

# Community-level determinants of smooth brome (*Bromus inermis*) growth and survival in the aspen parkland

Alec A. Carrigy · Gisela C. Stotz ·  
Margarete A. Dettlaff · Gregory J. Pec · Inderjit ·  
Nadir Erbilgin · James F. Cahill Jr.

Received: 1 May 2016 / Accepted: 25 July 2016 / Published online: 10 August 2016  
© Springer Science+Business Media Dordrecht 2016

**Abstract** During the initial establishment phase, both biotic and abiotic conditions of the resident community can be important in determining the persistence of invasive plant populations. Invaders may act as passengers by tracking variation in environmental conditions (passenger model), or alternatively, may drive changes in environmental conditions which facilitate their continued invasion (driver model). We distinguish between these two models by comparing variation in resource availability among multiple plant community types to invader initial growth and survival. This study took place in the aspen

parkland ecoregion of Alberta, Canada, which is a savanna-type habitat consisting of multiple plant community types and invaded by nonnative smooth brome (*Bromus inermis*). We characterized four community types by a suite of biotic and abiotic variables (brome seed density, plant richness, plant cover, soil pH, soil moisture, and organic and inorganic N) and performed a brome seed addition experiment. Brome seedling growth and survival were greater with increased levels of soil moisture, while growth decreased with increases in dissolved organic N, but did not vary with other environmental conditions. Both survival and growth of brome seedlings were lowest in brome-dominated areas. These results show support for the passenger model of invasion, as variation in local environmental conditions were associated with variation in brome performance. Further, brome appears to have a negative effect on its own growth, a pattern uncommon among plant invaders.

---

Communicated by Prof. Lauchlan Fraser, Dr. Chris Lortie, Dr. JC Cahill.

---

A. A. Carrigy (✉)  
Department of Biology, University of New Mexico,  
Albuquerque, NM, United States  
e-mail: acarrigy@unm.edu

A. A. Carrigy · G. C. Stotz · M. A. Dettlaff ·  
G. J. Pec · J. F. Cahill Jr.  
Department of Biological Sciences,  
University of Alberta, Edmonton, AB, Canada

Inderjit  
Department of Environmental Studies, University of  
Delhi, Delhi, India

N. Erbilgin  
Department of Renewable Resources, University of  
Alberta, Edmonton, AB, Canada

**Keywords** Smooth brome · Invasion · Aspen parkland · Passenger · Driver hypothesis

## Introduction

Plant invasions involve several distinct phases, including long-distance dispersal into the community, successful germination, establishment, reproduction,

population growth, spread, and naturalization (Theoharides and Dukes 2007). The initial establishment phase plays an important role in the invasion process, as this is when invaders form self-sustaining populations (Sakai et al. 2001). The survival and growth of the invader in the establishment phase may depend on its traits (Rejmanek and Richardson 1996; Hamilton et al. 2005), or by biotic or abiotic aspects of the resident community into which it has entered (Elton 1958; Lonsdale 1999), partly explaining why only a small proportion of species become invasive (Williamson and Fitter 1996). We use multiple community types to determine the relationship between the biotic and abiotic aspects of a local community and the initial growth and survival of a widespread nonnative invader, smooth brome (*Bromus inermis* Leyss.).

Both the composition of a resident plant community and the availability of resources in the environment are thought to influence the establishment success of invaders (Elton 1958; Davis et al. 2000). For example, increased diversity (species, phylogenetic, and functional) can lead to invasion resistance (Naeem et al. 2000; Fargione and Tilman 2005) through competitive interactions (Levine et al. 2004) a process commonly referred to as biotic resistance (Elton 1958; Levine et al. 2004). Alternatively, plant–herbivore (Parker and Hay 2005; Pearse and Hipp 2014), or plant–soil microbe interactions (Klironomos 2002; Reinhart and Callaway 2006) can also confer biotic resistance (Levine et al. 2004). Some studies have found a positive relationship between diversity and biotic resistance (Wiser et al. 1998; Stohlgren et al. 2003), while others have found no such relationship (Cully et al. 2003; Smith et al. 2004), indicating variability in the role of diversity determining biotic resistance to establishment. High resource availability is often also associated with increased invasion success (Davis and Pelsor 2001; Foster et al. 2009; James et al. 2011), whereby some invasive species can become stronger competitors for available resources under high resource conditions (Vilà and Weiner 2004; Vinton and Goergen 2006; Funk and Vitousek 2007). Although we might find variation in diversity and resource availability across invaded and uninvaded communities, in many cases, it is unknown whether these patterns are a cause or consequence of invasion.

To address this uncertainty, the ‘passenger/driver’ model for invasion has been proposed (MacDougall and Turkington 2005). As initially proposed, the driver

model operates when an invader directly induces changes to the environment to *drive* patterns of subsequent invasion. For example, by adding novel chemicals (Inderjit et al. 2011), altering nutrient cycling (Ehrenfeld 2003; Piper et al. 2015), disturbance regimes (Brooks et al. 2004), or soil biota (Kourtev et al. 2003), a driver may facilitate its future establishment. In contrast, the original presentation of the passenger model occurs when invaders are *tolerant* of and colonize areas with new or altered disturbance regimes that may suppress native species, or colonize habitats with open niches (MacDougall and Turkington 2005). Passengers are thus not the cause of changes in ecosystems, but instead establish because of alterations to an ecosystem. However, the passenger/driver models only represent opposite ends of a continuum and an invader may be a passenger and a driver simultaneously (Didham et al. 2005). Further, the interpretation of the passenger model has been expanded to include changes in ecosystem properties other than disturbance (e.g., N deposition) which favor invasive species (White et al. 2013). For example, brome responds to levels of both soil moisture and N in the environment (Nernberg and Dale 1997; Vinton and Goergen 2006) which could increase its invasion potential; more generally, it is thought that higher resource levels increase the invasibility of an ecosystem (Alpert et al. 2000; Davis et al. 2000). Thus, the abundance of invaders in the environment may be correlated with resource availability as a consequence of such conditions and not the cause (HilleRisLambers et al. 2010; White et al. 2013).

We tested the passenger/driver models by using natural variation in the environment across multiple community types in place of direct manipulation of resource levels to indirectly infer brome’s behavior as a passenger or driver. In four common community types in the aspen parkland ecoregion of Alberta, Canada, we sampled the seed bank and performed a seed addition experiment to determine how initial brome growth and initial survival vary among community types in relation to aspects of the existing plant community and abiotic factors. This system is a savanna-type habitat with trembling aspen (*Populus tremuloides* Michx.) stands alternating with native grasslands. It provides a particularly relevant context for testing the passenger/driver models with respect to resource availability, as it captures aspects of both forest and grasslands, hosting a mosaic of vegetative

and topographic variation (Su and Bork 2007). We used this information to answer the following three research questions:

- (1) How do the community types within the aspen parkland differ in community composition, abiotic conditions, and brome seed density?
- (2) Are there differences in brome seedling growth and survival among the different community types within the aspen parkland?
- (3) Are brome growth and survival associated with local conditions across native communities, and is this consistent with the passenger or driver model?

If brome's establishment corresponds with variation in resource levels in the environment, this would support the passenger model. If brome invasion facilitates its own growth and survival, this would suggest that brome is a driver of its own invasion, especially if its invasion is associated with differences in resource availability.

## Materials and methods

### Study area and species

This study took place in an approximately 50 ha area of native parkland at the Roy Berg Kinsella Research Ranch in Kinsella, Alberta, Canada (53°59'N, 111°39'W). The parkland is a savanna-type habitat, which contains mixed community types, predominantly native rough fescue [*Festuca hallii* (Vasey) Piper] grasslands, interspersed with patches of trembling aspen (*P. tremuloides*). Smooth brome can be found not only in native grasslands, but also in and along patches of trembling aspen. At even small spatial scales, there is high spatial turnover in species composition (Su and Bork 2007) and abiotic resources, including light, water, N, and P across different community types within the aspen parkland (Lamb et al. 2007; Bennett et al. 2014). Thus, the natural conditions of the aspen parkland provide substantial variation in initial abiotic conditions, which provides an excellent study system to determine the mechanisms controlling invasive plant establishment, allowing differentiation between the roles of an invader as passenger or driver.

Smooth brome is a C<sub>3</sub> perennial grass that has invaded many areas worldwide (White et al. 1993; Stacy et al. 2005), including native grasslands of western Canada (Otfinowski et al. 2007). Brome invasion is associated with decreases in native plant diversity (Romo et al. 1990; Fink and Wilson 2011; Bennett et al. 2014) and changes in ecosystem function, such as nutrient cycling (Vinton and Goergen 2006; Piper et al. 2015). Another key concern about brome invasion is its ability to penetrate into native systems, even in the absence of apparent disturbances. Further, the role of the biotic and abiotic conditions that facilitate or inhibit the initial establishment of smooth brome is not clear.

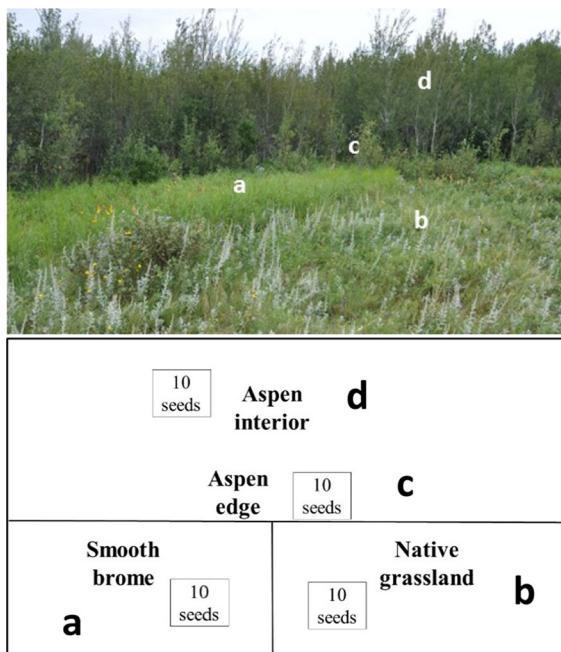
### Experimental design

#### Layout

We used a randomized block design, totalling 14 blocks in a 50 ha area. Within each block, there were four plots (1 m<sup>2</sup>), each consisting of one of four community types, determined prior to setup: smooth brome, native grassland, aspen edge, or aspen interior (total 56 plots), with all plots within 10 m of each other (Fig. 1). Blocks were selected where native grasslands and brome patches abutted a patch of aspen with a minimum distance of 25 m from the nearest blocks. Where possible, we used separate aspen patches for each block, but the number of separate aspen patches that fit these criteria was low—thus, some large patches of aspen housed multiple blocks. Plots were chosen that fit the following criteria: (1) brome plots contained >40 % brome cover and were always located in native grasslands, while native grassland plots did not have brome, and (2), aspen edge plots were located at the edge of an aspen stand, while the aspen interior plot was located at least 5 m into the aspen patch from the edge plot.

#### Environmental and community variables

To test (1) how biotic and abiotic conditions vary among community types and (2) whether these conditions are associated with brome growth and survival, we measured a variety of biotic and abiotic resources in each community type during the time of local seed dispersal. We also sampled the seed bank to test the impacts of resource availability on initial



**Fig. 1** Photograph (*top*) and top-down view (*bottom*) showing the relative position of the four community types in the aspen parkland landscape: smooth brome [dominated by *Bromus inermis*, left, in front of aspen; (a)], native grassland [foreground, right; (b)], aspen edge (c), and aspen interior [further into the trees; (d)]. Shown here is one site; there are 14 sites total Photo credit: A. A. Carrigy

brome establishment (see Table 1 for a summary of variables measured). During July 2014, we identified herbaceous and woody perennials by species within a 1 m<sup>2</sup> sampling area adjacent to each plot and calculated species richness. In addition, at each sampling area, percent cover was visually estimated by plant species (see Appendix Table 4 for a detailed list of species by community type).

Soil resources, including soil N and moisture, were measured in each plot as they are known to be limiting in this system (Cahill and Lamb 2007) and important for smooth brome growth (Vinton and Goergen 2006). Dissolved organic N (DON) and pH were also measured as both may play a role in plant community dynamics and may change following plant invasion (Kourtev et al. 2003; Van Der Heijden et al. 2008). Two soil samples were taken from each plot using 5-cm wide and 15-cm deep soil cores, which were combined, mixed, placed in a plastic bag and immediately put on ice in a cooler. Soil was sieved through a 2-mm sieve and then analyzed for pH and different

forms of nitrogen. We extracted nitrogen from a 7.5 g subsample of soil from each plot for 2 h in 2 M KCl (Robertson et al. 1999) and the supernatant was frozen until it was sent to the Biogeochemical Analytical Service Laboratory at the University of Alberta for analysis where total N, ammonia, nitrate, and nitrite were measured by flow injection analysis (Lachat QuickChem QC8500 FIA Automated Ion Analyzer, Loveland, CO, USA). We focused primarily on total inorganic N and DON. DON is produced by the extracellular enzymes of soil microbes, which break down complex insoluble N polymers, forming a pool of soluble N that may be taken up by plants (Bardgett et al. 2003; Schimel and Bennett 2004). Total inorganic N was calculated as the sum of NO<sub>2</sub>, NO<sub>3</sub>, and NH<sub>4</sub> and dissolved organic N was calculated as (total N–total inorganic N). To measure pH, we mixed a 10 g subsample of soil with 20 mL of deionized water. This mixture was shaken and then analyzed with a pH meter (Thermo Scientific, Waltham, MA, USA). Relative soil moisture was measured using a ThetaProbe soil moisture sensor (Delta-T Devices, Cambridge, UK) at three random locations in each plot in July 2014.

To determine how brome seed density varies among community types, we sampled the persistent seed bank in each plot during the following growing season in May 2015. The persistent seed bank contains seeds that are viable for more than 1 year, and are thus present at the start of a growing season (Thompson and Grime 1979). In brief, four soil cores (3 cm wide × 17 cm deep) were taken at the four corners of each 1-m<sup>2</sup> plot and pooled together. Soils were sampled for smooth brome seeds by removing coarse (shoots, roots, soil invertebrates) and fine debris through the washing of soils through two sieves (6 and 0.212 mm) (Heerdt et al. 1996). It is highly unlikely that brome seeds fell through the fine sieve, as the seeds are relatively large (5–8 mm; Otfinowski et al. 2007). The coarse debris was visually inspected for seeds, and the remaining soil in the fine sieve was spread in a thin layer over 3 cm of seedling starter mix (ProMix High Porosity Growing Medium, Premier Horticulture Inc., Quakertown, PA, USA) in 96 × 96 cm greenhouse trays subdivided into eight 12 × 12 cm squares. One control cell per tray, filled only with seedling starter mix, was used to identify seed contamination in the greenhouse. We randomly rearranged the trays three times to account for

**Table 1** Summary of variables measured in four common community types (native grassland, smooth brome, aspen edge, and aspen interior) at 14 locations within the aspen parkland ecoregion of Kinsella, AB, Canada

| Variables               | Source  | Units                            | Sampling period  |
|-------------------------|---|----------------------------------|------------------|
| Environmental variables |   |                                  |                  |
| Soil moisture           | Average of three 0–5 cm deep soil probe measurements  | Percent volumetric water content | July 2014        |
| Total inorganic N       | Two 5 cm diameter, 15 cm deep core  | mg/g soil                        | July 2014        |
| Dissolved organic N     | Two 5 cm diameter, 15 cm deep core  | mg/g soil                        | July 2014        |
| pH                      | Two 5 cm diameter, 15 cm deep core  | pH                               | July 2014        |
| Vegetation variables    |   |                                  |                  |
| Species richness        | 1 m <sup>2</sup> plot   | No. of species/m <sup>2</sup>    | July 2014        |
| Total plant cover       | 1 m <sup>2</sup> plot   | Percent cover/m <sup>2</sup>     | July 2014        |
| Brome seed density      | Four pooled 3 cm diameter, 17 cm deep cores   | Seeds/cm <sup>2</sup>            | May–August 2015  |
| Response variables      |   |                                  |                  |
| Survival                | Proportion survival of ten planted brome seeds  | Proportion                       | June–August 2014 |
| Total biomass           | Sum of aboveground and belowground biomass of all surviving brome seedlings at harvest (integrates both survival and average biomass) | mg                               | June–August 2014 |
| Average biomass         | Average of biomass of brome survivors at harvest  | mg                               | June–August 2014 |

Ten seeds of smooth brome (*B. inermis*) were planted in each community type

variation in growing conditions and turned over the soil after 3 months to promote germination of as many seeds as possible. We assessed seedlings for a total of 4 months, after which germination ceased. This amount of time was deemed sufficient to allow brome to germinate, as brome often emerges quickly after planting and has high germination rates (Grilz et al. 1994).

#### Seed addition

Ten seeds of smooth brome, obtained from the Roy Berg Kinsella Research Ranch, were hand dispersed within a 7 × 7 cm area onto all plots during mid-June 2014. Seeds were covered by a small wire mesh to prevent small mammal herbivory, and were allowed to

germinate and grow within each plot without supplemental watering or fertilizer for 8 weeks prior to harvest. Small mammals disturbed one plot, which we removed from analysis. At harvest, we counted the number of survivors, roots were separated from stems and washed (plants were small enough to allow full collection of roots), and individual parts were dried at 70 °C for 48 h and weighed to determine biomass.

#### Statistical analysis

To identify differences in species composition across community types, a perMANOVA (Permutational Multivariate Analysis of Variance) was performed on cover estimate/species data using the “slow and thorough procedures” with Sorensen distances and



10,000 randomizations (McCune et al. 2002) in PC-ORD v5.10 (MjM Software, Gleneden Beach, Oregon, USA). A perMANOVA tests the response of one or more variables to one or multiple factors using permutation methods and a distance measure (Anderson 2001). Pairwise comparisons on differences based on community types were conducted with permutation tests ( $\alpha = 0.05$ ). To test for differences in species richness, total cover, DON, total inorganic N, pH, and soil moisture among community types, we performed individual linear mixed models in R v3.1.2 (R Core Team 2014) using the *lme* function in the R package *nlme* (Pinheiro et al. 2016). All models included the categorical variable ‘community type’ as a fixed factor (four levels: native grassland, smooth brome, aspen edge, and aspen interior) and ‘block’ as a random factor. We ran pairwise comparisons to test where differences occurred using the *glht* function in the package *multcomp* (Hothorn et al. 2008).

We ran a generalized linear mixed model with a Poisson distribution using the *glmer* function in the R package *lme4* to test for differences in survival among all four community types, changing the baseline community to allow for all possible pairwise comparisons (Bates et al. 2015). To answer whether there were differences in brome growth among all four community types, we ran linear mixed models using the function *lme* in the R package *nlme* (Pinheiro et al. 2016) and performed post hoc pairwise comparisons of total biomass and average biomass using the *glht* function in the package *multcomp* (Hothorn et al. 2008). We calculated average biomass as the average weight of the seedlings that survived per plot to the end of the experiment, while survival was the number of brome seedlings alive at harvest. Total biomass is a composite measure, which incorporates both growth and survival, and was calculated as the sum of the biomass of all the surviving seedlings per plot. Survival represents the ability of brome seedlings to successfully germinate and is the source of new brome plants in each community type. Average biomass represents the potential for growth of brome seedlings in each community type, while total biomass represents total brome pressure, including both survival and growth potential.

To test for biotic and abiotic conditions associated with brome growth and survival across native communities, we ran three linear mixed models, one for each response variable (brome survival, total biomass,

and average biomass) in relation to a suite of biotic and abiotic factors. Here, our focus is on brome growth and establishment in native plant communities; therefore, brome plots were excluded from this analysis. Total biomass was square root transformed in order to meet the assumptions of analysis. Both measures of biomass included above and belowground biomass. For each response variable, we tested a global model that included the fixed factors community type (three levels: native grassland, aspen edge, aspen interior), species richness, total species cover, soil moisture, DON, total inorganic N, and pH. ‘Block’ was used as a random factor in all models. Total and average biomass models were analyzed using the *lme* function in the R package *nlme* (Pinheiro et al. 2016), while survival was analyzed with a Poisson error distribution using the *glmer* function in the R package *lme4* (Bates et al. 2015).

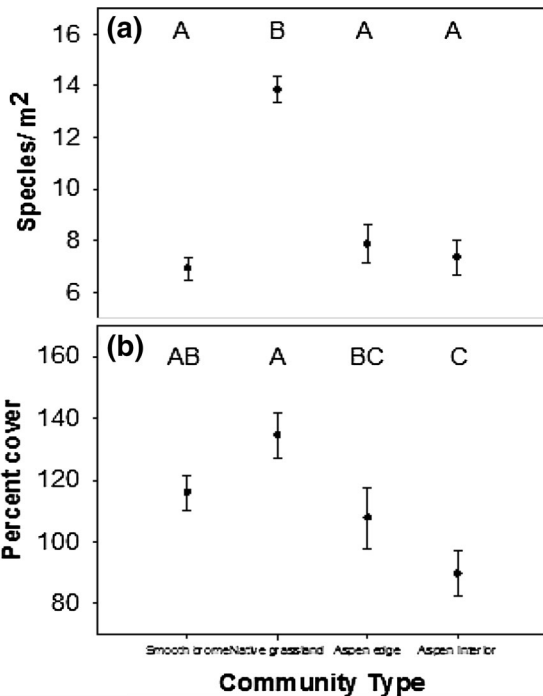
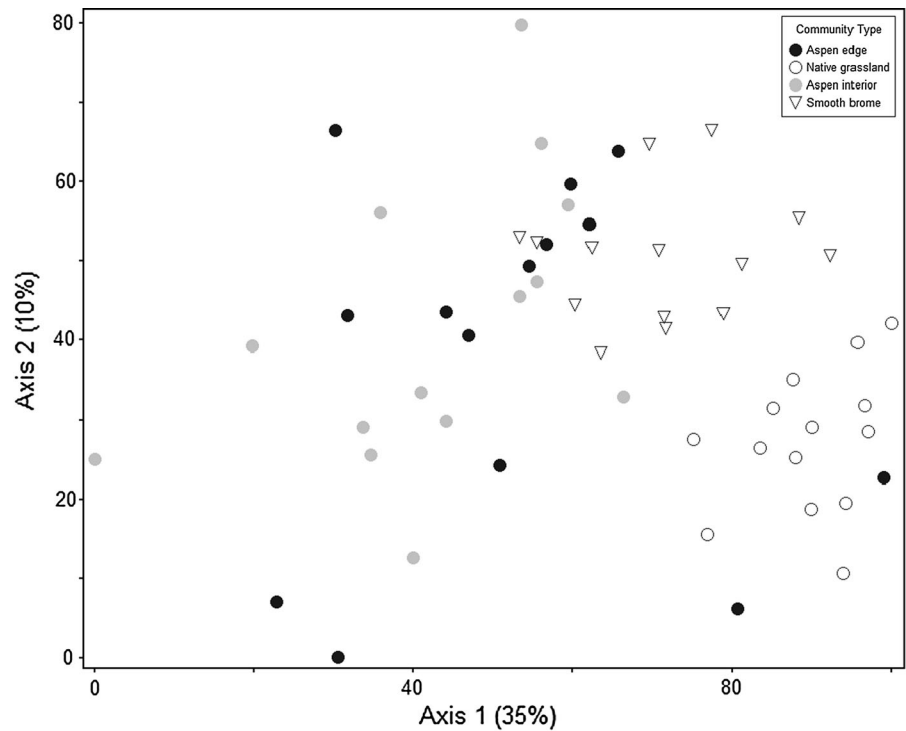
## Results

### Community variation

Species composition varied among community types (PerMANOVA;  $pseudoF = 10.624$ ,  $p = 0.0001$ ). All community types differed from each other ( $p < 0.05$ ) except for aspen edge and aspen interior ( $p > 0.5$ ) (Fig. 2). Species richness, total plant cover, total inorganic N, and DON differed among community types ( $F_{3,39} = 30.9$ ,  $p = < 0.0001$ ;  $F_{3,39} = 6.7$ ,  $p = < 0.0001$ ;  $F_{3,39} = 4.6$ ,  $p = < 0.0001$ ;  $F_{3,39} = 7.3$ ,  $p = 0.0075$ ). Native grasslands had nearly double the species richness compared to all other community types, which were not different from each other (Fig. 3a; see Appendix Table 5 for results of pairwise comparisons). Total plant cover was the highest in native grasslands and smooth brome, and was the lowest in the aspen interior (Fig. 3b). Total inorganic N was the highest in native grasslands and lowest in aspen edge and aspen interior, and was intermediate in brome (Fig. 4a). DON was the highest inside aspen stands, intermediate in the aspen edge, and the lowest in brome and native grasslands (Fig. 4b). Soil pH and moisture did not differ among community types ( $F_{3,39} = 1.2$ ,  $p = 0.34$ ;  $F_{3,39} = 1.2$ ,  $p = 0.33$ ) (Fig. 4c, d).

A total of 590 seedlings of 24 species emerged from the seedling trays, including 263 forbs (15 species) and

**Fig. 2** Nonmetric multidimensional scaling (NMDS) ordination of species composition by community type: native grassland, smooth brome, aspen edge, and aspen interior (see *inset* legend). 35 % of variation is explained by *axis 1* and 10 % by *axis 2*. Species data were collected in a 1-m<sup>2</sup> area of each plot

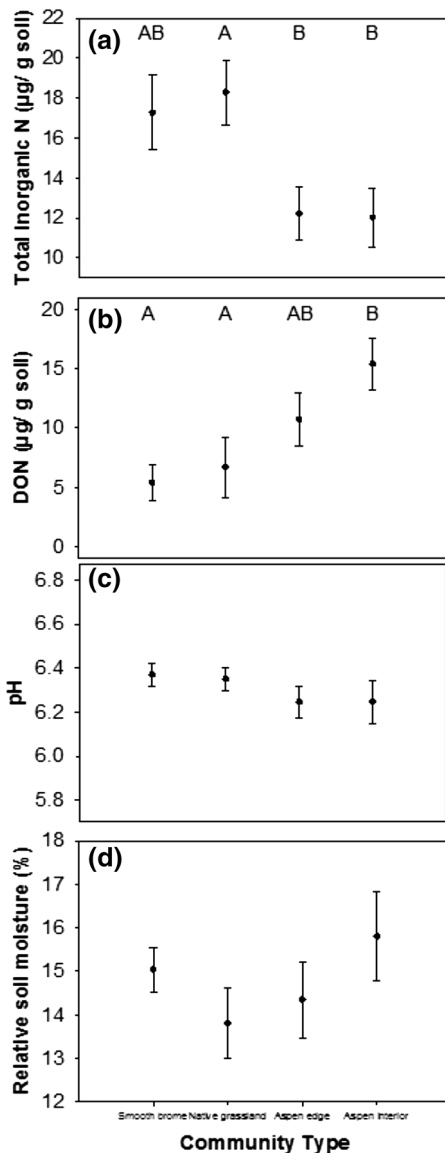


**Fig. 3** Differences in biotic variables across community types: species richness (a) and percent plant cover (b). Species data were collected in a 1-m<sup>2</sup> area of each plot. *Shared letters* indicate no significant difference. *Error bars* indicate ±SE

327 grasses (9 species), with no smooth brome seedlings emerging from any community type (see Appendix Table 6). The number of seedlings that emerged varied by community type: 14 seedlings/cm<sup>2</sup> emerged from soil in smooth brome plots, 16 from aspen interior, 24 from aspen edge, and 29 from native grasslands. None of these seedlings were smooth brome and as such, there appears to be no evidence of a persistent brome seed bank in any community type in this system.

**Brome initial growth and survival**

Initial mean survival, total biomass, and average biomass were all lowest in the smooth brome community type (Fig. 5; see Appendix Table 7 for pairwise comparisons). Brome seedling survival was the lowest in the smooth brome community (mean = 0.214 ± 0.192 SE) and highest in the aspen interior (mean = 0.564 ± 0.227 SE) (Fig. 5a). Total biomass was lowest in brome and native grasslands, though total biomass was significantly lower in brome than aspen edge and aspen interior, while native grasslands and both aspen plots were no different (Fig. 5b). Average biomass was the highest in native

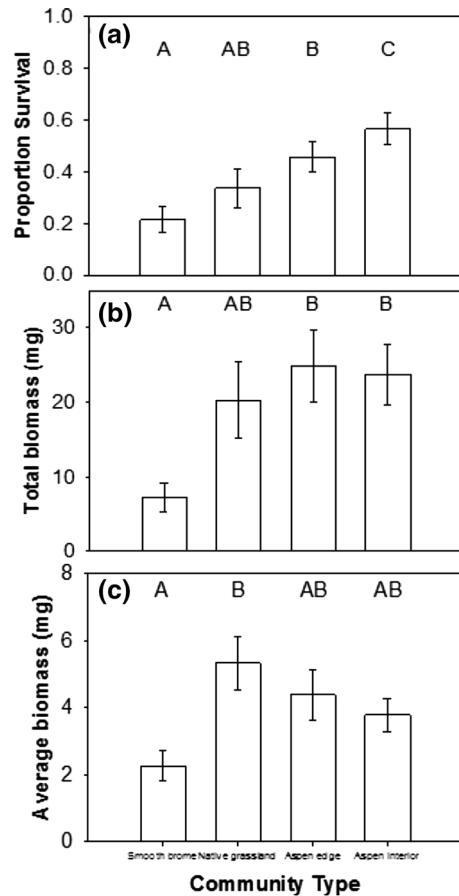


**Fig. 4** Abiotic variables: total inorganic N (a), DON (b), pH (c), and soil moisture (d) by community type. *Shared letters* indicate no significant difference; Soil pH and moisture did not vary among community types, thus *letters* were not included. *Error bars* indicate  $\pm$ SE

grasslands, but not different among other community types (Fig. 5c).

#### Biotic and abiotic conditions and brome initial establishment

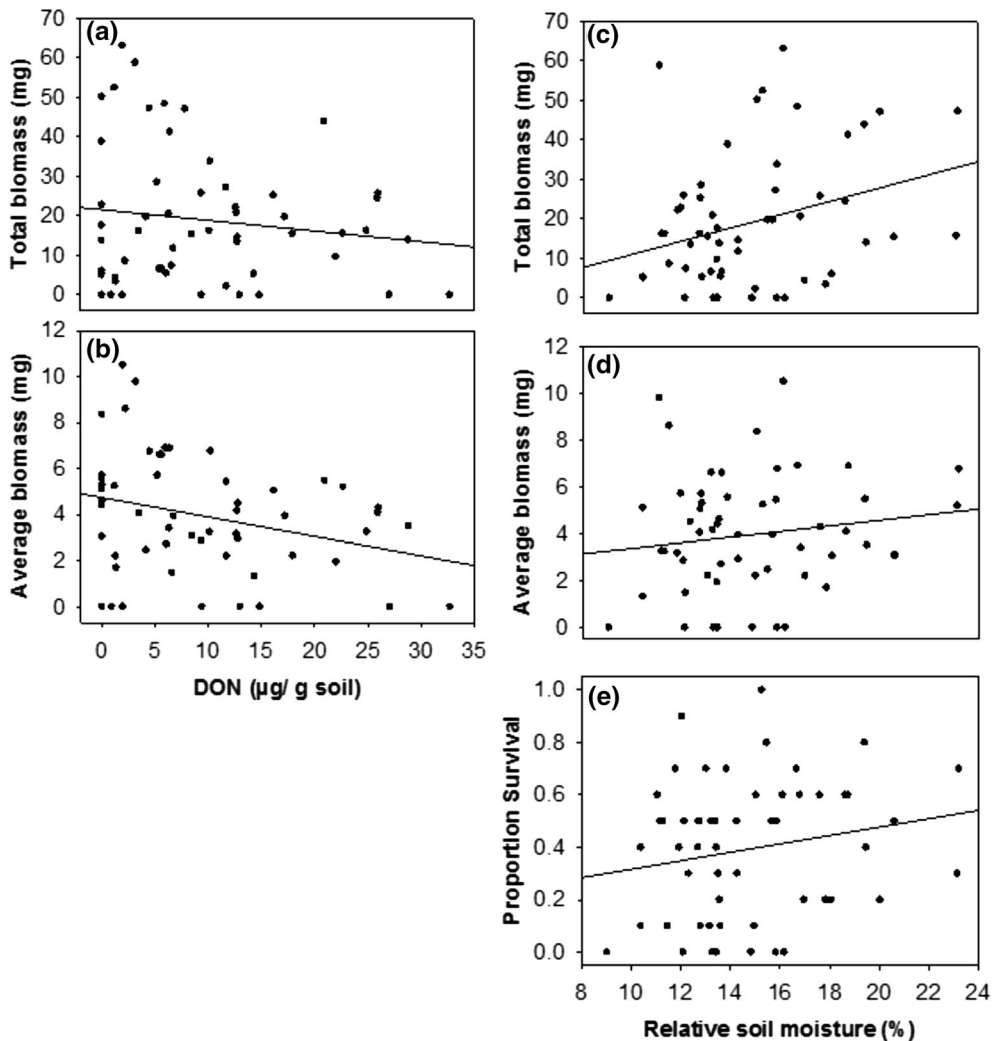
There was a negative association between DON and brome total biomass and average biomass



**Fig. 5** Survival (a), total biomass (b), and average biomass (c) of ten brome seeds sown into four community types at 14 locations of the aspen parkland. *Shared letters* indicate no significant difference. *Error bars* indicate  $\pm$ SE

( $F_{1,20} = 7.64$ ,  $p = 0.012$ ;  $F_{1,20} = 12.72$ ,  $p = 0.019$ ) (Fig. 6a, b), while soil moisture was positively associated with total and average biomass ( $F_{1,20} = 10.67$ ,  $p = 0.0039$ ;  $F_{1,20} = 4.58$ ,  $p = 0.0449$ ) (Fig. 6c, d). Total plant cover, species richness, total inorganic N, pH, and community type were not associated with total and average biomass ( $p > 0.05$ ; Table 2). There were no factors associated with brome survival across native communities ( $p > 0.05$ ; Table 3). However, when factors were tested individually, soil moisture was positively associated with survival ( $z = 2.02$ ;  $p = 0.04$ ) (Fig. 6e; Appendix Table 8), in line with soil moisture's effect on total and average biomass. The results differ between models due to the low degrees of freedom when all factors are included. Other than soil moisture's relationship with survival, the results from these three models with all factors





**Fig. 6** Relationship between DON and total and average biomass of brome seedlings (a, b) and soil moisture and total biomass, average biomass, and survival (c, d, e)

included matched the results when the factors were tested individually (see Appendix Table 8).

## Discussion

We found that brome survival and growth were the lowest in brome-invaded areas. Although we found differences between community types in a variety of conditions (e.g., community composition, richness, cover, inorganic N, and DON), brome was able to establish in all community types. We found that brome growth and survival were consistent with the passenger model, as measured by brome's growth and

survival by responding to variation in some environmental conditions (DON and soil moisture), supporting earlier studies (MacDougall and Turkington 2005; HilleRisLambers et al. 2010). On the other hand, many other conditions did not affect brome growth and survival, despite variation across community types (e.g., community composition, richness, cover, and total inorganic N), and thus, brome is only a passenger of certain conditions. Consistent with the driver model, brome appears to be driving environmental change within brome patches, causing low growth and survival of brome seedlings. As such, brome appears to be a 'negative driver,' which is in contrast to the typical view of invaders altering conditions to its own

**Table 2** General linear mixed models testing for biotic and abiotic conditions associated with smooth brome (*B. inermis*) total and average biomass across native communities ( $n = 42$ )

|                   | Total biomass |          | Average biomass |          |
|-------------------|---------------|----------|-----------------|----------|
|                   | <i>F</i>      | <i>p</i> | <i>F</i>        | <i>p</i> |
| Total inorganic N | 0.34          | 0.56     | 1.35            | 0.26     |
| Soil moisture     | 10.67         | 0.0039*  | 12.72           | 0.0019*  |
| DON               | 7.64          | 0.012*   | 4.58            | 0.0449*  |
| pH                | 0.13          | 0.72     | 0.09            | 0.77     |
| Species richness  | 0.98          | 0.33     | 1.30            | 0.27     |
| Total cover       | 0.00          | 0.98     | 2.38            | 0.14     |
| Community type    | 0.06          | 0.95     | 2.47            | 0.11     |

Total and average biomass were analyzed using a normal distribution, while survival was analyzed using a Poisson distribution

Significant differences marked with \*

**Table 3** General linear mixed models testing for biotic and abiotic conditions associated with smooth brome (*B. inermis*) survival across native communities ( $n = 42$ )

|                              | Survival |          |
|------------------------------|----------|----------|
|                              | <i>z</i> | <i>p</i> |
| Total inorganic N            | -0.27    | 0.79     |
| Soil moisture                | 1.04     | 0.30     |
| DON                          | -1.84    | 0.07     |
| pH                           | -0.44    | 0.66     |
| Species richness             | -0.07    | 0.94     |
| Total cover                  | 0.67     | 0.51     |
| Native grassland—aspens edge | -1.23    | 0.22     |
| Aspens edge—aspens interior  | -1.56    | 0.12     |

Total and average biomass were analyzed using a normal distribution, while survival was analyzed using a Poisson distribution

advantage. Because we do not have data showing that brome is causing change to these environmental conditions, follow-up studies are needed to establish the role of brome as a driver. Overall, these results are consistent with the idea that an invader can be both a passenger and a driver (Wilson and Pinno 2013). Although we lack data on brome reproduction and long-term patch persistence, these findings have important implications for the maintenance of

diversity and the long-term ecological trajectories of the community types in the aspen parkland system.

### Community variation

While we had close to 600 germinating seedlings in our greenhouse trays, no brome seedlings emerged, suggesting that there is no persistent brome seed bank in this system. The absence of seeds in the seed bank can be a function of many factors, which we did not measure in this study, including limited seed dispersal, seed predation pre- (McKone 1985) and post-dispersal (Hulme 1998), post-dispersal transport (Vander Wall et al. 2005), and seed pathogens (Blaney and Kotanen 2001). Brome seeds may be targeted by granivores; however, in feeding trials with other forage grasses, brome seeds were generally avoided by deer mice (*Peromyscus maniculatus*) (Everett et al. 1978). Previous reports of seed decomposition by fungus have been recorded in brome seeds (Blaney and Kotanen 2001), where seeds germinated from upland soils only after being treated with fungicide, and no seeds emerged from wetland areas in Ontario, Canada. Alternatively, brome seeds may simply have germinated earlier in the season before soil cores were taken as brome germination can be >90 % and up to 100 % under a range of warm-period temperatures, osmotic potentials, and light conditions (Grilz et al. 1994).

### Brome growth and survival across all community types

Although brome seedlings had the lowest growth and survival in brome patches, levels of biotic and abiotic resources in brome patches are comparable to other community types suggesting that the low growth and survival brome seedlings experience in brome patches are caused by another unmeasured variable. Brome may limit its own recruitment in invaded patches due to competition with already established brome plants. For example, in plots with >85 % brome cover, MacDougall and Wilson (2007) reported low recruitment success (<1 seedling per plot in 1 m<sup>2</sup> plots with 3000 seeds/m<sup>2</sup>) of five different plant species (1 grass, 2 legumes, 2 forbs) in undisturbed and N-amended plots. This suggests that there may be strong competition with established brome plants for available resources. Alternatively, the soil community may play

an important role in limiting brome's establishment. For example, pathogen accumulation in brome patches has been previously documented, limiting its growth and leading to patch die-off (Myhr et al. 1966), consistent with predictions based on density-dependent soil pathogen accumulation (Janzen 1970; Connell 1971).

We did not find support for biotic resistance related to species richness or total cover (Levine et al. 2004). This is similar to Bennett et al. (2014), who found that species richness and diversity were not related to biotic resistance to brome invasion. In contrast, DiAllesandro et al. (2013) found that species richness was inversely related to smooth brome biomass. However, DiAllesandro et al. (2013) used nutrient additions and planted artificial communities as opposed to natural field conditions used here, which could explain the discrepancy between studies. Bennett et al. (2014) reported strong biotic resistance to brome survival by competition with the native grassland community depending on the levels of P and N. This is likely because they tested biotic resistance over 4 years, as opposed to the single growing season in the current study. Additionally, we considered brome invasion into aspen stands and within brome patches as opposed to native grasslands only.

#### Biotic and abiotic conditions and brome establishment

Although soil moisture and dissolved organic N were found to be associated with brome growth, only soil moisture explained the variation in brome survival across native community types. That abiotic resources such as N were unrelated to survival was unexpected, given that additions of these resources can in general increase seedling survival (Liancourt et al. 2005). However, this is consistent with other studies in that brome may perform well and maintain dominance across a wide range of moisture and N levels (Nernberg and Dale 1997; Wilson and Pinno 2013).

In contrast, differences in both total and average biomass were negatively associated with variation in levels of DON, while total and average biomass and survival were positively associated with soil moisture (Table 2; Fig. 6c, d, e). These results suggest an effect of DON on growth but not survival, since abiotic

conditions may not only have a direct effect on growth, but may also mediate the interaction with neighbors. Neighbor interactions can be strong in this system: competition with neighboring plants can reduce plant growth in the seedling stage by up to 90 % (Haag et al. 2004; Lamb et al. 2007). Brome has been previously shown to be negatively impacted by low soil moisture, and yet can still retain its competitive dominance at low moisture levels (Nernberg and Dale 1997). This could explain why we found an effect of moisture on brome growth and survival, yet brome is still able to survive and grow in all community types. Where environments are N-limited, DON can become an important form of N for plants (Bardgett et al. 2003; Nordin et al. 2004), such as in this system (Lamb et al. 2007). However, it is still unclear which species in this system are capable of taking up organic N in appreciable quantities. The negative association between DON and brome growth may influence aspen-brome dynamics as DON is higher in aspen stands (Fig. 4b), likely due to secondary chemical inputs from aspen leaves or root exudates (Kraus et al. 2003). Alterations in the rate of nutrient cycling can also contribute to plant invasions (Ehrenfeld 2003; Allison and Vitousek 2004; Rothstein et al. 2004), for example, levels of total soil N were higher in brome-invaded patches than uninvaded soils but the rate of mineralization was also significantly higher in invaded soils (Piper et al. 2015). Other species in the same genus also alter soil nitrogen cycling, including *Bromus hordeaceus*, (Hawkes et al. 2005), *Bromus rubens* (Parker and Schimel 2010), and *Bromus tectorum* (Stark and Norton 2015). Thus, the importance of nitrogen cycling independent of nitrogen levels for smooth brome invasion dynamics deserves further attention. We also recognize the role of other unmeasured abiotic variables, particularly night-time temperature (Baker and Jung 1968), light, or other macronutrients that could be related to initial brome establishment.

#### Conclusion

We found that brome established in a number of plant community types in a small area, even in the absence of apparent disturbance and across a range of environmental conditions. We also found support for the passenger model of brome

invasion with respect to DON and soil moisture, but not all environmental factors. Given the high rate of establishment of brome seeds found here, targeting brome preseed dispersal may be an effective means of controlling further spread. As well, areas with higher levels of soil moisture and low levels of DON may be at a higher risk of brome invasion. Based on our results and the previously documented impacts of brome invasion on native plant communities (Romo et al. 1990; Fink and Wilson 2011; Bennett et al. 2014), we suggest that more attention be paid to the planting and management of smooth brome in its nonnative range.

**Acknowledgments** We thank Tan Bao for helpful discussions during the preparation of the manuscript, Mika Wrightson-Rivard, Iryna Stryapunina, and Sydney Wild for providing help with sample processing, Charlotte Brown for providing assistance in the greenhouse, Ashton Sturm for assistance in the field, Lysandra Pyle for help in identifying seed bank seedlings, and Steven Williams for logistical support in the greenhouse. We also thank Roy Turkington for providing a rich body of work on plant community ecology and invasion which has been foundational to this work and many other studies from the Cahill lab. This work

was supported by an NSERC USRA awarded to AAC, GJP was supported by a University of Alberta Doctoral Recruitment Scholarship, and GCS was supported by CONICYT Becas-Chile scholarship. NSERC Discovery, NSERC Discovery Accelerator Supplement, and Alberta Conservation Association research grants were awarded to JFC.

**Author's contributions** Alec A. Carrigy wrote and revised the manuscript, collected data, and performed statistical analysis. Gisela C. Stotz performed field work, and helped with statistical analysis. Margarete A. Dettlaff aided with field work. Gregory J. Pec helped with statistical analysis and field work. Alec A. Carrigy, Gisela C. Stotz, Margarete A. Dettlaff, Inderjit, Nadir Erbilgin contributed to idea generation and experimental design. James F. Cahill secured research funding, led the integration of the study as part of a larger research program, contributed to experimental design and the analytical approach, and was substantially involved in the writing of the manuscript. All authors contributed to the revising of this manuscript.

## Appendix

See Tables 4, 5, 6, 7 and 8.

**Table 4** Community composition data collected from four common community types in the aspen parkland ecoregion (native grassland, smooth brome, aspen edge, aspen interior) at 14 locations

| Species  | Native grassland |                | Smooth brome   |                |
|--|------------------|----------------|----------------|----------------|
|  | Plots occupied   | Mean cover (%) | Plots occupied | Mean cover (%) |
| <i>Achillea millefolium</i> L.                         | 13               | 2.54           | 7              | 1.29           |
| <i>Agrostis scabra</i> Willd.                          | 2                | 1.5            |                |                |
| <i>Amelanchier alnifolia</i> (Nutt.) Nutt. Ex M. Roem. | 1                | 50             | 1              | 25             |
| <i>Anemone canadensis</i> L.                           |                  |                |                |                |
| <i>Apocynum androsaemifolium</i> L.                    |                  |                |                |                |
| <i>Aralia nudicaulis</i> L.                            |                  |                |                |                |
| <i>Artemisia ludoviciana</i> Nutt.                     | 10               | 8.6            | 5              | 1.8            |
| <i>Astragalus agrestis</i> Douglas ex G. Don           | 9                | 4.89           | 2              | 1              |
| <i>Bromus inermis</i> Leyss.                           |                  |                | 14             | 62.5           |
| <i>Bromus porteri</i> (J.M. Coult.) Nash               | 1                | 1              |                |                |
| <i>Campanula rotundifolia</i> L.                       | 5                | 1              |                |                |
| <i>Carex stenophylla</i> Wahlb.                        | 13               | 4              | 13             | 4.77           |
| <i>Cirsium arvense</i> (L.) Scop.                      | 1                | 3              |                |                |
| <i>Collomia linearis</i> Nutt.                         | 1                | 1              |                |                |
| <i>Comandra umbellata</i> (L.) Nutt                    | 2                | 1              | 1              | 1              |
| <i>Dactylis glomerata</i> L.                           |                  |                |                |                |
| <i>Danthonia intermedia</i> Vasey                      | 1                | 1              |                |                |
| <i>Elymus glaucus</i> Buckley                          | 14               | 6.15           |                |                |
| <i>Chamerion angustifolium</i> (L.)                    |                  |                |                |                |
| <i>Erigeron caespitosus</i> Nutt.                      | 1                | 2              |                |                |
| <i>Erigeron glabellus</i> Nutt.                        | 1                | 1              |                |                |
| <i>Festuca hallii</i> (Vasey) Piper                    | 7                | 4.43           | 1              | 1              |
| <i>Fragaria virginiana</i> Duchesne                    | 4                | 5.75           | 3              | 3.67           |
| <i>Gaillardia aristata</i> Pursh                       | 1                | 1              |                |                |
| <i>Galium boreale</i> L.                               | 14               | 22.71          | 13             | 3.15           |
| <i>Geum triflorum</i> Pursh                            | 2                | 9.5            |                |                |
| <i>Hesperostipa curtiseta</i> (Hitc.) Barkworth        | 13               | 8.92           | 5              | 1              |
| <i>Heuchera richardsonii</i> R. Br.                    |                  |                |                |                |
| <i>Lactuca tatarica</i> (L.) C.A. Mey.                 | 5                | 8.25           | 2              | 30             |
| <i>Lathyrus ochroleucus</i> Hook.                      | 6                | 1.83           | 4              | 1.75           |
| <i>Lilium philadelphicum</i> (L.)                      |                  |                |                |                |
| <i>Maianthemum canadense</i> Desf.                     |                  |                |                |                |
| <i>Maianthemum stellatum</i> (L.) Link                 |                  |                | 1              | 1              |
| <i>Muhlenbergia richardsonis</i> (Trin.) Rydb.         | 2                | 2.5            |                |                |
| <i>Nasella viridula</i> (Trin.) Barkworth              | 2                | 5.5            |                |                |
| <i>Oxytropis campestris</i> L. DC.                     | 1                | 3              |                |                |
| <i>Petasites frigidus</i> (L.) Fr.                     |                  |                | 2              | 2              |
| <i>Poa palustris</i> L.                                | 1                | 2              |                |                |
| <i>Poa pratensis</i> L.                                | 14               | 19.21          | 14             | 6.5            |
| <i>Polygonum convolvulus</i> L.                        | 1                | 1              | 2              | 2              |
| <i>Populus tremuloides</i> Michx.                      |                  |                |                |                |
| <i>Potentilla arguta</i> Pursh                         | 3                | 7              |                |                |
| <i>Prunus virginiana</i> L.                            |                  |                |                |                |

**Table 4** continued

| Species   | Native grassland |                | Smooth brome   |                |
|---|------------------|----------------|----------------|----------------|
|   | Plots occupied   | Mean cover (%) | Plots occupied | Mean cover (%) |
| <i>Pulsatilla patens</i> (L.) Mill.                       | 1                | 3              |                |                |
| <i>Ribes americanum</i> Mill.                             |                  |                |                |                |
| <i>Rosa arkansana</i> Porter                              | 11               | 8.36           | 9              | 10             |
| <i>Rubus idaeus</i> L.                                    | 3                | 10.67          | 3              | 9.67           |
| <i>Rubus pubescens</i> Raf.                               |                  |                |                |                |
| <i>Solidago gigantea</i> Aiton                            |                  |                |                |                |
| <i>Solidago missouriensis</i> Nutt.                       | 6                | 1.83           | 1              | 1              |
| <i>Stellaria longifolia</i> Muhl. Ex Willd.               |                  |                |                |                |
| <i>Stellaria longipes</i> Goldie                          |                  |                | 1              | 1              |
| <i>Symphyotrichum ericoides</i> (L.) G.L. Nesom           | 2                | 2              |                |                |
| <i>Symphyotrichum falcatum</i> (Lindl.) G.L. Nesom        | 2                | 2              |                |                |
| <i>Symphyotrichum laeve</i> A. Love & D. Love             | 13               | 5.08           | 8              | 4.71           |
| <i>Symphoricarpos occidentalis</i> Hook.                  | 12               | 22.25          | 14             | 17             |
| <i>Taraxacum officinale</i> F.H. Wgg.                     | 2                | 1              |                |                |
| <i>Thalictrum venulosum</i> Trel.                         |                  |                | 1              | 8              |
| <i>Thermopsis rhombifolia</i> (Nutt. Ex Pursh) Richardson | 10               | 6.9            | 2              | 5              |
| <i>Tragapogon dubius</i> Scop.                            | 1                | 1              |                |                |
| <i>Vicia americana</i> Muhl. Ex Willd                     | 12               | 4.92           | 8              | 3.25           |
| <i>Viola adunca</i> Sm.                                   | 6                | 2              | 1              | 1              |
| Species   | Aspen edge       |                | Aspen interior |                |
|   | Plots occupied   | Mean cover (%) | Plots occupied | Mean cover (%) |
| <i>Achillea millefolium</i> L.                            | 2                | 1.5            |                |                |
| <i>Agrostis scabra</i> Willd.                             | 2                | 1              |                |                |
| <i>Amelanchier alnifolia</i> (Nutt.) Nutt. Ex M. Roem.    | 4                | 11.75          | 5              | 12.8           |
| <i>Anemone canadensis</i> L.                              | 1                | 3              |                |                |
| <i>Apocynum androsaemifolium</i> L.                       | 1                | 4              | 1              | 12             |
| <i>Aralia nudicaulis</i> L.                               |                  |                | 1              | 15             |
| <i>Artemisia ludoviciana</i> Nutt.                        | 2                | 1.5            |                |                |
| <i>Astragalus agrestis</i> Douglas ex G. Don              | 1                | 2              |                |                |
| <i>Bromus inermis</i> Leyss.                              | 10               | 24.1           | 9              | 8.56           |
| <i>Bromus porteri</i> (J.M. Coult.) Nash                  |                  |                |                |                |
| <i>Campanula rotundifolia</i> L.                          | 1                | 1              | 1              | 2              |
| <i>Carex stenophylla</i> Wahlb.                           | 10               | 3.2            | 11             | 3.55           |
| <i>Cirsium arvense</i> (L.) Scop.                         |                  |                |                |                |
| <i>Collomia linearis</i> Nutt.                            |                  |                |                |                |
| <i>Comandra umbellata</i> (L.) Nutt                       |                  |                |                |                |
| <i>Dactylis glomerata</i> L.                              | 2                | 1              | 2              | 2.5            |
| <i>Danthonia intermedia</i> Vasey                         |                  |                |                |                |
| <i>Elymus glaucus</i> Buckley                             | 2                | 2.5            | 1              | 10             |
| <i>Chamerion angustifolium</i> (L.)                       | 1                | 2              |                |                |
| <i>Erigeron caespitosus</i> Nutt.                         | 1                | 1              |                |                |
| <i>Erigeron glabellus</i> Nutt.                           |                  |                |                |                |



**Table 4** continued

| Species   | Aspen edge     |                | Aspen interior |                |
|---|----------------|----------------|----------------|----------------|
|   | Plots occupied | Mean cover (%) | Plots occupied | Mean cover (%) |
| <i>Festuca hallii</i> (Vasey) Piper                       | 1              | 1              |                |                |
| <i>Fragaria virginiana</i> Duchesne                       | 3              | 3.33           | 3              | 2              |
| <i>Gaillardia aristata</i> Pursh                          |                |                |                |                |
| <i>Galium boreale</i> L.                                  | 12             | 3.75           | 9              | 1.67           |
| <i>Geum triflorum</i> Pursh                               |                |                |                |                |
| <i>Hesperostipa curtisetata</i> (Hitcch.) Barkworth       | 3              | 7              |                |                |
| <i>Heuchera richardsonii</i> R. Br.                       | 1              | 1              |                |                |
| <i>Lactuca tatarica</i> (L.) C.A. Mey.                    | 1              | 6              | 1              | 2              |
| <i>Lathyrus ochroleucus</i> Hook.                         | 7              | 4.14           | 8              | 3.75           |
| <i>Lilium philadelphicum</i> (L.)                         |                |                | 1              | 2              |
| <i>Maianthemum canadense</i> Desf.                        | 1              | 3              | 3              | 1.67           |
| <i>Maianthemum stellatum</i> (L.) Link                    | 4              | 4.75           | 4              | 1.5            |
| <i>Muhlenbergia richardsonis</i> (Trin.) Rydb.            |                |                |                |                |
| <i>Nasella viridula</i> (Trin.) Barkworth                 |                |                |                |                |
| <i>Oxytropis campestris</i> L. DC.                        |                |                |                |                |
| <i>Petasites frigidus</i> (L.) Fr.                        | 1              | 1              |                |                |
| <i>Poa palustris</i> L.                                   |                |                |                |                |
| <i>Poa pratensis</i> L.                                   | 10             | 6.8            | 10             | 4.6            |
| <i>Polygonum convolvulus</i> L.                           | 1              | 1              |                |                |
| <i>Populus tremuloides</i> Michx.                         |                |                |                |                |
| <i>Potentilla arguta</i> Pursh                            | 1              | 3              |                |                |
| <i>Prunus virginiana</i> L.                               |                |                | 3              | 18.33          |
| <i>Pulsatilla patens</i> (L.) Mill.                       |                |                |                |                |
| <i>Ribes americanum</i> Mill.                             | 2              | 10             | 3              | 6.67           |
| <i>Rosa arkansana</i> Porter                              | 11             | 21.91          | 12             | 30.42          |
| <i>Rubus idaeus</i> L.                                    | 11             | 21             | 11             | 15.78          |
| <i>Rubus pubescens</i> Raf.                               |                |                | 1              | 35             |
| <i>Solidago gigantea</i> Aiton                            | 1              | 2              |                |                |
| <i>Solidago missouriensis</i> Nutt.                       | 1              | 1              |                |                |
| <i>Stellaria longifolia</i> Muhl. Ex Willd.               |                |                | 1              | 1              |
| <i>Stellaria longipes</i> Goldie                          |                |                |                |                |
| <i>Symphyotrichum ericoides</i> (L.) G.L. Nesom           |                |                |                |                |
| <i>Symphyotrichum falcatum</i> (Lindl.) G.L. Nesom        | 1              | 5              |                |                |
| <i>Symphyotrichum laeve</i> A. Love & D. Love             | 4              | 2.5            | 3              | 4              |
| <i>Symphoricarpos occidentalis</i> Hook.                  | 7              | 24.57          | 8              | 20.63          |
| <i>Taraxacum officinale</i> F.H. Wgg.                     | 2              | 1.5            |                |                |
| <i>Thalictrum venulosum</i> Trel.                         | 5              | 4.6            | 6              | 3.67           |
| <i>Thermopsis rhombifolia</i> (Nutt. Ex Pursh) Richardson | 2              | 1.5            |                |                |
| <i>Tragopogon dubius</i> Scop.                            |                |                |                |                |
| <i>Vicia americana</i> Muhl. Ex Willd                     | 4              | 1.75           | 4              | 1.75           |
| <i>Viola adunca</i> Sm.                                   | 4              | 2.25           | 5              | 3.8            |

Percent cover of all vascular plant species was taken in a 1 m<sup>2</sup> area in each plot

**Table 5** Pairwise comparisons of environmental variables measured across the four common community types of the aspen parkland (native grassland, smooth brome, aspen edge, aspen interior)

|                                 | Species richness |          | Total cover |          | Dissolved organic N |          | Total inorganic N |          | pH       |          | Soil moisture |          |
|---------------------------------|------------------|----------|-------------|----------|---------------------|----------|-------------------|----------|----------|----------|---------------|----------|
|                                 | <i>z</i>         | <i>p</i> | <i>z</i>    | <i>p</i> | <i>z</i>            | <i>p</i> | <i>z</i>          | <i>p</i> | <i>z</i> | <i>p</i> | <i>z</i>      | <i>p</i> |
| Native grassland—aspens edge    | 7.2              | <0.001*  | 2.6         | 0.047*   | -2.2                | 0.13     | 2.8               | 0.03*    | 1.2      | 0.63     | -0.4          | 0.97     |
| Aspen interior—aspens edge      | -0.6             | 0.93     | -1.7        | 0.30     | 1.6                 | 0.37     | -0.1              | 0.99     | -0.01    | 0.99     | 1.3           | 0.59     |
| Smooth brome—aspens edge        | -1.1             | 0.68     | 1.1         | 0.67     | -2.4                | 0.07     | 2.3               | 0.09     | 1.4      | 0.50     | 0.8           | 0.83     |
| Aspen interior—native grassland | -7.8             | <0.001*  | -4.3        | <0.001*  | 3.8                 | <0.001*  | -2.9              | 0.02*    | -1.2     | 0.62     | 1.7           | 0.33     |
| Smooth brome—native grassland   | -8.4             | <0.001*  | -1.5        | 0.46     | -0.3                | 0.99     | -0.5              | 0.97     | 0.2      | 0.99     | 1.3           | 0.358    |
| Smooth brome—aspens interior    | -0.5             | 0.96     | 2.9         | 0.02*    | -4.1                | <0.001*  | 2.4               | 0.07     | 1.4      | 0.49     | -0.4          | 0.98     |

Significant differences marked with \*

**Table 6** Species list of seedlings, identified as part of the seed bank study, collected from four community types in the aspen parkland ecoregion (native grassland, smooth brome, aspen edge, aspen interior) at the Kinsella Research Ranch in Kinsella, AB, Canada

| Community type                   |
|----------------------------------|
| Native grassland                 |
| <i>Achillea millefolium</i>      |
| <i>Agrostis scabra</i>           |
| <i>Androsace septentrionalis</i> |
| <i>Artemisia ludoviciana</i>     |
| <i>Carex synocephala</i>         |
| <i>Cirsium undulatum</i>         |
| <i>Mertensia paniculata</i>      |
| <i>Muhlenbergia cuspidata</i>    |
| <i>Poa palustris</i>             |
| <i>Poa pratensis</i>             |
| Smooth brome                     |
| <i>Agropyron subsecundum</i>     |
| <i>Agrostis scabra</i>           |
| <i>Androsace septentrionalis</i> |
| <i>Carex synocephala</i>         |
| <i>Geum triflorum</i>            |
| <i>Mertensia paniculata</i>      |
| <i>Poa palustris</i>             |
| <i>Poa pratensis</i>             |
| <i>Taraxacum officinale</i>      |
| Aspen edge                       |
| <i>Achillea millefolium</i>      |
| <i>Agrostis scabra</i>           |
| <i>Androsace septentrionalis</i> |

**Table 6** continued

|                                  |
|----------------------------------|
| <i>Bouteloua gracilis</i>        |
| <i>Carex synocephala</i>         |
| <i>Geum triflorum</i>            |
| <i>Lepidium densiflorum</i>      |
| <i>Mertensia paniculata</i>      |
| <i>Poa palustris</i>             |
| <i>Rubus idaeus</i>              |
| <i>Solidago missouriensis</i>    |
| <i>Taraxacum officinale</i>      |
| Aspen interior                   |
| <i>Achillea millefolium</i>      |
| <i>Agropyron trachycaulum</i>    |
| <i>Androsace septentrionalis</i> |
| <i>Carex synocephala</i>         |
| <i>Geum triflorum</i>            |
| <i>Hesperostipa curtisetata</i>  |
| <i>Mertensia paniculata</i>      |
| <i>Poa palustris</i>             |
| <i>Poa pratensis</i>             |
| <i>Rubus idaeus</i>              |
| <i>Solidago canadensis</i>       |
| <i>Stellaria longifolia</i>      |
| <i>Stellaria</i> sp.             |
| <i>Taraxacum officinale</i>      |

Seeds were collected by taking four 3 cm wide × 17 cm depth soil cores at the four corners of a 1 m<sup>2</sup> plot and pooling them. Following a sieve treatment to remove large debris, soil was spread in seedling trays in a greenhouse and allowed to grow for 4 months (soil was turned over after 3 months)

**Table 7** Pairwise comparisons of survival, total biomass, and average biomass of smooth brome (*B. inermis*) seedlings across four community types

|                                 | Total biomass |          | Average biomass |          | Survival |          |
|---------------------------------|---------------|----------|-----------------|----------|----------|----------|
|                                 | <i>z</i>      | <i>p</i> | <i>z</i>        | <i>p</i> | <i>z</i> | <i>p</i> |
| Native grassland—aspens edge    | −0.87         | 0.82     | 1.06            | 0.72     | −1.61    | 0.11     |
| Aspen interior—aspens edge      | −0.01         | 0.99     | −0.66           | 0.91     | 1.25     | 0.21     |
| Smooth brome—aspens edge        | −3.10         | 0.01*    | −2.32           | 0.09     | −3.42    | <0.001*  |
| Aspen interior—native grassland | 0.88          | 0.82     | −1.75           | 0.3      | 2.82     | 0.005*   |
| Smooth brome—native grassland   | −2.24         | 0.11     | −3.45           | 0.003*   | −1.92    | 0.055    |
| Smooth brome—aspens interior    | −3.11         | 0.01*    | −1.70           | 0.33     | −4.52    | <0.001*  |

Ten brome seeds were planted in each community type in 2014 and allowed to grow for 2 months before harvest

Significant differences marked with \*

**Table 8** Individual linear mixed models testing for associations between smooth brome (*Bromus inermis*) seedling total biomass, (b) average biomass and (c) survival and a variety of biotic and abiotic conditions measured across native communities

|                                  | Total biomass |          | Average biomass |          | Survival |          |
|----------------------------------|---------------|----------|-----------------|----------|----------|----------|
|                                  | <i>F</i>      | <i>p</i> | <i>F</i>        | <i>p</i> | <i>z</i> | <i>p</i> |
| Total inorganic N                | 0.1           | 0.76     | 0.57            | 0.46     | −1.53    | 0.13     |
| Soil moisture                    | 8.74          | 0.0064*  | 5.04            | 0.033*   | 2.02     | 0.04*    |
| DON                              | 4.04          | 0.054*   | 6.76            | 0.015*   | −0.65    | 0.51     |
| pH                               | 0.14          | 0.71     | 1.64            | 0.21     | −0.17    | 0.86     |
| Species richness                 | 0.51          | 0.48     | 0.1             | 0.76     | −1.74    | 0.08     |
| Total cover                      | 0.05          | 0.83     | 0.12            | 0.73     | −0.59    | 0.55     |
| Community type                   | 0.46          | 0.64     | 1.01            | 0.38     |          |          |
| Native grassland—aspens edge     |               |          |                 |          | 1.61     | 0.11     |
| Native grassland—aspens interior |               |          |                 |          | 2.82     | 0.005*   |
| Aspens edge—aspens interior      |               |          |                 |          | 1.25     | 0.21     |

Significant differences marked with \*

**References**

Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. *Oecologia* 141:612–619

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect Plant Ecol Evol Syst* 3:52–66

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46

Baker BS, Jung GA (1968) Effect of environmental conditions on the growth of four perennial grasses in response to controlled temperature. *Agron J* 60:155–158

Bardgett RD, Streeter TC, Bol R (2003) Soil microbes compete effectively with plants for organic-nitrogen inputs to temperate grasslands. *Ecology* 84:1277–1287

Bates D, Maechler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48

Bennett JA, Stotz GC, Cahill JF (2014) Patterns of phylogenetic diversity are linked to invasion impacts, not invasion resistance, in a native grassland. *J Veg Sci* 25:1315–1326

Blaney CS, Kotanen PM (2001) Effects of fungal pathogens on seeds of native and exotic plants: a test using congeneric pairs. *J Appl Ecol* 38:1104–1113

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. *Bioscience* 54:677–688

Cahill JF, Lamb EG (2007) Interactions between root and shoot competition and plant traits. *HortScience* 42:1110–1112

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Den Boer PJ, Gradwell G (eds) *Dynamics of populations*. PUDOC, San Vicente, pp 298–312

Cully AC, Cully JF, Hiebert RD (2003) Invasion of exotic plant species in tallgrass prairie fragments. *Conserv Biol* 17:990–998

Davis MA, Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasibility. *Ecol Lett* 4:421–428

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534

- DiAllesandro A, Kobiela BP, Biondini M (2013) Invasion as a function of species diversity: a case study of two restored North Dakota grasslands. *Ecol Restor* 31:186–194
- Didham RK, Tylisanakis JM, Hutchison MA, Ewers RM, Gemmell NJ (2005) Are invasive species the drivers of ecological change? *Trends Ecol Evol* 20:470–474
- Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–523
- Elton C (1958) *The ecology of invasions by animals and plants*. Methuen, London
- Everett RL, Meeuwig RO, Stevens R (1978) Deer mouse preference for seed of commonly planted species, indigenous weed seed, and sacrifice foods. *J Range Manag* 31:70–73
- Fargione JE, Tilman D (2005) Diversity decreases invasion via both sampling and complementarity effects. *Ecol Lett* 8:604–611
- Fink KA, Wilson SD (2011) *Bromus inermis* invasion of a native grassland: diversity and resource reduction. *Botany* 89:157–164
- Foster BL, Kindscher K, Houseman GR, Murphy CA (2009) Effects of hay management and native species sowing on grassland community structure, biomass, and restoration. *Ecol Appl* 19:1884–1896
- Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–1081
- Grilz PL, Romo JT, Young J (1994) Comparative germination of smooth brome and plains rough fescue. *Prairie Nat* 26:157–170
- Haag JJ, Coupe MD, Cahill JF (2004) Antagonistic interactions between competition and insect herbivory on plant growth. *J Ecol* 92:156–167
- Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ, Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. *Ecol Lett* 8:1066–1074
- Hawkes CV, Wren IF, Herman DJ, Firestone MK (2005) Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecol Lett* 8:976–985
- Heerd G, Verweij GL, Bekker RM, Bakker JP (1996) An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. *Funct Ecol* 10:144–151
- HilleRisLambers J, Yelenik SG, Colman BP, Levine JM (2010) California annual grass invaders: the drivers or passengers of change? *J Ecol* 98:1147–1156
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363
- Hulme PE (1998) Post-dispersal seed predation: consequences for plant demography and evolution. *Perspect Plant Ecol Evol Syst* 1:32–46
- Inderjit, Wardle DA, Karban R, Callaway RM (2011) The ecosystem and evolutionary contexts of allelopathy. *Trends Ecol Evol* 26:655–662
- James JJ, Drenovsky RE, Monaco TA, Rinella MJ (2011) Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? *Ecol Appl* 21:490–502
- Janzen D (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67–70
- Kourtev PS, Ehrenfeld JG, Häggblom M (2003) Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biol Biochem* 35:895–905
- Kraus TEC, Dahlgren RA, Zasoski RJ (2003) Tannins in nutrient dynamics of forest ecosystems—a review. *Plant Soil* 256:41–66
- Lamb EG, Shore BH, Cahill JF (2007) Water and nitrogen addition differentially impact plant competition in a native rough fescue grassland. *Plant Ecol* 192:21–33
- Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecol Lett* 7:975–989
- Liancourt P, Corcket E, Michalet R (2005) Stress tolerance abilities and competitive responses in a watering and fertilization field experiment. *J Veg Sci* 16:713–722
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536
- MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55
- MacDougall AS, Wilson SD (2007) Herbivory limits recruitment in an old-field seed addition experiment. *Ecology* 88:1105–1111
- McCune B, Grace JB, Urban DL (2002) *Analysis of ecological communities*. MjM Software Design, Gleneden Beach
- McKone MJ (1985) Reproductive biology of several brome-grasses (*Bromus*): breeding system, pattern of fruit maturation, and seed set. *Am J Bot* 72:1334–1339
- Myhr KE, Tesar MB, Davis RA, deZeeuw DJ (1966) Death of smooth brome (*Bromus inermis* Leyss.) on organic soil. *Crop Sci* 6:221
- Naeem S, Knops JMH, Tilman D, Howe KM, Kennedy T, Gale S (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91:97–108
- Nernberg D, Dale MRT (1997) Competition of five native prairie grasses with *Bromus inermis* under three moisture regimes. *Can J Bot* 75:2140–2145
- Nordin A, Schmidt IK, Shaver GR (2004) Nitrogen uptake by arctic soil microbes and plants in relation to soil nitrogen supply. *Ecology* 85:955–962
- Otfinowski R, Kenkel NC, Catling PM (2007) The biology of Canadian weeds. 134. *Bromus inermis* Leyss. *Can J Plant Sci* 87:183–198
- Parker JD, Hay ME (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecol Lett* 8:959–967
- Parker SS, Schimel JP (2010) Invasive grasses increase nitrogen availability in California grassland soils. *Invasive Plant Sci Manag* 3:40–47
- Pearse IS, Hipp AL (2014) Native plant diversity increases herbivory to non-natives. *Proc R Soc Lond B* 281:20141841
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) *Nlme: linear and nonlinear mixed effects models*, R package version 3.1-127. <http://CRAN.R-project.org/package=nlme>
- Piper CL, Lamb EG, Siciliano SD (2015) Smooth brome changes gross soil nitrogen cycling processes during

- invasion of a rough fescue grassland. *Plant Ecol* 216:235–246
- Reinhart KO, Callaway RM (2006) Soil biota and invasive plants. *New Phytol* 170:445–457
- Rejmanek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology* 77:1655–1661
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Robertson GP, Coleman DC, Bledsoe CS, Sollins P (1999) Standard soil methods for long-term ecological research. Oxford UP, New York, 480 p
- Romo JT, Grilz PL, Driver EA (1990) Invasion of the Canadian prairies by an exotic perennial. *Blue Jay* 8:130–135
- Rothstein DE, Vitousek PM, Simmons BL (2004) An exotic tree alters decomposition and nutrient cycling in a Hawaiian montane forest. *Ecosystems* 7:805–814
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Annu Rev Ecol Syst* 32:305–332
- Schimel JP, Bennett J (2004) Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85:591–602
- Smith MD, Wilcox JC, Kelly T, Knapp AK (2004) Dominance not richness determines invasibility of tallgrass prairie. *Oikos* 106:252–262
- Stacy MD, Perryman BL, Stahl PD, Smith MA (2005) Brome control and microbial inoculation effects in reclaimed cool-season grasslands. *Rangel Ecol Manag* 58:161–166
- Stark JM, Norton JM (2015) The invasive annual cheatgrass increases nitrogen availability in 24-year-old replicated field plots. *Oecologia* 177:799–809
- Stohlgren TJ, Barnett DT, Kartesz J (2003) The rich get richer: patterns of plant invasions in the United States. *Front Ecol Environ* 1:11–14
- Su JG, Bork EW (2007) Characterization of diverse plant communities in Aspen Parkland rangeland using LiDAR data. *Appl Veg Sci* 10:407–416
- Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol* 176:256–273
- Thompson K, Grime JP (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J Ecol* 67:893–921
- Van Der Heijden MGA, Bardgett RD, Van Straalen NM (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol Lett* 11:296–310
- Vander Wall SB, Kuhn KM, Beck MJ (2005) Seed removal, seed predation, and secondary dispersal. *Ecology* 86:801–806
- Vilà M, Weiner J (2004) Are invasive plant species better competitors than native plant species? Evidence from pairwise experiments. *Oikos* 105:229–238
- Vinton MA, Goergen EM (2006) Plant–soil feedbacks contribute to the persistence of *Bromus inermis* in tallgrass prairie. *Ecosystems* 9:967–976
- White DJ, Haber E, Keddy C (1993) Invasive plants of natural habitats in Canada. Canadian Wildlife Service, Environment Canada, Ottawa, 121 p
- White SR, Tannas S, Bao T, Bennett JA, Bork EW, Cahill JF (2013) Using structural equation modelling to test the passenger, driver and opportunist concepts in a *Poa pratensis* invasion. *Oikos* 122:377–384
- Williamson M, Fitter A (1996) The varying success of invaders. *Ecology* 77:1661–1666. doi:[10.2307/2265769](https://doi.org/10.2307/2265769)
- Wilson SD, Pinno BD (2013) Environmentally-contingent behaviour of invasive plants as drivers or passengers. *Oikos* 122:129–135
- Wiser SK, Allen RB, Clinton PW, Platt KH (1998) Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79:2071–2081