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ORIGINAL PAPER

Manual weeding of *Rumex obtusifolius* and its effects on plant species composition in organically managed grassland

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Abstract *Rumex obtusifolius* is a troublesome weed especially in organically managed grasslands. Manual weeding is commonly used for *R. obtusifolius* control, but its effectiveness and effect on plant species composition in upland grassland has never been investigated. Therefore the aim of our study was to reveal the effect of manual weeding by digging out *R. obtusifolius* taproots to depths of 5 or 15 cm, either once or twice, in: (i) presence of *R. obtusifolius* plants; (ii) plant species composition. Additional treatments were grazed and unmanaged grassland (both without digging out *R. obtusifolius* taproot). Digging out taproots twice, to 15 cm, reduced the presence of *R. obtusifolius* significantly. Grazing without digging out taproots was the treatment that was most favourable for *R. obtusifolius* plants. Manual weeding had no significant effect on species richness. The empty spaces after plant removal were filled by nutrient-demanding species (*Poa pratensis, Poa trivialis, Festuca pratensis* and *Lolium perenne*, *Trifolium repens* and *Taraxacum* sp.). On unmanaged grassland the number of *R. obtusifolius* plants decreased, species richness was reduced, but this allowed the spread of other tall weedy species (*Urtica dioica*, *Galium album* and *Elytrigia repens*). Digging out taproots to a depth of 15 cm, performed twice, can be an effective method for *R. obtusifolius* control in organically managed grasslands, as this procedure eliminated the majority of *R. obtusifolius* plants. However, the use of this weeding method over large areas of grassland is limited due to time-consuming and hard physical work.

Keywords Broad-leaved dock · Taproot · Digging out · Pasture · Weed

Key message

- Manual weeding can be effective in the eradication of *Rumex obtusifolius.*
- The effectiveness of manual weeding together with its effect on plant species composition in upland grassland had not been investigated previously.
- Empty spaces left after manual weeding were filled by nutrient-demanding grasses and forbs.
- Digging out the taproots twice, to 15 cm depth, can be an effective method for *R. obtusifolius* control in permanent grasslands under the conditions of organic farming.

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Introduction

Rumex obtusifolius L. (broad-leaved dock) is one of the most troublesome weed species in temperate grasslands and can also colonise permanent agricultural crops (Novák 1994; Brant et al. 2006), where they can survive for ten or more years (Martinková et al. 2009). It produces high plant biomass and large numbers of seeds, and is generally avoided by grazing livestock; these attributes combined with its perennial character, persistent soil seed bank and high ability to regenerate from fragmented underground organs (Cavers and Harper 1964; Zaller 2004) can lead it to becoming a persistent weed that reduces the quality of herbage for grazing or forage conservation. Its regeneration strategy includes its ability to regenerate from buds on the strong underground stem system above the root collar (Pino et al. 1995). In conventionally managed grasslands, *R. obtusifolius* can be controlled by selective herbicides (Hopkins and Johnson 2003), but chemical control requires very specific attention to detail in the timing of spraying. Factors such as the growth stage of docks at spraying (Brock 1972; Dimitrova and Marinov-Serafimov 2008; DiTomaso et al. 2013), the technique of application (Power et al. 2013; Jursík et al. 2008) and weather conditions (Pimentel 1995) can affect the success of herbicidal treatment.

Under organic farming, however, the use of herbicides is prohibited and only biological or mechanical methods of weed control are allowed. Biological methods that have been used or investigated for *R. obtusifolius* control include using specific insects, e.g. *Gastrophysa viridula* (Hatcher et al. 1997; Honěk and Martinková 2004), pathogenic fungi-like *Uromyces rumicis* (Keary and Hatcher 2004), or specific grazers such as goats (Hejcman et al. 2014). Nevertheless, the application of biological methods on farmland is still problematic. Cessation of management has also been shown to reduce the numbers of *R. obtusifolius* plants in grassland (Martinková et al. 2009; Hejcman et al. 2012). Mechanical methods that have been investigated include using different intensities of defoliation (Hopkins and Johnson 2002), heating of plants (Latsch et al. 2007, 2011), motorised milling of roots (Pötsch and Griesebner 2007) and manual digging of taproots (Strnad et al. 2010). In a study by Stilmant et al. (2010) frequent cutting of *R. obtusifolius* reduced the vigour of the aboveground organs, particularly decreasing the number of leaves, the size of the largest leaf and also the amount of herbage production contributed by *Rumex*. Plants of *R. obtusifolius* can, however, tolerate a high cutting frequency for several years, and three cuts per year may not be sufficient for its elimination from grassland (Niggli et al. 1993; Hopkins and Johnson 2002; Stilmant et al. 2010; Hann et al. 2012).

After plants of *R. obtusifolius* become established in grassland they develop deep taproots with a high storage capacity for assimilates and nutrients. Persistence is allowed by the high regeneration ability of the root collar after disturbance and by a high clonal reproduction potential (Pino et al. 1995; Strnad et al. 2010). Buds are common on dock root crowns in the upper 10 cm layer of the soil. Therefore digging plants out from <10 cm below the soil surface is not an effective method for *R. obtusifolius* control (Dierauer 1993; Bond et al. 2007; Strnad et al. 2010), at least in soils with high contents of plant-available nutrients, as in the cited studies. However, the effects of root digging to soil depths of 5 and 15 cm, performed once or twice, on the survival of *R. obtusifolius* in upland grasslands dominated by *A. capillaris* have never been investigated. Furthermore, there have been no studies of the effects on plant species composition and species richness of manual dock control in permanent grasslands.

The aim of our study was therefore to answer the following questions: (i) How effective is digging out *R. obtusifolius* taproots to 5 or 15 cm soil depth, performed once or twice, for its control in *A. capillaris* grassland, assessed over 5 years? (ii) Which plant species replace *R. obtusifolius* after its removal by digging? (iii) Is the absence of grassland management a less effective method of control than digging out *R. obtusifolius* taproots? and (iv) How do different weeding treatments affect the species richness of vascular plants?

Materials and methods

Study site

The experimental grassland was situated in Krásná Studánka, Liberec, Czech Republic (50°48′29.24″N, 15°2′17.56″E, 394 m.a.s.l.). The bedrock is biotite granite covered by Cambisol with a pH (KCl) value of 5.45 and an organic C concentration of 4.53 %. Contents of plant-available (Mehlich III; Mehlich 1984) P, K, Ca and Mg were 28, 67, 1728 and 58 mg kg^{-1}, respectively. The mean annual temperature is 7.2 °C and the mean annual precipitation is 803 mm (Liberec meteorological station). The grassland was classified as upland hay mesophile meadow (alliance *Arrhenatherion*; Chytrý 2007). The dominant vascular plant species before the introduction of management treatments were *A. capillaris* (cover 64 %), *Taraxacum* sp. (14 %), *Trifolium repens* (14 %) and *R. obtusifolius* (7 %). At the beginning of the experiment, the mean density of *R. obtusifolius* was about two plants per square metre. The 8 ha experimental pasture was managed organically and rotationally stocked by Gasconne suckler cows with their calves during four grazing cycles per vegetation season. To reduce the number of inflorescences of *R. obtusifolius* plants, ungrazed sward patches were cut twice (after the second and fourth grazing cycles) per vegetation season.

Experimental design

The experiment was established in the centre of the 8 ha pasture in four complete randomised blocks with individual

3 m × 3 m plots. Six treatments were applied: (i) grazed, taproot of *R. obtusifolius* dug out to a depth of 15 cm below ground twice ($GD_{15}T$); (ii) grazed, taproot of *R. obtusifolius* dug out to a depth of 15 cm once ($GD_{15}O$); (iii) grazed, taproot of *R. obtusifolius* dug out to a depth of 5 cm below ground twice (GD_5T); (iv) grazed, taproot of *R. obtusifolius* dug out to a depth of 5 cm below ground once (GD_5O); (v) grazed, without digging out *R. obtusifolius* taproot (GND—the traditional farm management which was the control); (vi) no grassland management—unmanaged pasture without digging out *R. obtusifolius* taproot (UND). Digging of *R. obtusifolius* taproots was performed manually using two special narrow spade for each of the two depths (Fig. 1). The first weeding was performed on 14th August 2007 and the second on 20th May 2008. There was no weeding in the years 2009–2011.

Data collection

The percentage cover of vascular plant species and the numbers of broad-leaved dock plants were monitored in 2 m × 2 m plots located in the middle of each of the 3 × 3 m experimental plots from 2007 to 2011. The cover of all vascular plant species was assessed once in the spring (from the end of May to the beginning of June) and the numbers of *R. obtusifolius* plants were counted twice in spring (the end of May to beginning of June) and autumn (from end of October to beginning of November) during each of the 5 years of the experiment. One *R. obtusifolius* plant was defined as having all visible shoots growing from buds inside a circle of 30 cm diameter around the main shoot. Young seedlings were counted if the leaf length was at least 5 cm. The nomenclature of vascular plant species follows Kubát et al. (2002).

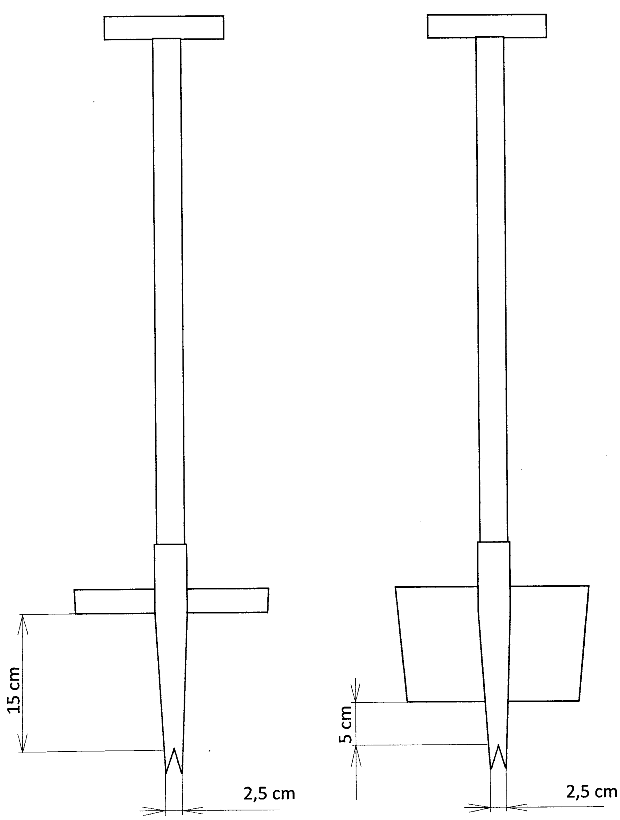


Fig. 1 Schematic drawing of special metal narrow spade for 15 and 5 cm depth of digging out. Width of the blade was 2.5 cm

Statistical analyses

A one-way ANOVA was used to analyse the treatment effects on the number of *R. obtusifolius* plants (recalculated per square metre) in the spring and autumn sampling dates of a particular year. The effect of time, treatment and their interaction on the cover of dominant plant species and species richness was evaluated by a repeated ANOVA. The success rate of manual weeding was expressed as the ratio of the final (year 2011) to initial (year 2007) number of *R. obtusifolius* plants and it was tested by one-way ANOVA. Post hoc comparison using the Tukey HSD test was applied to identify significant differences between treatments on a particular sampling date. Ratio data were log transformed in order to meet the assumptions of ANOVA. All univariate analyses were performed using STATISTICA 12 software (StatSoft, Tulsa, USA). The community response was analysed using constrained ordinations. Redundancy analysis (RDA) in the CANOCO 5 programme (terBraak and Šmilauer 2012) was used to evaluate multivariate plant species composition data in particular years. The blocks were used as covariables in all analyses to restrict permutations to the blocks. Cover data in RDA were logarithmically transformed [$y = \log 10 (y + 1)$] to down-weight dominant species and 999 permutations were used in all analyses. An ordination diagram, constructed by the CANOCO 5 programme, was used to visualise the results of the RDA analysis of data collected in 2011.

Results

There were no significant differences in *R. obtusifolius* numbers among treatments after the first weeding treatment in August 2007 (Fig. 2). The first significant differences in *R. obtusifolius* numbers among treatments appeared after the second digging in May 2008. After spring 2008, there were strong variations in *R. obtusifolius* numbers depending on the applied treatments. Generally, the lowest numbers of *R. obtusifolius* plants were recorded in treatments where manual weeding was applied twice (GD_5T, $GD_{15}T$).

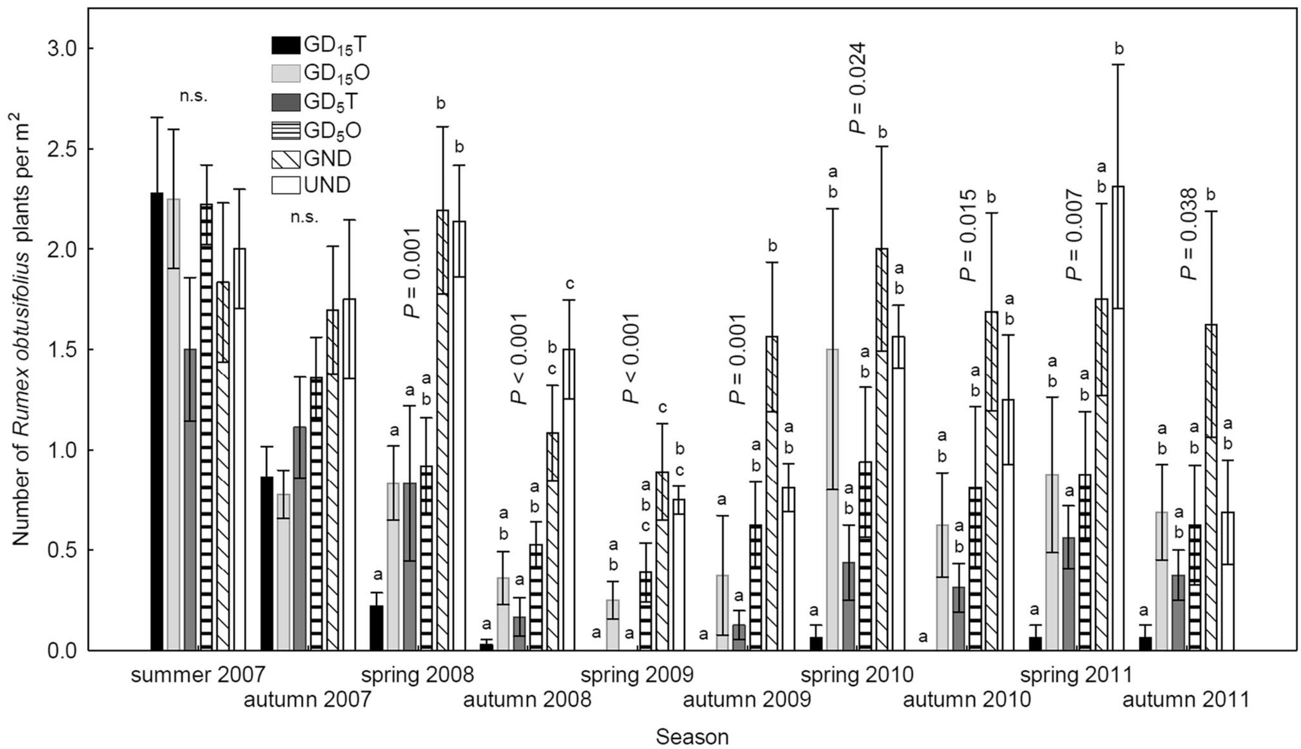
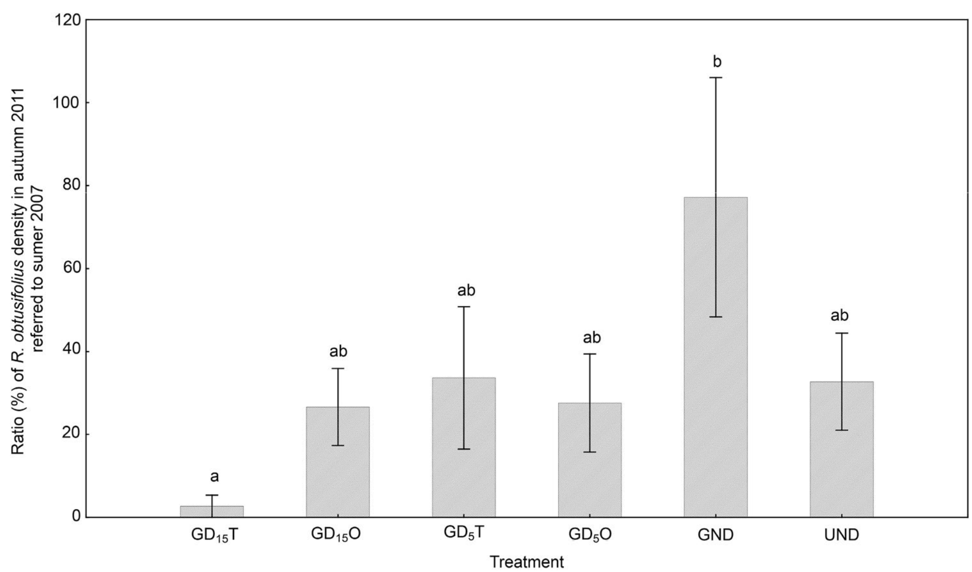


Fig. 2 Number of *Rumex obtusifolius* per 1 m^2 under different treatments for the years 2007–2011. *P* represents the probability value for differences between treatments obtained by one-way ANOVA for each year, n.s.—non-significant result. According to a Tukey post hoc test, treatments with the same letter were not significantly different on 0.05 probability value. *Error bars* represent the standard error of the mean. Treatment abbreviations are explained in Table 1

Fig. 3 Survival rate of *R. obtusifolius* in autumn 2011 referred to the initial number of plants in summer 2007. Probability value for differences between treatments obtained from one-way ANOVA analyses was $P < 0.05$. According to a Tukey post hoc test, treatments with the same letter were not significantly different on 0.05 probability value. *Error bars* represent standard error of the mean. Treatment abbreviations are explained in Table 1



Only a slight reduction was recorded in treatments with one digging treatment and in UND treatment. Higher numbers of *R. obtusifolius* plants were usually recorded in the spring under UND treatment than under other treatments. In 2011, we recorded 3, 26, 28, 33, 34 and 77 % of the initial number of *R. obtusifolius* plants recorded in 2007 in the $GD_{15}T$, $GD_{15}O$, GD_5O, UND, GD_5T and GND treatments, respectively (Fig. 3). Although at the end of the experiment, a 23 % reduction in the number of *R. obtusifolius* plants was recorded in GND treatment, there was a high

Table 1 Results of RDA analyses of cover estimates performed separately for each year

Year	Explanatory variables	Covariables	% Expl. var. 1st axis (all axes)	*F* ratio 1st axis (all axes)	*P* value 1st axis (all axes)
2007	GD_5O, GD_5T, $GD_{15}T$, $GD_{15}O$, UND, GND	Blocks	15.74 (28.93)	2.8 (1.2)	0.094 (0.192)
2008	GD_5O, GD_5T, $GD_{15}T$, $GD_{15}O$, UND, GND	Blocks	35.01 (47.67)	8.1 (2.7)	0.001 (0.001)
2009	GD_5O, GD_5T, $GD_{15}T$, $GD_{15}O$, UND, GND	Blocks	32.09 (43.84)	7.1 (2.3)	0.006 (0.004)
2010	GD_5O, GD_5T, $GD_{15}T$, $GD_{15}O$, UND, GND	Blocks	36.92 (51.16)	8.8 (3.1)	0.004 (0.002)
2011	GD_5O, GD_5T, $GD_{15}T$, $GD_{15}O$, UND, GND	Blocks	39.42 (53.84)	9.8 (3.5)	0.007 (0.002)

Applied treatments were *$GD_{15}T$* grazing with digging the taproot of *R. obtusifolius* out from a depth of 15 cm below ground twice, *$GD_{15}O$* grazing with digging the taproot of *R. obtusifolius* out from a depth of 15 cm below ground only once, *GD_5T* grazing with digging the taproot of *R. obtusifolius* out from a depth of 5 cm below ground twice, *GD_5O* grazing with digging the taproot of *R. obtusifolius* out from a depth of 5 cm below ground only once, *GND* grazing without digging the taproot of *R. obtusifolius* out (traditional farm management as a control), *UND* unmanaged treatment, *% expl.* var. species variability explained by one (all) ordination axis (measure of explanatory power of the explanatory variables), *F-ratio F* statistics for the test of particular analysis, *P value* probability value obtained by the Monte Carlo permutation test, *Tested hypothesis* is there any effect of treatment on plant species composition in any particular year?

degree of variation caused by differences amongst individual plots. In several cases, the numbers of *R. obtusifolius* plants were even higher in 2010 than in 2007.

No significant effect of the treatments on plant species composition as calculated by RDA was recorded in 2007 (Table 1). The variability of plant species composition explained by the treatments was more than 50 % after 5 years of the experiment in 2011. Three groups of treatments with similar plant species composition were recognised on the ordination diagram based on RDA analysis of data collected in 2011 (Fig. 4): GD_5T, $GD_{15}T$ and $GD_{15}O$ treatments form the first group, GND and GD_5O treatments make up the second group and UND comprises the third group. The association of individual species with particular management treatments is clearly visible from the ordination diagram. GD_5T, $GD_{15}T$ and $GD_{15}O$ treatments had low coverage of *R. obtusifolius*, which was replaced particularly by *Poa pratensis*. Tall weedy forbs *Urtica dioica*, *Galium album* and tall grasses *Elytrigia repens* and *Dactylis glomerata* were associated with UND treatment. The GND and GD_5O treatments supported the productive grasses *Poa trivialis, Festuca pratensis* and *Lolium perenne.* All of the grazed treatments were favourable for the development of the prostrate forbs *T. repens* and *Taraxacum* sp. The majority of the most abundant plant species in the sward (*Agrostis capillaris*, *D. glomerata*, *E. repens*, *F. pratensis*, *G. album*, *L. perenne*, *P. pratensis* and *Trifolium repens*) were significantly affected by time and treatment but not by their interactions (Figs. 5, 6; Table 2). *Rumex obtusifolius, Taraxacum* sp. and *U. dioica* were the only three dominant species whose cover was affected not only by time and treatment but also by their interactions (Fig. 6; Table 2). No effect of time, treatment or their interaction was revealed for *Veronica chamaedrys.*

Species richness of vascular plants was significantly affected by time, treatment and their interaction (Table 2). Species richness was stable in all managed treatments, but it decreased from 15 to 9 species per 4 m^2 in the UND treatment (Fig. 7).

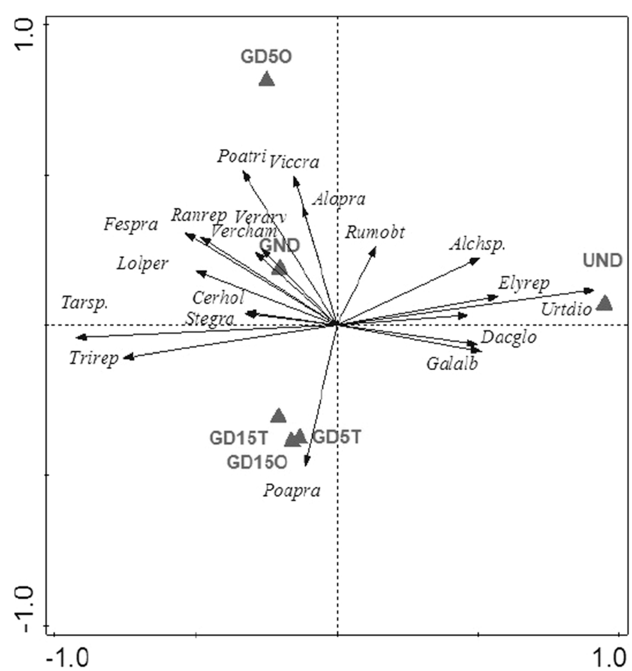


Fig. 4 Ordination diagram showing results of a RDA analysis of plant species composition data collected after 5 years of the experiment in 2011 (see Table 1 for details). Treatment abbreviations are explained in Table 1. Species abbreviations: *Alchsp, Alchemilla* sp.; *Alopra, Alopecurus pratensis*; *Cerhol, Cerastium holosteoides; Dacglo, Dactylis glomerata; Elyrep, Elytrigia repens; Fespra, Festuca pratensis; Galalb, Galium album; Lolper, Lolium perenne; Poapra, Poa pratensis; Poatri, Poa trivialis; Ranrep, Ranunculus repens; Rumobt, Rumex obtusifolius; Stegra, Stellaria graminea; Tarsp., Taraxacum* sp.; *Trirep, Trifolium repens; Urtdio, Urtica dioica; Verarv, Veronica arvensis; Vercha, Veronica chamaedrys; Viccra, Vicia cracca*

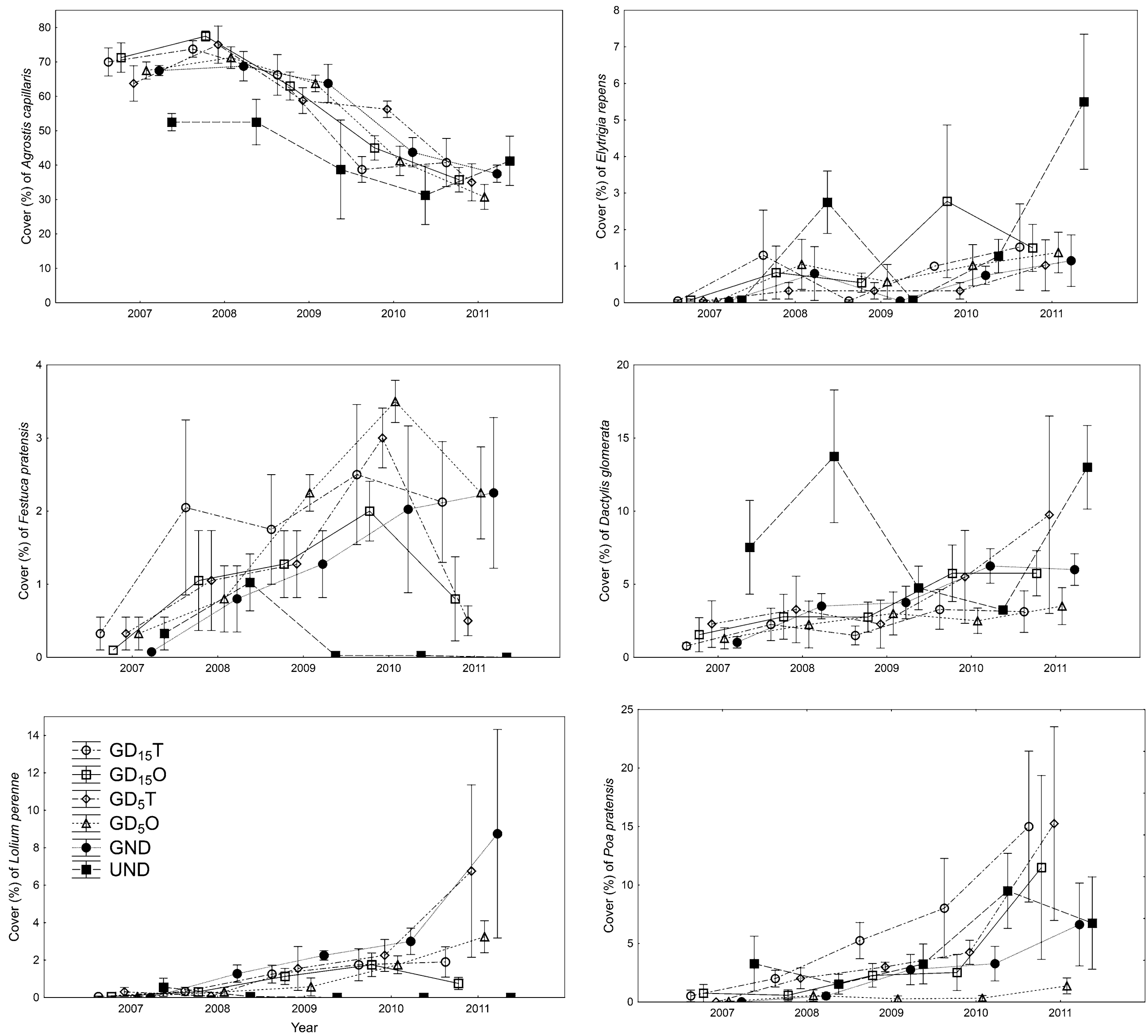


Fig. 5 Cover (%) of the dominant grass species under different treatments for the years 2007–2011. *Error bars* represent the standard error of the mean. Treatment abbreviations are explained in Table 1

Discussion

The main finding of this study was that all of the manual weeding treatments, as well as the treatment of no grassland management, resulted in a significantly reduced density of *R. obtusifolius* plants in *A. capillaris*-dominated grassland. The repeated digging to a depth of 15 cm was the most successful treatment for reducing *R. obtusifolius* as 97 % of plants were eradicated. This depth was also recommended by Pötsch and Griesebner (2007) who used an innovative motorised rotating milling cutter system for mechanical destruction of *R. obtusifolius* plants in Austrian alpine pastures. Likewise, Dierauer (1993) and Bond et al. (2007) concluded that, under conditions of organic farming, the only effective method for control of *R. obtusifolius* is to remove the entire root or to cut the root at least 10 cm below ground. This means that it is necessary to remove the majority of buds, which are responsible for the vegetative reproduction of *R. obtusifolius* (Pino et al. 1995). Manual weeding at a depth of 5 cm, however, could still result in a reduction in the number of *R. obtusifolius* plants, as also noted by Dierauer (1993). Nevertheless this reduction was not statistically significant due to high standard errors resulting from limited replication of the treatments. Conversely, Strnad et al. (2010) reported that manual weeding by digging of the plants to 5 cm below the

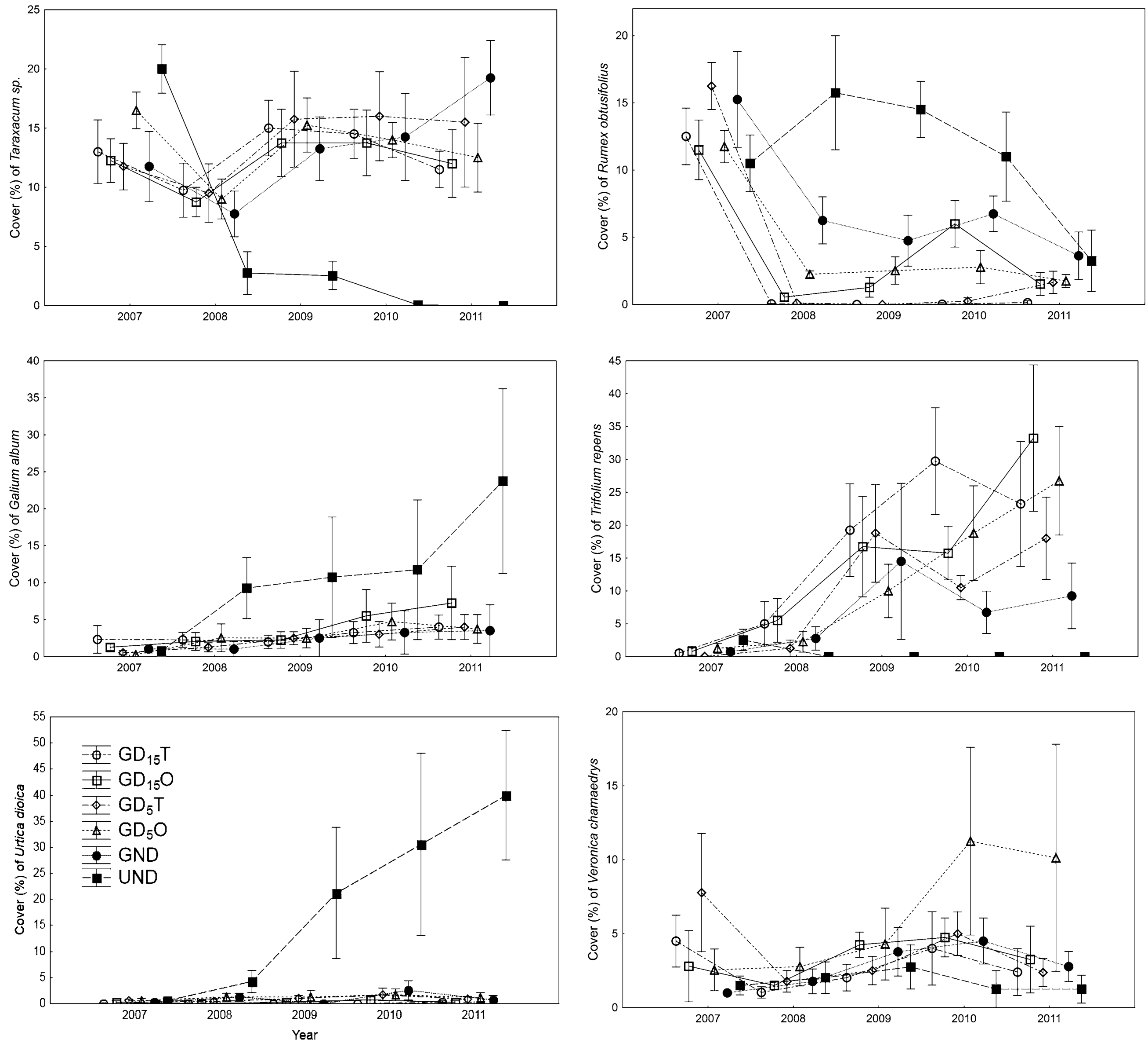


Fig. 6 Cover (%) of dominant forb species under different treatments for the years 2007–2011. *Error bars* represent the standard error of the mean. Treatment abbreviations are explained in Table 1

ground is not sufficient for *R. obtusifolius* control even when applied eight times during three vegetation seasons. The differences in results between these studies were probably caused by the different content of plant-available nutrients in the soil. In the study of Strnad et al. (2010) there were N fertiliser applications and the soil had levels of plant-available P and K that were five and four times higher than that found in our study. It seems that manual weeding is much more efficient under conditions of lower soil nutrient availability (especially N, P and K), as low nutrient supply does not allow fast regrowth of *R. obtusifolius* plants after manual weeding. On the other hand, in soil with high Ca and Mg availability, the density of *R. obtusifolius* plants was weakly positively related to K availability but showed no relation to P availability (Hann et al. 2012).

Manual weeding of *R. obtusifolius* not only reduced its presence in the sward but also had a significant successional effect on the cover of the dominant vascular plant species in *A. capillaris* grassland. Plants of *R. obtusifolius* were mainly replaced by nutrient-demanding grasses (*P. pratensis, P. trivialis, F. pratensis* and *L. perenne*) and also by prostrate forbs (*T. repens* and *Taraxacum* sp.) which quickly colonised the gaps created by the manual removal of *Rumex*. These plant species are of relatively high value for grazing livestock because of their high forage value

Table 2 Results of repeated measurements ANOVA (time, treatment, time × treatment) for the coverage of plant species and number of vascular plant species

	Effect					
	Time, *Df* = 4		Treatment, *Df* = 5		Time × treatment, *Df* = 20	
	F ratio	*P* value	*F* ratio	*P* value	*F* ratio	*P* value
Agrostis capillaris	46.65	<0.001	6.32	<0.001	1.39	0.15
Dactylis glomerata	3.94	0.01	5.60	<0.001	1.09	0.37
Elytrigia repens	7.17	<0.001	2.87	0.02	1.40	0.14
Festuca pratensis	8.90	<0.001	4.92	<0.001	1.31	0.19
Galium album	2.68	0.04	4.34	0.001	0.60	0.90
Lolium perenne	5.67	<0.001	2.81	0.02	1.07	0.40
Poa pratensis	8.80	<0.001	2.40	0.04	0.79	0.72
Rumex obtusifolius	**37.12**	**<0.001**	**16.70**	**<0.001**	**3.55**	**<0.001**
Taraxacum sp.	4.92	0.001	8.33	<0.001	2.50	0.002
Trifolium repens	12.01	<0.001	5.43	<0.001	1.40	0.14
Urtica dioica	2.54	0.05	13.61	<0.001	2.18	0.007
Veronica chamaedrys	1.49	0.21	2.06	0.08	0.76	0.75
Number of plant species	3.67	0.01	14.68	<0.001	3.26	<0.001

Df Degree of freedom, *F* value derived from *F* statistics in repeated measurements ANOVA, *P* probability value

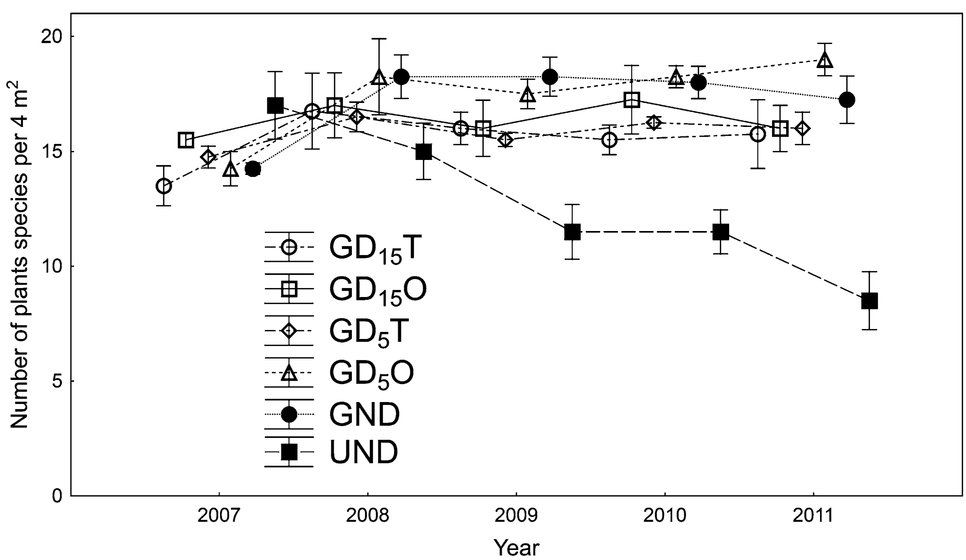


Fig. 7 Species richness of vascular plants (per 4 m^2) under different treatments for the years 2007–2011. *Error bars* represent standard error of the mean. Treatment abbreviations are explained in Table 1

(Frame 1992). Manual weeding of *R. obtusifolius* had no substantial effect on species richness. Species richness was reduced in the treatment with no grassland management, a finding also observed previously in temperate grasslands (Pavlů et al. 2012). There was almost no regeneration of *R. obtusifolius* plants via seedlings in all of the managed treatments, based on personal observations (Vilém Pavlů) (data not presented). It is likely that repeated defoliation of ungrazed patches prevented seed production and generative reproduction of *R. obtusifolius.* Any young seedlings of *R. obtusifolius* are likely to have been grazed or damaged by cutting or by hooves of the cattle during the grazing. Similarly, Stilmant et al. (2010) recorded a reduction in the vigour of the aerial parts of *R. obtusifolius* under grazing treatment, associated with a reduction in the number of leaves, the size of the largest leaf and the herbage mass. In the spring we found a higher number of *R. obtusifolius* plants in the treatment with no grassland management due to the presence of seedlings close to mother plants (personal observation, Vilém Pavlů). These seedlings did not survive until the autumn of the same year, however, as they were suppressed by overgrowing tall grasses and forbs.

This confirmed the low competitive ability of *R. obtusifolius* seedlings in closed grassland stands (Weaver and Cavers 1979). The low presence of *R. obtusifolius* plants in the treatment with no grassland management in the final year of the experiment is in accordance with previous studies (Pavlů et al. 2008; Martinková et al. 2009; Hejcman et al. 2012) in which high mortality of *R. obtusifolius* plants was recorded in unmanaged grassland after several years, probably due to the effects of competition from tall grasses and forbs. Under conditions of no grassland management, however, mature plants of *R. obtusifolius* can produce a large number of germinable seeds; these seeds may be able to survive in the soil seed bank for decades (Toole and Brown 1946). Additionally, unmanaged grassland supported tall weedy species with high nutrient requirements, such as *U. dioica, G. album* and *E. repens*; these are not considered desirable plant species in agricultural grasslands (Frame 1992).

Manual weeding of *R. obtusifolius* can be an effective method for its control in temperate grasslands. Manual digging of *R. obtusifolius* taproots is commonly made by farmers (Pötsch and Griesebner 2007) but has not been adequately tested under experimental conditions. In addition to being an appropriate technique for use in organic farming, this method of manual weeding of *R. obtusifolius* can also be used in grasslands managed according to agri-environment and conservation schemes, where the use of herbicides approved for dock control might present problems for other dicotyledons of conservation interest. It is also a weed-control method which is also suitable for conventional farmers who prefer not to use herbicides, including many horse keepers. However, the use of this weeding method over large areas of grassland is limited due to time-consuming and hard physical work.

Conclusion

Manual or mechanical weeding of *R. obtusifolius* by digging out the taproots can be an effective method for *R. obtusifolius* control in organically managed grasslands dominated by *Agrostis capillaris*. Digging of *R. obtusifolius* taproots to the depth of 15 cm, performed twice, was the most successful method as this procedure eliminated the majority of *R. obtusifolius* plants. Bare ground gaps created by digging are colonised by nutrient-demanding grasses and forbs with high forage value. Although removal of grassland management, thereby allowing the sward to grow unmown and ungrazed, can reduce the number of *R. obtusifolius* plants in the sward, the plants present can produce seeds which can contribute further to weed infestation of surrounding areas. Additionally, the absence of grassland management supports tall weedy species and considerably reduces the species richness of vascular plants.

Author contributions

VP, JG and LP conceived and designed the research. JG, VP, LP, VL and RH conducted the experiments. RH and VP analysed the data. VP, RH, LP and MH wrote the manuscript. All authors read and approved the manuscript.

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