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Reference:
Michielsen Mathias, Szemák László, Fenesi Annamária, Nijs Ivan, Ruprecht Eszter.- Resprouting of w oody species encroaching temperate European grasslands after cutting and burning
Applied vegetation science - ISSN 1402-2001 - 20:3(2017), p. 388-396
Full text (Publisher's DOI): http://dx.doi.org/doi:10.1111/AVSC.12300
To cite this reference: http://hdl.handle.net/10067/1400650151162165141

Resprouting of woody species encroaching temperate European grasslands after cutting and burning

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Printed journal page estimate: 5894 words (7.25 pages), figure 0.5 pages, total 7.75 pages.

Abstract

Questions: Are there interspecific differences in the resprouting after cutting and burning among woody species encroaching temperate grasslands? Are alien woody species more successful than natives in their resprouting after the two treatments proposed to control shrub encroachment? Is resprouting influenced by age of the individuals? Does resprouting differ between cutting and burning?

Location: Temperate grasslands encroached by shrubs, Transylvania, Romania.

Methods: We investigated the resprouting after cutting or burning of four shrub species (*Cornus sanguinea*, *Crataegus monogyna*, *Prunus spinosa* and *Rosa canina*) encroaching grasslands in field sites three years following treatments. We compared the resprouting ability of shrubs between species and treatments and analyzed the relationship between the number of resprouts and stump diameter, as a proxy for age. In a common garden experiment on one-year-old individuals we compared resprouting after cutting and burning between three native (*C. sanguinea*, *C. monogyna* and *P. spinosa*) and three alien woody species (*Ailanthus altissima*, *Elaeagnus angustifolia* and *Hippophae rhamnoides*) during one growing season.

Results: *C. monogyna* produced the largest number of resprouts in the field study, and *H. rhamnoides* in the experimental study. Overall, resprouting ability of alien woody species did not differ from that of the natives. In the field study, we found an increasing number of resprouts with increasing stump diameter, and the rate of increase in the number of resprouts was greatest in *C. monogyna*. We detected no difference in the resprouting of woody species between cutting and burning treatments either in the field or in the experimental study.

Conclusions: Our study suggests that the success of encroachment control in grasslands does not depend on treatment type, but on the woody species composition and age of individuals. Grasslands encroached by *C. monogyna* or *H. rhamnoides* will be more labour-intensive to restore and maintain free of shrubs. Restoration measures should be implemented in the early stage of shrub encroachment since younger shrubs have a lower resprouting ability. Burning and cutting may be equally effective in controlling shrub encroachment, but treatments should be more intensive than in the current study in order to damage the resprouting buds and arrest resprouting.

Keywords: Alien; Clipping; *Crataegus monogyna*; Fire; Grassland conservation; *Hippophae rhamnoides*; Invasive; Romania; Shrub; Stump diameter; Tree; Woody encroachment

Nomenclature: Tutin et al. (1968-1993)

Running head: Controlling woody encroachment in grasslands

Introduction

Large areas of semi-natural grassland are abandoned from traditional management throughout Europe, and these grasslands become susceptible to secondary succession, inducing shrub encroachment (Heisler et al. 2004; Lett & Knapp 2005; Valkó et al. 2012; Petersen & Drewa 2014). The major effect of shrub encroachment in grasslands is the displacement of herbaceous species through competition for light, moisture and nutrients (Petersen & Drewa 2014). Thus, there is a serious threat that many grassland species adapted to open areas and continuous human management will disappear (Pykälä 2000). Besides native shrubs and trees, woody aliens invade abandoned grassland, aggravating nature conservation concerns (Boulant et al. 2008 and literature therein).

One solution to restore abandoned temperate grassland is the reintroduction of a disturbance regime that reduces shrub presence. The European Union developed a subsidiary program to stimulate farmers to keep their grasslands free of shrubs by introducing management practices (Angileri et al. 2011). In Romania, additional agri-environment payments are available for grassland maintenance through the Ministry of Agriculture and Rural Development (http://www.madr.ro/en/). Due to this program, Romanian farmers began to clear their land from woody species. Some farmers use cutting as a method to eradicate shrubs and trees, while others use fire as a more simple and cost-effective way of clearance. Despite the fact that the use of fire as a land management option is forbidden in Romania (and in many other European countries), illegal burning is an ongoing practice (Castellnou et al. 2010; Valkó et al. 2014; Deák et al. 2014).

Prescribed burning is successfully applied in North America in a large number of grassland conservation projects, not only as a replacement for but also in combination with other management tools, e.g. mowing (MacDougall & Turkington 2007, Valkó et al. 2014). Twidwell et al. (2013, 2016) gave new insight into the use of fire in restoring grassland from encroached sites. Case studies testing the North American techniques in European grasslands concluded that prescribed burning could be used to maintain an open landscape (Goldammer & Bruce 2004). However, in some studies, fire was found to be inadequate to preserve grassland composition and diversity. In these studies, grassland species richness was reported to decline in yearly burned plots, most probably as a result of increased abundance of some highly competitive species, e.g. *Brachypodium pinnatum* (Moog et al. 2002; Wahlman & Milberg 2002; Köhler et al. 2005).

The use of prescribed burning as a regular tool for grassland conservation and management in Europe attracts more and more interest (Goldammer 2009; Valkó et al. in press). However, to introduce it e.g. in the restoration of encroached grassland, carefully designed case studies are needed to understand the interaction between woody species and burning. This is especially important in management plans targeting control of alien species. For example, Hutchinson et al. (2004) found that fire may even increase the spread of *Ailanthus altissima*, one of the most noxious alien tree species of Europe. Moreover, it is important to determine the response of grassland species to burning in order to conserve the target communities of nature conservation (Driscoll et al. 2010).

Resprouting, i.e. the production of secondary shoots, is a plant response to disturbance damaging the aboveground biomass (Del Tredici 2001). Resprouting ensures the long-term persistence of plant individuals. Resprouting species can vary much in the percentage of individuals that resprout and in the number of resprouts they produce after a disturbance. Some species are unable to resprout at all, e.g. *Juniperus communis* or *J. phoenicea* (Quevedo et al. 2007), while others possess a high resprouting ability. The ability of woody species to resprout depends on the natural regime of their biome (e.g. fire, wind throw, localized gap disturbances), thus it shows regional patterns (Vesk & Westoby 2004). Therefore, great differences might exist between native and introduced species regarding their resprouting behaviour after certain disturbances (e.g. Busby et al. 2010). In addition, several widespread invasive species are proposed to be successful as a result of their vigorous resprouting ability (e.g. *Robinia pseudacacia*, Cierjacks et al. 2013; *Ailanthus altissima*, Call et al. 2003). Thus, we expect successful alien woody species encroaching temperate grasslands to have a higher resprouting ability compared to most common natives.

Intraspecific differences in resprouting occur as well. Shibata et al. (2014) found increasing resprouting with age in temperate shrub species from Japan, while in sub-canopy and canopy trees resprouting ability was lost after attaining a certain age.

There is limited information about the resprouting ability of common woody species from temperate Europe after disturbances, such as cutting and burning, causing the complete loss of the aboveground biomass. In many shrubs and trees from fire-prone ecosystems resprouting ability is a major way of regeneration, which ensures the survival and thus the persistence of individuals between fire events. We do not know to what extent non-fire-adapted woody species from temperate regions of Europe are able to resprout after fire, and whether resprouting ability differs from that after cutting. Burning may damage at least part of the bud bank, while nutrient inputs into the soil from burned biomass could advance growth (Blodgett et al. 2000).

The aim of this study is to improve the knowledge about the resprouting ability after cutting and burning (treatments causing complete aboveground biomass loss) of shrub and tree species encroaching temperate grasslands in many parts of Europe. A better understanding of the resprouting process in temperate shrubs can lead to the implementation of more suitable management strategies to eradicate woody species from abandoned grassland and to restore semi-natural grasslands of high nature conservation value. To achieve this, we investigated the resprouting ability of four common shrub species encroaching grasslands after a cutting or burning treatment in a field study. In order to complement our field observations with a more rigorous test regarding differences between the two treatments and to involve alien woody species invading or potentially invading abandoned grasslands, we conducted a common garden experiment on one-year-old individuals of three native and three alien shrub or tree species, and compared their resprouting after experimental cutting and burning. Our research questions were: (i) Are there interspecific differences in the resprouting after cutting and burning among woody species encroaching temperate grasslands? (ii) Are alien woody species more successful than natives in their resprouting after cutting and burning? (iii) Is resprouting influenced by basal stem diameter as a proxy for age? (iv) Does resprouting differ between cutting and burning treatments?

Methods

Field study

We haphazardly selected grassland sites in the vicinity of Cluj-Napoca in Transylvania, Romania, where shrubs had been eradicated by farmers in 2012 by two methods, i.e. cutting or burning. The sites were abandoned dry grassland, except Inucu and the cut site in Puini, which were extensively grazed by sheep after the treatment. The dominant graminoid species of the study sites were: *Agrostis capillaris*, *Brachypodium pinnatum*, *Carex humilis*, *Elymus hispidus*, *Festuca rupicola* and *Stipa pulcherrima*. The sites selected for our study were representative for the region and comprehended around 300 m variation in altitude. Unfortunately, the sites were slightly unbalanced with respect to cutting and burning, since we included three burned and two cut sites (Appendix S1). In one of the burned sites, Inucu, burning was not intentional but caused by malpractice. In most of the cases we could not find out the exact date of the treatments, not even the season. Both shrub removal treatments caused the total destruction of the aboveground biomass, but lead to the resprouting of treated individuals from the collar, which is defined as the place where root and shoot tissues come together (Sutton & Tinus 1983; Del Tredici 2001).

We investigated the resprouting ability of the four most common shrub species encroaching temperate Europe's extensively used or abandoned dry grasslands, i.e. *Crataegus monogyna*, *Prunus spinosa, Rosa canina* and *Cornus sanguinea*, three growing seasons after cutting or burning. Several species within the genus *Crataegus* occur in the study region, and for small plants the identity cannot be easily determined. However, *C. monogyna* is by far the most common species, and thus this name is used throughout this study. In all studied species resprouting is the most important way of post-disturbance regeneration. While the first three species were sampled in each of the sites, the last one was sampled in one cut and one burned site only (Appendix S1). We encountered only a very small number of dead individuals in burned sites, while finding dead stumps in cut sites was almost impossible due to vegetation and litter cover. Thus, we considered only successfully resprouted woody individuals in our field study. During July-August 2014, we selected 32–67 individuals per species in each site, covering the whole size range, for our measurements. The selection process started with collecting data from randomly selected individuals, followed by adding specific individuals with stump diameters fitting the gaps in the prevailing stump diameter range. Consequently, this procedure aimed at obtaining accurate allometric relationships between stump diameter and resprouting ability, rather than at estimating the mean stump diameter of each population.

During data collection, we measured the basal diameters of the single or several stumps remaining after cutting or burning. Basal diameters were measured 3–5 cm above the ground in two perpendicular directions with a calliper (0.01 mm accuracy), using the average of the widest stump as a proxy for the age of an individual (Quevedo et al. 2007; Grady & Hoffman 2012; Matula et al. 2012). In order to quantify the resprouting ability, the total number of resprouts was counted per individual. We considered resprouts from the stem base only, since root resprouts were not possible to identify.

Experimental study

In a common garden experiment at the University Botanical Garden at Cluj-Napoca we exposed six shrub or tree species to removal management similar to the field situation, i.e. three native (*C. sanguinea*, *C. monogyna* and *P. spinosa*) and three alien species (*Ailanthus altissima*, *Elaeagnus angustifolia* and *Hippophae rhamnoides*). Seeds of the study species were collected from one to three sites each in the surroundings of Cluj-Napoca, Romania (except *A. altissima* and *E. angustifolia*, which were collected in Dobrogea region, Romania) in 2012. Seeds were germinated in the common garden in 2013. The seedlings were grown individually in 3-L pots until they were one year old, when they were submitted to three experimental treatments in March 2014 (in accordance with the most common period of shrub clearance in the study region): aboveground parts cut, burned or left intact as a control. For the burning treatment, pots were arranged randomly one besides the other, and covered with dry litter (365 g m^{-2}), which was then burned. Litter was collected from dry grasslands near Cluj-Napoca. Litter amount was determined based on field measurements in grassland sites of Transylvania, Romania in early spring. This amount corresponds to a medium litter quantity found in different grassland types worldwide (Loydi et al. 2013). Each species had 45 individuals, 15 per treatment type. Before the treatments, the height of each individual was measured (precision 0.5 cm). Initial height (mean ± SD) of the study species was 44.5 ± 6.0 cm in *C. sanguinea*, 13.0 ± 6.0 cm in *C. monogyna*, 29.0 ± 9.5 cm in *P. spinosa*, 11.5 ± 2.5 cm in *A. altissima*, 62.5 ± 10.5 cm in *E. angustifolia* and 26.0 ± 7.5 cm in *H. rhamnoides*. After the treatments, the saplings were arranged in five randomized blocks (each block containing three individuals of each species and treatment combination) in the common garden, and allowed to regrow until September 2014. Pots were regularly watered according to the multiannual mean monthly precipitation of the studied region (27.8–90.5 mm m^{-2}, Cluj-Napoca Meteorological Station). Monthly water quantities were divided, and watering was done once per week during March and April and twice per week between May and September. From the 270 saplings, only three (one control *H. rhamnoides*, one cut and one burned *E. angustifolia*) died until the end of the experiment. Before harvesting, we counted the number of resprouts. At harvesting, the roots were washed free of soil, and roots and shoots were separated and oven-dried at 60 °C for 48 hours before weighing. Above- and belowground biomass produced by individuals until the end of the experiment were used in subsequent analyses.

Data analyses

In order to compare the resprouting ability of shrubs between species and treatments in the field study, the effect of species (n = 4, fixed), treatment (n = 2, fixed), stump diameter as a proxy for age (covariate), and site (n = 5, random) on the total number of resprouts produced by an individual was investigated with a general linear mixed effect model (LMM). Biologically relevant interactions such as species × treatment and species × stump diameter were also included in the model. We used the *r.squaredGLMM* function in 'MuMIn' package in R to calculate marginal R^2, which is concerned with variance explained by fixed factors, as a measure of effect size (Nakagawa & Schielzeth 2013). As allometric relationship may exist between stump diameter and the number of resprouts, both variables were log-transformed before the analysis. In the case of a significant main factor or interaction, pairwise comparisons were performed with Tukey's post-hoc test (*multcomp* package, *glht* function in R).

To analyze the data of the experimental study, we built a GLMM with Poisson error distribution in order to determine which factors influenced the resprouting potential of one-year-old treated (cut or burned) shrubs and trees. Note that untreated individuals (control) had no resprouts, thus they were excluded from this analysis. Species (n = 6) was introduced as fixed factor nested within the native or alien group (n = 2), treatment (n = 2) as fixed factor and block (n = 5) as random term. Initial plant height (measured before the treatment) was introduced as covariate. Species × treatment and status of species × treatment interactions were also included in the model. Further, two GLMMs with Gaussian error distribution were built to analyze the effects of species (nested within the native or alien group), native or alien status (n = 2), treatment (n = 3, control, cut and burned) as fixed factors, and block as random term, on the aboveground and belowground biomass of the shrubs and trees at the end of the experimental study. In the case of a significant main factor or interaction, pairwise comparisons were performed with Tukey's post-hoc test. All analyses were performed using the R statistical environment (version 3.1.2, R Core Team 2014, Vienna, Austria).

Results

Differences in the resprouting of woody species after cutting and burning

We found significant differences in the total number of resprouts produced after cutting and burning among the four shrub species in the field study (χ^2 = 50.80, p < 0.001, R^2m = 0.07, Fig. 1) and among the six shrub and tree species in the experimental study as well (χ^2 = 69.75, p < 0.001, R^2m = 0.29, Fig. 2). From the four native shrub species analyzed in the field study, *C. monogyna* produced the highest number of resprouts per individual and *P. spinosa* the lowest (Fig. 1). Among the experimentally grown one-year-old plants, the alien shrub *H. rhamnoides* had the highest, the native shrubs (*C. sanguinea, C. monogyna* and *P. spinosa*) an intermediate, and the two alien trees (*A. altissima* and *E. angustifolia*) the weakest resprouting ability (Fig. 2). Overall, resprouting of the alien species was not different from that of the natives ($\chi^2 = 1.65$, $p = 0.198$, $R^2m = 0.001$).

Effect of stump diameter on the resprouting of shrubs in the field study

Stump diameter, a proxy for age, significantly influenced resprouting ability ($\chi^2 = 228.19$, $p < 0.001$, $R^2m = 0.22$), with younger individuals producing a smaller number, and older individuals a larger number of resprouts (Fig. 3). The age-specific resprouting ability was different among species (interaction between species and log(stump diameter), $\chi^2 = 32.67$, $p < 0.001$), and the greatest in *C. monogyna* (Fig. 3).

Effect of treatment type on the resprouting of woody species

Whether the aboveground biomass of shrubs and trees has been cut or burned, had no significant effect on the number of resprouts they produced neither in the field ($\chi^2 = 0.03$, $p = 0.847$, $R^2m = 0.01$) nor in the experimental study ($\chi^2 = 0.32$, $p = 0.570$, $R^2m = 0.001$). We found a significant interaction between species and treatment in the field data ($\chi^2 = 14.49$, $p = 0.002$), but not in the experimental study ($\chi^2 = 0.16$, $p = 0.990$). In the case of the field study, Tukey's post-hoc test did not result in any intraspecific differences between treatments (difference between resprouting after cutting and burning for *C. sanguinea* $z = 1.755$, $p = 0.530$; *C. monogyna* $z = -0.749$, $p = 0.980$; *P. spinosa* $z = 0.494$, $p = 0.990$; *R. canina* $z = 0.117$, $p = 0.990$).

Treatment significantly influenced the aboveground ($\chi^2 = 113.63$, $p < 0.001$, $R^2m = 0.10$) and belowground biomass ($\chi^2 = 10.19$, $p = 0.006$, $R^2m = 0.3$) of individuals in the experimental study. Burned one-year-old shrub and tree species had 28% less aboveground ($z = -3.479$, $p = 0.001$) and 6% less belowground biomass ($z = -2.388$, $p = 0.045$), while cut individuals had 28% less aboveground ($z = -3.788$, $p < 0.001$) and 9% less belowground biomass ($z = -3.194$, $p = 0.004$) compared to control individuals. Alien species did not react differently to the treatments compared to native species ($\chi^2 = 1.65$, $p = 0.198$; $R^2m = 0.01$).

Discussion

Interspecific differences in resprouting

Based on our field investigations, *C. monogyna* produced the largest number of resprouts. It is very probable that *C. monogyna* stores a large amount of energy reserves in its roots, which ensures a high resprouting after the loss of its aboveground biomass, as it was revealed for successful resprouters in general (Bond & Midgley 2001; Clarke et al. 2010). Mobilization of root reserves after the treatments may explain the lower belowground biomass observed in treated individuals at the end of the garden experiment.

On average, alien or native status did not influence the resprouting ability of woody species in our experiment. Even so, young individuals of *H. rhamnoides*, a shrub species alien to the region, had a higher potential of resprouting after cutting and burning compared with native shrubs. Grasslands invaded by this species will probably need additional efforts in eradication projects. On the contrary, young individuals of the other two alien woody species, *E. angustifolia* and *A. altissima*, were found to have a relatively low resprouting ability as a result of cutting or burning of their aboveground parts.

Intraspecific differences in resprouting ability

We found a significant effect of the stump diameter, a proxy for age, on the number of resprouts produced by the shrub species in the field study. This observed positive relation between age and resprouting ability is in agreement with the results of Quevedo et al. (2007) on *C. sanguinea*, *C. monogyna* and *P. spinosa*. The same relation was found in other ecosystems, e.g. Central-European coppices (Matula et al. 2012) and in some temperate shrub species in Japan (Shibata et al. 2014). The age dependent resprouting ability, i.e. the rate of increase in the number of resprouts with stump diameter, differed among species and was greatest in *C. monogyna*.

Differences in resprouting ability of individuals belonging to the same species may be caused by varying availability of nutrients, carbohydrates and water to the active meristems (Hogkinson 1998). A superior root development and mobilization of resources for resprouting at older life stages may cause a positive relation between resprouting ability and age. In the same way, such a relation may be explained by the greater amount of viable bud meristems in older individuals (Sennerbyforsse & Zsuffa 1995). On the other hand, the bark thickness of individuals can increase with age, resulting in a higher resistance against protruding resprouts in older life stages (Matula et al. 2012). That is why, in some species, resprouting ability has been found to increase with pre-fire size (e.g. Matula et al. 2012), while in others resprouting has been observed in juveniles but it decreased with age (e.g. Dey & Jensen 2002; Sands & Abrams 2009; Shibata et al. 2014).

Treatment effect on the resprouting of woody species

Two different treatments (i.e. cutting or burning), causing the complete loss of the aboveground biomass of woody species, induced similar resprouting rates, both in the field and experimental study. This similarity indicates that none of the applied treatments damaged the collar meristems, which are vital for resprouting, although the treatments were severe enough to induce the resprouting process (see also Petersen & Drewa 2014). Despite the nutrient input to the soil from the burned aboveground biomass (Blodgett et al. 2000), the resprouting of woody species after burning was not higher compared to cutting. In several other studies, burning and cutting did not result in a different resprouting of individuals either (Pyke et al. 2010; Petersen & Drewa 2014), but our study is the first to demonstrate this for temperate European woody species.

Implications for restoration of grasslands encroached by shrubs

Given the interspecific differences in resprouting, i.e. the production of secondary shoots from the collar to recover after the complete loss of aboveground biomass, observed among the study species, the species composition of shrubs in grasslands is an important factor to take into account when considering a management plan. Temperate grasslands encroached by *C. monogyna* or *H. rhamnoides* will be more labour-intensive to restore and maintain free of shrubs due to the larger number of resprouts, which develop immediately after the shrub removal treatment. Also, the longer shrubs thrive in grasslands and advance in age, the stronger the resprouting reaction will be when a treatment is introduced and the more intense or frequent the treatment has to be (irrespective of treatment type). As a consequence, the introduction of a treatment regime in encroached grasslands should be implemented as soon as possible following shrub establishment, because younger shrubs have a lower resprouting ability than older ones.

Burning and cutting may be equally effective in controlling shrub encroachment, but restoration measures should be carefully designed. In our study, the severity of the applied treatments at the field sites was too low to damage the resprouting buds, since treated shrubs had a high resprouting ability. When burning is applied, which is a much cheaper solution, higher fire intensities may be needed to damage the collar meristems and to preclude resprouting (Cruz et al. 2003, Twidwell et al. 2016). This could be accomplished by increasing the fuel load in grasslands, i.e. by waiting for more biomass to accumulate. While applying a high intensity fire may be appropriate to restore grasslands from shrub encroachment in degraded or economically valuable areas, it cannot be proposed for grasslands of particularly high conservation value. In this case it is important to consider the long-term effects of the proposed biomass removal regimes on the floristic composition of grasslands (e.g. Ruprecht et al. 2016). One alternative solution for the efficient control of woody encroachment in grassland could be a properly timed intensive cutting, damaging collar meristems of woody species, followed by introducing grazing right after the cutting intervention (e.g. Barbaro et al. 2001, Dostálek and Frantík 2008). However, further studies are needed whether these solutions are viable within the economic and social context of the region.

Acknowledgements

We are grateful to the farmers who burned or cut the shrubs in their grassland and by this means made our field study possible. We are very grateful to H. Téglás, Z. Nyika and P. Domokos for their assistance with preparing and accomplishing the experimental study. We thank the "Alexandru Borza" Botanical Garden from Cluj-Napoca for ensuring the necessary infrastructure during the experiment. We thank O. Valkó and one anonymous reviewer for constructive comments and J. Dengler for his editorial attention and suggestions. This work was supported by the Romanian Ministry of Education and Research (CNCS-UEFISCDI, project PN-II-RU-TE-2014-4-0381, Nr. 228/01.10.2015). During writing the manuscript, ER was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences.

References

Angileri, V., Loudjani, P. & Serafini, F. 2011. GAEC implementation in the European Union situation: and perspectives. *Italian Journal of Agronomy* 6: e2.

Barbaro, L., Dutoit, T. & Cozic, P. 2001. A six-year experimental restoration of biodiversity by shrub-clearing and grazing in calcareous grasslands of the French Prealps. *Biodiversity and Conservation* 10: 119-135.

Blodgett, H., Hart, G. & Stanislaw, M. 2000. Annual burning decreases seed density in the upper soil layers of the seed bank. *Tillers* 2: 31-38.

Bond, W.J. & Midgley, J.J. 2001. Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology and Evolution* 16: 45-51.

Boulant, N., Kunstler, G., Rambal, S. & Lepart, J. 2008. Seed supply, drought, and grazing determine spatio-temporal patterns of recruitment for native and introduced invasive pines in grasslands. *Diversity and Distributions* 14: 862-874.

Busby, P.E., Vitousek, P. & Dirzo, R. 2010. Prevalence of tree regeneration by sprouting and seeding along a rainfall gradient in Hawai'i. *Biotropica* 42: 80-86.

Call, L.J. & Nilsen, E.T. 2003. Analysis of spatial patterns and spatial association between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). *American Midland Naturalist* 150: 1-14.

Castellnou, M., Kraus, D. & Miralles, M. 2010. Prescribed burning and suppression fire techniques: from fuel to landscape management. In: Montiel, C. & Kraus, D. (eds.) *Best practices of fire use – prescribed burning and suppression fire programmes in selected case-study regions in Europe*, pp. 3–16. European Forest Institute [Research Report No. 24], Porvoo, FI.

Cierjacks, A., Kowarik, I., Joshi, J., Hempel, S., Ristow, M., Lippe, M. & Weber, E. 2013. Biological flora of the British Isles: *Robinia pseudoacacia*. *Journal of Ecology* 101: 1623-1640.

Clarke, P.J., Lawes, M.J. & Midgley, J.J. 2010. Resprouting as a key functional trait in woody plants – challenges to developing new organizing principles. *New Phytologist* 188: 651-654.

Cruz, A., Perez, B. & Moreno, J.M. 2003. Resprouting of the Mediterranean-type shrub *Erica australis* with modified lignotuber carbohydrate content. *Journal of Ecology* 91: 348-356.

Deák, B., Valkó, O., Török, P., Végvari, Z., Hartel, T., Schmotzer, A., Kapocsi, I. & Tótmérész, B. 2014. Grassland fires in Hungary – Experiences of nature conservationists on the effects of fire on biodiversity. *Applied Ecology and Environmental Research* 12: 267-283.

Del Tredici, P. 2001. Sprouting in temperate trees: A morphological and ecological review. *The Botanical Review* 67: 121-140.

Dey, D.C. & Jensen, R.G. 2002. Stump sprouting potential of oaks in Missouri Ozark forests managed by even- and uneven-aged silviculture. In: Shifley, S.R. & Kabrick, J.M. (eds.) *Proceedings of the second Missouri Ozark Forest Ecosystem Project Symposium: Post-treatment results of the landscape experiment*, pp. 102-113. North Central Research Station, Forest Service – U.S. Department of Agriculture, St. Paul, US.

Dostálek, J. & Frantík, T. 2008. Dry grassland plant diversity conservation using low-intensity sheep and goat grazing management: case study in Prague (Czech Republic). *Biodiversity and Conservation* 17: 1439-1454.

Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., (…) & York, A. 2010. Fire management for biodiversity conservation: Key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.

Goldammer, J.G. 2009. White paper on use of prescribed fire in land management, nature conservation and ferestry in temperate-boreal Eurasia. *International Forest Fire News* 38: 133-152.

Goldammer, J.G. & Bruce, M. 2004. The use of prescribed fire in the land management of Western and Baltic Europe: An overview. *International Forest Fire News* 30: 2-13.

Grady, J.M. & Hoffman, W.A. 2012. Caught in a fire trap: Recurring fire creates stable size equilibria in woody resprouters. *Ecology* 93: 2052-2060.

Heisler, J.L., Briggs, J.M., Knapp, A.K., Blair, J.M. & Seery, A. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. *Ecology* 85: 2254-2257.

Hogkinson, K.C. 1998. Sprouting success of shrubs after fire: Height-dependent relationships for different strategies. *Oecologia* 115: 64-72.

Hutchinson, T., Rebbeck, J. & Long, R. 2004. Abundant establishment of *Ailanthus altissima* (tree-of-heaven) after restoration treatments in an upland oak forest. In: Yaussy, D.A., Hix, D.M., Long, R.P. & Goebel, P.C. (eds.) *Proceedings 14th Central Hardwood Forest Conference, 2004 March 16-19, Wooster, Ohio. General Technical Report NE-316*, pp. 514–514. U.S. Department of Agriculture Forest Service, Northeastern Research Station, Delaware, US.

Köhler, B., Gigon, A., Edwards, P.J., Krüsi, B., Langenauer, R., Lüscher, A. & Ryser, P. 2005. Changes in the species composition and conservation value of limestone grasslands in Northern Switzerland after 22 years of contrasting managements. *Perspectives in Plant Ecology, Evolution and Systematics* 7: 51-67.

Lett, M.S. & Knapp, A.K. 2005. Woody plant encroachment and removal in mesic grassland: Production and composition responses of herbaceous vegetation. *American Midland Naturalist* 153: 217-231.

Loydi, A., Eckstein, R.L., Otte, A. & Donath, T.W. 2013. Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis. *Journal of Ecology* 101: 454-464.

MacDougall, A.S. & Turkington, R. 2007. Does the type of disturbance matter when restoring disturbance dependent grasslands? *Restoration Ecology* 15: 263-272.

Matula, R., Svátek, M., Kúrová, J., Úradnícek, L., Kadavý, J. & Kneifl, M. 2012. The sprouting ability of the main tree species in Central European coppices: implications for coppice restoration. *European Journal of Forest Research* 131: 1501-1511.

Moog, D., Poschlod, P., Kahmen, S. & Schreiber, K.-F. 2002. Comparison of species composition between different grassland management treatments after 25 years. *Applied Vegetation Science* 5: 99-106.

Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effect models. *Methods in Ecology and Evolution* 4: 133-142.

Petersen, S.M. & Drewa, P.B. 2014. Effects of biennial fire and clipping in woody and herbaceous ground layer vegetation: Implications for restoration and management of oak barren ecosystems. *Restoration Ecology* 22: 525-533.

Pykälä, J. 2000. Mitigating human effects on European biodiversity through traditional animal husbandry. *Conservation Biology* 14: 705-712.

Pyke, D.A., Brooks, M.L. & D'Antonio, C.M. 2010. Fire as a restoration tool: A decision framework for predicting the control or enhancement of plants using fire. *Restoration Ecology* 18: 274-284.

Quevedo, L., Rodrigo, A. & Espelta, J.M. 2007. Post-fire resprouting ability of 15 non-dominant shrub and tree species in Mediterranean areas of NE Spain. *Annals of Forest Science* 64: 883-890.

Ruprecht, E., Enyedi, M.Z., Szabó, A. & Fenesi, A. 2016. Biomass removal by clipping and raking vs burning for the restoration of abandoned *Stipa*-dominated European steppe-like grassland. *Applied Vegetation Science* 19: 78-88.

Sands, B.A. & Abrams, M.D. 2009. Effects of stump diameter on sprout number and size for three oak species in a Pennsylvania clearcut. *Northern Journal of Applied Forestry* 26: 122-125.

Sennerbyforsse, L. & Zsuffa, L. 1995. Bud structure and resprouting in coppiced stools of *Salix viminalis* L., *S. eriocephala* Michx, and *S. amygdaloides* Anders. *Trees – Structure and Function* 9: 224-234.

Shibata, R., Shibata, M., Tanaka, H., Iida, S., Masaki, T., Hatta, F., Kurokawa, H. & Nakashizuka, T. 2014. Interspecific variation in the size-dependent resprouting ability of temperate woody species and its adaptive significance. *Journal of Ecology* 102: 209-220.

Sutton, R.F. & Tinus, R.W. 1983. Root and root system terminology. *Forest Science, Monograph* 24 (Supplement to Number 4, 1 December 1983): a0001-z0001(1).

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1968-1993. *Flora Europaea*, vols. 1–5. Cambridge University Press, Cambridge, UK.

Twidwell, D., Fuhlendorf, S.D., Taylor, C.A. & Rogers, W.E. 2013. Refining thresholds in coupled fire–vegetation models to improve management of encroaching woody plants in grasslands. *Journal of Applied Ecology* 50: 603-613.

Twidwell, D., Rogers, W.E., Wonkka, C.L., Taylor, C.A. & Kreuter, U.P. 2016. Extreme prescribed fire during drought reduces survival and density of woody resprouters. *Journal of Applied Ecology* 53: 1585-1596.

Valkó, O., Török, P., Matus, G. & Tóthmérész, B. 2012. Is regular mowing the most appropriate and cost-effective management maintaining diversity and biomass of target forbs in mountain hay meadows? *Flora* 207: 303-309.

Valkó, O., Török, P., Deák, B. & Tóthmérész, B. 2014. Review: Prospects and limitations of prescribed burning as a management tool in European grasslands. *Basic and Applied Ecology* 15: 26-33.

Valkó, O., Deák, B., Magura, T., Török, P., Kelemen, A., Tóth, K., Horváth, R., Nagy, D.D., Debnár, Z., Zsigrai, G., Kapocsi, I. & Tóthmérész, B. in press. Supporting biodiversity by prescribed burning in grasslands – a multi-taxa approach. *Science of the Total Environment*. DOI: 10.1016/j.scitotenv.2016.01.184.

Vesk, P.A. & Westoby, M. 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* 92: 310-320.

Wahlman, H. & Milberg, P. 2002. Management of semi-natural grassland vegetation: evaluation of a long-term experiment in southern Sweden. *Annales Botanici Fennici* 39: 159-166.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Location and altitude of grassland sites, treatment type and woody species sampled in the field study.

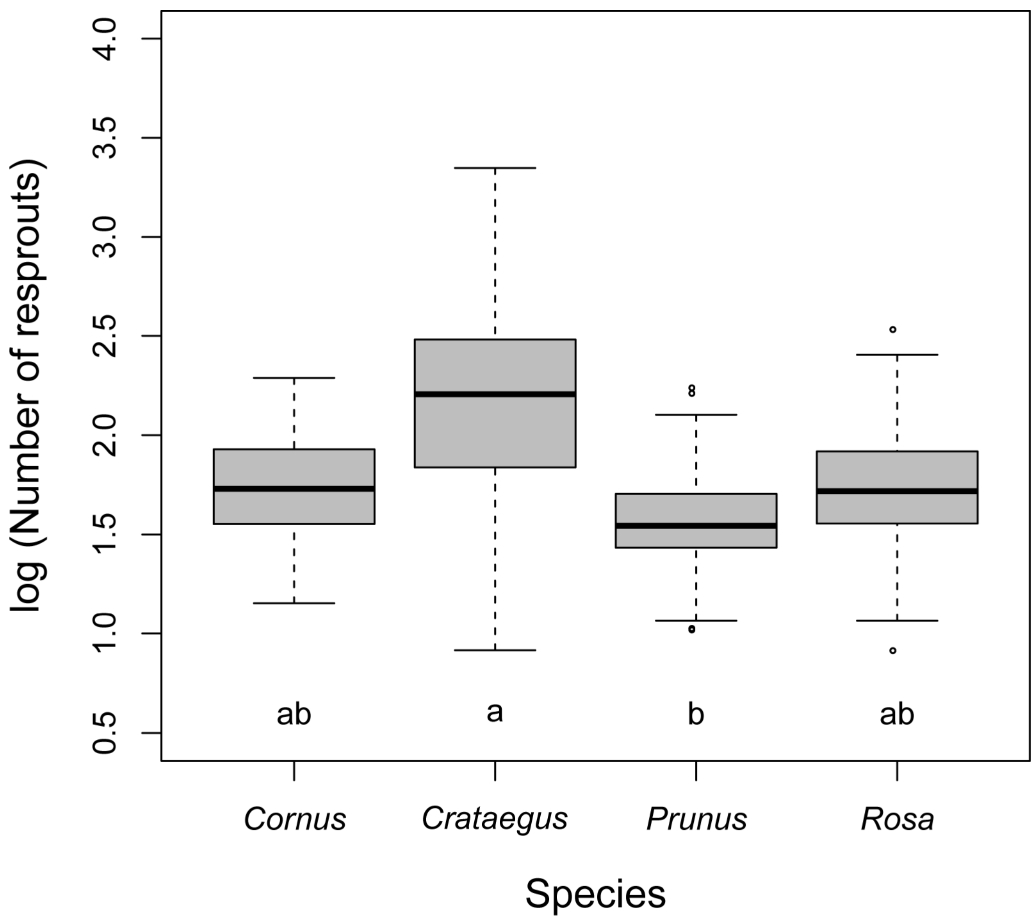

Fig. 1. Differences in the total number of resprouts produced during three growing seasons following treatments (cutting or burning) between shrub species (*Cornus sanguinea*, *Crataegus monogyna*, *Prunus spinosa* and *Rosa canina*) in the field study. The values represent fitted values, i.e. the standardized values after removing the effects of all other considered variables, from LMM where species, treatment and stump diameter were used as explanatory variables (see Methods). Letters denote significant differences at $p < 0.05$, based on Tukey's post-hoc test. Medians, interquartile ranges (IQRs, box) and 1.5 × IQRs (whiskers) are shown; dots are outliers.

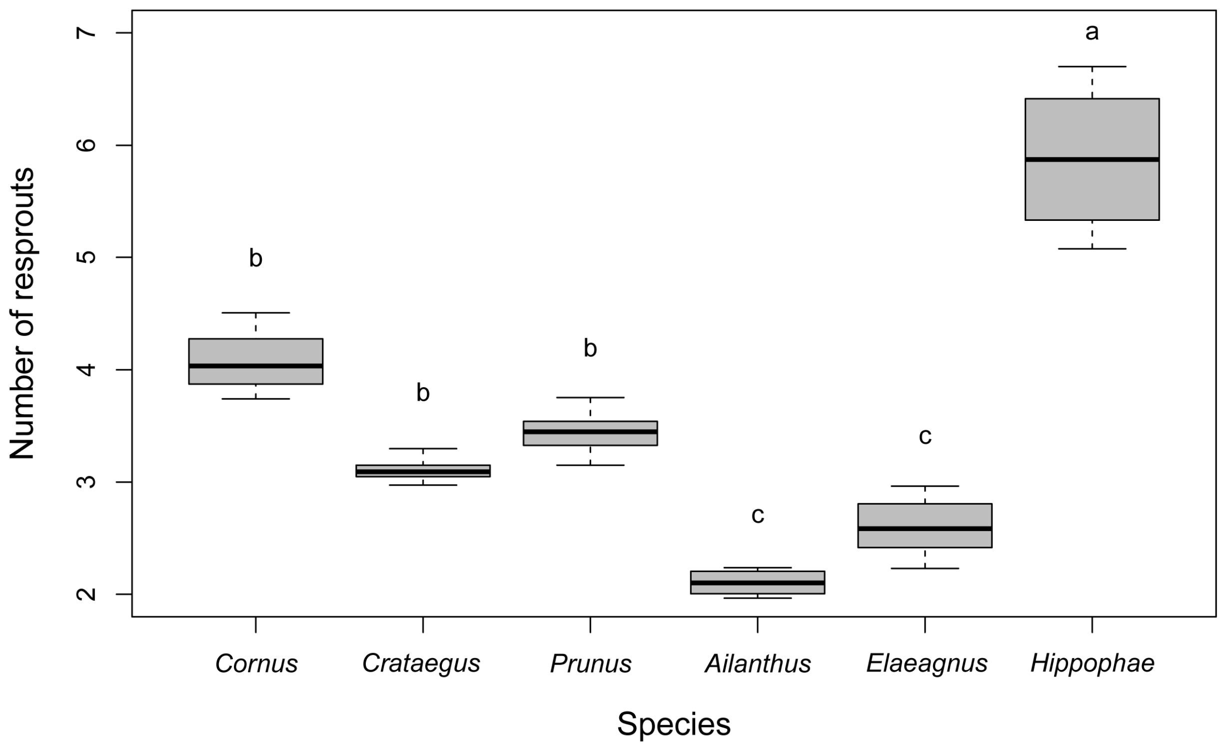

Fig. 2. Differences in the number of resprouts produced during one growing season following treatments (cutting or burning) between one-year-old native (*Cornus sanguinea*, *Crataegus monogyna* and *Prunus spinosa*) and alien shrub and tree species (*Ailanthus altissima*, *Elaeagnus angustifolia* and *Hippophae rhamnoides*) in the experimental study. The values represent fitted values, i.e. the standardized values after removing the effects of all other considered variables, from GLMM where species, status and treatment were used as explanatory variables (see Methods). Letters denote significant differences at $p < 0.05$, based on Tukey’s post-hoc test. Medians, interquartile ranges (IQRs, box) and 1.5 × IQRs (whiskers) are shown.

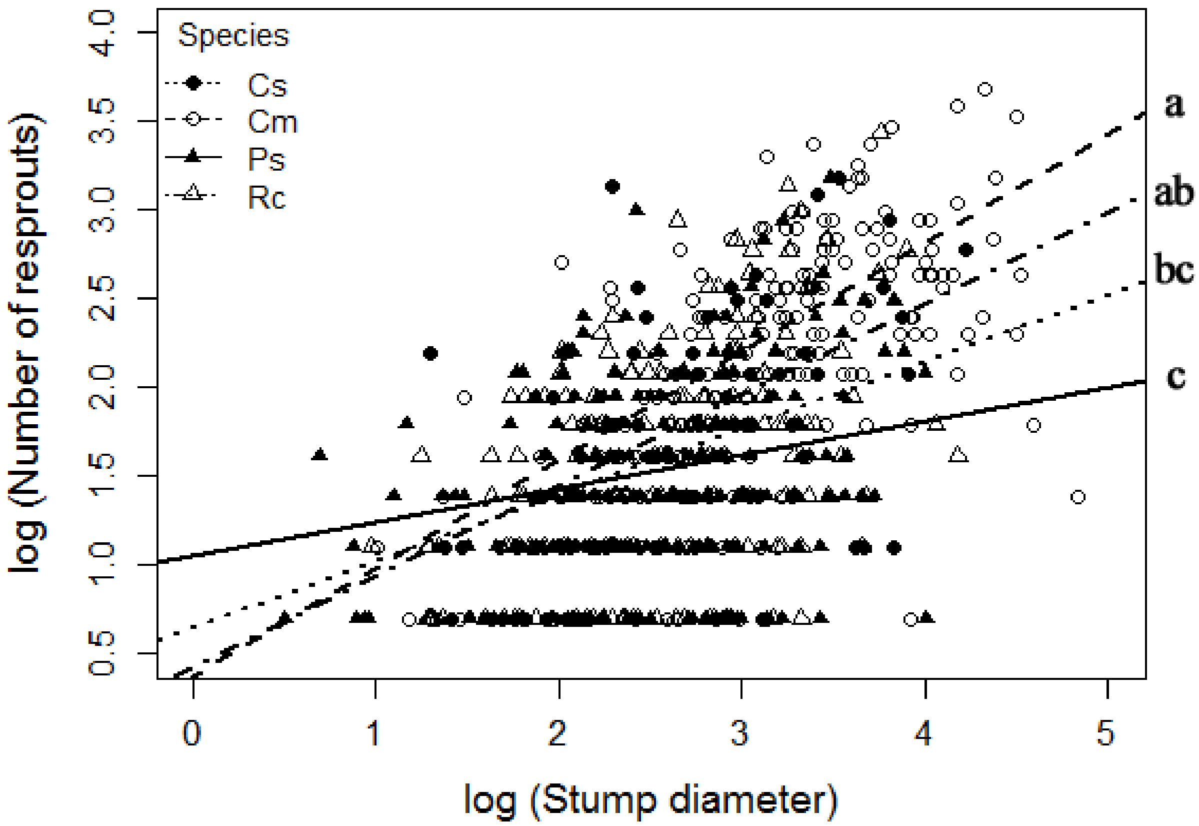

Fig. 3. Number of resprouts per individual produced by the four shrub species during three growing seasons following treatments (cutting or burning) in the field study as a function of stump diameter, as a proxy for age. Cs = *Cornus sanguinea*, Cm = *Crataegus monogyna*, Ps = *Prunus spinosa*, Rc = *Rosa canina*. Letters denote significant differences at $p < 0.05$, based on Tukey's post-hoc test.