Competitive ability of *Rhinanthus minor* L. in relation to productivity in the Rengen Grassland Experiment

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ABSTRACT

Rhinanthus minor (yellow-rattle) can be used for restoration of species-rich grasslands but is vulnerable to competitive exclusion from high total aboveground biomass production of vascular plants. We asked (1) whether there is a threshold limit for total annual aboveground biomass production of vascular plants above which *R. minor* cannot establish viable population in grasslands and (2) how is cover of *R. minor* in grassland related to standing biomass of bryophytes. Data were collected in the Rengen Grassland Experiment (RGE) established in Germany in 1941 with following fertilizer treatments: unfertilized control, application of Ca, CaN, CaNP, CaNPKCl and $CaNPK_2SO_4$. Cover of *R. minor* and total annual aboveground biomass production of vascular plants were determined from 2005 to 2009. Further relationship between standing biomass of bryophytes and cover of *R. minor* was analyzed in 2006. Mean cover of *R. minor* over five years ranged from 0.7% to 12.3% in $CaNPK_2SO_4$ and control treatments, respectively. Cover of *R. minor* was significantly negatively related to total annual aboveground biomass production of vascular plants and cover of *R. minor* was below 3% in all plots with total annual aboveground dry matter biomass production of vascular plants higher than 5 t/ha. Although cover of *R. minor* was markedly reduced in highly productive plots in the RGE, high standing biomass of bryophytes (1.8 t/ha) in low productive control was not an obstacle for establishment of its viable population. We concluded, that viable population of *R. minor* can be established in grasslands only if total annual aboveground dry matter biomass production of vascular plants is below 5 t/ha regardless on standing biomass of bryophytes.

Keywords: biomass production; long-term fertilizer application; plant nutrition; yellow-rattle; semi-natural grassland restoration

The first step for the restoration of species-rich plant communities from highly productive improved grasslands is the substantial decrease in nutrients availability and consequently aboveground biomass production. This can be achieved by long-term cutting and biomass removal (Bakker et al. 2002, Hejcman et al. 2010a) or by very expensive and irreversible removal of nutrients rich upper soil layer (Rasran et al. 2007, Diaz et al. 2008). A cheap and environmentally friendly alternative has been proposed recently, i.e. the introduction of hemi-parasitic species, of which *Rhinanthus minor* L. is most frequently used (e.g. Davies et al. 1997, Pywell et al. 2004, Westbury et al. 2006, Cameron et al. 2009). This is because *R. minor* decreases biomass production of dominant species which is not compensated by biomass of *R. minor* (Cameron et al. 2005). This is explained by low nutrient and water use efficiencies of hemi-parasites compared to other sward components (Matthies 1995, Těšitel et al. 2010) and by negative effects of the parasite on host photosynthesis (Cameron et al. 2008). Decrease in total aboveground biomass of vascular plants induced by *R. minor* introduc-

Supported by the Czech Science Foundation, Project No. 521/08/1131 and by the Ministry of Agriculture of the Czech Republic, Project No. MZE 0002700604.

tion was marginal (Westbury and Dunnett 2007, Mudrák and Lepš 2010) up to approximately 30% of the control value in field experiments reviewed by Ameloot et al. (2005). Negative effect of *R. minor* on plant community biomass production can be increased in the presence of arbuscular mycorrhizal fungi indicating possible synergistic effect of host plant infection by fungi and parasitism on biomass production (Stein et al. 2009).

R. minor is present in many grassland plant communities and has wide range of host species from legumes to highly productive forage grasses (Gibson and Watkinson 1989, Westbury 2004, Cameron and Seel 2007). The question of current research is into which plant communities *R. minor* can successfully be introduced? In temperate Europe, *R. minor* is characteristic species of low productive cut grasslands from acid to calcareous soils (Regal 1967, Grime et al. 1988, Ellenberg et al. 1991). According to Westbury et al. (2006) *R. minor* failed to establish long-term persistent populations in all of the agriculturally improved grasslands with aboveground dry matter (DM) biomass production above 5 t/ha. According to van Hulst et al. (1987), *R. minor* is an effective invader in relatively unproductive grassland because its finite rate of increase is a nonlinear function of the biomass of the surrounding vegetation, being maximized when the surrounding vegetation is dense enough to allow effective root parasitism but not so dense that young *R. minor* plants are outcompeted for light. Ameloot et al. (2006) recorded successful establishment of viable *R. minor* population in grasslands with DM biomass production below 4 t/ha. In a study by Mudrák and Lepš (2010), plant community in which *R. minor* had high cover exhibited aboveground DM biomass production of 3–4 t/ha. According to a model by Fibich et al. (2010), abundance of hemiparasites in grasslands is negligible if the aboveground DM biomass production is higher than 5 t/ha.

Relationship between abundance of *R. minor* and total annual aboveground biomass production of vascular plants and standing biomass of grassland bryophytes can be well investigated in the Rengen Grassland Experiment. The RGE, established by Prof. Ernst Klapp in the Eifel Mountains (Germany) on low productive *Nardus stricta* grassland in 1941, is probably the oldest still running and properly designed (with five randomized replications) grassland fertilizer experiment worldwide (Schellberg et al. 1999). Long-term fertilizer application created a steep gradient of plant communities within the distance of several meters from low productive *Violion caninae* with average aboveground DM biomass production 3 t/ha up to highly productive *Arrhenatherion* meadow with DM biomass production 8 t/ha (Chytrý et al. 2009, Hejcman et al. 2010a). In contrast to short-term fertilizer experiments, the major advantage of the RGE is in the adaptation of plant species composition to nutrients availability as fertilizers have been applied over more than 60 years. In this experiment, *R. minor* is common in low productive plots which are completely randomized with highly productive plots (Hejcman et al. 2007). Further, *R. minor* is common in the surroundings of the experiment indicating that there is no limitation of *R. minor* distribution because of low seed availability even in plots with its absence or low cover.

No seed limitation of *R. minor* distribution in all plots of the RGE enables to investigate how is competitive ability of *R. minor* affected by fertilizers application, by total annual aboveground biomass production of vascular plants and by bryophyte standing biomass. In this respect, following research questions were asked: Is there any threshold limit for total annual aboveground biomass production of vascular plants above which *R. minor* cannot establish viable population in grasslands and (2) how is cover of *R. minor* in grassland related to standing biomass of grassland bryophytes?

MATERIAL AND METHODS

Study site. In 1941, the fertilizer experiment was set up at the Rengen Grassland Research Station of the University of Bonn in the Eifel Mountains (Germany, 50°13'N, 6°51'E) at 475 m a.s.l. At the study site, the mean annual precipitation is 811 mm and mean annual temperature is 6.9°C (Rengen meteorological station). The soil is a pseudogley indicated by temporarily wet conditions in the turf layer after rainfall in winter and spring and the slow vertical rise of capillary water in summer. Further soil information is given in Schellberg et al. (1999).

Experimental design. The experiment is arranged in a completely randomized block design with five fertilizer treatments (Ca, CaN, CaNP, CaNPKCl and $CaNPK_2SO_4$) and five replicates (Table 1, Figure 1). As an unlimed control was originally missing in the RGE, five replicates of a treatment without any fertilizer input (further referred to as control) were added in 1998. Control plots were introduced in the vicinity of the existing

Table 1. Amounts of nutrients (kg/ha) supplied annually to the treatments since 1941 according to Schellberg et al. (1999), classification of vegetation into alliances according to Chytrý et al. (2009), total annual aboveground dry matter biomass production of vascular plants according to Hejcman et al. (2010a) and standing dry matter biomass of bryophytes in 2006 according to Hejcman et al. (2010c)

Treatment abbrev.	Applied nutrients (kg/ha)	Alliance	Biomass production of vascular plants (t/ha)	Standing biomass of bryophytes (t/ha)
Control	non fertilized control	*Violion caninae*	2.5	1.8
Ca	Ca = 715; Mg = 67	*Polygono-Trisetion*	2.9	0.46
CaN	Ca = 752; N = 100; Mg = 67	*Polygono-Trisetion*	4.9	0.02
CaNP	Ca = 936; N = 100; P = 35; Mg = 75	*Arrhenatherion*	6.5	0.25
CaNPKCl	Ca = 936; N = 100; P = 35; K = 133; Mg = 90	*Arrhenatherion*	8.9	0.15
$CaNPK_2SO_4$	Ca = 936; N = 100; P = 35; K = 133; Mg = 75	*Arrhenatherion*	9.6	0.09

Fertilizers used: Ca – CaO; N – NH_4NO_3; P – Thomas slag.

plots on an area exhibiting the same soil properties. This area was protected as an unfertilized control, has never been fertilized and has been cut at the same time in which the experimental plots were harvested. Individual plot size was 3 × 5 m.

According to previous studies on phyto-sociological classification of vegetation, long-term fertilizer application created significantly different plant communities within near neighborhood (Chytrý et al. 2009). Unfertilized control supported oligotrophic *Nardus* grassland (*Violion caninae* alliance) whereas vegetation in the Ca and CaN treatments mostly resembled montane meadow (*Polygono-Trisetion* alliance). *Arrhenatherum elatius* hay meadow (*Arrhenatherion* alliance) developed in the CaNP, CaNPKCl and $CaNPK_2SO_4$ treatments, respectively. Long-term fertilizer application resulted in high gradient of total annual aboveground biomass production of vascular plants (Hejcman et al. 2010a, Table 1) and its chemical properties (Hejcman et al. 2010d), standing biomass of bryophytes (Hejcman et al. 2010c, Table 2) and soil chemical properties (Hejcman et al. 2009, Table 2).

Figure 1. Aerial photograph of the Rengen Grassland Experiment taken in late June 2006 (photo M. Hejcman©)

Table 2. Results of basic soil chemical analyses of 0–10 cm layer (mg/kg of soil, according to Hejcman et al. 2009). Numbers represent mean values of five replicates

Treatment	P	K	Mg	pH	N (%)	C (%)	C:N
Control	15	43	132	4.9	0.373	4.9	13.1
Ca	6	25	199	6.5	0.350	4.2	12.0
CaN	4	23	195	6.5	0.364	4.4	12.0
CaNP	311	32	199	6.6	0.363	4.3	11.8
CaNPKCl	226	94	207	6.5	0.363	4.4	12.0
$CaNPK_2SO_4$	222	105	207	6.6	0.367	4.5	12.3

Soil pH was potentiometrically measured in a suspension with 0.01 mol/dm^3 $CaCl_2$. Plant available P and K were extracted by a calcium-acetate-lactate solution and measured colorimetrically and photometrically, respectively. Mg was extracted with 0.01 mol/dm^3 $CaCl_2$ and measured with flame atomic absorbance spectrometry (AAS). Total carbon (C) and N were quantified by elemental analyses (Carbo-Erba, Italy)

Data collection and analysis. Cover of *R. minor* was visually estimated directly in percentages (based on the Braun-Blanquet methodology) in late June from 2005 to 2009. To eliminate edge effects, cover of *R. minor* was estimated in the centre of each 3 × 5 m plot in an area of 1.8 × 3.2 m. Aboveground fresh biomass of vascular plants was measured by cutting the sward in each plot at a height of approximately 2 cm in swaths of 1 m by 5 m in early July and mid-October. Subsamples of approximately 0.5 kg were then taken from the cut material and oven-dried at 60°C for 48 h to determine the dry matter content of the harvest and its total yield. Determination of bryophyte biomass was carried out in late June 2006 to coincide with the time of cover estimates of *R. minor* (Hejcman et al. 2010c). In the central part of each 3 × 5 m experimental plot, one 30 × 30 cm metal frame was located (6 treatments × 5 replications = 30 plots). Sampling squares were located at exactly the same relative position in each experimental plot. Bryophytes were manually scraped up and directly stored in plastic bags. In the laboratory, soil and vascular plant debris were removed before bryophytes were oven dried at 80°C for 24 h and dry matter biomass was determined.

Repeated measures ANOVA was used to analyze effect of year, treatment and their interactions on cover of *R. minor* and then one-way ANOVA followed by post-hoc comparison using Tukey's test was used to identify significant differences among treatments in individual years. Regression analysis was used to investigate relationship between cover of *R. minor* and aboveground DM biomass production of vascular plants and standing biomass of bryophytes. All analyses were performed in Statistica 8.0 program (StatSoft, Tulsa).

RESULTS

Calculated by repeated measures ANOVA, cover of *R. minor* was significantly affected by treatment (df = 5, F = 101, P < 0.001), year (df = 4, F = 13, P < 0.001) and by treatment × year interaction (df = 20, F = 2.8, P < 0.001). Mean cover of *R. minor* together with standard errors of the mean in individual treatments and in individual years are given in Figure 2. Mean cover of *R. minor* over five years was 12.3%, 6.7%, 1%, 0.9%, 0.3% and 0.7% in control, Ca, CaN, CaNP, CaNPKCl and $CaNPK_2SO_4$ treatments, respectively. Mean cover of *R. minor* over all treatments was 5.4%, 2.6%, 2.8%, 2.2% and 5.3% in 2005, 2006, 2007, 2008 and 2009, respectively. Cover of *R. minor* was significantly negatively related to total annual aboveground biomass production of vascular plants and the cover of *R. minor* was below 3% in plots with biomass production higher than 5 t/ha (Figure 3). On the other hand, cover of *R. minor* was significantly positively related to standing biomass of bryophytes in 2006 (Figure 4).

DISCUSSION

The main message of this paper is that competitive ability of *R. minor* is low if the total annual aboveground dry matter biomass production of vascular plants exceeds 5 t/ha. This is clear from negligible cover of *R. minor* in plots with biomass production higher than 5 t/ha. Therefore introduction of *R. minor* into existing improved grasslands to decrease their biomass production and to increase their species richness can be probably successful only if the total annual aboveground

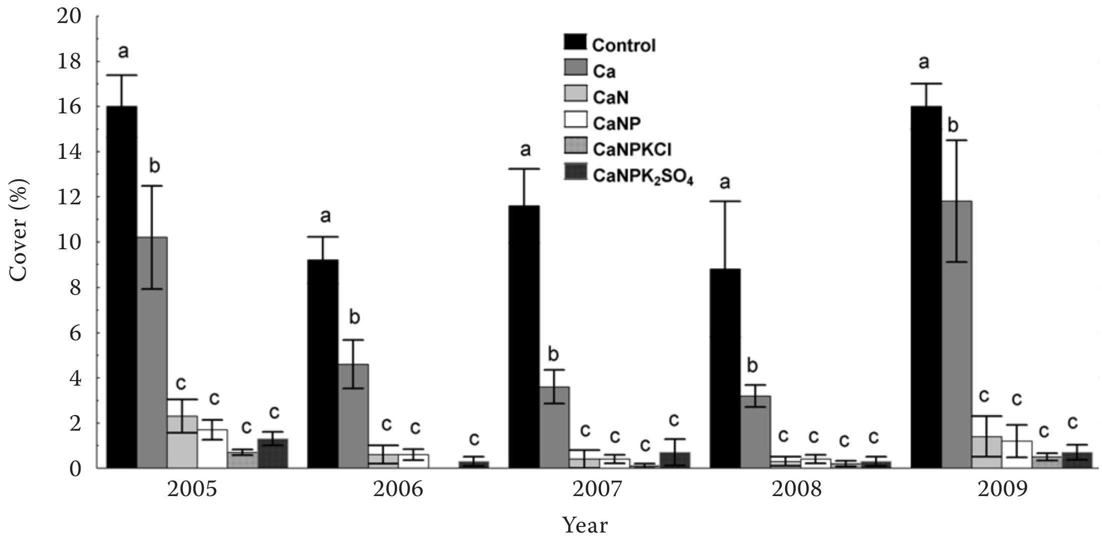

Figure 2. Effect of fertilizer treatments on cover of *Rhinanthus minor*. Error bars represent the standard error of the mean (SE). Using Tukey post-hoc test, treatments with the same letter in each year were not significantly different on 0.05 probability value

biomass production of vascular plants decreases at least below 5 t/ha under the late two cut management. Above this limit, long-term viable population of *R. minor* in grasslands can hardly be established and effect of *R. minor* on total aboveground biomass production will be therefore none or negligible. Low competitive ability of *R. minor* in swards with total aboveground biomass production higher than 5 t/ha was probably the main reason why *R. minor* failed to establish long-term persistent populations in all of the agriculturally improved grasslands in experiments by Westbury et al. (2006). According to model by Fibich et al. (2010) based on real data collected in the Tatra Mts. (Slovak Republic), there was no occurrence of hemi-parasitic species when total aboveground DM biomass production of grassland exceeded 5 t/ha. Total aboveground DM biomass production of plots with viable population of *R. minor* was 3–4 t/ha in study by Davies et al. (1997) or by Mudrák and Lepš (2010) and this is in accordance with results from the RGE. If the biomass production exceeds 5 t/ha, *R. minor* evidently suffer from shading in tall canopy of potential host plants as high sensitivity of *R. minor* to shading was experimentally confirmed by Keith et al. (2004). The upper aboveground DM biomass production limit for successful establishment of *R. minor* is

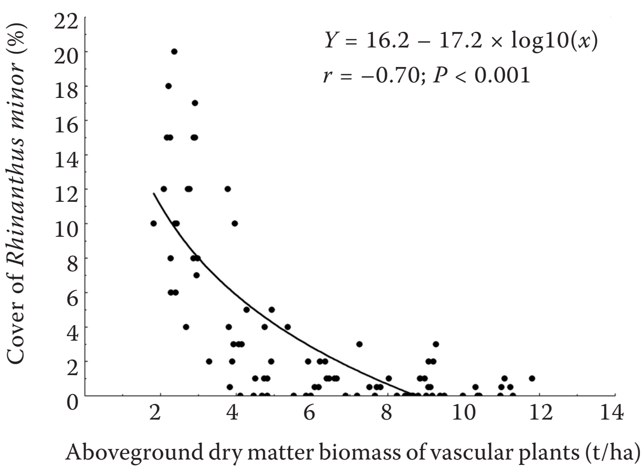

Figure 3. Cover of *Rhinanthus minor* as a function of total annual aboveground dry matter biomass production of vascular plants

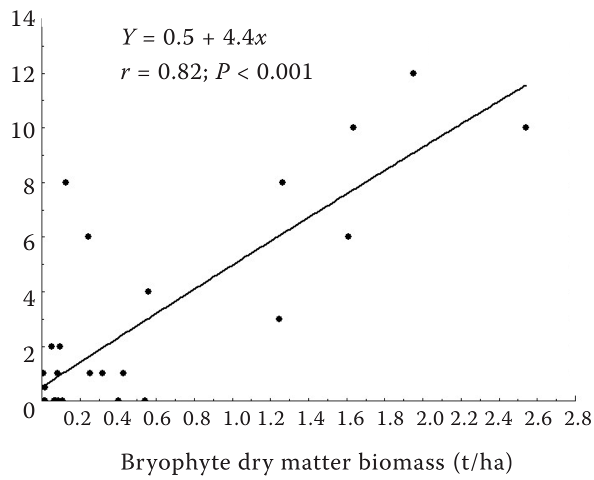

Figure 4. Cover of *Rhinanthus minor* in 2006 as a function of bryophyte dry matter standing biomass in 2006

consistent with threshold limit proposed by Bakker et al. (2002) for successful restoration of species rich grasslands.

The next message of this paper is that *R. minor* suffers from long-term N, NP or NPK application in grasslands. This becomes clear from its low cover in CaN, CaNP, CaNPKCl and $CaNPK_2SO_4$ treatments. In CaN treatment, the mean cover of *R. minor* was only 1% although the N concentration in biomass of potential host plats was highest of all treatments (Hejcman et al. 2010d) and *R. minor* is known to well profit from N rich hosts (Ameloot et al. 2008). This was probably because of very dense sward preventing its seedlings emergence in CaN treatment as *R. minor* was recognized to be highly sensitive to high biomass production or to high sward density (Lindborg et al. 2005). The second possible explanation is the change in host root morphology directly affecting probability of host-parasite association as was previously described for *R. minor* or other hemi-parasitic species (Gibson and Watkinson 1991, Murera and Below 1993).

It is likely that cover of *R. minor* below 1% in CaNP, CaNPKCl and $CaNPK_2SO_4$ treatments was caused by (i) shading of tall vegetation as well as by (ii) direct negative effect of high P availability on host-parazite association. This is in agreement with Davies and Graves (2000) that high P availability impacted the outcome of the host-parasite interaction although unattached plants of *R. minor* planted in monoculture well profit from high P availability in the soil (Seel et al. 1993). At high P availability in soil, effect of parasite on host plant is minimal while performance of parasite is markedly reduced. This is because of reduced flux of water and nutrients from host to parasite because of changes in host plant roots morphology, increased meristematic activity of host, decreased formation of haustoria and therefore attachement succes of the parasite (Davies and Graves 2000). High plant available concentration of P in soil is therefore not compatible with occurence of *R. minor* in grasslands.

Although competitive ability of *R. minor* was markedly reduced in highly productive or dense swards in the RGE, high biomass production of bryophytes was not an obstacle for establishment of its viable population in the low productive control plots. This was evident from high cover of *R. minor* in control with dense and 7 cm tall canopy of bryophyte species *Rhytidiadelphus squarrosus* with standing DM biomass 1.8 t/ha (Hejcman et al. 2010c). In all treatments, late cutting (early July and mid-October) have been applied for decades. Therefore low cover or absence of *R. minor* in particular plots cannot be ascribed to too early cutting regime preventing its seeds ripening and their dispesion.

Acknowledgements

Special thanks for help with data collection go to Michaela Češková.

REFERENCES

Ameloot E., Hermy M., Verheyen K. (2006): *Rhinanthus*: an effective tool in reducing biomass of road verges? An experiment along two motorways. Belgian Journal of Botany, *139*: 173–187.

Ameloot E., Verlinden G., Boeckx P., Verheyen K., Hermy M. (2008): Impact of hamiparasitic *Rhinanthus angustifolius* and *R. minor* on nitrogen availability in grasslands. Plant and Soil, *311*: 255–268.

Ameloot E., Verheyen K., Hermy M. (2005): Meta-analysis of standing crop reduction by *Rhinanthus* spp. and its effect on vegetation structure. Folia Geobotanica, *40*: 289–310.

Bakker J.P., Elzinga J.A., de Vries Y. (2002): Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. Applied Vegetation Science, *5*: 107–120.

Cameron D.D., Geniez J., Seel W.E., Irving L.J. (2008): Suppression of host photosynthesis by the parasitic plant *Rhinanthus minor*. Annals of Botany, *101*: 573–578.

Cameron D.D., Hwangbo J., Keith A.M., Geniez J., Kraushaar D., Rowntree J., Seel W.E. (2005): Interactions between the hemiparasitic abgiosperm *Rhinanthus minor* and its hosts: from the cell to the ecosystem. Folia Geobotanica, *40*: 217–229.

Cameron D.D., Seel W.E. (2007): Functional anatomy of haustoria formed by *Rhinanthus minor*: linking evidence from histology and isotope tracing. New Phytologist, *174*: 412–419.

Cameron D.D., White A., Antonovics J. (2009): Parasite-grass-forb interactions and rock-paper-scissor dynamics: predicting the effects of the parasitic plant *Rhinanthus minor* on host plant communities. Journal of Ecology, *97*: 1311–1319.

Chytrý M., Hejcman M., Hannekens S.M., Schellberg J. (2009): Changes in vegetation types and Ellenberg indicator values after 65 years of fertilizer application in the Rengen Grassland Experiment, Germany. Applied Vegetation Science, *12*: 167–176.

Davies D.M., Graves J.D., Elias C.O., Williams P.J. (1997): The impact of *Rhinanthus* spp. on sward productivity and composition: implications for the restoration of species-rich grasslands. Biological Conservation, *82*: 87–93.

Davies D.M., Graves J.D. (2000): The impact of phosphorus on interactions of the hemiparasitic angiosperm *Rhinanthus minor* and its host *Lolium perenne*. Oecologia, *124*: 100–106.

Diaz A., Green L., Tibbett M. (2008): Re-creation of heathland on improved pasture using top soil removal and sulphur amendments: edaphic drivers and impacts on ericoid mycorrhizas. Biological Conservation, *141*: 1628–1635.

Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W., Paulissen D. (1991): Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica, *18*: 1–248.

Fibich P., Lepš J., Berec L. (2010): Modeling the population dynamics of root hemiparasitic plants along a productivity gradient. Folia Geobotanica, *45*: 425–442.

Gibson C.C., Watkinson A.R. (1989): The host range and selectivity of a parasitic plant: *Rhinanthus minor* L. Oecologia, *78*: 401–406.

Gibson C.C., Watkinson A.R. (1991): Host selectivity and the mediation of competition by the root hemiparasite *Rhinanthus minor*. Oecologia, *86*: 81–87.

Grime J.P., Hodgson J.G., Hunt R. (1988): Comparative Plant Ecology: a Functional Approach to Common British Species. Unwin Hyman, London.

Hejcman M., Klaudisová M., Schellberg J., Honsová D. (2007): The Rengen Grassland Experiment: plant species composition after 64 years of fertilizer application. Agriculture Ecosystems and Environment, *122*: 259–266.

Hejcman M., Száková J., Schellberg J., Šrek P., Tlustoš P. (2009): The Rengen Grassland Experiment: soil contamination by trace elements after 65 years of Ca, N, P and K fertiliser application. Nutrient Cycling in Agroecosystems, *83*: 39–50.

Hejcman M., Češková M., Schellberg J., Pätzold S. (2010a): The Rengen Grassland Experiment: effect of soil chemical properties on biomass production, plant species composition and species richness. Folia Geobotanica, *45*: 125–142.

Hejcman M., Schellberg J., Pavlů V. (2010b): Long-term effects of cutting frequency and liming on soil chemical properties, biomass production and plant species composition of *Lolio-Cynosuretum* grassland after the cessation of fertilizer application. Applied Vegetation Science, *13*: 257–269.

Hejcman M., Száková J., Schellberg J., Šrek P., Tlustoš P., Balík J. (2010c): The Rengen Grassland Experiment: bryophytes biomass and element concentrations after 65 years of fertilizer application. Environmental Monitoring and Assessment, *166*: 653–662.

Hejcman M., Száková J., Schellberg J., Tlustoš P. (2010d): The Rengen Grassland Experiment: relationship between soil and biomass chemical properties, the amount of applied elements and their uptake. Plant and Soil, *333*: 163–179.

Keith A.M., Cameron D.D., Seel W.E. (2004): Spatial interactions between the hemiparasitic angiosperm *Rhinanthus minor* and its host are species-specific. Functional Ecology, *18*: 435–442.

Lindborg R., Cousins A.O., Eriksson O. (2005): Plant species response to land use change – *Campanula rotundifolia*, *Primula veris* and *Rhinanthus minor*. Ecography, *28*: 29–36.

Matthies D. (1995): Parasitic and competitive interactions between the hemiparasites *Rhinanthus serotinus* and *Odontites rubra* and their host *Medicago sativa*. Journal of Ecology, *83*: 245–251.

Mudrák O., Lepš J. (2010): Interactions of the hemiparasitic species *Rhinanthus minor* L. with its host plant community at two nutrient levels. Folia Geobotanica, *45*: 407–424.

Murera L.M., Below F.E. (1993): Role of nitrogen in resistance to *Striga* parasitism of maize. Crop Science, *33*: 758–763.

Pywell R.F., Bullock J.M., Walker K.J., Coulson S.J., Gregory S.J., Stevenson M.J. (2004): Facilitating grassland diversification using the hemiparasitic plant *Rhinanthus minor*. Journal of Applied Ecology, *41*: 880–887.

Rasran L., Vogt K., Jensen K. (2007): Effects of topsoil removal, seed transfer with plant material and moderate grazing on restoration of riparian fen grasslands. Applied Vegetation Science, *10*: 451–460.

Regal V. (1967): Ecological indicator values of common grassland species in Czechoslovakia. Rostlinná výroba, *13*: 77–88. (In Czech)

Schellberg J., Möseler B.M., Kühbauch W., Rademacher I.F. (1999): Long-term effects of fertilizer on soil nutrient content, yield, forage quality and floristic composition of a hay meadow in the Eifel Mountains, Germany. Grass and Forage Science, *54*: 195–207.

Seel W.E., Parsons A.N., Press M.C. (1993): Do inorganic solutes limit growth of the facultative hemiparasite *Rhinanthus minor* L. in the absence of a host? New Phytologist, *124*: 282–289.

Stein C., Rissmann C., Hempel S., Renker C., Buscot F., Prati D., Auge H. (2009): Interactive effects of mycorrhizae and a root hemiparasite on plant community productivity and diversity. Oecologia, *159*: 191–205.

Těšitel J., Plavcová L., Cameron D.D. (2010): Heterotrophic carbon gain by the root hemiparasites, *Rhinanthus minor* and *Euphrasia rostkoviana* (Orobanchaceae). Planta, *231*: 1137–1144.

van Hulst R., Shipley B., Theriault A. (1987): Why is *Rhinanthus minor* (Scrophulariaceae) such a good invader? Canadian Journal of Botany, *65*: 2373–2379.

Westbury D.B. (2004): *Rhinanthus minor* L. Journal of Ecology, *92*: 906–927.

Westbury D.B., Davies A., Woodecock B.A., Dunnett N.P. (2006): Seeds of change: The value of using *Rhinanthus minor* in grassland restoration. Journal of Vegetation Science, *17*: 435–446.

Westbury D.B., Dunnett N.P. (2007): The impact of *Rhinanthus minor* in newly established meadows on a productive site. Applied Vegetation Science, *10*: 121–129.

Received on July 27, 2010

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