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# Does disturbance enhance the competitive effect of the invasive *Solidago canadensis* on the performance of two native grasses?

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**Abstract** The impact of invasive species on native plant communities can strongly depend on habitat disturbances. Thus, the joint study of invasion and disturbances are necessary to distinguish whether invasive species (1) are just 'passengers' of major environmental changes, (2) are the real cause (drivers) of native species decline, or (3) do disturbances and invasive species additively suppress native species (back-seat drivers). Therefore, we experimentally explored both the single and additive effect of competition by an invasive species and fire as disturbance on the performance of native species. We examined the responses of two native rhizomatous perennial grass species (*Elymus repens* and *Brachypodium pinnatum*) to competition with European invasive and American native *Solidago canadensis*. This was done under burned and unburned conditions, a novel disturbance type in this system. We found that competition with *S. canadensis* had a very strong negative effect on the performance of *B. pinnatum* irrespective of disturbance. In contrast, disturbance and competition had a cumulative negative influence on the performance of *E. repens*, with competition having greater effect than burning. Fire reduced the number of shoots of European *S. canadensis* individuals, but did not affect the frequently burned American populations. However, these differences did not translate into increased competitive ability of European populations compared with American ones. Thus, the competitive superiority of *S. canadensis* irrespective of continent of origin explained the performance loss in *B. pinnatum* ('driver' model); whereas reduced performance after burning of grass species and competitive superiority of the invasive species jointly decreased the performance of *E. repens* ('back-seat driver' model).

**Keywords** Competition · Fire · Burning · Pre-adaptation · Root-competition

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## Introduction

Changes in biodiversity are often caused by multiple, interacting drivers such as land-use change, invasion

of non-native species, climate change, nitrogen deposition, pollution and overexploitation (Sala et al. 2000; Thomas et al. 2006). Despite numerous studies focusing on the changes induced by these drivers, it is becoming clear that we lack understanding of how the interactive effects of these drivers affect ecosystems (Didham et al. 2007).

As invasive species may competitively displace native species within invaded communities (Callaway and Aschehoug 2000), strong correlations are often shown between the abundance of invasive species and loss of biodiversity of the local flora. However, the impact of invasive species can be strongly dependent on the effect of other drivers acting in concert, especially by habitat disturbance (Lonsdale 1999; Didham et al. 2005). Among the myriad of studies dealing with invasive species and habitat disturbance, only a minor fraction address both drivers simultaneously, and even less explicitly investigate the interaction between them (Didham et al. 2007). The parallel and not synergistic study of these drivers makes it impossible to distinguish between causal mechanisms of population decline: whether invasive species take advantage of habitat disturbance and are thus just passengers of the more fundamental environmental changes, or are essential drivers of change themselves (MacDougall and Turkington 2005). The 'driver' model assumes strong biotic interactions between the native and invasive species due to the invasive species' competitive superiority, irrespective of disturbance, with competitive exclusion as the main cause of native species decline. In contrast, according to the 'passenger' model, the invasive species has the ability to capitalize on disturbance, thus weak biotic interaction exists between invasive and native species without the presence of disturbance (Didham et al. 2005). However, the interactions of drivers are much more complex, and these models should be considered as extremes of a continuum, which incorporates the combined effect of the factors acting in concert (Didham et al. 2005; Chabrerie et al. 2007; White et al. 2013). Therefore, the 'passenger'/'driver' model has been expanded to include an intermediate 'backseat driver' model, where habitat disturbances and invasion act synergistically (Bauer 2012). In this model, invasive species take effect when disturbances have suppressed native species, but also become the cause of further change (Bauer 2012).

Plant invasions frequently occur in areas where the disturbance regime is altered, especially when disturbance frequencies are increased or new forms of disturbance are introduced, leading to an increase in the abundance of non-native species (Catford et al. 2012). In this scenario, the new disturbance conditions would be less suitable for native species that had evolved under historical disturbance conditions and may be poorly adapted to the new disturbance regime (Shea et al. 2004). In contrast, if an invasive species has the adaptations necessary for success in the newly altered environment or is at least more tolerant to such conditions than natives, it may have a competitive advantage over natives (Facon et al. 2006). Hence, the match between invaded habitat with altered disturbance and adventive species pre-adapted to that disturbance type may result in a successful plant invasion.

Here, we explore the ecological implications of additive effects between competition by an invasive species and fire as novel disturbance on two native species under controlled experimental conditions. The invasive species was chosen to be pre-adapted, while native species were evolutionarily naïve to disturbance by fire. We chose Central-Eastern European temperate grasslands as a model system. Fire was not an integral part of the disturbance regime of the plant communities of this region in the last several centuries (Feurdean et al. 2013). However, recently, burning is increasingly being used as an alternative land-use to mowing and grazing, to keep grasslands from being encroached by shrubs and trees and to remove accumulated dry biomass (Valkó et al. 2014). A probable outcome of frequent fires can be a depauperate native flora, since native species are not adapted to fire (Ruprecht et al. 2013), and colonization of grasslands by non-native species pre-adapted to fire (Gómez-González et al. 2011).

We have chosen *Solidago canadensis* L. (Canada goldenrod) an exceptionally successful worldwide invader as the focal invasive species, as it is increasingly abundant in our study system (Fenesi et al. 2009), however, the actual cause underlying its invasive success remains unknown. For example, it was often cited as superior competitor over native species due to its prolific vegetative growth (Weber 2001), suggesting that *S. canadensis* is invading via the driver model. However, it colonizes disturbed

areas such as abandoned fields and successional habitats (Dong et al. 2006), thus the passenger model may also explain its invasiveness. We used three European invasive populations of *S. canadensis* to test our hypotheses, as well as three native populations from frequently burned sites of North America to serve as a control. This was important because European *S. canadensis* populations may not have encountered fire since their introduction to Europe, and may have lost tolerance in favour of adaptations to local conditions. As competitive targets, we have chosen two common native grass species, a disturbance tolerant competitor (*Elymus repens*) and a stress-tolerant grassland-specialist (*Brachypodium pinnatum*) to measure the combined effect of biotic interactions with an invasive forb and fire as disturbance. We have chosen two native grass species, because they are functionally distinct from the invasive forb, thus we can expect (1) a less intense competition between them, as much stronger biotic interactions are expected among species from the same functional guilds (Fargione et al. 2004), and (2) different responses to disturbance, as functionally similar species have high probability to react similarly to the same disturbance (MacDougall and Turkington 2005).

We compared the performance of native species grown alone and with *S. canadensis* under burned and unburned conditions. First, we quantified the effect of both chosen causal factors (fire disturbance and invasive competition) on species' performance alone; second, we considered the effect of the two factors in an additive manner. We had three alternative hypotheses based on the driver—passenger theory of MacDougall and Turkington (2005) complemented by the 'back-seat driver' model of Bauer (2012). According to the 'invasive species as a driver' scenario, competition by invasive species would have strong effect on native species with and without disturbance (H1); according to the 'passenger' scenario, invasive competition would have week effect on the native species without disturbance (H2); while according to the 'back-seat driver' model, both invasive competition and disturbance would impact the native species in an additive manner (H3). Based on expansion of the invasive species in these non-fire adapted systems, we expected that native species would be strongly affected by fire, but also by the competition with *S. canadensis*, in support of the back-seat driver

hypothesis. We also aimed to find out whether there are differences between the invasive European and native American *S. canadensis* populations regarding their competitive ability and reaction to fire. We expected that European *S. canadensis* populations would manifest stronger effect on native species due to local adaptation, but that native *S. canadensis* populations would better tolerate fire and would benefit more from post-fire conditions.

## Materials and methods

### Study species

*Solidago canadensis* L. (Asteraceae) was introduced to Europe in the seventeenth century from its wide North-American native range, and has become one of the most aggressive invasive species of the continent (Weber 2001). It has a perennial rhizome which produce aerial shoots annually (van Kleunen and Schmid 2003). Its competitive ability as an invasive species has been chiefly attributed to its rapid and prolific vegetative and generative growth. Moreover, exudation of allelopathic compounds that natives have not evolved with (Abhilasha et al. 2008; Yuan et al. 2012), and disruption of links between native host and arbuscular mycorrhizal fungi (Zhang et al. 2010) also contribute to its competitiveness. It is reported to tolerate fire (Gibson et al 1993) or even benefit from regular burning (Towne and Kemp 2003) in its native range.

*Elymus repens* (L.) Gould (couch grass) is a strongly rhizomatous perennial grass with a guerrilla strategy, having prolific vegetative expansion by means of few ramets with longer spacers, creating a large clonal patch (Amiaud et al 2008). *E. repens* is an aggressive weed in arable lands, but also widespread along road-sites and pastures, and according to Grime's ecological strategies is a competitive-ruderal species (C/CR strategist) (Grime 2001). *Brachypodium pinnatum* (L.) Beauv. (tor-grass) is also a perennial, rhizomatous grass, but with a moderate relative growth rate, and vegetative propagation with phalanx strategy (De Kroon and Schieving 1990), thus producing short internodes which result in a tightly-packed advancing front; and was classified as a stress tolerant competitor (SC) according to Grime (2001). It is a common species of nutrient-poor semi-dry

grasslands of primary and secondary origin (Illyés et al. 2007).

Seeds and preparatory work

Seeds of *S. canadensis* were collected from three native (Illinois, USA) and three invasive populations (Cluj and Sibiu county, Romania, Table 1) in September-October 2012, from at least 30 individuals at each site. After dark and wet stratification at 4 °C for 3 months, seeds of both native and invasive *S. canadensis* populations were separately put on the surface of soil in 30 containers (14×40×12 cm, 5 containers/population) in March 2013. Containers were filled with 2:1 mixture of commercial potting soil and sand. After germination, seedlings were thinned to avoid interspecific competition and grown for three months. Pots were watered twice a week with the same amount of water. The experiment took place in an open air facility in the University Botanical Garden in Cluj-Napoca, Romania.

Competition experiment

In June 2013, 72 *S. canadensis* individuals from each population were individually transplanted to 3-L pots (18 cm diameter) filled with the same mixture of soil and sand described formerly. In one American population (A3) we did not have enough plants, so sample size was reduced to 60 pots. As *S. canadensis* plants were small and fragile (5–10 cm tall) by that time, we decided to let them grow for two month before we plant the native grass species in the pots to equalize their competitive abilities. After two months of growth, in one third of the pots we planted one individual of *B. pinnatum* next to *S. canadensis* individuals, and in one third an individual of *E. repens*, while one third of the pots were left as controls. With this competition setup, we simulated a community where the invasive species was already established, and none of the species had pre-emptive effect over the other. Grass species were also planted without competition in 24 replicates each. We had altogether 468 pots. Before planting, we measured the height of the aerial shoot of each *S. canadensis* plant, as an estimate of initial plant size, to form three homogenous groups within all six populations. The two grass species were collected from a disturbed, xero-mesic grassland, washed free of soil and planted next to *S. canadensis* individuals. Before transplantation, we carefully removed all but three adventitious buds from each grass individual to standardize their competitive vigour.

Pots were regularly watered according to the mean monthly precipitation amount of the studied region (min. 2.18–max. 3.16 dl/week).

Disturbance experiment

On 1 March 2014, half of the pots from all competition and control treatments for each population were arranged randomly one besides the other, and covered with dry litter (365 g m$^{-2}$), which was then burned. The other half of the pots were not treated and served as control. Litter was collected from xero-mesic grasslands near Cluj-Napoca, and contained

**Table 1** Origins of *Solidago canadensis* populations

| Population | Continent, state/country | Location | Fire frequency | Coordinates |
|---|---|---|---|---|
| A1 | North-America, Illinois | Richardson Wildlife Foundation, West Brooklyn | Burned regularly (every 2–3 years) | Lat 41.70734, Lon −89.18674 |
| A2 | North-America, Illinois | Douglas Hart Nature Center, Mattoon | Burned regularly (every 2–3 years) | Lat 39.49258, Lon −88.31090 |
| A3 | North-America, Illinois | Rock Springs Conservation Area, Decatur | Burned regularly (every 2–3 years) | Lat 39.82382. Lon −89.01321 |
| E1 | Europe, Romania | Abandoned grassland, Cluj-Napoca | Burned once in the last 10 years | Lat 46.79435, Lon 23.52775 |
| E2 | Europe, Romania | Disturbed grassland, Ciucea | Not burned in the last 20 years | Lat 46.95682, Lon 22.81145 |
| E3 | Europe, Romania | Old-field, Ruja | Not burned in the last 20 years | Lat 46.00620, Lon 24.65687 |

predominantly grass biomass, but did not contain *S. canadensis*. Litter amounts were determined based on field measurements in grassland sites of Transylvania, Romania in early spring. Following the burn treatment, treated and control pots were arranged using a randomized block design in four blocks in the same open air facility. Pots were re-randomized within blocks twice in the course of the experiment. To avoid genetic mixing between resident *S. canadensis* populations and those used in this study, plants were destructively harvested before flowering, during the first week of August 2014. All shoots of *S. canadensis*, and all tillers of grasses were counted. Aboveground parts of *S. canadensis* and the grasses were collected separately. Roots were washed free of soil and carefully separated. Aboveground and belowground biomass was dried at 60 °C for 72 h then weighed. Total biomass was calculated as the sum of the two fractions, while shoot-root ratio as the proportion of aboveground and belowground biomass.

Statistical analysis

To test the competitive effect of *S. canadensis* of different origin (European and American) on the two native species separately, we used the measured traits of undisturbed (unburned) pots including both with and without competition data. For normally distributed dependent variables (total biomass, shoot-root ratio), we used LMMs with Gaussian error distribution; variables were transformed when necessary to meet normality and homoscedasticity requirements of the residuals. We used GLMM with a Poisson error distribution and log link function for count variables (number of tillers). Competition (with or without *S. canadensis*) and continent of origin of *S. canadensis* (America, Europe) and their interactions were included as fixed factors, while blocks and populations of *S. canadensis* nested within continents were included as random factors in the model. We reduced the models by removing the fixed factors by stepwise deletion of non-significant ones and compared the resulting model to the previous one by using log likelihood-ratio tests (Zuur et al. 2009). We performed similar analyses on the vegetative traits of *S. canadensis* as well (number of aerial shoots instead of tillers) to test their response to competition with the grass species. Fixed factors were the identity of the competitive grass species and the continent of *S. canadensis* origin, while random factors were the same as in the above models.

To isolate the effect of burning on the performance of the native species, we used data from plants grown without competition. We performed the same type of analyses for the dependent variables as above, but disturbance (burned, unburned) was the fixed factor, and block the random factor. Similarly, we also tested the effect of burning on *S. canadensis*, with disturbance and continent of origin, and their interaction as fixed factors, whereas block and population nested within continent as random factors. We also applied model simplification as presented above.

Finally, we performed LMMs to determine whether fire disturbance had an additional effect on the outcome of competition between native grasses and *S. canadensis*. To include the effect of competition, we used the relative total biomass, relative shoot-root ratio and relative number of tillers of the two species as dependent variables in the analyses. Relative total biomass of a grass species was calculated as total biomass of individual grasses grown with *S. canadensis* as a percentage of the mean biomass for each species when grown alone. The other two relative variables were calculated in a similar way. First, we performed the LMMs with both grass species included to compare their relative performance. Fixed factors were species (*E. repens, B. pinnatum*), disturbance and continent of origin, and their pairwise interaction, while block and populations nested within continents were random factors. Second, as the identity of species had significant effect in the former models, we tested the individual responses of the native species with similar LMMs separately on the two grass species.

All statistical analyses were carried out in the R statistical environment version 3.0.1 (R Core Team 2014). 'lme4' R package was used to LMM and GLMM analyses (Bates and Maechler 2009). We used glht with Tukey contrasts in the R package 'multcomp' after LMMs and GLMMs to test for differences among the levels of significant explanatory variables.

Results

The effects of competition

*Solidago canadensis* had an overall strong negative effect on the performance of both native grass species (Fig. 1). When grown with *S. canadensis*, the total biomass of *B. pinnatum* decreased by an average of

71.12 % ($\chi^2 = 47.66$, $p < 0.001$); while growth of *E. repens* decreased by 58.15 % ($\chi^2 = 57.40$, $p < 0.001$; Fig. 1A). Similarly, there were 68.84 % fewer tillers in *B. pinnatum* ($\chi^2 = 105.80$, $p < 0.001$) and 61.64 % fewer in *E. repens* ($\chi^2 = 193.22$, $p < 0.001$) under competition (Fig. 1B). Moreover, the invasive species altered the resource allocation strategy of the native species differently ($\chi^2 = 38.24$, $p < 0.001$), as the shoot-root ratio of *B. pinnatum* in competition with *S. canadensis* was lowered by 54.14 % ($\chi^2 = 25.01$, $p < 0.001$), while this value was 33.86 % for *E. repens* ($\chi^2 = 6.47$, $p = 0.01$, Fig. 1C). We also tested whether the American and European *S. canadensis* populations had different competitive effects on native species, but continent of origin and continent × competition interaction never had a significant effect on either measured traits and were always removed during model simplification.

In contrast, competition with neither of the native grass species had a strong effect on *S. canadensis*: it showed a significant growth decrease by an average 9.15 % ($\chi^2 = 46.71$, $p < 0.001$) and 25.53 % ($\chi^2 = 10.12$, $p < 0.001$) in total biomass in competition with *B. pinnatum* and *E. repens*, respectively (Fig. 1A). There were no significant changes in number of shoots (*B. pinnatum*: 14.89 %; $\chi^2 = 0.17$, $p = 0.67$ and *E. repens* 15.50 %; $\chi^2 = 1.45$, $p = 0.22$) or change in shoot-root ratio (7.92 %; $\chi^2 = 0.91$, $p = 0.33$ and 0.01 %; $\chi^2 = 0.22$, $p = 0.63$). The effect of the two native species was marginally significantly different on the total biomass of *S. canadensis* ($\chi^2 = 3.63$, $p = 0.056$), but not on the two other traits. There were no significant differences between the American and European *S. canadensis* populations regarding their response to competition, but American *S. canadensis* individuals had higher shoot-root ratio ($\chi^2 = 18.72$, $p < 0.001$), and fewer shoots ($\chi^2 = 8.76$, $p = 0.003$) compared with European individuals (Fig. 1B and C).

### The effects of disturbance

Burning influenced none of the traits in *B. pinnatum* when grown alone: total biomass ($\chi^2 = 1.97$, $p = 0.15$), shoot-root ratio ($\chi^2 = 0.76$, $p = 0.38$) or number of tillers ($\chi^2 = 0.003$, $p = 0.95$). In *E. repens*, burning significantly reduced the total biomass ($\chi^2 = 3.87$, $p = 0.04$), but influenced neither the shoot-root ratio ($\chi^2 = 0.42$, $p = 0.51$), nor the number of tillers ($\chi^2 = 0.02$, $p = 0.86$).
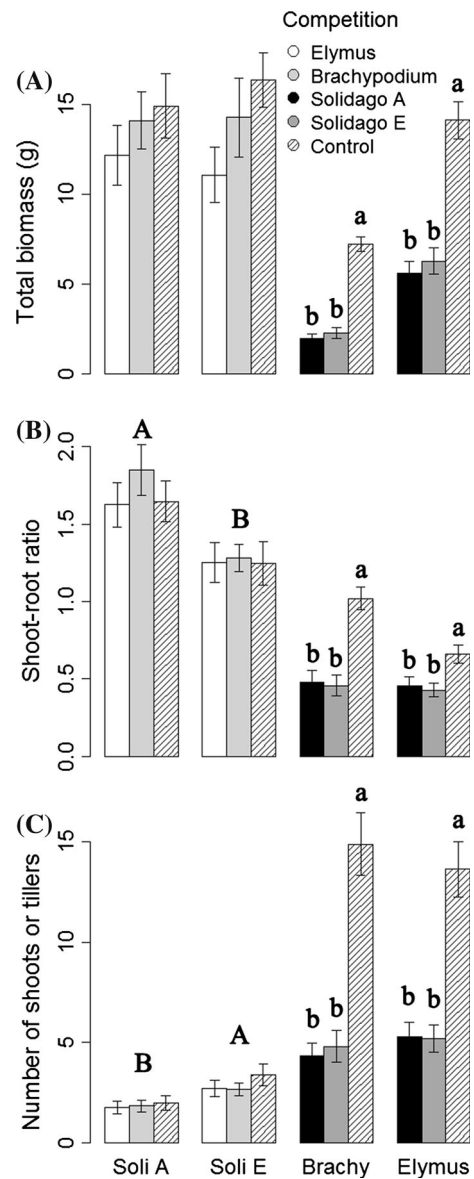


**Fig. 1** Total biomass (**A**), shoot-root ratio (**B**) and number of shoots/tillers (**C**) of *Solidago canadensis* (Soli A—American populations, Soli E—European populations) in competition with *Elymus repens* and *Brachypodium pinnatum*, and without competition (control); and the same traits of *B. pinnatum* and *E. repens* in competition with American or European *S. canadensis* and without competition. Mean ± SE are shown. Capital letters denote significant differences between the performance of American and European populations of *S. canadensis*, while lowercase letters show significant differences between control and competition situation in case of *E. repens* and *B. pinnatum*

Burning had no effect on the total biomass ($\chi^2 = 0.02$, $p = 0.86$) or number of aerial shoots ($\chi^2 = 1.22$, $p = 0.26$) of *S. canadensis* grown alone, but increased

the shoot-root ratio of the invasive species ($\chi^2 = 4.07$, $p = 0.04$). The continent of origin had no effect on total biomass ($\chi^2 = 0.22$, $p = 0.88$), but significantly influenced the shoot-root ratio ($\chi^2 = 7.52$, $p = 0.006$) and aerial shoot numbers ($\chi^2 = 3.61$, $p = 0.05$) of *S. canadensis*. American *S. canadensis* individuals had higher allocation to aboveground biomass than European ones and the number of aerial shoots was greater in European individuals. We found a significant burning × continent interaction for the number of shoots ($\chi^2 = 4.57$, $p = 0.03$), with significantly more aerial shoots in unburned compared to burned European *S. canadensis* (Fig. 2).

## The additive effect of invasive competition and disturbance

The invasive species had a significantly stronger competitive effect on the performance of *B. pinnatum* compared to *E. repens* shown by their different relative total biomass ($\chi^2 = 39.33$, $p < 0.001$, Fig. 3A) and relative shoot-root ratio ($\chi^2 = 52.56$, $p < 0.001$, Fig. 3B). Burning had no additional effect on the outcome of competition between *S. canadensis* and *B. pinnatum* on any vegetative trait, but it had a marginally significant additional effect on the outcome of competition between *S. canadensis* and *E. repens*. We found significantly higher total biomass ($\chi^2 = 3.61$, $p = 0.047$) and shoot-root ratio ($\chi^2 = 3.58$, $p = 0.048$) in unburned *E. repens* individuals (Fig. 3A, B). Continent of origin of the invasive competitor influenced the outcome of competition between *S. canadensis* and *B. pinnatum*, since the native grass species had a significantly higher relative total biomass in competition with European *S. canadensis* ($\chi^2 = 4.50$, $p = 0.03$). In the same way, the shoot-root ratio of *E. repens* was lower in competition with European *S. canadensis* individuals ($\chi^2 = 4.10$, $p = 0.04$) when compared to American ones (Fig. 1).

## Discussion

### The effect of competition on the performance of native and invasive species

Former experimental studies have shown that invasive species may have strong competitive effects on native species even without disturbance. According to a
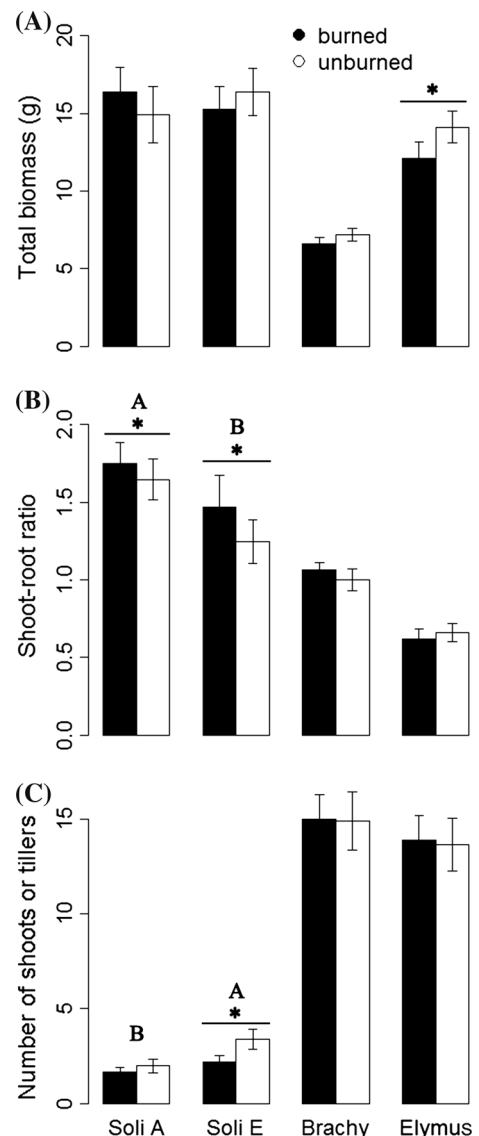


**Fig. 2** Total biomass (**A**), shoot-root ratio (**B**) and number of shoots/tillers (**C**) of American (Soli A) and European *Solidago canadensis* (Soli E), *Brachypodium pinnatum* (Brachy) and *Elymus repens* in burned or unburned conditions. Mean ± SE are shown. '*' denote significant differences at $p < 0.05$ between burned and unburned conditions, while capital letters show significant differences between the performance of American and European populations of *S. canadensis*

review, non-native species suppress native biomass by an average of 46.6 % (Vilà and Weiner 2004). In our experiment, native species also lost more than 50 % of their total biomass in competition with *S. canadensis*.

*B. pinnatum* was reported to have strong competitive abilities linked with its ability to form dense
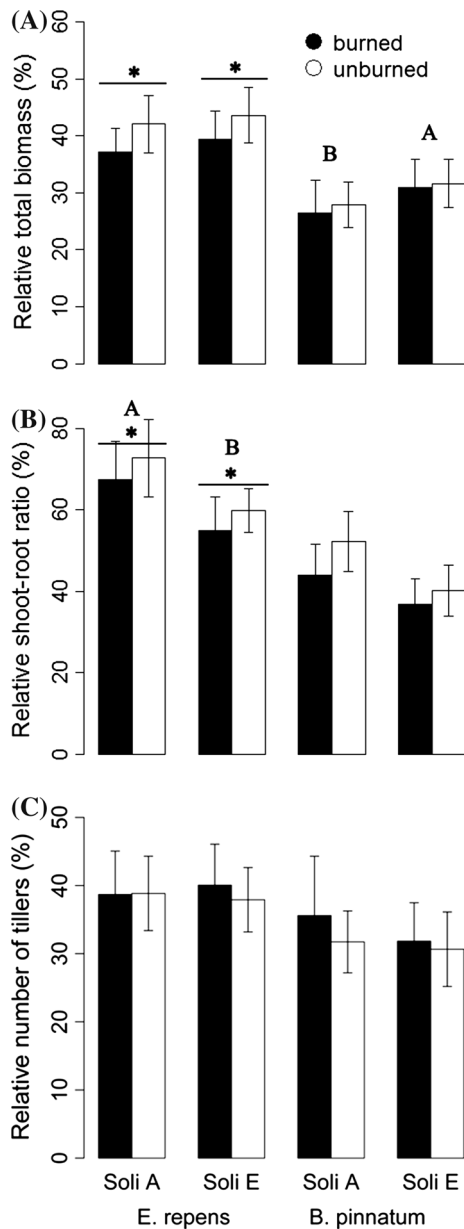
**Fig. 3** Changes in total biomass (**A**), shoot-root ratio (**B**) and number of shoots/tillers (**C**) of *Brachypodium pinnatum* and *Elymus repens* to competition with American (Soli A) and European *Solidago canadensis* populations (Soli E) in burned and unburned conditions. All values are relative to plants grown without competition from *S. canadensis*. Mean ± SE are shown. '*' denote significant differences at $p < 0.05$ between burned and unburned conditions, while capital letters show significant differences between the performance of American and European populations of *S. canadensis*

patches due to high tiller density and productivity (Carson and Barrett 1988), high phenotypic plasticity (Mojzes et al. 2003), and a vigorous rhizome system that allows rapid vegetative propagation after disturbances (de Kroon and Bobbink 1997). Similarly, *E. repens* is also reported to have strong competitive abilities because it can respond to competitive pressure by shifting from a guerrilla strategy towards a phalanx strategy by producing dense canopy and long aerial shoots (Amiaud et al. 2008; Pottier and Evette 2010). This is achieved by reducing the length of rhizome internodes, increasing branch frequency, and preferential allocation to aerial shoots and leaves (Amiaud et al. 2008). Despite these abilities, both species suffered large reductions in biomass in the presence of *S. canadensis,* perhaps due to the competitive advantage of the higher statured invasive species over the shorter grass species. *Solidago canadensis* is reported as superior adult competitor due to its large size (Walck et al. 1999) and its ability to grow at least as tall as neighbouring species (Goldberg and Werner 1983). The importance of plant size as a mediator of competitive ability is shown by strong competitive interactions when *S. canadensis* is grown with smaller species (Sun and He 2010; Yuan et al. 2012), but not when in competition with large grass species such as *Calamagrostis epigejos* (Rebele 2000) or *Festuca arundinacea* (Walck et al. 1999).

Being taller than the two native grasses, *S. canadensis* likely decreased light availability of native grasses. As the growth of rhizomes is negatively dependent on the quantity of light received by the leaves in *E. repens* (Palmer 1958), shading by *S. canadensis* could induce the prolific vegetative growth in this species, thus higher allocation to belowground tissues. Increased belowground biomass can enhance resource acquisition by root extension (perhaps the case of *B. pinnatum*), and also allow the colonization of surrounding gaps by elongation of vegetative organs (rhizomes and stolons) to avoid competition with a superior competitor (Amiaud et al. 2008). This intense root competition can be an effect of resource depletion by the larger invasive species; but also the effect of allelopathy of *S. canadensis* (Abhilasha et al. 2008; Yuan et al. 2012) which might inhibit the access of the other competitor's roots to resources (Schenk 2006).

Based on our results, it seems that competition for soil resources caused the differences in native species' response to the invader, as *B. pinnatum* suffered more from competition than *E. repens* (Fig. 3A). The belowground biomass of *E. repens* in competition (4.27 ± 1.60 g) was quite similar to that of *S. canadensis* (5.01 ± 2.50 g), suggesting balanced resource acquisition between the two species. In contrast, *B. pinnatum* produced much smaller belowground structures (1.49 ± 0.62 g) than its competitor (5.87 ± 2.93 g). These differences can also explain the smaller competitive effect of *B. pinnatum* on the invasive species.

### The effect of burning on the performance of native and invasive species

Grasses are highly combustible as they have low moisture content and produce a large quantity of fine fuel (Vilà et al. 2001). Therefore, fire can eliminate all aboveground plant parts with active meristematic tissues, and may also reduce the viability and/or activation of axillary buds of perennial grasses (Busso et al. 1993). However, burning might have several advantages for grasses: fire accelerates the mineralization of organic matter thus increasing nutrient availability (Canals et al. 2014); fire may stimulate resprouting and promote growth by depleting allelopathic substances (Vilà et al. 2001), and also reduce pathogen density in soil (Keeley and Fotheringham 2000). Despite these potential effects, our experimental burning had no impact on the vegetative performance and allocation of *B. pinnatum* grown without competition. In contrast, *E. repens* responded negatively to fire showing a 14.17 % reduction in total biomass in burned conditions, but no change in number of tillers or shoot-root ratio.

Species from non-fire-prone systems can survive fire without specific adaptations if they regenerate from rhizomatous structures after burning. For example, *B. pinnatum* was reported to be fire-resistant or even take advantage of fire due to its belowground stolons which are not damaged during burning (Moog et al. 2002; Kahlert et al. 2005). In contrast, *E. repens* showed decreased abundance after burning in its North-American introduced range (Howe 1995; Tester 1996) despite its highly vigorous rhizome system (Palmer and Sagar 1963), or unchanged frequency in European temperate grasslands (Antonsen and Olsson 2005). The main differences between the two species' response to fire may result from their phenology. Tillers of *E. repens* are formed during autumn from the erect tips of the rhizomes (Palmer and Sagar 1963), while *B. pinnatum* produce its shoots early in the season (Kahlert et al. 2005). During our experimental burning in early spring, *E. repens* suffered greater damage because it had already invested much in growth by that time, and had more tillers (3.09 ± 1.08) than *B. pinnatum* (1.00 ± 0.81). Thus *E. repens* probably lost a higher quantity of aboveground biomass than *B. pinnatum* during burning and it was not able to overcome this biomass loss later in the season. While, the axillary bud bank was not destroyed during fire in either species, burning did not induce the intense vegetative growth common to grasses of fire-prone ecosystems (Svejcar and Browning 1988; Cuomo et al. 1998).

Burning did not change the performance of *S. canadensis* based on total biomass or number of aerial shoots. However, fire did cause an important allocation change in this species to achieve the same total biomass: increased shoot-root ratio (i.e. lower allocation into roots, which permits a higher allocation into aboveground parts) under burned compared with unburned conditions. The decrease in root biomass in post-fire conditions is consistent with increased nutrient availability, and thus a more relaxed competitive environment (Reich 2002).

### The additive effect of invasive competition and disturbance on the performance of native grasses

While the study of individual drivers of plant community change is very common, the impacts caused by the combination of causal factors generate a lot of uncertainty (Seastedt et al. 2008). We aimed to test whether a disturbance that native species are naïve to (in our case fire) may change the competitive outcome between invasive and native species. Competition by *S. canadensis* had an overall very strong negative effect on the performance of *B. pinnatum*, irrespective of disturbance. In contrast, disturbance and competition had a cumulative negative influence on the performance of *E. repens*, with competition having a greater effect than burning (58.15 vs. 10.41 % decrease in total biomass). Disturbance did not alter the strength of the interspecific interactions, thus it did not escalate the competitive effect of the invasive *S. canadensis* on *B. pinnatum*. This result fits into the 'invasive species as a driver' scenario (our first hypothesis, H1). However, we found that the

additive effect of invasive competition and disturbance on the performance of *E. repens* was higher than the impact of competition alone, which supports the 'back-seat driver' model (H3). Therefore, two functionally similar native species' responses to *S. canadensis* fall at or near to the driver end of the passenger-driver continuum. As the disturbance–invasive competition–native performance interaction is a tangled web of synergistic effects, the position of the invasive species along this continuum may vary individualistically among target species. Therefore, more native species should be involved to correctly draw the invasive species' place on this continuum (Didham et al. 2005; Chabrerie et al. 2007).

Successful invasive species are predicted to maintain their performance and dominance under altered environmental conditions (Vitousek 1990). *Solidago canadensis* was explicitly reported to tolerate or even take advantage of fire in its native range (Gibson et al. 1993; Towne and Kemp 2003). However, rapid evolutionary chances often cause differences between populations from native and introduced range regarding their size (Müller and Martens 2005; Barney et al. 2008), life cycle (Müller-Schärer and Steinger 2004), and resistance to herbivores (Blossey and Notzold 1995). Müller-Schärer et al. (2004) also hypothesized that plants may show decreased tolerance to herbivory or other stress factors, but increased competitive ability in introduced populations, if tolerance has fitness costs.

Therefore, as Central-Europe is a non-fire prone ecosystem with no or very rare natural fire events, we expected that invasive *S. canadensis* populations might have lost fire tolerance and evolved increased competitive ability compared to native populations. To test such differences between populations of different origin, American populations were intentionally chosen from frequently burned sites. A probable loss of fire tolerance was found in *S. canadensis*, as European populations were affected by burning (reduced number of shoots), while American populations were not. However, we cannot conclude that there has been a shift towards increased competitive ability in introduced European populations (Blossey and Notzold 1995), because we detected no enhanced or even lower competitive effects of these populations compared to American once. These findings are not in line with earlier studies on the competitive ability of *S. canadensis* (Abhilasha

et al. 2008; Yuan et al. 2012). These authors conclude that allelopathy drive the competitive effect of invasive *S. canadensis*, but the accumulation of soil pathogens can also modify the interspecific relationship between invasive and native species (Abhilasha et al. 2008). As we did not isolate these aspects of competition, we must rely on the measured vegetative traits as overall measures of competitive effects (see above).

Studying the joint effect of essential drivers on grassland change may be helpful to plan management actions, as it is impossible to distinguish the causal link between the drivers simply by observations alone (Didham et al. 2005). For example, if the presence of invasive species is a symptom rather than the cause of native diversity loss (Reid et al. 2009), the removal of dominant invasive species is unlikely to restore the community (MacDougall and Turkington 2005; Stromberg et al. 2007). Because competition was the main driver of change in our study, the elimination of invasive species should help the recovery of native species. However, fire caused different responses in two rhizomatous perennial species, which are generally known as fire tolerant (Wright 1985). As burning had a contrasting effect on two functionally similar species, we can expect a diverse palette of responses to burning across other functional groups as well. In line with this, a previous study in this system has shown large differences among plant species and families in their seed recruitment after fire (Ruprecht et al. 2013), while case studies based on few species also report variable effects of burning (Deák et al. 2014; Valkó et al. 2014). As native and fire-tolerant invasive species have different colonization and spreading probabilities in frequently burned grasslands, burning may dramatically change and depauperate native vegetation.

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