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RHINANTHUS: A TOOL FOR RESTORING DIVERSE GRASSLAND?

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Abstract: The restoration of species-rich grasslands is often hindered by high residual soil fertility as a result of, e.g., intensive farming. The establishment of a diverse range of target species on such sites requires the reduction of soil fertility or of the vigour of competitive plants. Current methods to achieve these aims are often unsuccessful or complicated and expensive. It has been suggested that *Rhinanthus* species could be used to decrease the growth of competitive plants and enhance species diversity. We review evidence for this potential and suggest five key attributes that make *Rhinanthus* species a practical restoration tool. *Rhinanthus* species are natural components of species-rich grasslands (attribute 1), and seed of some species is relatively low cost and easily obtainable (2). Recent work has shown that certain *Rhinanthus* species reduce the vigour of competitive species, especially agricultural grasses, and allow establishment and persistence of target species (3). We analyze demographic data and show that certain *Rhinanthus* species have the ability for rapid population growth and spread, even in fertile grasslands (4). We also show that it is relatively easy for land managers to limit the population size of *Rhinanthus* species and prevent damage (e.g. excessive loss in production or invasion by weeds) to grasslands by excessive densities (5). We give suggestions for further research, including: the range of species-poor grasslands into which *Rhinanthus* can be introduced successfully and which *Rhinanthus* species should be used; the mechanisms by which *Rhinanthus* enhances diversity in restored grasslands; whether the ecotype or subspecies of *Rhinanthus* used affects restoration success; how management methods affect population growth and spread of *Rhinanthus*; and whether other parasitic plants could be used in habitat restoration.

Keywords: Biodiversity, Competition, Ecosystem function, Facilitation, Habitat creation, Hemiparasite, Parasitism

Nomenclature: TUTIN et al. (2001)

INTRODUCTION

The restoration of degraded or damaged habitats is a vital aspect of modern biodiversity conservation. For example, the UK Biodiversity Action Plan (www.ukbap.org.uk) currently has conservation plans for 45 habitats (e.g. calcareous grassland, dry acid grassland, meadows), many of which include targets for restoration (e.g. to restore 1000 ha of calcareous grassland by 2010). A major problem for such ambitious targets is that previous land management of restoration sites, such as intensive agriculture, has often left high residual soil fertility, particularly in phosphorus. This generally constrains attainment of the high levels of plant diversity characteristic of the desired habitats (MARRS 1993, PYWELL et al. 2002a). Many ways of depleting soil nutrients have been studied, but all have problems (WALKER et al. 2004). Removing nutrients by arable cropping, cutting or grazing is often slow or ineffective, as is diluting nutrient-rich soil by adding inert materials or deep cultivation. Adsorbing nutrients, e.g. phosphorus with iron and aluminium oxides, is also slow and can have toxic effects in some soils. Soil stripping or de-turfing is effective but it is a very expensive and extreme option.

The approaches listed above target the root problem of high soil fertility, but it may be more appropriate to attempt to control the ultimate effect of this fertility, i.e., the vigorous growth of competitive species, especially agricultural grasses. These restrict the establishment and persistence of target species (characteristic of the target habitat and usually uncompetitive in fertile conditions) that may have been sown as part of the restoration process. Nutrients will deplete (albeit slowly) over time, so an alternative approach is to reduce the vigour of competitive species to allow less competitive species to increase. Disturbance, such as rotovation, harrowing or slot-seeding is often used to create gaps for establishment from added seed (WALKER et al. 2004), but this only has short-term effects until the disturbed areas re-vegetate. Grazing or cutting may help if the competitive species are affected selectively (BULLOCK et al. 2001), but effects vary, fast-growing grasses may be encouraged and the intensity of grazing or cutting needed to suppress competitive species may not be appropriate for the target habitat type.

Some authors have suggested that *Rhinanthus* species might be a useful tool for the restoration of diverse grasslands by directly reducing the growth of dominant, productive species, especially certain grasses and legumes (DAVIES et al. 1997, SMITH et al. 2003). However, until recently this approach had not been tested explicitly. In this paper we assess the potential of this approach by reviewing the literature, carrying out some re-analysis of published data and presenting some new data.

Characteristics of hemiparasites as a restoration tool

For a *Rhinanthus* species to be a practical restoration tool, we suggest it should demonstrate the following characteristics.

(1) It is a species commonly associated with the target vegetation type.

(2) Seed is relatively low cost and easily obtainable for restoration projects.

(3) It reduces the vigour of competitive species and allows establishment and persistence of target species.

(4) It can colonize rapidly and persist in fertile grasslands.

(5) Excessive population size (which can lead to weed problems or extreme declines in yield for the farmer) can be controlled readily by commonly-used management practices.

We address these characteristics below.

Rhinanthus is a characteristic grassland plant

If one is attempting to restore a particular type of grassland, then any species sown should be typical of that vegetation. The Flora Europaea (TUTIN et al. 2001) lists 26 accepted *Rhinanthus* species. All of these are generally found in grasslands (TER BORG 1985). Three species that have been particularly well studied, *R. minor*, *R. angustifolius* and

R. alectorolophus, are widespread in Europe and are common components of a range of grassland types (TER BORG 1985). For example, in Britain, *R. minor* is found in 14 grassland vegetation types (National Vegetation Classification) characteristic of calcareous, neutral and acid soils (RODWELL 1992).

The cost of *Rhinanthus* as a restoration tool

We suggest that *Rhinanthus* is a relatively cheap option compared to other restoration methods. In the UK *R. minor* seed is sold by a number of seed merchants and it is relatively easy to harvest large quantities from semi-natural grasslands (STEVENSON et al. 1995, PYWELL et al. 2005). In 1999 we set up an experiment comparing several approaches to diversifying grassland (R. PYWELL, unpubl. data). *R. minor* seed costs £120 kg^{-1} (2004 price from Emorsgate Seeds in the UK was £ 190 kg^{-1}) and was sown at 2.4 kg ha^{-1}, totalling £ 288 ha^{-1}. Power harrowing and rolling cost £ 130 ha^{-1}, while soil stripping (removal of turf) costs £ 2720 ha^{-1}. So set up costs for *Rhinanthus* may be quite high if conventional sowing rates of 2–2.5 kg ha^{-1} (SMITH et al. 2000, PYWELL et al. 2005) are used. However, a sowing rate as low as 0.1 or 0.5 kg ha^{-1} can be effective (PYWELL et al. 2005) and slot seeding may allow lower than usual sowing rates (e.g. 0.8 ha^{-1}, COULSON et al. 2001). If subsequent management is effective in allowing rapid population build up (see below), then a low (and thus cheap) sowing rate may be sufficient.

Can *Rhinanthus* change grassland communities?

GIBSON & WATKINSON (1992) suggested key attributes that would allow a parasitic species to change plant community structure.

(1) The parasite has adverse effects on host fitness.
(2) Severity of attack varies among species in the community.
(3) The host species are significant components of the community.
(4) The parasite is abundant enough to attack a high proportion of the hosts.

Pot experiments have shown negative effects of *R. minor* and *R. angustifolius* on the growth and fecundity of parasitized plants (TER BORG & BASTIAANS 1973, GIBSON & WATKINSON 1991, SEEL & PRESS 1996), which are stronger than simple competitive effects (MATTHIES 1995). *Rhinanthus* species have wide host ranges. GIBSON & WATKINSON (1989) report at least 50 species for *R. minor* and 17 for *R. alectorolophus*, and the total number of potential hosts is probably much more. *Rhinanthus* species show selectivity when growing in grasslands, but selected host species vary among sites and over time (GIBSON & WATKINSON 1989). Selection does not seem to be related to dominance or nutrient status of the host (GIBSON & WATKINSON 1989) nor does it seem to have a genetic basis (MUTIKAINEN et al. 2000). However, important and potentially dominant species of grasslands are parasitized; for example *R. minor* attacks *Agrostis* sp., *Lolium perenne*, *Holcus lanatus*, *Dactylis glomerata* and *Trifolium repens* (GIBSON & WATKINSON 1989), and *R. angustifolius* attacks *Agrostis stolonifera* and *Lolium perenne* (TER BORG & BASTIAANS 1973).

How does this translate into effects on communities? Pot experiments have shown that the outcome of competition between two species can be affected by *R. minor* (GIBSON &

WATKINSON 1991). In the field there is increasing evidence for effects of *Rhinanthus* species on the structure of the species-rich grasslands in which they occur naturally. The evidence is of three types (Table 1). Correlation studies have compared community variables between patches with differing *Rhinanthus* abundances. It is dangerous to rely on these because community structure may not be related to *Rhinanthus* abundance but to other factors that affect *Rhinanthus*, such as local productivity (TER BORG & BASTIAANS 1973). Experimental manipulations are more informative. These have mostly involved removal of *Rhinanthus* from plots and comparing community structure with controls after a recovery period. These have the slight problem that the community is recovering from a disturbance (plant removal), not just the exclusion of the parasite. Less common, but more informative, are addition experiments, where areas with no *Rhinanthus* (within grasslands containing the parasite) are sown with the species and compared with controls after a period of establishment. It is perhaps best to do removal and addition experiments in tandem, but only MIZIANTY (1975) has done so.

Table 1 shows that these different types of evidence give generally similar results for three different *Rhinanthus* species (*R. minor*, *R. angustifolius*, *R. alectorolophus*) and across a wide range of grassland types and geographic regions. *Rhinanthus* presence always decreases the total dry biomass of the vegetation per unit area (i.e., yield), where biomass is measured. Note that we have reported total biomass effects that include the biomass of *Rhinanthus* plants; some reported figures exclude *Rhinanthus*, which does not give a true reflection of community effects. This supports the suggestion by MATTHIES (1995) that *Rhinanthus*, in common with other hemiparasites, utilizes nutrients inefficiently. Where biomass is broken down into species groups, grass biomass, and sometimes legume biomass, are decreased, but other forbs are unaffected.

In terms of restoring species-rich communities, we are more directly interested in effects on species number and diversity indices, but these variables have been studied rarely. The only published analysis (GIBSON & WATKINSON 1992) reports decreased diversity in the presence of *R. minor*. MIZIANTY (1975) provided raw data that we analyzed by ANOVA. Removal of *R. angustifolius* from plots resulted in a 10% drop in species number over two years, which was significantly different to the 6.2% increase in the control plots ($F_{1,8} = 35.5$, $P < 0.001$). A 0.7% increase in the addition treatment was not different to the control ($F_{1,8} = 3.7$, n.s.). Increases in diversity at some sites and decreases in others in response to *Rhinanthus* contrasts with the generality of the decreases in biomass. An explanation may be found in the so-called hump-back model by which species richness increases with productivity to a non-zero mode and then declines (GRIME 1979, WAIDE et al. 1999). The effect of *Rhinanthus* on species number may depend on where the productivity of a system and the decline caused by *Rhinanthus* lie in relation to this mode (unfortunately GIBSON & WATKINSON (1992) did not measure biomass). Basic productivity in fertile restoration sites would probably be far to the right of the mode and so *Rhinanthus* should always increase species number in these cases (see below).

Effects of *Rhinanthus* in species-rich communities of which it is a natural component do not necessarily predict what may happen when *Rhinanthus* is introduced to a restoration project on a species-poor, fertile site. It is fortunate therefore, that there are now some field studies of more direct relevance (Table 2). Three of these new grasslands were created by

Table 1. A summary of studies of the effects of *Rhinanthus* species on community variables in species-rich grasslands in which *Rhinanthus* occurs naturally. Studies are of three types; correlation, removal experiments and addition experiments (see text). Note that the total biomass includes *Rhinanthus*. * – Species number data were taken from Table 4 in MIZIANTY (1975) and analyzed (see text).

Rhinanthus species	Vegetation	Region	Variables measured	Effects of higher *Rhinanthus* abundance	Reference
Correlation studies					
R. minor	18 species-rich grasslands	England	Species number	6–36% decrease in species number	GIBSON & WATKINSON (1992)
R. minor	Species-rich flood meadow	England	Total biomass	60% decrease in total biomass	DAVIES et al. (1997)
R. alectorolophus	4 species-rich calcareous grasslands	Italy	Grass, legume & forb biomass	8–43% decrease in total biomass 45–72% decrease in grass biomass	DAVIES et al. (1997)
Removal experiments					
R. angustifolius	Species-rich grassland	The Netherlands	Grass, legume, forb, lower plant biomass	6–60% decrease in total biomass 60–90% decrease in legume biomass 30–85% decrease in grass biomass	TER BORG & BASTIAANS (1973)
R. angustifolius	Species-rich meadow	Poland	Total biomass Species number*	28% decrease in total biomass 10% increase in species number*	MIZIANTY (1975)
R. minor	Species-rich flood meadow	England	Grass, legume & forb biomass	36–73% decrease in total biomass ≤ 79% decrease in grass biomass	DAVIES et al. (1997)
R. minor	4 species-rich sand dunes	England	Species richness Diversity indices	Decreased Simpson's and Shannon-Wiener diversity	GIBSON & WATKINSON (1992)
Addition experiments					
R. angustifolius	Floodplain meadows	Russia	Grass, legume & forb biomass	25–30% decrease in total biomass 35–60% decrease in legume biomass	RABOTNOV (1959)
R. angustifolius	Species-rich meadow	Poland	Total biomass Species number*	25% decrease in total biomass	MIZIANTY (1975)

Table 2. A summary of studies of the effects of *Rhinanthus* species on community variables in restored grasslands. *Rhinanthus* species were not previously present and were added as seed in experimental contrasts that comprised no *Rhinanthus vs. Rhinanthus* added, and in some cases different sowing rates of *Rhinanthus*. * – Calculated from $kg.ha^{-1}$, assuming 300 seeds g^{-1}. † – Mean percentage occupied of 25 cells per 1 m^2 quadrat. ‡ – Plant density.

Rhinanthus species	Vegetation	Region	*Rhinanthus* sowing rate-seeds m^{-2}	Maximum *Rhinanthus* density (after years)	Variables measured	Effects of higher *Rhinanthus* abundance	Reference
R. minor	Arable field margin sown with 3 grasses, 17 forbs	England	12–96*	20%–33%† (2 yrs)	Total biomass	None	PYWELL et al. (1999)
R. minor	Ex-arable field sown with 5 grasses, 6 forbs	England	600–1000	177–375 m^{-2}‡ (1 yr)	Grass and forb biomass Species number	21%–44% decrease in total biomass 30%–54% decrease in forb biomass 84%–87% decrease in grass biomass increase in species number (by 1)	WESTBURY & DUNNETT (2000)
R. alectorolophus	Experimental grassland sown with ≤ 48 species	Switzerland	800	130 m^{-2} ‡ (1 yr)	Grass, legume and forb cover Total biomass	8% decrease in total cover 18%–22% decrease in grass cover 38% increase in cover of weed (unsown) species	JOSHI et al. (2000)
R. minor	Species-poor grassland, previously fertilized and grazed. Now unfertilized and hay cut. 10 forb species sown.	England	3–75*	60%–90%† (4 yrs)	Sward height Frequency of sown species	52%–67% decrease in sward height 60% increase in number of sown species Increased frequency in 7 of 10 sown species	PYWELL et al. (2004)
R. minor	Species-poor grassland, previously fertilized and grazed. Now unfertilized and hay cut. Sown with 4 grasses, 15 forbs.	England	72*	1250 m^{-2} † (4 yrs)	Grass and forb biomass Forb species number	55% decrease in grass biomass 45% increase in forb species number	R. PYWELL, unpubl. data

sowing seed mixes onto unvegetated sites (e.g. arable fields). The benefits of *Rhinanthus* in these situations are not obvious, maybe because exposure through lack of vegetation cover inhibits some species when re-creating grassland on arable soils (PYWELL et al. 2002a, 2003) and so reducing biomass at this early stage may be detrimental. WESTBURY & DUNNETT (2000) sowed *R. minor* at the same time as the other sown species and found biomass of both forbs and grasses was decreased although there was a very small increase in species number. JOSHI et al. (2000) and PYWELL et al. (1999) added *Rhinanthus* after one and two years respectively. PYWELL et al. (1999) found no effect on biomass. JOSHI et al. (2000) found some decrease in grass cover, no effect on added species, but an increase in invasion by unsown species.

Establishment of target species is more of a problem in productive grasslands than on bare, ex-arable sites (PYWELL et al. 2002a, 2003). Only two studies have used *Rhinanthus* to facilitate this process, but both suggest strong positive effects (Table 2). PYWELL et al. (2005) sowed *R. minor* into a species-poor grassland and greatly increased the number and abundance of target forbs from seed added two years later; these included *Centaurea nigra*, *Leontodon autumnalis* and *Leucanthemum vulgare*. In an experiment in Buckinghamshire, England we sowed *R. minor*, at the same time as 19 species, into a species-poor grassland (among many other treatments, see PYWELL et al. 2002b). Quadrats with a higher *R. minor* density had much decreased grass biomass (but no change in forb or total biomass) and large increases in the number of forb species (Fig. 1); forbs that seemed to benefit particularly included *Centaurea nigra* and *Trifolium pratense*.

How to facilitate *Rhinanthus* colonization and persistence

Rhinanthus species are characteristic of species-rich grasslands of low or moderate fertility. They tend to disappear when grasslands are managed intensively by fertilizer addition and heavy grazing or frequent cutting (DE HULLU 1985) and this, along with habitat destruction, is probably the cause of the decline in *R. minor* in Britain through the 20th century (PRESTON et al. 2002). However, it is possible to establish *Rhinanthus* populations in moderately fertile conditions. PYWELL et al. (2005) achieved mean frequencies of *R. minor* of more than 90% (percentage of 25 cells occupied in a 1 m^2 quadrat) after four years with soil phosphorus at 9 mg l^{-1}. The Buckinghamshire experiment had similar soil nutrient levels (P 8.5 mg l^{-1}) and local densities of > 600 m^{-2} *R. minor* were common after five years. In another experiment with similar soil nutrients COULSON et al. (2001) recorded rapid spread of *R. minor* from seeded strips with percentage cover reaching a maximum of 40% after three years.

It seems that appropriate sward management can allow colonization, spread and persistence of *Rhinanthus* species (or at least *R. minor*, *R. alectorolophus* and *R. angustifolius*) even in fertile conditions. We gathered demographic data for *R. minor* and *R. angustifolius* from a number of studies and used them to calculate population growth rates λ using stage-structured matrix models (CASWELL 2000) (Table 3). These analyses show wide variation in λ among and within (among years) populations, but also that restored populations (either introduced to a site, or recovering following change to more appropriate management) can show very high λ values ($\lambda > 1$ indicates an increasing population) for a long

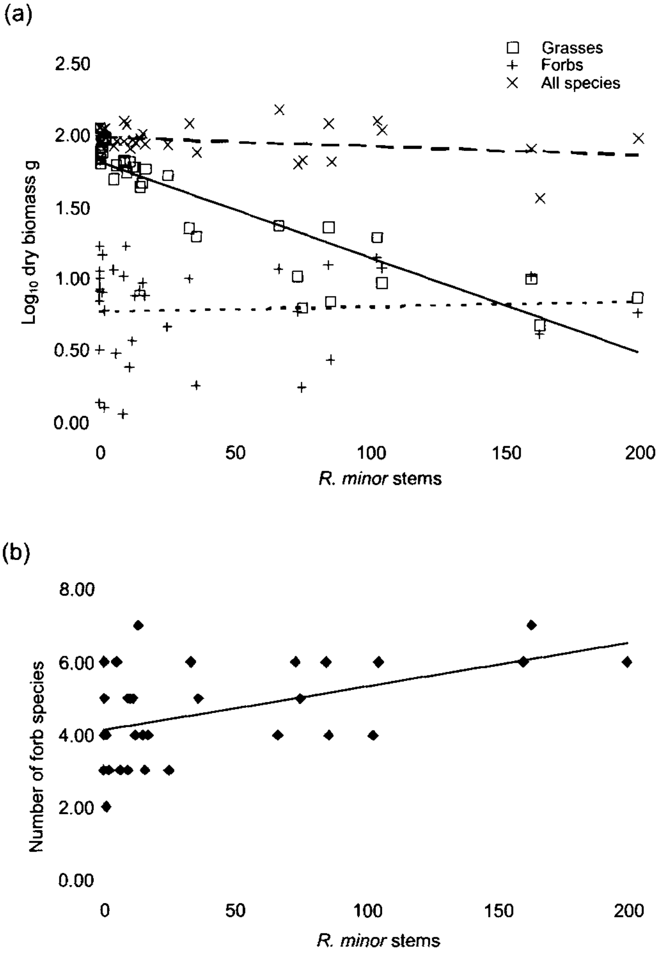

Fig. 1. Effects of *Rhinanthus minor* density on (a) vegetation biomass and (b) forb species number in a grassland restoration experiment in Buckinghamshire, England (R.F. PYWELL, unpubl. data). Data points represent individual quadrats of differing *Rhinanthus* density. All values are per 0.4 × 0.4 m quadrat. There was a significant negative effect of *Rhinanthus* density on grass biomass (solid line; linear regression; $r^2 = 0.80$, $n = 36$, $P < 0.001$), but not on total (dashed line) or forb (dotted line) biomass. Number of forbs also increased with *Rhinanthus* density (linear regression; $r^2 = 0.23$, $n = 36$, $P < 0.01$).

time after restoration (DE HULLU et al. 1985). Even established populations can have high λ values, suggesting an ability to show rapid increase. Meadow management (annual hay cutting) is probably more appropriate than grazing (TER BORG 1985, data), although a single season without a hay cut (after years of hay cutting), may be beneficial in increasing survival and seed production (MAGDA et al. 2004, data). Increased λ with aftermath grazing (COULSON et al. 2001, data) suggests an open sward during the germination period in early spring is important to enhance seedling establishment (see also DE HULLU 1985, VAN HULST et al. 1987, SMITH et al. 2000).

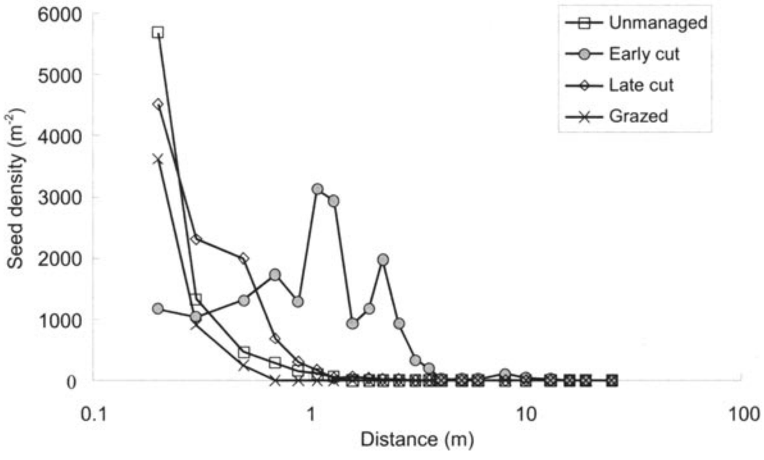

Fig. 2. Dispersal curves for *Rhinanthus minor* under different grassland management systems (BULLOCK et al. 2003b). Data are from seeds traps around groups of *R. minor* planted into managed fields. Lines connecting points are for illustrative purposes.

An important aspect of population increase in restored sites is an ability to spread rapidly from initial colonization points (especially if seed survival is poor). This can be assessed by combining demographic with dispersal data to project the rate of spread of a population (NEUBERT & CASWELL 2000, BULLOCK et al. 2002). BULLOCK et al. (2003b) showed that grassland management has strong effects on *R. minor* dispersal curves (see also TER BORG 1985 and STRYKSTRA et al. 1996). Seeds disperse short distances by wind under no management, but hay cutting machinery can disperse seeds further (Fig. 2). Early cutting as the seeds ripen results in long distance dispersal, but this effect is decreased by late cutting after much of the seed has already dispersed. Grazing animals trample plants and cause very short dispersal distances.

We combined the relevant dispersal data from BULLOCK et al. (2003b) with each *R. minor* demography data set to get indicative population spread rates (Table 3). These calculations suggest that the good seed dispersal by hay cutting can accelerate population spread up to 4–5 m yr^{-1}; which matches observed rates (R. PYWELL, unpubl. data). Therefore, under appropriate management, these *Rhinanthus* species can build up populations and colonize new areas rapidly and are able to maintain numbers to the extent of being able to recover quickly from dips in population size (see also TER BORG 1985).

Controlling dense *Rhinanthus* populations

The converse of these findings is that it is relatively easy to control *Rhinanthus* species if densities get too high. In the agricultural world, *Rhinanthus* species are seen as weeds of grasslands and crops (MAGDA et al. 2004) because of their effects on production. The high densities reported above may lead to declines in production which are unacceptable, for example, to farmers who have created diverse grasslands within agri-environmental schemes.

Table 3. Population growth rates λ for *Rhinanthus* species calculated from demographic data supplied in the references. Seed survival in the soil is thought to be low and none of the studies supply such data. So we calculated a λ assuming no survival and another λ using the maximum between year survival of 10% for *Rhinanthus* species reported by TER BORG (1985). Dispersal data for *R. minor* (see Fig. 2) were combined with demographic data to model the rate of spread of *R. minor* populations; using the dispersal data appropriate to the management applied to the population. Ranges in λ and spread rate reflect replication among sites or over years. "Restored" populations were either introduced to the site by seeding or were recovering from low numbers following new management. "Established" populations were long-established at the site.

Rhinanthus species	Grassland history	Region	Treatments	λ without seedbank (yr^{-1})	λ with seedbank (yr^{-1})	Modelled spread rate ($m\ yr^{-1}$)	Reference
"Restored" populations							
R. minor	Previously intensively cropped and grazed, now hay cut; existing population	France	Experimental				MAGDA et al. (2004)
			no cut	12.94	12.97	0.75	
			early cut	4.49	4.52	4.49	
			late cut	1.98	2.01	0.84	
R. minor	Previously fertilized and intensively grazed, now unfertilized and hay cut; *Rhinanthus* seeded in	England	Experimental				COULSON et al. (2001)
			hay cut only	0.11	0.21	0	
			hay cut and aftermath grazed	3.25	3.34	3.70	
R. angustifolius	Previously intensively cropped and fertilized, now unfertilized and hay cut; existing population	The Netherlands	2–6 years after new management	1.14–5.34	1.24–5.44	-	DE HULLU et al. (1985)
			7–11 years	0.19–1.87	0.29–1.96	-	
			> 12 years	0.28–5.72	0.38–5.81	-	
"Established" populations							
R. minor	Hay meadow, mown annually	Quebec		0.85–4.32	0.93–4.40	0–4.51	VAN HULST et al. (1987)
R. angustifolius	Hay meadow	The Netherlands		1.45	1.52	-	TER BORG (1985)
R. angustifolius	Horse pasture	The Netherlands		0.18	0.27	-	TER BORG (1985)

In England, abundant *R. minor* in certain nature reserves has caused the sward to become too open and invaded by undesirable species such as *Senecio jacobaea* (C. PINCHES, English Nature, pers. comm.). The most effective management to limit *Rhinanthus* populations seems to be very early cutting before the seed is ripe (see also MAGDA et al. 2004), and indeed killing plants before maturity (by pulling, ploughing or cutting) is a traditional way of controlling *R. minor* and *R. angustifolius* in Britain (CARRUTHERS 1903). Poor seed survival in the soil means a single year of this management could cause huge population declines. It is also possible that high densities are a transient phase typical of new *Rhinanthus* populations and density may fall to a lower equilibrium over time (DE HULLU 1985).

DISCUSSION

Rhinanthus species, or at least *R. minor*, *R. angustifolius* and *R. alectorolophus*, seem to meet the five criteria we suggested in the Introduction to make them effective tools for grassland restoration. These three species are associated with a number of grassland communities that are common targets for restoration projects. Seed is relatively easy to obtain either commercially or by harvesting. They also seem to be able to increase grassland diversity, to colonize fertile grasslands rapidly and their populations can be managed easily.

Evidence for the community effects of *Rhinanthus* species in existing infertile, species-rich grasslands is strong (Table 1), but it is dangerous to extrapolate from these conditions to a putative role of *Rhinanthus* species in increasing diversity in fertile restored grasslands. Therefore, it is useful that there are now a few studies using *Rhinanthus* species in projects involving grassland re-creation or diversification (Table 2). When grasslands are created on bare soil (e.g. ex-arable land) the effects of adding *Rhinanthus* species are ambiguous, but this conclusion is partly a consequence of the paucity of studies appropriate to our question. WESTBURY & DUNNETT (2000) have done the most relevant study, and the strong negative effect of *R. minor* on forb biomass might be seen as a hindrance to achieving good grassland restoration. In creating grasslands on arable sites it may be ineffective to sow all species together as many do not establish on bare soil with poor organic matter content (PYWELL et al. 2002a). A more appropriate, "phased", method may be to sow some generalist species that establish quickly to form a sward, which creates conditions more conducive to establishment of specialist grassland species (PYWELL et al. 2003). *Rhinanthus* species could be sown in this later stage to reduce effects of competitive dominants. The PYWELL et al. (1999) study, although limited, used this approach.

The two studies using *Rhinanthus* species to facilitate diversification of existing species-poor grassland are more conclusive. Grass biomass and sward height were reduced and added forb species established in greater numbers and abundance (Table 2). However the mechanism behind the effect of *Rhinanthus* species on both restored and established, species-rich grasslands is not fully understood. Different authors give subtly different mechanisms: a general depression in sward growth and biomass that allows less competitive species to survive and reproduce (DAVIES et al. 1997); reduction of the competitive advantage of certain species in interactions with less competitive species (GIBSON & WATKINSON 1992); and the death of the annual parasite leaving gaps that allow seedling establishment of certain species (JOSHI et al. 2000, PYWELL et al. 2005). It is likely that all mechanisms are important, with *Rhinanthus* species having positive effects on both the recruitment (in gaps) and established phases of less competitive species. However, we do suggest that studies need to be done to unravel these mechanisms by looking at how the presence of *Rhinanthus* species affects the demography of key species in terms of recruitment and gap dynamics, growth, survival and fecundity.

Thus, the use *Rhinanthus* species has great benefits over other tools for facilitating grassland restoration. It is relatively cheap, it is self-sustaining, it looks good and it seems to work. As natural components of many grassland types, *Rhinanthus* species may also have other functional roles in these communities. They seem to be an important nectar source for bees and other invertebrates early in the season (MEEK et al. 2002). Their litter might have high nitrogen concentrations, in common with related hemiparasites (e.g. *Bartsia*), which can affect decomposition processes (PRESS 1998, QUESTED et al. 2003). Such functional attributes could accelerate the development of restored communities to resemble closely target grasslands in terms of both community structure and ecosystem processes.

The ability of certain *Rhinanthus* species to increase rapidly even in moderately fertile grasslands (Table 3) is probably determined mostly by the fact that they parasitize potential competitors (VAN HULST et al. 1987) and that they can disperse very far under particular management regimes (BULLOCK et al. 2003b). A large seed with extensive reserves, high seed viability, and the short period between germination and seed production (4–5 months) (TER BORG 1985, COULSON et al. 2001, PYWELL et al. 2005) are probably important too. However, populations fare less well if the grassland is grazed during the *Rhinanthus* growing season (probably due to trampling) or if the sward is dense during the seedling establishment phase (TER BORG 1985, COULSON et al. 2001, J.M. BULLOCK, unpubl. data). This suggests hay cutting with aftermath grazing is the best management to enhance *Rhinanthus* populations.

It is early to suggest recipes for using *Rhinanthus* species in grassland restoration. For ex-arable sites the phased approach needs to be investigated further. However, we are more confident about the approach to be used in existing species-poor grasslands. The *Rhinanthus* species should be added as seed (the species establish well from seed and so pot-grown plants are an unnecessary expense). Sowing rates are generally quite high (Table 2), but fairly low sowing rates (e.g. 15 seeds m^{-2}) can be sufficient to produce large populations in a short time (Table 2). We have found slot-seeding or a short period of heavy stocking with cattle can create sufficient microsites (COULSON et al. 2001, PYWELL et al. 2005). The best management to allow spread is hay cutting (timed at the peak of seed production) followed by aftermath grazing. The *Rhinanthus* population should be allowed to build up to a large size over, e.g., 2–3 years (PYWELL et al. 2005) so that it creates a sufficiently open sward. Seed of target species can then be simply over-sown with no disturbance treatment being necessary. We have little knowledge of what is a sufficient *Rhinanthus* population density to facilitate establishment of target species. The studies summarized in Table 2 report densities of between 130–1250 m^{-2} after only a few years. All these densities facilitated diversification of the grassland sward, but Fig. 1 and the PYWELL et al. (2005) study show the highest densities gave the strongest positive effects. This suggests that one should try to get very high densities of *Rhinanthus*, but there must be diminishing returns in attempting to achieve such densities. So we are as yet unable to recommend a target densities.

Here we have tended to treat all *Rhinanthus* species interchangeably. The demographic characteristics and community impacts of the three widespread species, *R. minor*, *R. alectorolophus* and *R. angustifolius*, seem to be largely similar. Other species are poorly studied (but see ZOPFI (1995)). It is important, however, that the species used in any restoration is suitable to both the region and the grassland type, to ensure that the restored grassland is similar to local target communities and that the *Rhinanthus* species persists. In the Netherlands *R. alectorolophus* and *R. angustifolius* seem to prefer more mesic grasslands to *R. minor* (TER BORG 1985). There is also much infraspecific differentiation in some *Rhinanthus* species. STACE (1997) lists six possible subspecies of *R. minor* in Britain that differentiate morphologically and by habitat (region, soil moisture, geology and altitude). ZOPFI (1993) studied *R. alectorolophus* from 76 populations in eastern Switzerland and identified seven morphological and genotypic ecotypes that he hypothesized had evolved in response to variation in grazing and cutting management. Therefore, to both maximize success and preserve genetic diversity, it may be important to consider the provenance of *Rhinanthus* used in a restoration (BULLOCK et al. 2003a).

We have concentrated on *Rhinanthus* here. Could other parasitic plants have the same role in restoration? Certainly, other species have been shown to affect community structure in a range of vegetation types. Removal of the hemiparasitic annual *Triphysaria pusilla* (*Orobanchaceae*) from its native species-rich coastal prairie communities in California caused an increase in biomass of graminoids by 28%, although species number was unaffected (MARVIER 1998). In a Californian saltmarsh, quadrats containing the holoparasite *Cuscuta salina* (*Cuscutaceae*) had reduced biomass of the host *Salicornia virginica* and increased biomass of other species (PENNINGS & CALLAWAY 1996, CALLAWAY & PENNINGS 1998). Species-rich grasslands often have a range of parasitic plants; in Britain these include species of *Odontites*, *Euphrasia*, *Thesium* and *Orobanche* (RODWELL 1992). We would suggest that none of these have the same potential as *Rhinanthus* species for use in restoration because they are too small (*Euphrasia*), rare (*Thesium humifusum*), host-specific (*Orobanche*) or needing of disturbance (*Odontites*) to affect communities. However, some study of species other than *Rhinanthus* may be worthwhile, especially *Odontites* and *Euphrasia*.

RESEARCH NEEDS

It is only recently that experimental tests have been done using *Rhinanthus* species in restoration, and these are still few. We suggest future research should address the following questions.

(1) Can *Rhinanthus* species be established, cause significant reductions in productivity and facilitate success of target species in a wide range of species-poor grasslands varying, e.g. in soil type, species composition, geographical location, including those with high fertility?

(2) What are the appropriate sowing rates and target densities for *Rhinanthus* to enhance diversity?

(3) What are the ecological mechanisms by which *Rhinanthus* enhances diversity in restored grasslands; e.g. creating gaps or reducing competitive advantage, increasing seedling establishment or survival at the established phase, etc?

(4) Can species other than *R. minor*, *R. alectorolophus* and *R. angustifolius* be used to facilitate restoration?

(5) Does the provenance and ecotype of *Rhinanthus* used affect success of the restoration?

(6) Should there be a lag phase between *Rhinanthus* addition and sowing target species, and what densities should *Rhinanthus* reach before species are added?

(7) Which introduction and management methods best facilitate population growth and spread of *Rhinanthus* species following seed addition?

(8) Can *Rhinanthus* reach damaging densities in restored grassland and what are the best methods to keep populations at appropriate levels?

(9) Is it appropriate to use *Rhinanthus* species for restoration on ex-arable land, and would a phased approach be best?

(10) Can other parasitic plants be used in habitat restoration?

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