). It is through this organ that the parasite derives all its water and nutrients from its host's xylem and phloem (Aber & Salle, 1983; Aber, Fer & Salle, 1983; Dorr & Kollmann, 1995). The detailed morphology and processes involved in the infection of host plants by *Orobanche* are given by Sahai and Shivanna (1981) and Press and Graves (1995).

The parasite gradually enlarges a tuber outside the host's root whilst still attached to it. Once this tuber is sufficiently large, the flowering stem primordium will rapidly swell and enlarge. The plant accumulates high concentrations of various non-essential sugar alcohols, particularly mannitol, in order to draw water from its host root system prior to emergence (Harloff & Wegmann, 1993). Thus the flowering of plants can vary within and between years at a site depending on the climate and timing of attachment of the *Orobanche* seedlings to the host's roots.

Studies have also concentrated on how much damage various species of *Orobanche* inflict on a variety of crops (Arjonaberral *et al.*, 1987; Barker *et al.*, 1996; Manschadi *et al.*, 1996; Dhanapal *et al.*, 1997) and various methods of controlling the populations of *Orobanche* in fields (Eplee & Norris, 1995; Dhanapal & Struik, 1996; Jurado-Exposito *et al.*, 1996, 1997; Hershenhorn *et al.*, 1996). The timing of crop sowing has been shown to affect the infection rate by *O. crenata*, which decreased in the order autumn>winter>spring>summer (van Hezewijk *et al.*, 1994; López-Granados & Garcia-Torres, 1997). Generally, sowing crops earlier in the growing season increases the infection rate by *Orobanche* (Mesa-Garcia & Garcia-Torres, 1986). This can be explained by the pre-conditioning requirement of the seeds for warm and moist conditions, which tend to be predominant in autumn. A study of the population dynamics of *O. crenata* showed that the growth rate of the population was related to rainfall and soil temperatures during December to February, i.e. the period of crop vegetative growth (López-Granados & Garcia-Torres, 1996).

The yield of crops such as broad bean can be reduced by as much as 63% when *Orobanche crenata* seeds are sown at a density of 600 per kg soil (Manschadi *et al.*, 1996). The yield of tomato is reduced linearly with increasing seed densities in the soil up to a maximum of 10 mg dm^{-3} of soil in the case of *O. aegyptiaca* (Barker *et al.*, 1996). The yield of tobacco decreased with an increase in the number of *O. cernua* spikes per plant. The weight of the individual spikes of *O. cernua* decreased as the number of spikes per host plant increased. This suggests there is intraspecific competition between *Orobanche* plants for resources from its host plant (Linke *et al.*, 1991; López-Granados & Garcia-Torres, 1993a, 1993b). *O. crenata* parasitising *Vicia faba* can have a maximum spike density of 10 to 40 m^{-2}, and not suprisingly the population growth rate is fastest at the lowest population densities (López-Granados & Garcia-Torres, 1993b; Manschadi *et al.*; 1997).

Studies have shown that *Orobanche* have large and very persistent seed banks in the soil (Ashworth, 1976; López-Granados & Garcia-Torres, 1993). The seed bank of *O. crenata* can reach four million per m^2 with a viability of 53 to 68%. Only 0.003% of seeds become attached and of these only 9% actually emerge and flower, probably due to lack of nutrients available from the host plant. The seed output was estimated to be as much as 4 million per m^2 at a spike density of 53 per m^2.

Orobanche species are easily killed with glyphosate, but many more herbicides, including chlorsulfuron, sulfosate, imazethapyr, metham sodium, imidazolines, maleic hydrazide and mazapyr, are also effective in controlling them (Mesa-Garcia & Garcia-Torres, 1985; Foy *et al.*, 1988; Jacobsohn *et al.*, 1988; Castejon-Munoz *et al.*, 1990; Garcia-Torres & López-Granados, 1991; Kotoulasyka & Eleftherohorinos, 1991; Garcia-Torres *et al.*, 1994, 1995; Lolas, 1994; Goldwasser *et al.*, 1995; Gressel, Segel & Ransom, 1996; Jurado-Exposito *et al*, 1996, 1997). Potential biological control agents such as various insects and fungi that attack *Orobanche* have also been investigated (Almenoufi, 1982; Linke *et al.*, 1990, 1992; Raju *et al.*, 1995). There are various models of the population dynamics of *O. crenata* and their host plants in a variety of cropping regimes (Castrotendero & Garcia-Torres, 1995; Garcia-Torres *et al.*, 1996; Schnell *et al.*, 1996; López-Granados & Garcia-Torres, 1997).

The taxonomy and systematics of *Orobanche* have to date primarily relied upon morphology: from habit, pigmentation, etc., through to micro-characters such as seed and pollen ornamentation (Musselman, 1986; Rumsey & Jury, 1991: Kreutz, 1995, etc.). The limitations imposed by character loss through reduction associated with parasitism (see Rumsey, 1998) may be overcome by the application of phytochemical and molecular techniques; however, little has been published to date on these techniques employed on *Orobanche*. Some authors, e.g. Wolfe and de Pamphilis (1997), have concentrated on the evolutionary aspects of the parasitic condition at the gene level; most, however, have sought to investigate genetic variation within and among species based on molecular markers. This work has concentrated on weed species; Verkleij *et al.* (1986, 1989, 1991, 1994) investigated alloymic variation in *O. crenata* and *O. aegyptiaca* in Spain and Syria, and Paran *et al.* (1997) used DNA (RAPD) markers to study the five main species in Israel. Both studies investigated intraspecific variation in relation to host and found no correlation. The genetic variation within taxa was primarily held within populations as opposed to between populations. This indicates that high levels of gene flow occur between populations, which Paran *et al.* (1997) ascribe to efficient seed dispersal and presumably not to transfer of pollen between populations. It might be argued, however, that regular introduction through unwitting human transport is mostly responsible for the patterns of diversity now witnessed. The advent of quick, relatively cheap DNA methods which require very little plant material, e.g. the characterisation of RAPD profiles from individual seeds (Joel, Portnoy & Katzir, 1996; Portnoy *et al.*, 1997), superficially offers great potential. Care must be taken in the interpretation of such studies using RAPD methods, as these have been widely criticised for their lack of reproducibility and unknown, and unknowable genetic basis.

A selected list of recent and pertinent literature on the biology and ecology of species of *Orobanche* is given below.

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FIELD NOTE

Two species of Marsh Fly (Diptera: Sciomyzidae) in the Barnsley area

I should like to place on record the occurrence of *Coremacera marginata* (Fab.) and *Sepedon sphegea* (Fab.), two rather local and highly distinctive 'snail-killing' flies not included for this district in Roy Crossley's excellent review (Notes on the Marsh Flies (Diptera: Sciomyzidae) of Yorkshire, *Naturalist* **122**: 93-97) recently published.

First recorded locally in 1994, *C. marginata* is known from three wasteground sites, viz, Carlton Marsh (SE 3710), Manvers (SE 4501) and Wombwell Ings (SE 4203). It is, however, perhaps best established at Houghton Common (SE 4308), a sandy tract of birch scrub and rank grassland.

S. sphegea favours damper places and has been recorded locally since 1989 from Gypsy Marsh (SE 4102), Smithies (SE 3408), Cortonwood (SE 3901) and Wombwell Ings, this last site harbours both species, an interesting indication of the often complex habitat diversity to be found at some 'mature' wasteground localities.

Since both species are readily identified in the field, it is possible that they are currently undergoing range expansion, particularly *C. marginata*, which is unlikely to have escaped notice for so long since regular diptera recording in the district commenced in 1982.

J. D. Coldwell,
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OBITUARY

JOHN HALLSWORTH FLINT, F.L.A., F.R.E.S. 1919-1997

John Flint at Pocklington Canal, August 1989. Photo: R. Crossley

Iohn Flint, doyen of Yorkshire entomologists, died on 23rd December 1997, and with his
oassing an era of Yorkshire entomology has come to an end.

John Hallsworth Flint was born in Leeds on 6th September 1919. As a boy he lived in Jpper Armley and was educated at Christ Church and West Leeds High Schools. After natriculation he joined Leeds City Council's Public Library Service. He passed his A.L.A. exams, with distinction, in 1938, at Leeds College of Commerce and his F.L.A. thesis was accepted in 1948. He rose through various Branch Librarianships to become Central Lending Librarian, moving in 1964 to the City's Education Service to co-ordinate and establish the library of the embryo Leeds Polytechnic (now Leeds Metropolitan Jniversity). He retired as Polytechnic Librarian in 1983 and his contribution to its successful development was acknowledged with the conferment of an Honorary Fellowship of which he was justifiably proud. He spent the war in the army maintaining radar equipment in the south of England. On one of these radar sites, in 1944, he met Hilda ('Tim') Steward and they were married in her village church, at Woodham Ferrers in Essex, in January 1945. After the war they settled in Chapel Allerton, Leeds.

John's interest in natural history started early, fostered by his maternal grandfather, and his teenage diaries reveal a wide-ranging enthusiasm for birds, plants and insects. This broad view lasted throughout his life though from the beginning his main interest was entomology. His capture of a specimen of the spectacular Velvet-ant, *Mutilla europaea*, on the North York Moors in 1937 spurred his mother to find an expert entomologist to help him in his hobby. This led to his introduction to the legendary W. Douglas Hincks who remained a close friend until his untimely death in 1961. Hincks' influence on the youthful beginner was obvious to all who knew John well, for he often spoke of Douglas with great respect and affection. He introduced him to the Leeds Co-operative Field Naturalists' Club and in 1938 John also joined the Leeds Naturalists' Club and Scientific Association, besides attending meetings of the Entomological Section of the Yorkshire Naturalists' Union which he formally joined in 1940. In these societies he enjoyed the company and mentorship of other prominent entomologists of the day including John Dibb, J. Digby

Firth, and T. Basil Kitchen who became another firm friend. In 1944, he was elected a Fellow of the Royal Entomological Society.

At his request his prize for achieving a distinction in his A.L.A. exams was a copy of N. H. Joy's *Handbook of British Beetles*. This weighty tome travelled with him throughout the war and he spent every available moment collecting and identifying beetles. He also studied the haunts and habits of Orthoptera, Heteroptera, Homoptera, aculeate Hymenoptera and brachyceran and syrphid Diptera. Tim took up Odonata and together they collected and reared symphytan Hymenoptera, while under John's guidance their sons, Peter and Jeremy, also became competent entomologists.

After the war he became actively involved with the Y.N.U. Entomological Section, being Section Secretary 1953-63, Survey Committee Chairman 1968-73, and Section Chairman 1973-83; he also served for many years on the Union's Executive Committee. He was Recorder, sometimes concurrently, for Coleoptera, Hemiptera and Neuroptera, assiduously maintaining the Y.N.U. records and regularly producing comprehensive reports of new and significant discoveries, always preceded by an erudite introduction; his contributions to the published reports of Union field meetings were always equally scholarly. He also assisted Tim when she was Hymenoptera Recorder. John was a member of the Spurn Survey Team in 1951 and 1952, and with Hincks organised the 5-year survey by the Entomological Section at Malham, 1954-1958, and wrote the introduction to the report which was published in 1963. John was also a member of the survey team which worked at Freshfield from 1959-1963. He published many short field notes over the years in *The Naturalist*, and also in *The Entomologist's Monthly Magazine* between 1946 and 1976, and for many years he was a regular book reviewer for *The Naturalist*. Involvement with the Yorkshire Naturalists' (now Wildlife) Trust began in 1964 and John served as a member of Council from 1965 until 1984. He acted for several years as Potential Reserves Officer, and it was on the basis of his recommendations in that period that the Trust pursued the acquisition of a number of properties as reserves. He was also instrumental in initiating entomological recording on reserves, a task for which he was well suited.

Towards the end of his active fieldwork, John had the pleasure of adding a new insect to the British List. This was the hopper *Cicadula ornata*, of which he found several specimens at Aughton Ings in 1987, and an account of this discovery was published in the *Entomologist's Gazette* (**40**: 345-346, 1989). What is most remarkable is that identification depends upon examination of minute internal parts of the insect, demanding delicate dissection and microscopic examination, and this was at a time when he had difficulty in controlling the hand trembles that marked the early stages of Parkinson's disease!

John revelled in the company of fellow enthusiasts and had a special flair for encouraging beginners, especially those prepared to make a determined effort to get to grips with their chosen subject. At indoor meetings his exhibition boxes were always instructive and set a high standard for others to emulate. His full and productive life was marred towards the end by a prolonged and progressively debilitating illness, but his influence will last among those fortunate to have known his friendship and wise counsel. During his lifetime John was honoured by his fellow naturalists in recognition of his contributions to those organisations he served so loyally: President of the Leeds Naturalists' Club and Scientific Association 1951 and 1979; President of the Yorkshire Naturalists' Union 1970; Honorary Life Member of the Yorkshire Naturalists' Union 1994; Vice-President of the Yorkshire Wildlife Trust 1979-1984 and Honorary Life Vice-President of the Yorkshire Wildlife Trust 1984.

The respect and affection in which he was widely held was amply demonstrated by the large attendance at his funeral in Leeds. John enjoyed the unfailing support and companionship of Tim and she was always the perfect hostess to all who visited their home and enjoyed their warm hospitality. To Tim, and to Peter, I am indebted for information about John's early life, and our condolences are extended to her and the family in their sad loss.

Ross Crossley

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