

Rhinanthus minor L.

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Scrophulariaceae, Pedicularieae. Yellow-rattle. *Rhinanthus minor* L. *sensu lato* is a summer annual, facultative hemiparasitic therophyte. Stem erect, simple or branched and up to 500 mm, 4-angled and often streaked or spotted black. Leaves 20–30 mm × (2–)5–8 mm, opposite, sessile, subcordate at base, ovate to lanceolate and entire to dentate, scabrid at least above, hairy or not. Flowers solitary, subsessile, in axils of leaf-like bracts in terminal spike-like racemes. Bracts triangular, glabrous or somewhat scabrid, longer to slightly shorter than calyx; lower teeth of bracts not much longer than the upper. Intercalary leaves (at nodes on the main stem between the highest branches and the lowest bract) 0–6 pairs. Calyx 4-toothed and flattened, usually mid-green or with a reddish-tinge, hairy only on the margins, or all over. Corolla 12–15(–17) mm, yellow to brownish-yellow; mouth of corolla somewhat open. Lower lip 3-lobed, turned down away from upper lip. Upper lip compressed, with two violet teeth (rounded) below the apex, < 1 mm, shorter than wide. Dorsal line of corolla ± straight proximally, merging into convexly curved upper lip. Didynamous; stamens included in upper lip of corolla. Stigma included or slightly exserted. Anther-lobes hairy, not mucronate. Seed capsules shorter than calyx, compressed and loculicidal, seeds few. Seeds ± discoid, always winged, without oil-body. Seeds 4.9 × 3.8 mm; mean seed mass 2.84 mg (Grime *et al.* 1988).

Rhinanthus minor is highly variable in several characters and displays ecotypic variation. Identification of subspecies in the field is further confounded by its hemiparasitic habit as this can result in stunted, unbranched individuals. It has been suggested that these individuals are best ignored unless they are the prevalent sort (Stace 1997).

Six subspecies may be recognized in the British Isles.

Subsp. *minor*. Aestival flowering ecotype. Stem 120–400 mm, usually with only short non-flowering branches but sometimes with longer suberect flowering branches from the middle and upper part of the stem. Internodes (except lowest) ± equal. Leaves on main

stem (10–)20–40(–50) × (3–)5–7 mm, linear-oblong to narrowly oblong. Intercalary leaves 0(–1) pair (rarely more). Lowest flowers usually from 6th–9th node. Calyx hairy only on the margins. Corolla yellow, teeth violet (rarely white).

Subsp. *stenophyllus* (Schur) O. Schwarz (*R. stenophyllus* (Schur) Druce). Autumnal flowering ecotype. Stem (150–)250–500 mm, usually with several long arcuate-ascending flowering branches from middle and lower part of stem. Lower internodes much shorter than upper. Leaves on main stem 15–45 × 2–5(–7) mm, narrowly lanceolate or linear-lanceolate, ± tapering from near the base. Intercalary leaves (0–)1–2(–4) pairs. Lowest flowers usually from (8th–)10th–13th(–15th) node. Calyx hairy only on the margins. Corolla yellow, sometimes becoming brown, teeth violet.

Subsp. *monticola* (Sterneck) O. Schwarz (*R. monticola* (Sterneck) Druce; *R. spadiceus* Wilmott). Montane ecotype. Plant often tinged purple. Stem (50–)100–200(–250) mm, usually with short or medium length branches from near the base, sometimes also with 1–3 longer flowering branches. Lower internodes usually very short, the upper much longer. Leaves on main stem 10–20(–25) × 2–4 mm, linear-lanceolate, ± tapering from near the base, often more erect than in ssp. *stenophyllus*. Intercalary leaves usually 1–2(–3) pairs. Lowest flowers mostly from (7th–)8th–11th(–12th) node. Calyx hairy only on the margins and often tinted purple. Corolla dull yellow becoming light brown, or constantly light brown, teeth violet.

Subsp. *calcareus* (Wilmott) E. F. Warb. (*R. calcareus* Wilmott). Autumnal flowering ecotype. Stem 250–500 mm, usually with long arcuate-ascending flowering branches from about the middle. Lower internodes short, upper very long. Leaves on main stem 10–25 × 1.5–3 mm, linear, ± spreading. Intercalary leaves usually (2–)3–6 pairs. Lowest flowers usually from 14th–19th node. Calyx hairy only on margins. Corolla yellow, teeth violet.

Subsp. *borealis* (Sterneck) P. D. Sell (*R. borealis* (Sterneck) Druce). Autumnal flowering ecotype. Stem (50–)90–200(–280) mm, unbranched or occasionally with short axillary non-flowering (very rarely flowering) branches, with internodes (except lowest) ± equal. Intercalary leaves 0. Stem leaves 10–30 × 3–7 mm, oblong or oblong-linear, ± parallel-sided. Lowest flowers

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*Abbreviated references are used for standard works: see *Journal of Ecology* (1975), 63, 335–344. Nomenclature of vascular plants follows Stace (1997).

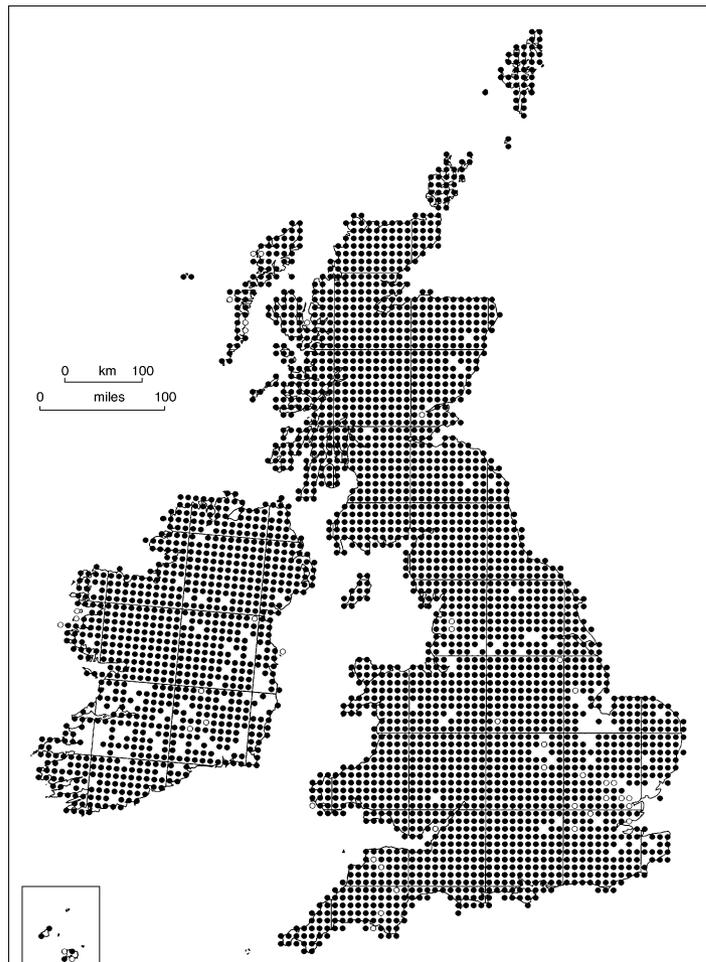


Fig. 1 The distribution of *Rhinanthus minor* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. Mapped by Henry Arnold, Biological Records Centre, Centre for Ecology and Hydrology. (○) Pre-1950, (●) 1950 onwards.

from 5th–7th(–8th) node. Calyx hairy all over. Corolla bright yellow, teeth violet or white.

Subsp. *lintonii* (Wilmott) P. D. Sell (*R. lintonii* Wilmott, *R. lochabrensis* Wilmott, *R. gardineri* Druce). Autumnal flowering ecotype. Stem to 300 mm; similar to sp. *borealis* in a pubescent calyx and suggested to be a hybrid (see section VIII B). Simple, or with 1–2 pairs of branches from the lower or middle part of the stem. Internodes \pm equal, or the lower shorter. Stem leaves (8–)10–20(–30) \times 1.5–3(–4) mm, very narrow linear–lanceolate, \pm tapering from the base. Intercalary leaves 0–3 pairs. Flowering from 7th–10th node.

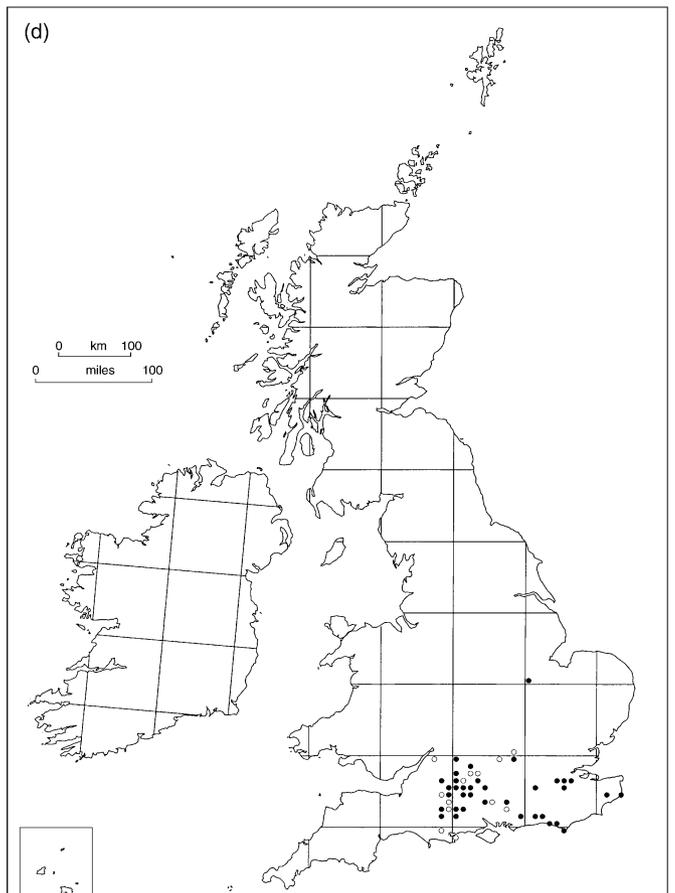
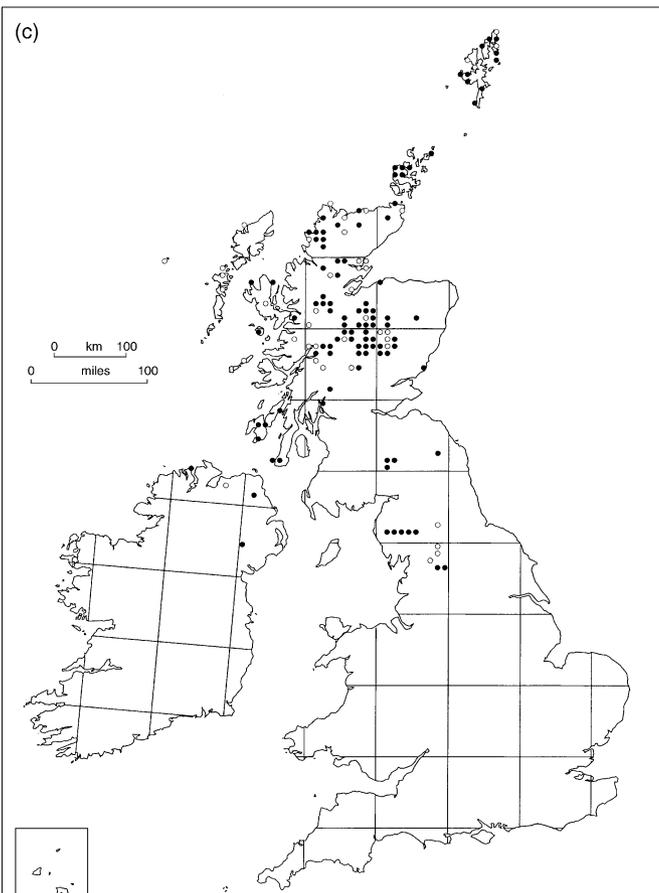
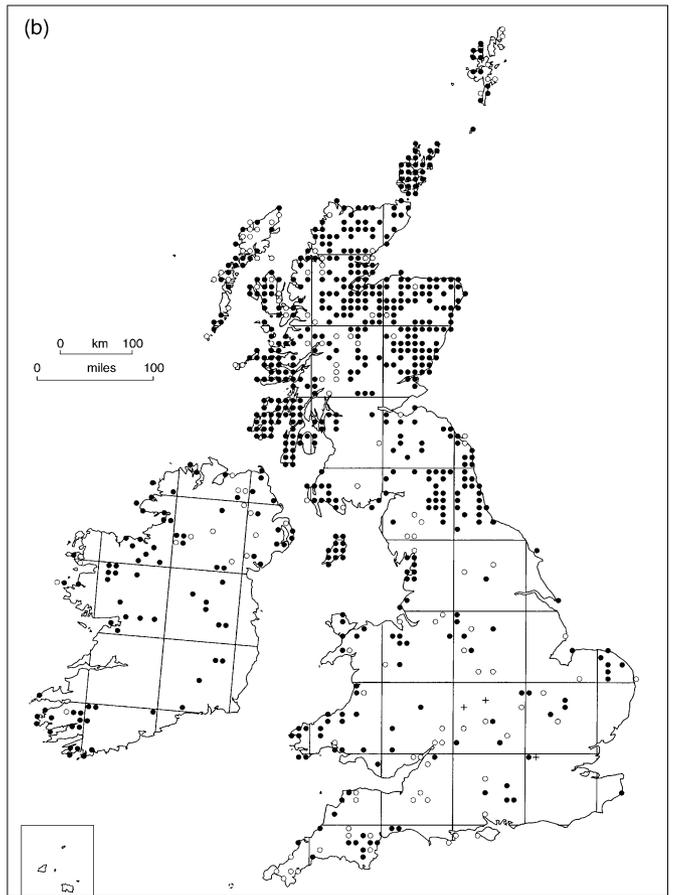
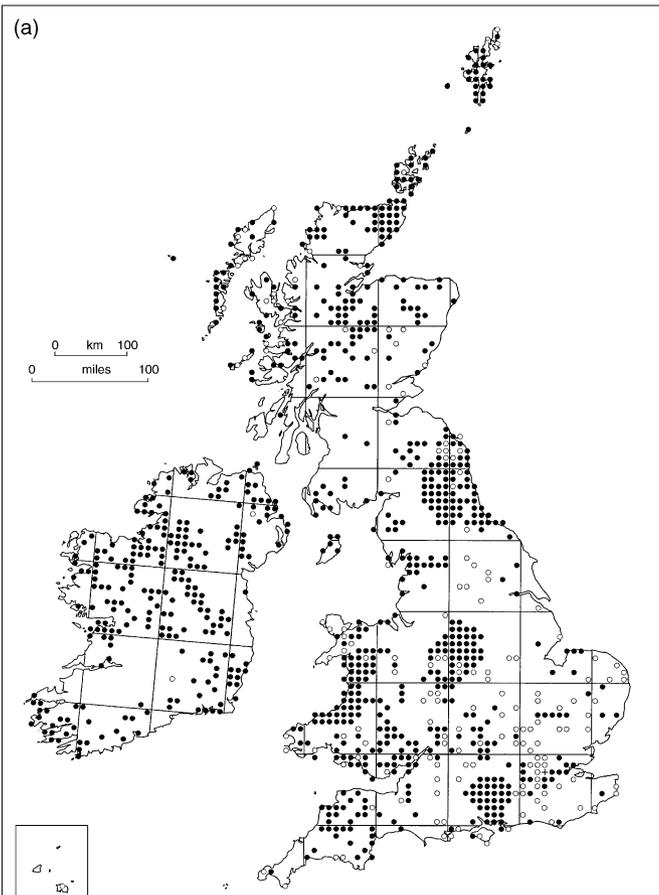
Linnaeus gave the original generic name for *Rhinanthus* in 1753 when the name *Rhinanthus crista-galli* was published. However, in 1939 this name was recognized as a *nomen dubium* by Schwartz (cited in van Hulst *et al.* 1986) and replaced by *R. minor*. The two main *Rhinanthus* species in the British Isles, *R. minor* and *R. angustifolius* (*R. serotinus*, *R. major*) were also once collectively grouped under *R. crista-galli* (Parker & Riches 1993).

Rhinanthus minor is native to the British Isles and common throughout, growing mainly in meadows, but is also found in ungrazed grassland, mire, road verges, and as a component of sand-dune vegetation.

I. Geographical and altitudinal distribution

Rhinanthus minor is found throughout most of the British Isles being recorded in all vice-counties (Fig. 1). The distribution of *R. minor* throughout the British Isles shows greater variation at the subspecies level (Fig. 2). Subsp. *minor* occurs particularly in lowland central and southern Britain. Subsp. *stenophyllus* is common northwards from the Isle of Man and Northumberland. Subsp. *monticola* is restricted to the mountain districts of Yorkshire and from Selkirk to Shetland. Subsp. *calcareus* is mainly found from Dorset and Kent to Gloucester and Buckinghamshire. Subsp. *borealis* is largely restricted to mountains ascending to over 1000 m in Scotland, and mostly has a central and northern distribution. Subsp. *lintonii* is also present on mountains in central and northern Scotland, but often occupies areas lacking other subspecies of *R. minor*.

Rhinanthus minor is widespread throughout most of Europe, although rare in the Mediterranean region. *Rhinanthus minor* has been given as frequent in most parts of lowland Iceland, but has been recorded only once from the interior (Grøntved *et al.* 1942). In northern Sweden, *R. minor* grows as an alien (Seel & Press 1993).



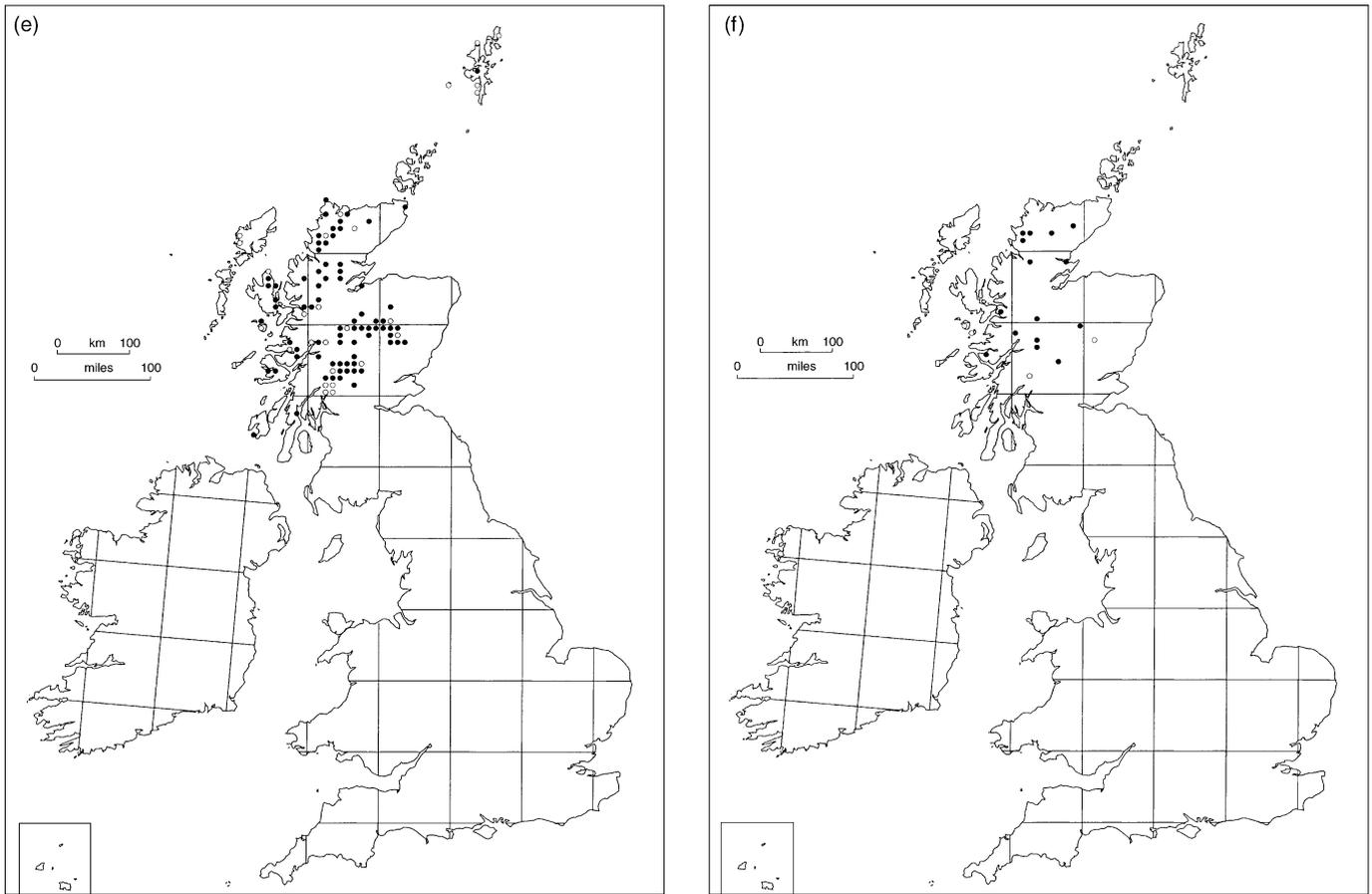


Fig. 2 The distribution of the subspecies of *Rhinanthus minor* in the British Isles. (a) *minor*, (b) *stenophyllus*, (c) *monticola*, (d) *calcareus*, (e) *borealis*, and (f) *lintonii*. Each dot represents at least one record in a 10-km square of the National Grid. Mapped by Henry Arnold, Biological Records Centre, Centre for Ecology and Hydrology. (○) Pre-1950, (●) 1950 onwards.



Fig. 3 The distribution of *Rhinanthus minor* in Eurasia and North America. The map is reproduced with permission from ter Borg (1985).

Rhinanthus minor is widespread throughout North America (van Hulst *et al.* 1987) and within Asia (ter Borg 1985) (Fig. 3). In North America, *R. minor* (*R. crista-galli*) is found from Labrador to Alaska and southward to New England and New York (Steere 1966a). It is also found in the Rocky Mountains and to north-western Oregon (Steere 1966b). In Canada, dis-

tinct northern and southern *R. minor* populations have been identified using seed protein analysis; a hybrid between these two populations has also been recorded (van Hulst *et al.* 1986). The southern population was described as *R. minor* ssp. *minor* and may have been introduced as a contaminant in hay from continental Europe (Fernald 1907), whereas the northern populations

were native and defined as *R. minor* ssp. *borealis* (van Hulst *et al.* 1986). *Rhinanthus minor* (*R. crista-galli*) has also been recorded in New Zealand, but is not accepted as part of the naturalized flora (Webb *et al.* 1988).

The altitudinal range of *R. minor* in the British Isles extends from sea level up to 594 m in North Yorkshire, England, to 831 m on Snowdon in North Wales and to 1021 m in Perthshire, Scotland (Alt. range Br. Pl.). However, it is more commonly observed to 350 m (Grime *et al.* 1988).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

The widespread distribution of *R. minor* indicates that it encounters no regional climatic limits in Britain or Ireland. However, variation is shown at the subspecies level. In general, *R. minor* is absent from most skeletal soils and steep slopes in Britain (Grime *et al.* 1988), which may be a consequence of its hemiparasitic behaviour and the scarcity of suitable hosts in these habitats.

Species of *Rhinanthus* are mainly found in open grassland, and ter Borg & Bastiaans (1973) have queried whether they are present in low and open vegetation owing to habitat preference, or if this vegetation type is a result of their presence. *Rhinanthus minor* is not shade tolerant and an open sward is likely to be important for its initial establishment. The distribution of *R. minor* is given by Preston & Hill (1997) as European Boreo-temperate, but widely naturalized.

(B) SUBSTRATUM

Rhinanthus minor occurs on a wide range of substrates including clay, sand, chalk and occasionally peat, but is absent from sites with a soil pH below 5.0 (Grime *et al.* 1988). Of the many National Vegetation Classification (NVC) communities with which *R. minor* is associated, it is most abundant in the *Anthoxanthum odoratum*–*Geranium sylvaticum* grassland (MG3), which is frequently associated with soils derived from superficial deposits: alluvium, head, glacio-fluvial material or, most commonly, glacial till often laid down in moraines or as drumlins (Rodwell 1992). This soil type can either have poor to impeded drainage or be free-draining. When soils are free-draining, the traditional application of lime and farmyard manure buffers the loss of minerals to leaching and so maintains soil pH in favour of *R. minor*.

At Castle Hill National Nature Reserve (Sussex), *R. minor* is abundant in association with soils derived from Cretaceous chalk, having a pH range of 7.5–7.8. These soils are well drained and are low in organic matter and nutrients (Kelly 1989a). *Rhinanthus minor* has also been found in calcareous grassland at Bessingby and Flamborough Head, North Humberside (Gibson & Watkinson 1992). In West Yorkshire, *R. minor* is

reported as having a widespread but scattered distribution, becoming locally abundant in neutral or base-rich grassland (Lavin & Wilmore 1994). It is also common in neutral grassland at Strensall, North Yorkshire (Gibson & Watkinson 1992) and has been successfully established in association with a sown meadow mix on a substrate of crushed brick waste containing a high proportion of fines; soil pH was 8.6 (Westbury 2001).

Rhinanthus minor is absent from droughted habitats, but may be a component of sand dune vegetation (Vallance 1952; Gibson 1986), mainly in association with areas having a high cover of perennial species (Watkinson & Davy 1985). In particular, it has been found in: semi-fixed dunes; calcareous fixed dunes and sand plains; dunes kept moist by fluctuating base-rich ground waters; dry dune slacks that are rarely flooded to any great extent; and damp or wet dune slacks kept moist by fluctuations in less base-rich, ground waters (Rodwell 2000). In northern Sweden, *R. minor* has been recorded in dry fields on coarse mineral soils (Danell & Ericson 1990).

Rhinanthus minor is tolerant of grassland habitats that become waterlogged in winter (Grime *et al.* 1988). For example, Davies *et al.* (1997) studied a population of *R. minor* in an alluvial flood-meadow in North Yorkshire. *Rhinanthus minor* is also associated with fen peats having a moderate to high summer water table and some winter flooding with base-rich, calcareous and often oligotrophic waters (Rodwell 1995). It is also found in and around well-developed springs, flushes and mires, or in other areas influenced by surface or ground waters (Rodwell 1991). On the Isle of Man, it is associated with bogs, marshes, wet fields, mine rubble, damp roadsides and dry grassland (Allen 1984).

III. Communities

Rhinanthus minor is found in a wide range of grassland habitats in the British Isles, being typically associated with hay meadow communities. Of the habitats studied by Grime *et al.* (1990), *R. minor* was most commonly associated with meadows (16%), limestone pastures/rock outcrops (2%) and enclosed pastures (1%), typically being associated with a high floristic diversity. It is absent from aquatic, arable, woods and several types of spoil habitats and is classified as having an established strategy intermediate between a ruderal and a stress-tolerant ruderal (Grime *et al.* 1988). However, although *R. minor* is now usually absent from arable land, formerly it was observed in cereal crops following grassland reversion (Long 1924).

The NVC has recorded *R. minor* in 22 British plant communities (six mesotrophic grasslands, six calcicolous grasslands, two calcifugous grasslands, two mires, one fen community and five maritime communities) with varying abundance (Rodwell 1991, 1992, 1995, 2000).

Rhinanthus minor is most frequent in the *Briza media* subcommunity of *Anthoxanthum odoratum*–*Geranium*

sylvaticum grassland (MG3), occurring in 61–80% of vegetation samples recorded, with an abundance ranging from 2 to 3 on the Domin scale (Rodwell 1992). MG3 grassland is a northern submontane community almost entirely confined to a few upland valleys in northern England, around Teesdale and Weardale in Durham, Swaledale and Wensleydale in North Yorkshire and parts of the Lake District where traditional hay-meadow management has been applied. No Scottish samples have been recorded, although fragments of the community are present along the riverbanks in Tayside (Rodwell 1992). The constant species of the MG3 community are: *Agrostis capillaris*, *Alchemilla glabra*, *Anthoxanthum odoratum*, *Cerastium fontanum*, *Conopodium majus*, *Dactylis glomerata*, *Festuca rubra*, *Geranium sylvaticum*, *Holcus lanatus*, *Plantago lanceolata*, *Poa trivialis*, *Ranunculus acris*, *Rumex acetosa*, *Sanguisorba officinalis* and *Trifolium repens*. In addition to the MG3 constant species, the *Briza media* subcommunity is characterized by an abundance of species common to unimproved grasslands, e.g. *Briza media*, *Centaurea nigra*, *Leontodon hispidus*, *Lotus corniculatus* and *Luzula campestris*, and the near absence of species associated with improvement/or re-seeding (Rodwell 1992).

Rhinanthus minor is also relatively frequent in the *Alopecurus pratensis*–*Sanguisorba officinalis* grassland (MG4). This community is found in the lowlands on alluvial soils in the Midlands and southern England where traditional hay-meadow management has been applied to land that seasonally floods. *Rhinanthus minor* has been recorded in 41–60% of samples with an abundance of 1–5 (Rodwell 1992).

Rhinanthus minor has been recorded in the following communities with a moderate constancy: *Centaureo*–*Cynosuretum cristati* grassland (MG5), typical of circumneutral brown soils throughout the lowlands of Britain where traditional hay-meadow management has been applied; *Cynosurus cristatus*–*Caltha palustris* grassland (MG8), characteristic of traditionally managed pasture that is periodically inundated. It is recorded on the flat or slightly sloping land by rivers and streams and also as fragmentary stands below springs, flushes and seepage lines which produce moderately calcareous water. The community has a widespread but rather local distribution throughout the British lowlands; *Dryas octopetala*–*Silene acaulis* ledge community (CG14), invariably confined to ungrazed crags and ledges of calcareous bedrocks, mainly in the central and southern Scottish Highlands, although localized communities are found in the north-west Highlands; *Saxifraga aizoides*–*Alchemilla glabra* community (U15), widespread but local in the Scottish Highlands through the mountains between Breadalbane and Clova. It is confined to steep, continuously irrigated, calcareous cliff faces and earth banks and is therefore usually ungrazed; *Potentilla anserina*–*Carex nigra* dune-slack community (SD17), widespread in dune systems around the British coast, particularly in

northern Britain. It is characteristic of damp or wet dune slacks kept moist by the fluctuating, less base-rich, ground waters.

Rhinanthus minor also occurs with a lower constancy in a number of other NVC communities, namely *Arrhenatheretum elatioris* grassland (MG1), *Lolio-Cynosuretum cristati* grassland (MG6), *Festuca ovina*–*Carlina vulgaris* grassland (CG1), *Festuca ovina*–*Avenula pratensis* (*Helictotrichon pratense*) grassland (CG2), *Bromus erectus* (*Bromopsis erecta*) grassland (CG3), *Bromus erectus* (*Bromopsis erecta*–*Brachypodium pinnatum*) grassland (CG5), *Sesleria albicans*–*Scabiosa columbaria* grassland (CG8), *Luzula sylvatica*–*Geum rivale* tall-herb community (U17), *Peucedano*–*Phragmitetum australis* community (S24), *Juncus subnodulosus*–*Cirsium palustre* fen-meadow (M22), *Molinia caerulea*–*Crepis paludosa* mire (M26), *Ammophila arenaria*–*Festuca rubra* mire community (SD7), *Festuca rubra*–*Galium verum* dune-slack community (SD8), *Salix repens*–*Campylium stellatum* dune-slack community (SD14) and *Salix repens*–*Holcus lanatus* dune-slack community (SD16). Floristic tables of associated species and the geographical distribution of the associated communities of *R. minor* throughout the British Isles are provided by Rodwell (1991, 1992, 1995, 2000).

Grime *et al.* (1988) reported that *R. minor*, expressed as a percentage similarity, was frequently associated with the following species: *Bromus hordeaceus* (93%), *Festuca pratensis* (82%), *Phleum pratense* (79%), *Alopecurus pratensis* (78%) and *Ranunculus bulbosus* (71%). Association analysis has also been carried out for *R. minor* in sand dunes at Holme-next-the-Sea, Norfolk to determine its host range and selectivity (Gibson 1986). Only two species were found to be significantly positively associated with *R. minor*: *Ononis repens* and *Plantago lanceolata*. In contrast, 12 species were significantly negatively associated with *R. minor*. Hodgson (1973) found that *R. minor* was positively associated with *Plantago lanceolata*, in addition to *Festuca rubra* and *Lathyrus pratensis*, but negatively with *Briza media*, *Dactylis glomerata*, *Ranunculus acris* and *Viola riviniana*. These associations may be a consequence of host–parasite interactions. Negative associations may also result if species have environmental tolerance limits outside those of *R. minor* (Gibson 1986).

In central Europe, *R. minor* is associated with the Molinio-Arrhenatheretea cultivated meadow and pasture communities (Ellenberg 1988). Specifically, in Germany, *R. minor* is found in all orders of Molinietales and mown Arrhenatheretalia. It is also found in Nardetalia of the Nardo-Callunetea community (Pfl. Exk.). In northern Sweden, *R. minor* has been recorded in a species-rich *Anthoxanthum odoratum* meadow (Danell & Ericson 1990). Populations in Sweden are also found to cluster along roadsides (Seel & Press 1993). Studies on the distribution of *R. minor* in S. Netherlands (Hillegers 1981) and the North Holland dunes indicated a preference for low, open turf (Mesobromion and Koelerio-Corynephoretea) (ter Borg 1985).

In lowland Iceland, *R. minor* is associated with uncultivated grassland, home-fields, grassy slopes, heaths and dry moors (Grøntved *et al.* 1942).

In north-eastern USA, *R. minor* (*R. crista-galli*) is found in fields and thickets (Steere 1966a) and hay fields in Canada (van Hulst *et al.* 1987).

IV. Response to biotic factors

Generally, for an individual plant to establish successfully in existing vegetation it must develop a sufficiently large root system to extract water and nutrients (Watkinson & Gibson 1988). Hemiparasites can overcome this initial barrier to establishment through the formation of haustoria (xylem–xylem continuity), which enables the existing root system of the host to be utilized. Subsequent survival, especially in a productive grass sward, is then based on the ability of *R. minor* to acquire water and solutes from its host(s).

The density of *R. minor* in a sward has been suggested to be a function of host density and vigour (van Hulst *et al.* 1987). Owing to its hemiparasitic habit, treatments that influence the abundance and/or vigour of the host vegetation can influence the number of *R. minor* individuals supported. Consequently, the presence of *R. minor* in grassland is strongly related to management and the associated soil fertility/productivity.

RESPONSES TO CUTTING

The reliance of *R. minor* on its hosts for much of its nutrition suggests that the partial defoliation of a host could reduce the performance of *R. minor*. However, when all meadow vegetation except *R. minor* was clipped at the soil surface, no significant effect on its fecundity or survival was observed (van Hulst *et al.* 1987).

The cost of apical dominance in *R. minor* was investigated in a natural population in a sward dominated by *Agrostis capillaris* and *Poa pratensis* in Lapland, Finland (Huhta *et al.* 2000). It was found that the removal of terminal buds by clipping 10% of the prevailing height did not induce vigorous branching. Furthermore, there was no effect on the final height of *R. minor*, the number of nodes, the amount of above-ground biomass or the number of fruits, although root biomass increased slightly. However, the control plants had slightly more sterile branches (lacking flowers). With 50% removal, plants were ultimately shorter, produced fewer branches and fruits and had lighter seeds and less above-ground biomass. However, root biomass did not differ. No regrowth was observed with 75% removal, leaving only short stalks with small rootstocks (Huhta *et al.* 2000).

A population of *R. minor* was established by sowing 1000 seeds m⁻² in a recently established sward, dominated by *Lolium perenne* in Shelley, West Yorkshire (D. B. Westbury and N. P. Dunnett, unpublished). During March, a cutting treatment was applied to promote the establishment of *R. minor* by reducing sward dominance. The vegetation was cut above the *R. minor* plants

to a height of 40 mm. June assessments of *R. minor* density indicated that the treatment was associated with a reduction in its number, with an average 228 (± 50) individuals m⁻² compared to 407 (± 162) m⁻² in the uncut plots. When a spring cut was applied to meadow vegetation established on ex-arable land in Wetherby, West Yorkshire, the mean number of individuals present was 570 (± 211) m⁻², compared to 400 (± 195) m⁻² in the control plots (Westbury 2001). However, the large standard errors indicate that not all populations responded in the same way.

RESPONSES TO SWARD SCARIFICATION

Sward scarification providing 50% disturbance was applied to a recently established *Lolium perenne* sward at Shelley, West Yorkshire, in November, before over-sowing *R. minor* in experimental plots at 1000 seeds m⁻² (D. B. Westbury and N. P. Dunnett, unpublished). The number of individuals present in these scarified plots the following June was greater than in the control plots, with average densities of 496 (± 57) and 336 (± 21) individuals m⁻², respectively. Scarification was also associated with a 42% increase in *R. minor* above-ground biomass from 64.0 g m⁻² to 91.0 g m⁻².

The same *R. minor* and scarification treatment was applied to two different meadows which had been grassland for at least 20 years. Scarification of a sward dominated by *Agrostis capillaris*, *Anthoxanthum odoratum* and *Cynosurus cristatus* at Richmond, North Yorkshire, resulted in a slight increase in *R. minor* density, with 361 (± 45) individuals m⁻², compared to 346 (± 27) m⁻² in the absence of scarification (D. B. Westbury and N. P. Dunnett, unpublished). Scarification of a sward consisting chiefly of *Agrostis capillaris*, *Dactylis glomerata*, *Holcus lanatus*, *Plantago lanceolata* and *Ranunculus repens* at Thunderbridge, West Yorkshire, also increased the establishment success of *R. minor*. The mean number of individuals present in June was 255 (± 50) individuals m⁻² compared to 184 (± 34) m⁻² in the control plots (D. B. Westbury and N. P. Dunnett, unpublished).

RESPONSES TO THE APPLICATION OF HERBICIDE

To reduce grass abundance and promote the establishment of *R. minor* in a *Lolium perenne* sward, the selective graminicide fluazifop-P-butyl (Syngenta Crop Protection Ltd, Cambridge, UK) was applied at a rate of 125 g active ingredient ha⁻¹ in April. The average density of *R. minor* present in the sprayed plots in June was 507 (± 40) m⁻² compared to 336 (± 21) m⁻² for the control (D. B. Westbury and N. P. Dunnett, unpublished). The application of fluazifop-P-butyl was also associated with a greater above-ground biomass of *R. minor* at the time of harvest in July. The mean value in the control plots was 64.0 g m⁻² compared to 120.8 g m⁻² in the graminicide treated plots, equivalent to an increase of 89%.

In a *Lolium perenne*–*Cynosurus cristatus* grassland (MG6, NVC community, Rodwell 1992) at Ingleborough, North Yorkshire, the establishment of *R. minor* was observed to benefit from a late July hay-cut followed by autumn grazing with cattle (Smith *et al.* 1996a). This type of traditional management opens up the sward for many species including *R. minor*, by reducing standing biomass and creating bare ground through trampling, the effect being greater on soils with a low to moderate fertility.

Rhinanthus minor is very vulnerable to changes in agricultural practices away from the traditional methods of hay meadow management, where survival depends on its ability to shed seed before harvest. The lack of a long-term persistent seed bank also means that *R. minor* is heavily dependent on the yearly establishment from seed produced the previous year. Consequently, modern techniques of grassland management including cutting for silage and the application of inorganic fertilizer are all detrimental to the long-term persistence of *R. minor*.

Rhinanthus minor has been shown to be moderately resistant to the 'broad-leaved' herbicides MCPA-salt and 2,4-D amine when applied to existing grassland at a rate of 1.7 kg ha⁻¹ and 1.4 kg ha⁻¹, respectively. However, it is susceptible to Mecoprop-salt when applied to existing grassland at 2.8 kg ha⁻¹ (Fryer & Makepeace 1978).

In the glasshouse, it has been found that *R. minor* is susceptible to the fungicide Calixin. Calixin interferes with the metabolism of mannitol, required to produce high osmotic pressure in the sap of *R. minor* enabling it to obtain host solutes (Gibson 1986).

V. Response to environment

(A) GREGARIOUSNESS

Rhinanthus populations are often observed as transient patches within swards, frequently forming dense populations (Salter 1935; de Hullu 1985b; Gibson 1986, 2000; Kelly 1989b). Gibson (1986) investigated *R. minor* populations on a sand dune system at Holme-next-the-Sea, Norfolk, over an area of about 3 ha; dense patches of 100–200 flowering plants m⁻² and areas of lower density (0–50 plants m⁻²) were observed. Yearly variation in plant density also occurs and, over a 4-year period, populations of *R. minor* in calcareous grassland in Sussex varied between 15 plants m⁻² and 135 plants m⁻² (Grubb *et al.* 1982). However, in contrast, populations of *R. minor* on a limestone outcrop that had remained undisturbed for at least 100 years in the mountains of Caenlochan Nature Reserve (Scotland) varied from 1.0 plants m⁻² to 2.3 plants m⁻², over 3 years (de Hullu *et al.* 1985).

Natural population densities of *R. minor* in a SSSI (Site of Special Scientific Interest) meadow (Pye Flatts)

near Barnsley, West Yorkshire, ranged from 596 individuals m⁻² to 1004 individuals m⁻². The mean of five samples was 752 ± 70 individuals m⁻², although areas of high density were specifically selected. According to van Hulst *et al.* (1987), these values are relatively low, as observations of natural *R. minor* densities in a 12-year-old meadow in Canada, averaged 4382 ± 1236 individuals m⁻². This was classified as a high density, compared to 1409 ± 190 individuals m⁻² for medium density and 405 ± 183 individuals m⁻² for low density. However, the values given were for densities at the beginning of the growing season, with losses of plants occurring throughout the year, and to a greater extent at the higher starting density.

To investigate the diversification of an upland *Lolium perenne*–*Cynosurus cristatus* meadow (MG5; Rodwell 1992), Smith *et al.* (2000) sowed various species, including *R. minor*, into experimental plots under several cutting and grazing treatments. *Rhinanthus minor* was the most successful species to be introduced and soon established in the unsown plots if associated with a suitable management regime, such as a late summer hay-cut. After 5 years, population numbers in the unsown plots were greater than in the sown plots. Consequently, it was suggested that the initial colonization of *R. minor* had peaked after 4–5 years. Of the sown plots, the greatest density of individuals was approximately 68 m⁻², under a treatment of autumn and spring grazing combined with a late July hay-cut and fertilizer application (40 kg ha⁻¹ of 20 : 10 : 10, NPK) (Smith *et al.* 2000). However, when this treatment combination was applied without spring grazing, the density of *R. minor* was reduced to 14 individuals m⁻².

Populations of *R. minor* are strongly regulated by sward composition and structure. Overall, the number of *R. minor* individuals observed in productive swards is relatively low, indicating its limited ability to compete with the vigorous growth of its potential hosts. For example, when the commercial fertilizer 'Rapid Grow' was added at a rate of 24 g m⁻² to meadow plots on a weekly basis, a negative relationship was observed between the survivorship of *R. minor* and vegetation density (van Hulst *et al.* 1987). Despite the negative aspect of soil fertility on *R. minor* populations, if it survives in a productive sward, individuals are frequently larger and more fecund (ter Borg 1972; de Hullu 1984; van Hulst *et al.* 1987), with fecundity and plant size being positively correlated with the biomass of the surrounding vegetation (van Hulst *et al.* 1987).

At five experimental sites, *R. minor* was sown in the autumn at a rate of 1000 seeds m⁻². Three of the sites consisted of existing grassland and two investigated establishment from a bare ground start in conjunction with a complete meadow mix (80% grass : 20% forbs, by weight). The establishment success of *R. minor* differed between sites and whether or not existing vegetation was present (all assessments were made in June).

The lowest density of *R. minor* recorded was 117 (± 24) individuals m⁻², in plots established on recently

cultivated land in Kirkby, Merseyside (Westbury 2001). The relatively poor establishment at this site can most likely be attributed to the substrate, being nutrient poor, consisting of crushed brick waste with a high proportion of fines. The substrate was also hard and compact, which may have reduced root growth of *R. minor* and its potential hosts. Although *R. minor* can grow completely autotrophically, the very low soil fertility is likely to have further limited its success.

At Wetherby, West Yorkshire, *R. minor* density on ex-arable land was greater, with $377 (\pm 15)$ individuals m^{-2} , suggesting that establishment of *R. minor* is not hindered by the absence of vegetation cover at the time of sowing (D. B. Westbury and N. P. Dunnett, unpublished). The capacity of *R. minor* to establish the following spring in the absence of a sufficient host resource may be attributed to its ability to grow autotrophically, coupled with the fact that younger hosts can be more susceptible to the effects of parasitism (Seel & Press 1996). This is further supported by the observation that when non-dormant, pre-chilled *R. minor* seed was sown at 1000 seeds m^{-2} at the same time as a complete meadow mix during March, the average establishment density was $24 (\pm 5)$ individuals m^{-2} .

At Thunderbridge, West Yorkshire, the density of *R. minor* present in experimental plots established on permanent grassland was $184 (\pm 34)$ individuals m^{-2} , compared to $346 (\pm 27)$ individuals m^{-2} in a hay meadow at Richmond, North Yorkshire. At Shelley, West Yorkshire, $336 (\pm 21)$ individuals m^{-2} were recorded in a recently established sward dominated by *Lolium perenne* (D. B. Westbury and N. P. Dunnett, unpublished).

Overall, there was no apparent trend between levels of soil fertility and *R. minor* density. Differences between sites with respect to host quality is likely to be the main factor influencing the number of individuals present. Host quality will depend on the botanical composition and age of the sward, the growth conditions (e.g. soil fertility) of any potential hosts and their susceptibility to parasitism. However, the extent of seed predation and herbivory is also likely to influence numbers and would be expected to vary between sites. Clearly, numerous factors can be responsible for determining the density of *R. minor* populations.

(B) PERFORMANCE IN VARIOUS HABITATS

Rhinanthus minor, being a facultative root hemiparasite, can gain nutrition both autotrophically and heterotrophically. In the field, autotrophic growth rarely occurs, but in experimental systems it is commonly shown to be associated with reduced survival and fecundity, which is mainly due to the smaller size of plants. Nutrient addition can significantly stimulate growth of unattached individuals (Seel *et al.* 1993b), although *R. minor* has a limited ability to acquire and assimilate inorganic nitrogen from the soil (Seel *et al.* 1993a). The main advantage of autotrophic nutrition is that it allows the hemiparasite to develop and produce

some seed even when infecting a nutritionally poor host, or when the host resource is limited due to parasitism by several individuals (Atsatt 1970). Autotrophic nutrition also allows an individual to search actively for a host. Self-parasitism within clumps of *R. minor* can also occur, but when studied in the absence of a host, the efficiency of water and nutrient uptake was not increased (Gibson & Watkinson 1991). In the field, self-parasitism both within an individual and between neighbouring plants occurs infrequently (Gibson 1986). *Rhinanthus minor* has been observed to infect several hosts simultaneously, and of 65 *R. minor* plants studied in sand dune vegetation, five were attached to just one host and two to at least seven different hosts. The most frequent number of hosts was four (Gibson & Watkinson 1989).

The benefit to the hemiparasite infecting a suitable host is indicated by an increase in plant size and reproductive output. *Rhinanthus minor* can infect a wide range of hosts, enabling it to establish in different species assemblages and grassland types (van Hulst *et al.* 1987; Gibson & Watkinson 1989). Through utilizing the existing root systems of their hosts, hemiparasites can invade closed grassland habitats where other annual species are rare or absent. However, *R. minor* cannot invade all grassland communities equally well and has been found to produce fewer seeds than were originally sown into wet and dry grassland communities (van Hulst *et al.* 1987).

The list of potential hosts for *R. minor* determined from four sites in Britain (Gibson & Watkinson 1989) and one in central Europe (Weber 1976), includes 50 species from 18 plant families. Of these, the Fabaceae accounts for 11 species and the Poaceae 16. In addition, 9 species are annuals or short-lived perennials, 36 are herbaceous perennials and 5 are woody species (Gibson & Watkinson 1989). Although *R. minor* can infect many different host species, an equal nutritional benefit is not derived from all the hosts infected (Atsatt 1970), a scale of host quality existing. Furthermore, some families are completely avoided (e.g. Orchidaceae) (Weber 1976).

Preferred hosts and beneficial hosts have been identified for several species of *Rhinanthus*, but when grown in monocultures with these hosts, the parasite biomass produced is usually lower than with a more diverse sward (Joshi *et al.* 2000), even though the additional species may be of lower benefit to the parasite when grown in monoculture. However, growth tests can be very contradictory, as species may act as good hosts in one test and be poor in the next, possibly owing to genetic variation or different growing conditions (ter Borg 1985). Discords may also occur between pot and field studies; for example, Ramlan (1994) found that the presence of *R. minor* had no significant effect on the yield of pot-grown *Lolium perenne*, while in a *L. perenne* sward at Shelley, West Yorkshire, the above-ground biomass of *L. perenne* was strongly reduced by the presence of *R. minor*.

It is well documented that legume species are good hosts for hemiparasites (Govier *et al.* 1967; de Hullu 1984; Seel & Press 1993; Matthies 1996, 1997), enabling

surplus nitrogen to be accumulated without injurious effects (Govier *et al.* 1967), leading to an increased biomass and fecundity. Hemiparasites attached to legume species growing in nitrogen-deficient soil usually have a greater fitness than those growing with non-legume hosts (Gibson & Watkinson 1989). In a group of replacement series experiments, the potential hosts: *Festuca rubra*, *Holcus lanatus*, *Lolium perenne* and *Trifolium repens* were grown in different binary mixtures in the presence of *R. minor*. By examining the number of haustorial attachments between host and parasite (based on the relative haustorial frequency to host root weight), it was suggested that *R. minor* showed host preference in the order *Trifolium* > *Lolium* > *Festuca* > *Holcus* (Gibson 1986). Variation in host quality was then related to the degree of host selectivity (Gibson 1986), with nitrogen supply being the most important factor determining host quality (de Hullu 1984; Gibson & Watkinson 1991; Matthies 1997).

A pot study with *R. minor* and individual hosts showed that although shoot biomass of *Centaurea nigra* was suppressed to a greater extent than with *Achillea millefolium*, the overall benefit to *R. minor* in terms of above-ground biomass accumulation and fecundity was less (Westbury 2001). In turn, this suggests that although *C. nigra* was more susceptible to the presence of *R. minor*, its nutritional benefit was lower. Consequently, after successful infection of a host, host quality is more likely to be a function of the quality and quantity of nutrients received from the host(s) and not necessarily how strongly host biomass is reduced by parasitism. However, a reduced impact on the host can also be associated with a lower parasite performance (Davies & Graves 2000),

Leucanthemum vulgare is a poor host for *R. minor*, being associated with only a marginal increase in biomass and fecundity (Westbury 2001). *Plantago lanceolata* is also a poor host and despite haustorial connections being observed between host and parasite, *R. minor* performance was similar to unattached plants (Hodgson 1973; Seel *et al.* 1993a). However, based on the number of observed and expected haustorial connections between *R. minor* and *P. lanceolata* in sand-dune vegetation, *P. lanceolata* was identified as a 'preferred host' of *R. minor* (Gibson & Watkinson 1989).

The susceptibility of a species to parasitism and the quality of a host can also be a function of host age. Seel & Press (1996) studied repeated parasitism of *Poa annua* by *R. minor* and revealed that host age, and whether or not the host had been previously infected, to be important in determining host productivity. Plants infected for the first time in their second year of growth had a higher productivity than those infected in their first year only, suggesting that younger hosts were more susceptible to parasitism. Furthermore, plants infected for two consecutive years were suppressed by a greater margin. In this pot experiment, the nutrient-rich foliage produced by *R. minor* was not allowed to return to the soil after senescence. Nutrients, released from the

decaying vegetation in the absence of *R. minor* during late summer through to early spring, may have otherwise counteracted any negative impact that parasitism had on the host vegetation.

Rhinanthus minor is not shade tolerant, being absent from woodland, etc. (Grime *et al.* 1988). The effect of light availability on *R. minor* was investigated in a pot study with the host *Poa pratensis* (Hwangbo & Seel 2002). When individuals were approaching 5 weeks old and about to flower, a shading treatment was applied which had no effect on final *R. minor* biomass, haustoria number or the amount of ¹⁵N transferred from the host. However, *R. minor* responded to the shading with a significant increase in height (Hwangbo & Seel 2002). The ecological significance of shading is likely to be greater for *R. minor* seedlings before and soon after they have attached to suitable hosts.

Sward density is an important factor for the survival of *R. angustifolius*, especially at the seedling stage (de Hullu 1985a). The ability of a hemiparasite to reduce host biomass is paramount to its survival in productive swards. A greater overall survival of *R. minor* may be afforded through group suppression, if initial *R. minor* densities are sufficiently high to have a strong impact on the vegetation, reducing competitive exclusion. In such cases, individuals are usually smaller and less fecund, but owing to the greater numbers, high rates of seed production in a patch are maintained.

In support of this, species with an intermediate growth rate have been noted as 'preferred' hosts (ter Borg & Bastiaans 1973) as this increases the chances of a parasite to suppress the host, with the host still able to provide sufficient nutrients. Fast growing, ruderal species such as *Senecio vulgaris* have been suggested as unsuitable hosts for *Rhinanthus* spp. because they do not exert a sufficient competitive influence, making them vulnerable to competitive exclusion (ter Borg & Bastiaans 1973).

Despite the importance of *Rhinanthus* finding suitable hosts for parasitism, it appears that haustoria formation is initially a random process. This is because no host cues are required for germination and a wide range of hosts can be successfully infected. Consequently, owing to the attachment of haustoria to inert objects and unsuitable hosts that provide no nutritional benefit, host selection is probably random and dependent on the relative abundance of host roots and their distribution within the soil profile. In a pot study, host root length significantly affected the probability of infection by *R. minor*, with hosts with longer total root length having a higher probability of being parasitized than hosts with shorter roots (Saona 2002). If random foraging for host roots occurs, hosts with a certain root architecture or root size or type would be more available for infection, which could in turn suggest host specificity.

(C) EFFECT OF FROST, DROUGHT, ETC.

There is no information on the effect of frost on *R. minor*, although a parallel may be drawn with *R. angustifolius*,

where following frost the root tips of many seedlings emerging on bare soil were observed to be dead (ter Borg 1972). However, this may also be a result of desiccation, although re-growth in the proximal parts where side roots had developed was later observed in some samples. In contrast, when a cover of grass was present, this afforded a degree of protection as seedlings showed no visible damage. The presence of hosts may have increased the resistance of seedlings, or the cover of grasses ameliorated the microclimate (ter Borg 1972).

Rhinanthus minor is not frequent in habitats associated with drought, although, during periods of water stress, its host plants may wilt first. The parasitic behaviour of *R. minor* may buffer its sensitivity to water stress enabling survival in relatively dry areas, as found by Fresco (1980) for *R. angustifolius*. Under dry conditions, there is rubescence of the stem, bracts and calyx. Stem striolation can also occur and the pigmentation of the corolla teeth may be enhanced (Hamblen 1958).

VI. Structure and physiology

(A) MORPHOLOGY

Being hemiparasitic, the morphology of *Rhinanthus minor* is dependent on whether it is growing auto- or heterotrophically. Autotrophic individuals are frequently stunted (5–7.5 cm) and do not produce branches (Seel & Jeschke 1999). Severely stunted plants can also fail to flower. Total leaf area is also lower relative to individuals attached to a host, ranging from 400 mm² to 910 mm². In comparison, when attached to *Hordeum vulgare*, heights reached a maximum of 21 cm and total leaf area ranged from 4400 mm² to 5150 mm². Plants attached to *Trifolium alpestre* had better leaf development than with *H. vulgare* and leaves were narrower, larger and far less brittle (Seel & Jeschke 1999), indicating that morphology is also influenced by host type.

When three *R. minor* individuals were grown in pots with different individual hosts (*Achillea millefolium*, *Centaurea nigra* and *Leucanthemum vulgare*), the response of *R. minor* with respect to height, number of seed capsules, number of branches and number of nodes varied (Table 1). The greatest difference depended on whether a potential host species was present.

Rhinanthus minor mainly relies on the extensive root systems of its hosts and has a limited root volume. On contact with host roots, haustorial connections are made

which are about 1 mm in diameter, the size depending on host species (Gibson 1986). For example, haustoria formed with *Festuca rubra* were frequently smaller than those with *Lotus corniculatus* which were usually greater than 2 mm. Such large haustoria have also been found on *Lolium perenne* (Gibson 1986). Haustoria approximately twice the size of those associated with *Trifolium pratense* and *Bromus inermis* were observed with *Lupinus sericeus* (Saona 2002), while an individual attached to both *Festuca rubra* and *Lotus corniculatus* had both small and large haustoria (Gibson 1986).

Seed of *R. minor* undergoes an uncommon differentiation in developing both a chalazal and a micropylar endosperm haustorium. The main features of the chalazal haustorium are that it contains two highly polyploid nuclei with polytene chromosomes and complex nucleoli; the nuclei are extremely ramified and interdigitated with the cytoplasm; and the cell wall develops a prominent labyrinth that deeply penetrates into the haustorium at the chalazal end (Nagl 1992).

(B) MYCORRHIZA

Rhinanthus minor has been listed by Harley & Harley (1987) as an obligate non-mycorrhizal plant, confirmed by Davies & Graves (1998).

(C) PERENNATION: REPRODUCTION

Rhinanthus minor is a summer annual and according to the Raunkiaer system, a therophyte, over-wintering as seed. Reproduction is by seed only, which germinate in spring and do not form a persistent seed bank.

(D) CHROMOSOMES

The diploid chromosome number is $2n = 22$ (Chr. Eur. Pl.). The nuclear DNA content has been recorded as 7.9 pg per nucleus (Grime *et al.* 1988).

(E) PHYSIOLOGICAL DATA

Through the formation of haustoria, xylem–xylem continuity is established between *R. minor* and its host(s). Annual hemiparasites are capable of autotrophic growth, but have a greater benefit from the acquisition of xylem-dissolved minerals and some organic compounds from the host(s), such as reduced nitrogen in the form of

Table 1 The effect of host type on *Rhinanthus minor* attributes. Values in parentheses are \pm SE. Means per plant with the same superscript letter in each column do not differ significantly (Tukey's multiple comparison test $P < 0.05$). $n = 10$

Host species	Height (mm)	No. of seed capsules	No. of branches	No. of nodes
Control (no host)	273 ^a (± 17)	8.4 ^a (± 1.1)	4.8 ^a (± 0.8)	7.8 ^a (± 0.2)
<i>Achillea millefolium</i>	396 ^b (± 10)	18.3 ^c (± 1.2)	7.5 ^{ab} (± 0.5)	8.4 ^{ab} (± 0.2)
<i>Centaurea nigra</i>	380 ^b (± 12)	15.8 ^{bc} (± 1.4)	7.9 ^b (± 0.5)	8.7 ^{ab} (± 0.3)
<i>Leucanthemum vulgare</i>	307 ^a (± 15)	10.6 ^{ab} (± 1.5)	4.9 ^a (± 0.6)	9.3 ^b (± 0.2)

amino acids. Some organic carbon is also obtained from the xylem, but there is no evidence for the acquisition of phloem-borne photosynthates (Jiang *et al.* 2004).

To withdraw host xylem sap, the parasite must compete with the transpiration stream of the host. It has been suggested that the amount gained by the parasite is directly proportional to the host–parasite concentration gradient, and inversely proportional to host–parasite resistances (Press *et al.* 1990). High concentrations of sugar alcohols may help to maintain osmotic potentials below those of the host (Press *et al.* 1998), with relatively high levels of mannitol being found in *R. minor* (Hodgson 1973). The water potential of a hemiparasite can be 1–2 MPa or more, lower than that of the host, which is suggested to be a result of high transpiration rates and low hydraulic conductivity across the haustorium (Ehleringer & Marshall 1995). Klaren & van de Dijk (1976) found that following the attachment of *R. angustifolius* to a host, an increase in the content of potassium, calculated on the basis of tissue water, was partly responsible for the enhanced water retention of its cells. The accumulation of high concentrations of inorganic ions, especially potassium, magnesium and sodium, has also been reported for *R. minor* (Press *et al.* 1990; Seel & Jeschke 1999). The higher osmolarity found in the leaves of parasites may facilitate the acquisition of resources from its host (Kuijt 1969).

Cameron & Seel (2003) have observed two defence mechanisms as a response to *Rhinanthus* infection: hypersensitive cell death in *Plantago lanceolata* and encapsulation of the parasite endophyte with lignin in *Leucanthemum vulgare*, partially explaining the failure of the parasite to grow well with these species. In addition, Hodgson (1973) used radio-labelled carbon to show that the parasite derived relatively little carbon from *Plantago lanceolata*, *Veronica chamaedrys* and *Lolium perenne*. Conversely, these ‘host’ species actually appeared to derive carbon from the parasite. In contrast, minimal translocation was observed from the parasite to graminaceous hosts, or to *Trifolium repens* (Hodgson 1973), and these are generally considered good hosts for hemiparasites.

Based on field measurements in Abisko, northern Sweden, *R. minor* has been recorded as having high transpiration rates both day and night (Press *et al.* 1988). During the day, transpiration rates were 9.22 mmol m⁻² s⁻¹ compared to 7.71 mmol m⁻² s⁻¹ at night, producing a night : day quotient of 0.84. Normal stomatal closure at night was not observed, but there was no uptake of carbon dioxide. In contrast, other plants that open stomata at night possess crassulacean acid metabolism (CAM) (Press *et al.* 1988).

Relatively high transpiration rates during the day and night have been suggested to increase heterotrophic carbon supply and solute transfer from the host to the parasite (Marschner 1986). Furthermore, high transpiration rates have also been suggested to be the principal method of gathering nitrogen (Press *et al.* 1988). However, although rates of transpiration in *R. minor* are

greater in attached than unattached plants, no significant difference has been observed between *R. minor* associated with *Festuca rubra* and the legume, *Vicia cracca*, which had greater concentrations of foliar nitrogen (Seel & Press 1994). The stomata of *R. minor* also remain open for long periods under unfavourable conditions (e.g. heat and drought). Photosynthesis continues and more sugar alcohols will be produced, maintaining the osmotic gradient between host and parasite (Hodgson 1973).

No direct relationship between the amount of carbon translocated to *R. minor* and dry weight yield of *R. minor* was found. Consequently, it was suggested that hemiparasites are more dependent on the host for something other than carbohydrates (Hodgson 1973). This has also been confirmed for *R. angustifolius*, as unattached plants accumulated sugars, while concentrations in individuals attached to *Hordeum vulgare* decreased (Klaren & Janssen 1978). When attached to a suitable host, autotrophic carbon gain in *R. minor* is minimal (Press *et al.* 1988), although *Rhinanthus* spp. still have high light requirements (ter Borg 1985). As *R. minor* has a limited capacity to assimilate inorganic nitrogen, the transport of organic nitrogen from the host appears to be the most important factor in the growth of hemiparasites (Govier *et al.* 1967; Hofstra & Klaren 1973), and both growth and photosynthesis of *R. minor* are positively correlated with nitrogen supply (Seel *et al.* 1993a). When attached to nitrogen-rich hosts (legumes), finite partitioning of nitrogen into chlorophyll means that *R. minor* may accumulate more nitrogen than it can incorporate into photosynthetic machinery (Seel *et al.* 1993a).

The concentration of nitrogen in the leaves of *R. minor* is closely related to that of the host plant. For example, parasites growing with *Trifolium pratense* had leaf nitrogen concentrations almost three times greater than that of the host, while those attached to *Bromus commutatus* had over twice as much. Unattached *R. minor* individuals did accumulate some nitrogen, but the relationship between nitrogen supply and growth was not observed (Seel *et al.* 1993a). Unattached *R. minor* has quantities of chlorophyll similar to solely autotrophic species (Hodgson 1973), but after attachment, it has been found that individuals have significantly greater amounts of total chlorophyll than unattached plants, being 4-fold greater in plants associated with *T. pratense* (Seel *et al.* 1993a). Concentrations of leaf chlorophyll were also significantly greater than in unattached *R. minor* and, in turn, were associated with higher rates of light-saturated photosynthesis (carbon dioxide exchange rate).

Light-saturated rates of photosynthesis are stimulated by attachment to a host, the extent of which is dependent on the host species infected (Seel *et al.* 1993a). However, this is in contradiction to observations by Hodgson (1973), who found that rates of photosynthesis in unattached *R. minor* plants exceeded those following attachment. Conversely, *Rhinanthus* spp. do not

appear to have any detrimental effects on host photosynthesis (Hofstra & Klaren 1973; Seel & Press 1996). Under field conditions in Abisko, northern Sweden, it was found that the rate of light-saturated photosynthesis in the leaves of *R. minor* was $6.68 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Press *et al.* 1988). The rate of carbon loss in darkness was of similar magnitude, being $-5.53 \mu\text{mol m}^{-2} \text{s}^{-1}$. It was calculated that *R. minor* would need 10.9 h of light-saturated photosynthesis to achieve no net loss of carbon in the leaves. Although hemiparasites can fix carbon autotrophically, the high rates of respiration will limit net carbon gains (Press *et al.* 1988). Rates of dark respiration have also been found to be greater in individuals attached to nitrogen-rich hosts (legumes), although these carbon losses are likely to be compensated by the greater rate of light-saturated photosynthesis in association with such hosts (Seel & Press 1994). In addition, parasites associated with nitrogen-rich hosts may be more autotrophic for carbon than those on nitrogen-poor hosts (Cechin & Press 1993). $^{14}\text{CO}_2$ fed to *R. minor* leaves is rapidly fixed into mannitol and/or galactitol (Hodgson 1973). The other main products of photosynthesis are: a phenolic glycoside, hexoses, glucose, fructose, but not sucrose. Amino acids are also produced.

The attachment of *R. minor* to nitrogen-rich hosts leading to high concentrations of leaf nitrogen is associated with low photosynthetic nitrogen-use efficiencies (PNUE). For example, the mean PNUE for *R. minor* on *Trifolium pratense* was $1.5 \text{ mmol mol}^{-1} \text{ min}^{-1}$, compared to $10.6 \text{ mmol mol}^{-1} \text{ min}^{-1}$ when growing on *Plantago lanceolata* (Seel *et al.* 1993a). PNUE values are also greater in attached than in unattached plants (Seel & Press 1994).

Low rates of carbon dioxide fixation and high rates of water loss result in low values of water use efficiency (WUE, defined as the molar ratio of photosynthesis to transpiration). *Rhinanthus minor* plants attached to legumes have greater WUEs than those unattached or attached to grasses (Seel & Press 1994), suggesting a down-regulation of transpiration rates in response to nitrogen supply. However, in contrast to other parasites, *R. minor* may not regulate transpiration in direct response to host nitrogen supply (Seel *et al.* 1993a). It is more likely to be a result of greater rates of photosynthesis when growing with nitrogen-rich hosts (Seel & Press 1994). Field measurements in Abisko, northern Sweden, gave the WUE of *R. minor* as $0.72 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ (Press *et al.* 1988).

The ability of *R. minor* to complete its life cycle by attaining a minimum level of nutrition ultimately depends on the host-parasite relations and the availability of abiotic nutrients. ter Borg (1972) observed that aestival ecotypes of *R. angustifolius* could not tolerate conditions associated with modern agriculture, or survive low soil fertilities. Due to the low capacity of *R. minor* to assimilate inorganic nitrogen, in the absence of a host, individuals are usually stunted with low chlorophyll concentrations. The addition of inorganic solutes and, in particular, the addition of phosphate (Na_2HPO_4),

to unattached plants has been shown to stimulate growth, increasing plant height and biomass (Seel *et al.* 1993b). However, the addition of potassium (KCl) and nitrogen (NaNO_3 , NH_4Cl , NH_4NO_3) produced only small growth responses, exemplifying the limited capacity to assimilate inorganic nitrogen. Chlorosis in *R. minor* has been observed when the iron from ethylenediamine-*o*-hydroxy phenylacetate iron complex was provided as part of a complete nutrient solution (Seel & Jeschke 1999). This was overcome by adding additional iron as the sequestrene complex.

Leaf and stem concentrations of NO_3^- in unattached *R. minor* plants were found to be virtually nil, while the values in plants in association with the host *Hordeum vulgare* increased to $400\text{--}500 \mu\text{mol g}^{-1}$ dry wt, compared to $100 \mu\text{mol g}^{-1}$ dry wt with *Trifolium alpestre*. Phosphate concentrations almost quadrupled with *H. vulgare* and approximately doubled with *T. alpestre* (Seel & Jeschke 1999).

In the field, *R. minor* had significantly greater cover values in plots not treated with NPK fertilizer (20 : 10 : 10) applied at a rate of 25 kg ha^{-1} for nitrogen and 12.5 kg ha^{-1} for both phosphorus and potassium (Smith *et al.* 1996a). When NPK fertilizer was applied to an *Anthoxanthum odoratum*–*Geranium sylvaticum* grassland (MG3; Rodwell 1992) in Upper Teesdale in north England at a rate of 80 kg ha^{-1} for nitrogen and 40 kg ha^{-1} for phosphorus and potassium, less *R. minor* seed was harvested than in the controls not receiving any fertilizer (Smith *et al.* 1996b). The response of light-saturated rates of photosynthesis to mineral nutrients has also been investigated and were 91% lower in the high phosphorus treatment. WUE fell by up to an order of magnitude when phosphorus supply was increased. The impact of phosphorus on transpiration rates was less marked and varied over time (Davies & Graves 2000).

Values of total above-ground biomass (host and parasite) are usually lower than host biomass alone because *Rhinanthus* spp. have lower resource utilization efficiencies than their hosts (Matthies 1995). Therefore, on fertile soils, because *R. minor* appears to be less dependent on the host vegetation for resource requisition, the impact on host productivity might be expected to be lower. In support of this, less pronounced yield reductions of host vegetation have been observed with increased soil fertility (Gibson & Watkinson 1991; Matthies & Egli 1999; Davies & Graves 2000), although this is in contrast to the findings of ter Borg & Bastiaans (1973) and Davies *et al.* (1997), who observed greater reductions in host shoot biomass with increasing soil fertility. The type of host species present and their response to increased soil fertility may strongly influence the effect of the presence of *R. minor*.

Under high soil fertilities, the susceptibility of potential hosts to parasitism may decrease. This is based on observations that on fertile soils the number of haustorial connections between hemiparasites and their hosts tends to be lower (Gibson & Watkinson 1991; Cechin & Press 1993; Davies & Graves 2000), and this is commonly

associated with less pronounced yield reductions of the hosts (ter Borg 1986; Gibson & Watkinson 1991; Davies & Graves 2000) and lower parasite performance (Cechin & Press 1993; Davies & Graves 2000). A lower susceptibility of the host to parasitism under high levels of soil fertility has been related to changes in the physical structure of the host's cell walls (Cechin & Press 1993), suggested to account for the reduced number of attachments between *R. minor* and *Lolium perenne* when grown at high levels of phosphorus (Davies & Graves 2000).

Furthermore, the addition of fertilizer to a grass sward would be accompanied by an increase in meristem activity of the host vegetation, increasing the strength of the carbon sinks relative to those of the parasite. As a result, the flux of solutes from host to parasite could be limited. The ability of *R. minor* to gain carbon autotrophically might then gain importance if it is to persist in a productive sward. However, because of the lower nutritional gain from the host in combination with the limited capacity of *R. minor* to assimilate inorganic solutes (Seel *et al.* 1993b), its capacity to synthesize chlorophyll for photosynthesis would be limited. This may be another factor reducing the ability of *R. minor* to compete in productive grasslands.

The number of haustoria formed appears to be related to soil fertility. For example, when *R. minor* was grown with the legume host *Trifolium repens*, the number of haustorial attachments decreased with increasing levels of soil nitrogen (Gibson & Watkinson 1991). The number of secondary haustoria produced by *R. minor* with the host *Lolium perenne* was also severely reduced under conditions of high phosphorus. At the high phosphorus level, only 39% of the parasites formed a successful connection with *L. perenne*, compared to 72% with the low phosphorus treatment (Davies & Graves 2000).

Although increased CO₂ levels might be expected to increase the availability of both autotrophic and heterotrophic carbon gain, the response of *Rhinanthus alectorolophus* to elevated CO₂ levels (590 µL L⁻¹, compared to 374 µL L⁻¹), was shown to depend strongly on host species and nutrient level. Furthermore, the growth of both parasite and hosts was more strongly influenced by CO₂ concentration at high nutrient levels (Matthies & Egli 1999).

The mineral concentrations in *R. minor* have been determined for samples collected at two sites (data source: Environmental Chemistry Section, CEH Merlewood). At Ulpha Bridge, near Kendal, Cumbria, the percentage concentrations (g g⁻¹) were: 2.4 N, 0.36 P, 2.2 K, 0.17 Na, 2.7 Ca, 0.49 Mg, 0.018 Fe and 0.0063 Mn. Concentrations of Cu and Zn were 7.9 and 53 µg g⁻¹, respectively. Percentage concentrations (g g⁻¹) obtained from North Walney, Barrow-in-Furness, Cumbria, were: 2.2 N, 0.41 P, 1.9 K, 0.54 Na, 3.9 Ca, 0.67 Mg, 0.021 Fe and 0.016 Mn. Concentrations of Cu and Zn were 14 and 390 µg g⁻¹, respectively. The ash content of *R. minor* determined from material collected at Wetherby, West Yorkshire, was 0.113 g g⁻¹ (Morgan *et al.* 2003).

(F) BIOCHEMICAL DATA

Rhinanthus minor is strongly suspected of being poisonous owing to the presence of the iridoid glycoside rhinanthin (C₂₉H₅₂O₂₀) (also known as aucubin), but it is not clear how harmful it is to livestock (Long 1924). Over 4 days Lehmann (cited in Long 1924) fed a rabbit 1238 g of fresh *R. minor* plants bearing half-ripe seeds, without any apparent injury. Lehmann also ate, without harm, 35 g of *R. minor* seeds made into a cake and cooked. *Rhinanthus minor* has therefore been suggested of being poisonous only after a prolonged period of consumption (Long 1924), or in the unlikely event of animals consuming sufficient quantities (Cooper & Johnson 1998). If *R. minor* seeds are ground up with cereal grain it gives flour and bread a reddish or violet-brown colour and an unpleasant taste, most likely due to rhinanthin (Long 1924). Butter produced from cows grazing on pastures infested with *R. minor* has also been reported to have a bad taste (Long 1924). As previously mentioned, *R. minor* also has high concentrations of mannitol (Hodgson 1973).

Rhinanthus minor is also known to have medicinal properties, being used for alleviating the symptoms of asthma and dry coughs, loosening catarrh and serving as an eye-wash for various eye complaints (Johannsdottir 1992). *Rhinanthus crista-galli* has also been used for the treatment of epilepsy and fits (Lacey 1993).

VII. Phenology

Germination of *R. minor* in February/March after a period of winter stratification coincides with the growth of potential host roots. Prior to this, the availability of host roots for parasitism by *R. minor* can be restricted owing to low soil temperatures limiting root activity (de Hullu 1984). Successful infection when the host roots begin to grow could suppress host productivity from the outset, thereby increasing the probability of *R. minor* surviving once shoot growth increases.

The onset of flowering in *Rhinanthus* does not depend on a host, its phenological status, or on environmental conditions, remaining the same even when plants are not attached to a host. Consequently, the onset of flowering was suggested to be an independent characteristic with a strong genetic basis, only narrowly related to habitat (ter Borg 1987). In contrast, Seel & Jeschke (1999) found that flowering in *R. minor* commenced later when attached to *Hordeum vulgare* than in unattached plants. The induction of flowering in *Rhinanthus* is also strictly correlated with the number of nodes along the main stem below the inflorescence (ter Borg 1987), which may depend on the length of the growing season (ter Borg 1985). Differences in node number vary between *R. minor* populations in north-east Belgium, as plants on top of a slope in dry Thero-Airion/Violion caninae vegetation had *c.* 7 nodes, while lower in a more mesic Mesobromion grassland, plants had *c.* 9 nodes (Hillegers 1983).

Owing to the spike-like terminal inflorescence, different flowering stages of *R. minor* are displayed simultaneously once flowering commences. Flowering within a population mainly occurs from early May through to July/August but can continue until September, with seeds setting from June. Generally, aestival ecotypes flower from May to July and autumnal ecotypes from late July to September. After maturation, seed of *R. minor* can remain in the split capsules for several weeks, prolonging the period over which seed is dispersed.

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Rhinanthus minor is hermaphrodite and is either insect-pollinated or selfed. In a study of a population on a sand dune system at Holme-next-the-Sea, Norfolk, Gibson (1986) observed nine species of Hymenoptera to visit flowers of *R. minor*: *Bombus campestris* (*Psithyrus campestris*), *Bombus hortorum*, *B. lapidarius*, *B. lucorum*, *B. pratorum*, *B. ruderarius*, *Apis mellifera*, *Ammophila sabulosa* and *Megachile* sp. In contrast, observations by Kwak (1980) in the State Nature Reserve 'Stroomdallandschap Drentsche A' in the Netherlands, indicated that *Apis mellifera* never visited *R. minor*, and *Bombus campestris* (*Psithyrus campestris*) was recorded as an infrequent visitor. *Megachile* sp. and *Ammophila sabulosa* were not recorded in her study.

Different traits between the *Bombus* species have also been suggested to determine the type of pollination (Kwak 1979a). *Bombus hortorum* and *B. ruderarius* visit the flowers nototribically, landing on the lower lip of the corolla and removing nectar in the 'head up' position. In contrast, *B. lucorum*, *B. pratorum* and *B. lapidarius* visit sternetribically, landing on the upper lip and remove nectar 'head down'. Sternetribic visitors are suggested to promote self-pollination while nototribic visitors are likely to effect cross-pollination. Nectar is secreted at the base of the ovary and *B. lucorum* forages as a primary nectar thief, biting a hole in the corolla to reach it. *Bombus pratorum* and *B. lapidarius* are noted as occasionally acting as secondary nectar thieves, using holes created by the primary nectar thieves (Kwak 1979a). Nectar thieves have no value in cross-pollination as they do not come into contact with the pollen sacs. However, through their foraging activities they may cause self-pollination by dislodging pollen from the stigma (Gibson 1986).

(B) HYBRIDS

Flowers of *R. minor* may have rapid self-pollination (Bennema 1978), which restricts the extent of natural hybridization. However, hybridization has been reported between *R. minor* and *R. angustifolius* resulting in fertile F1 progeny, described as *R. × fallax* (Wimm. et Grab.) Sterneck (Kwak 1980). This hybrid has been recorded in a few localities in Britain (e.g. Vice-Counties

9, 96 and 105), but all herbarium specimens examined were believed to be large variants of *R. minor* (Hyb. Br. Is.). The Scottish subspecies *lintonii* (Wilmott) Sell is believed to be a fertile hybrid from two pairs of subspecies: *R. minor* ssp. *borealis* × ssp. *monticola* and *R. minor* ssp. *borealis* × ssp. *stenophyllus* (Sell 1967).

Populations of *R. minor* and *R. angustifolius* occasionally grow sympatrically and flowering may overlap. However, samples taken from a mixed field population of *R. minor* and *R. angustifolius* indicated that *R. minor* had remained pure, while introgression into *R. angustifolius* had occurred (Kwak 1980). Overall, the hybridization between *R. minor* and other *Rhinanthus* species may be limited owing to the poor transfer of pollen to the inaccessible stigmas of *R. minor* when bumblebees visit sternetribically (Kwak 1979a). A physiological barrier to the development of pollen tubes has also been suggested (Kwak 1979b).

(C) SEED PRODUCTION AND DISPERSAL

In the absence of a host and on low nutrient substrates, seed production is minimal, with only 1–2 seed capsules per plant. However, on examination of 171 *R. minor* plants growing in pasture, each plant on average had 17.3 ± 0.96 capsules containing an average 9.7 ± 0.1 seeds. The average seed output was calculated to be 168 ± 11 seeds per plant (Rep. Capac.). On the examination of 21 plants randomly selected from populations established in permanent pasture dominated by *Lolium perenne*, *Dactylis glomerata*, *Agrostis stolonifera* and *Poa trivialis*. *Rhinanthus minor* had a mean seed production of 92.9 ± 11.3 seeds per plant (Coulson *et al.* 2001), compared to 30–90 seeds on chalk grassland (Kelly 1989a). In meadow vegetation in Canada, *R. minor* has been recorded as having 10.5 seeds per capsule irrespective of the number of capsules on each plant (van Hulst *et al.* 1987). Gibson (1986) found no linear relationship between the number of seeds per capsule and the number of capsules per plant. However, a positive correlation between the number of branches and fruit production has been found (Huhta *et al.* 2000). The number of nodes on the main stem also determines the potential number of branches and the number of seeds produced.

Year-to-year variation in seed production has also been observed in *R. minor* populations on chalk grassland (CG2a, *Festuca ovina*–*Avenula pratensis* (*Helictotrichon pratense*)) in southern England (Kelly 1989a). During the first year of study, the mean number of seeds per capsule was 9.63 ± 1.71 , a value very similar to that recorded by Salisbury (Rep. Capac.), but plants had an average of only 3.14 capsules per plant (Kelly 1989a). This may reflect the different growth conditions and sward composition between the studied sites. Over the following 2 years, Kelly (1989a) found the number of capsules per plant to be 2.01 ± 0.22 and 4.93 ± 0.84 . However, in the fourth year, almost no plants set seed, attributed to it being a very dry season.

Yields of *R. minor* seed grown commercially can range from 40 to 100 kg ha⁻¹ (at *c.* 270 seeds g⁻¹) with a harvesting efficiency of 80% (G. Taylor, Technical officer, Johnsons Seeds, personal communication 1998). Yield is mainly dependent on the weather, but sometimes a sward can consist of a mosaic of dense and sparse *R. minor* patches, which ultimately reduces the overall yield. Furthermore, if flowering and seed set of *Rhinanthus* are delayed, seed production can be reduced or prevented (ter Borg 1987).

The dispersal of *Rhinanthus* seed has been suggested to be limited because of their large size and a lack of an active dispersal mechanism (ter Borg 1972). However, because the ripe capsules open at the apex, when the stiff stems are shaken by wind or a passing animal, seeds can be ejected. Furthermore, the seeds, being winged, are suited for wind dispersal (ter Borg 1972; Gibson 1986; Grime *et al.* 1988). Seeds may also float for several months (Disp. Pl.; ter Borg 1972) aiding dispersal by water (van Hulst *et al.* 1987). However, in late autumn the meadow plots at Wetherby, West Yorkshire, were flooded deeply when the River Wharfe burst its banks, but the dispersal of *R. minor* from experimental plots was not different from that of previous years.

Investigations of *R. minor* populations on a sand dune system at Holme-next-the-Sea, Norfolk, revealed that in areas previously cleared of *R. minor*, seedlings were located up to 1.45 m from the edge of an existing population (Gibson 1986). However, 48.9% of all seedlings germinated within 25 cm of the edge, and only 5% were found further than 1 m away. Poor dispersal may be because suitable sites occur reliably in the immediate environment of the plant as found for *Vulpia fasciculata* (Watkinson 1978).

Overall, the dispersal of *R. minor* seed is generally poor unless aided by man (van Hulst *et al.* 1987). This has been exemplified with studies on *R. angustifolius* as it was shown that mowing machinery was an effective dispersal agent both in terms of distance and the number of seeds dispersed (Strykstra *et al.* 1996). Hay cutting has also been shown to be more effective in dispersing seeds of *R. minor* than sheep grazing (Coulson *et al.* 2001; Bullock *et al.* 2003). Cutting dispersed seed at least 4 m, while grazing distributed seed a maximum of 0.9 m.

(D) VIABILITY OF SEEDS: GERMINATION

Rhinanthus minor has a transient seed bank with the majority of seedlings emerging the following spring. Under field conditions there is little carryover of seed for more than 6 months. Observations of seed persistence have been reported for two populations of *R. minor* (under field conditions), with seed persisting for over 3 years (Thompson *et al.* 1996). The large food reserves in the seed allow extensive growth of the radicle (see Fig. 4) while seeking a suitable host(s).

According to Baskin & Baskin (1998), at the time of dispersal, *R. minor* seed has intermediate physiological dormancy. To break dormancy about 3 months at temperatures between 2 °C and 6 °C seem to be needed

(Vallance 1952; Hodgson 1973; Gibson 1986). Attempts have been made to reduce the chilling requirement, including seed scarification, removal of the testa, extremes of temperature, leaching to remove any seed coat inhibitors, chemical treatment with gibberellins, cytokinins and host root extracts, but none of these treatments was shown to increase the rate of germination (Gibson & Watkinson 1991). Owing to this chilling requirement, in the UK, seedlings emerge from early February through to March/April following winter stratification. However, dormancy is usually broken earlier, as when seed was removed from the field and placed at an elevated temperature of around 21 °C, germination occurred before it was apparent in the field. This suggests that although dormancy had previously been broken, further development was restricted by low field temperatures. This has also been found for samples stratified in a refrigerator at 3 °C and then elevated to 16 °C (Table 2).

The temperature required to break dormancy varies depending on seed source. Seed of *R. minor* collected in the Alpine regions, up to *c.* 2100 m above sea level, germinated after exposure to 4–5 °C as well as at *c.* 2 °C, although germination percentages were rather low at both regimes. Seed from north and central Sweden, on the other hand, hardly germinated at 4–5 °C, but gave germination percentages up to 95% at 2 °C. This may indicate different systems of adaptation to arctic and alpine climates, a point that needs further testing (S. J. ter Borg, personal communication 2003).

To investigate embryo maturity at the time of being shed, seed of *R. minor* was placed on moist filter paper at 2 °C and 18 °C (Hodgson 1973). At weekly intervals, embryos were measured. After 12 weeks, seed at 2 °C started to germinate, but seed at 18 °C did not. At the time of germination, no significant difference was found between embryo size for the two treatments. It was suggested that at the time of seed shed, the embryo of *R. minor* is morphologically mature (Hodgson 1973), with cotyledons and radicle clearly distinguishable.

The effect of moist and dry storage on germination of *R. minor* has also been investigated (Westbury 2001). Seed was collected near Barnsley, West Yorkshire, still held in ripe (split) capsules. After 5 weeks' storage at 22 °C, seeds were given cumulative chilling treatments at 3 °C for up to 14 weeks in a dark refrigerator. Fresh seed having no prior storage and controls kept at 16 °C were also investigated. At weekly intervals, 100 seeds for each treatment were transferred to an illuminated growth cabinet at 16 °C for a further 2 weeks of observation.

Germination of seed placed immediately at 3 °C with no prior storage, was first observed after 7 weeks, but only if removed to the elevated temperature of 16 °C (Table 2); however, only one seed germinated. The main wave of germination began after 9 weeks of chilling, but only following transfer to the elevated temperature. Germination began in the refrigerator at 3 °C only after 12 weeks (Table 2).

After transfer to 16 °C, germination of seed previously stored moist was first observed after 9 weeks at

Table 2 Percentage germination of seed of *Rhinanthus minor* depending on chilling duration at 3 °C. Figures in parentheses give germination shown during a period of 2 weeks, after elevation to 16 °C

Treatment	Temperature at which germination occurred (°C)	Number of weeks' chilling at 3 °C									
		6	7	8	9	10	11	12	13	14	
Fresh (control)	3	0	0	0	0	0	0	2	35	69	
	3 > 16	(0)	(1)	(0)	(4)	(11)	(27)	(54)	(59)	(21)	
Moist storage at 22 °C	3	0	0	0	0	0	0	0	13	21	
	3 > 16	(0)	(0)	(0)	(2)	(1)	(3)	(20)	(31)	(25)	
Dry storage at 22 °C	3	0	0	0	0	3	10	5	33	55	
	3 > 16	(0)	(0)	(8)	(7)	(23)	(26)	(39)	(20)	(14)	

3 °C, compared to 8 weeks with dry storage. Germination at 3 °C began after 13 weeks in seed previously stored moist, compared to 10 weeks with dry storage (Table 2). The extent of dormancy was reduced following a period of dry storage, although this alone was not enough to eliminate dormancy completely. Overall, total percentage germination of the fresh seed was 90%, compared to 46% with moist pre-storage and 69% with dry pre-storage. All seed kept at a constant 16 °C failed to germinate.

After the 14-week experimental period, the effect of extended chilling on seed incubated at 16 °C was investigated for fresh seed and seed previously stored moist/dry. After 36 weeks at 3 °C, 84% of the fresh seed germinated, compared to 66% and 58% for the moist and dry stored seeds, respectively. On 19 September, the remaining seed was placed outdoors to enable natural chilling over winter. On 11 March seed viability had been maintained for 21 months, resulting in an overall total germination for each treatment of 99%. As with *R. minor*, low values of seed mortality are mainly found in species having low fecundity, poor dispersal and heavy seeds (Symonides 1988).

In other studies, after approximately 3 months at 2 °C, 70% germination was observed in *R. minor* (Gibson & Watkinson 1991), while the half-time value at 2 °C from seed collected at Gleadless, South Yorkshire, was 92 days (Hodgson 1973). Vallance (1952) investigated the chilling requirement of *R. crista-galli* and after 17 weeks at 2 °C mean germination percentage was 95%. However, when seed was stored moist at 20 °C for 5 months immediately after harvest, viability was maintained with a mean germination of 95% after 16 weeks. In contrast, when seed was stored dry at room temperature for 6 months prior to a moisture treatment at 2 °C, the rate of germination was greatly reduced, with sporadic germination occurring for more than a year, although mean germination percentage never exceeded 66% (Vallance 1952).

(E) SEEDLING MORPHOLOGY

Germination is epigeal. The hypocotyl elongates and carries the seed coat upwards on the cotyledons; the seed coat is then shed as they expand. The primary root is replaced by laterals (Fig. 4).

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

Rhinanthus spp. are usually avoided by grazing animals (Huxley 1992) although *R. minor* has been seen to be eaten by cattle.

To investigate the degradation of *R. minor* by microorganisms occurring in the rumen of cattle, five combinations of *R. minor* and hay (consisting of grasses, predominantly *Lolium perenne*) were examined (Morgan *et al.* 2003). Whole plants of *R. minor* consisting of seeds, flowers, leaves and stem were used to provide a sample similar to that which grazing cattle may consume. Initially, *R. minor* was fermented more rapidly than hay alone, probably as it contains a lower fibrous component. *Rhinanthus minor* was also found to have a lower *in vitro* dry matter degradation [iDMD] value than hay (0.537 and 0.610 g g⁻¹, respectively) and predicted iDMD values for the *R. minor*/hay combinations were lower than expected at all levels of *R. minor* inclusion. Consequently, *R. minor* appears to enhance the degradation of the diets examined, possibly by promoting certain species of microorganisms within the rumen which preferentially degrade fibre. However, above 50% inclusion of *R. minor*, the difference between predicted and observed values decreased. The downward trend of the observed values after this point was suggested to indicate that levels of inclusion of *R. minor* above 50% may be toxic to the rumen microorganisms (Morgan *et al.* 2003).

Seed predation

LEPIDOPTERA

Cochylidae: *Phalonidia permixtana* (Denis & Schiffmüller) is a local species, recorded in England from Kent, Sussex, Somerset and Devon. In Wales it has been found in Pembrokeshire and Carmarthenshire and there is one record from Scotland. The larva feeds in the flower heads, seeds and stems of *Rhinanthus* (Bradley *et al.* 1973).

Tortricidae: *Falseuncaria ruficiliana* (Haworth) and *Endothenia marginana* (Haworth) (Bradley *et al.* 1979). *Endothenia marginana* is widely distributed and locally

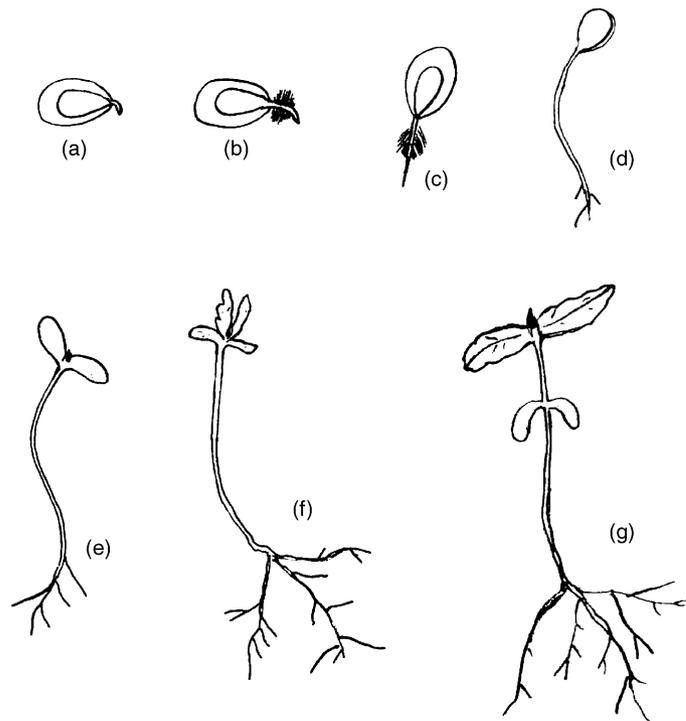


Fig. 4 Development stages of *Rhinanthus minor* seedlings. (a)–(c) $\times 2$, (d)–(g) $\times 1.5$.

common throughout the British Isles, north to the Outer Hebrides and Orkneys. The larvae eat the seeds and overwinter in the seed capsules of *R. minor* (Bradley *et al.* 1979).

Pyralidae: *Opsibotys fuscalis* (Denis & Schiffmüller) is locally common in meadows, marshes, open woodland and northern moorland. The larvae feed on the flowers and seed capsules (Emmet & Heath 1991).

Geometridae: *Eupithecia subumbrata* (Denis & Schiffmüller) is locally common and widespread in southern and eastern England but is less frequent and rather local elsewhere in the British Isles, as far north as Yorkshire and Lancashire. The larvae feed on the flowers and seed. *Perizoma albulata* (Denis & Schiffmüller) is entirely restricted to Shetland, where it has a wide distribution occurring wherever its larval food-plant, *R. minor*, grows (Ford 1955).

COLEOPTERA

Chrysomelidae: *Apteropeda* spp. (Kazsáb 1962).

DIPTERA

Agromyzidae: Pre-dispersal seed predation by *Phytomyza varipes* (Macquart) has been observed in colonies of *R. minor*. Capsules attacked frequently contained damaged seed, frass, larvae or pupae. Of 232 plants examined, 103 (44.4%) displayed evidence of seed predation (Gibson 1986). Furthermore, the number of capsules attacked increased with increasing capsule number on a plant: if a plant had one or two capsules, about a third of plants were attacked, while all plants were attacked if they had 16 or more

capsules. Seed predation was suggested to be density-dependent because the number of capsules present was inversely related to the density of plants (Gibson 1986).

HEMIPTERA

Aphididae: *Hyperomyzus rhinanthi* (Schouteden) (Phytophagous Insect Data Base).

Following the establishment of *R. minor* in meadow vegetation, 44% of juvenile losses were directly attributed to moisture stress (van Hulst *et al.* 1987). However, 47% of mortality was caused by herbivore damage, mainly by slugs, and 9% by fungal attack.

Post-dispersal seed predation by granivores such as *Microtus pennsylvanicus* (meadow vole) has also been suggested to account for losses of *R. minor* in a seeding-out experiment in a meadow in Canada (van Hulst *et al.* 1987).

(B) PLANT PARASITES AND (C) PLANT DISEASE

FUNGI

Mildews

Plasmopara densa (Rabenh.) Schröt. (downy mildew, Peronosporales), *Sphaerotheca fuliginea* (Schlect.) Pol-lacci (powdery mildew, Erysiphales) (Ellis & Ellis 1985) and *Sphaerotheca fusca* (Fr.) Blumer (Braun 1995).

British rust fungi

Coleosporium tussilaginis (Pers.) Berk. Uredinales (Ellis & Ellis 1985).

Uredospores and teliospores of *Coleosporium rhinanthacearum* Lév. have been reported on *R. minor* (Br. Rust Fungi).

British stem and leaf fungi (anamorphic Ascomycotina)

Phoma complanata (Tode) Desmaz. has been found on the dead stems of *R. minor* (*crista-galli*) but it is suspected of having been *Phoma deusta*, frequent in England and Scotland and found on the dry bracts, capsules, peduncles and dead stems of *R. minor* (*crista-galli*) (Br. Stem and Leaf F.1).

Ephelina lugubris (de Not.) Höhnelt on overwintered stems at soil level (Ellis & Ellis 1985).

Heteropatella umbilicata (Pers.) Jaap (Sutton 1980).

Phomopsis sp. (Dennis 1986).

Sarcopodium circinatum Ehrenb. (Dennis 1986).

Additional records from Europe

Uredinales: *Coleosporium euphrasiae* Schum. (Russia) (Kuprevich & Transhel 1957; Melnik & Pystina 1995) and *Coleosporium rhinanthacearum* Lév. (Germany) (Braun 1982). **Ustilaginales:** *Doassansia rhinanthi* Lagh. (Germany) (Zundel 1953). **Pleosporales:** *Leptosphaeria affinis* Karst. (Sweden) (Eriksson 1992).

X. History

All records for *Rhinanthus* given by Godw. Hist. are based on seed identification, except for one pollen record recorded in zone VIIb of the Flandrian at Loch Cuithir. The age distribution of *Rhinanthus* was remarkable (Godw. Hist.), with occurrences in five Middle Weichselian (about 68 000–19 000 BC) and one Late Weichselian (zone II) (19 000–11 000 BC). The next record is Roman at Godmanchester, and then a medieval record at Shrewsbury.

The first record for *R. minor* in the British Isles (as *Pedicularis pratensis lutea vel crista galli*) is 1699 in Oxfordshire (Morison (Bobart), cited in Druce 1927).

XI. Conservation

The impact of *R. minor* on sward productivity in England was noted by Carruthers (1898) after it was shown to reduce the vigour of both grasses and clover in meadow vegetation. The elimination of *R. minor* from swards was therefore considered agriculturally necessary. Studies on the loss of above-ground productivity in meadow vegetation also led to the classification of *Rhinanthus* as a 'very harmful meadow weed' (Mizianty 1975). However, because *R. minor* has been susceptible to recent cultural changes in grassland management, it is now believed to be in decline throughout the British Isles (Grime *et al.* 1988), and no longer an economic threat to agriculture (Parker & Riches 1993). In the Netherlands, comparisons between the frequency distribution maps of *R. minor* before and after 1950 indicate a decline of up to 60% (de Hullu 1985b).

Currently, there are no specific measures in the British Isles to conserve *R. minor*, although it is indirectly protected through the conservation of semi-natural grassland habitats under various agri-environmental schemes. Recently, the interest in *R. minor* has increased because of its ability to reduce the productivity of grasslands and promote forb abundance relative to that of the grass component (Davies *et al.* 1997; Westbury 2001; D. B. Westbury and N. P. Dunnett, unpublished). This in turn may raise the importance of *R. minor* in conservation schemes and promote its abundance throughout the British Isles. However, on the contrary, it has been suggested that the main impact of *R. minor* on the communities in which it grows is to reduce species diversity (Gibson & Watkinson 1992), promoting certain forb species at the expense of others, for example, *Plantago lanceolata* at Castor Hanglands National Nature Research, Cambridgeshire (Gibson 2000) and *Leucanthemum vulgare* in meadow communities established on ex-arable land (D. B. Westbury and N. P. Dunnett, unpublished data).

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