

Clonal integration facilitates the proliferation of smooth brome clones invading northern fescue prairies

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Abstract Predicting exotic invaders and reducing their impacts on the biodiversity and function of native ecosystems require understanding of the mechanisms that facilitate their success during key stages of invasion. We determined whether clonal growth, characteristic of the majority of successful invaders of natural areas, facilitates the proliferation of *Bromus inermis* (smooth brome), an exotic grass invading prairie ecosystems across the Great Plains. By manipulating the below-ground connections of proliferating rhizomes as well as the levels of soil nitrogen along the margins of clones invading northern fescue prairies in Manitoba, Canada, we hypothesized that physiological integration would most benefit ramets invading low resource environments. Severing clonal connections reduced the mass of smooth brome shoots invading native prairies and was exacerbated by the immobilization of soil nutrients with glucose. Clonal connections were equally important in the maintenance of smooth brome density and the horizontal proliferation of ramets. Our results demonstrate the role of physiological integration in the proliferation of a clonal exotic invader and may help explain the success of clonal invaders in other regions. Although integration among invading ramets suggests several

possibilities for successful management, future research must continue to elucidate differences in the invasiveness of native versus exotic species as well as the persistence of clonal connections among exotic invaders.

Keywords Invasive plant · Physiological integration · *Bromus inermis* · Native prairie · Clonal growth

Introduction

Exotic plant invasions pose a growing threat to the endemic biodiversity and function of ecosystems around the world (D'Antonio and Vitousek 1992; Davis 2003; Yurkonis et al. 2005). The success of exotic species is contingent upon their transition between several stages of invasion (Puth and Post 2005; Theoharides and Dukes 2007). For example, while the proliferation of exotic invaders is contingent on their interaction with native communities (Kolar and Lodge 2001), their establishment often depends on propagule pressure, disturbance, and the diversity and structure of invaded habitats (Lockwood et al. 2005; Pokorny et al. 2005; Hierro et al. 2006). Despite the large number of exotic species in most regional floras, few among them have become serious invaders and many simply contribute to local species richness (Rosenzweig 2001). Consequently, predicting exotic invaders and reducing their impacts on native

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communities require an understanding of the mechanisms that facilitate their success at each stage of invasion (Smith et al. 1999). Here, we determine whether clonal growth, characteristic of the majority of successful invaders of natural areas (Andersen 1995; Pyšek 1997; Reichard and Hamilton 1997; Acosta et al. 2006; Cadotte et al. 2006), facilitates the proliferation of an exotic grass invading northern fescue prairies.

Clonal plants, described as genetic individuals comprising of potentially independent modules (Kelly 1995), dominate most regional floras. In central Europe, clonal species comprise as much as 69% of the native flora and over 90% of alpine and arctic communities (Kelly 1995; Pyšek 1997). The success of clonal species is often attributed to their capacity to share resources among individual subunits. Translocation of resources, including water, carbohydrates, and minerals (Alpert and Mooney 1986; Lau and Young 1988; Tissue and Nobel 1988; Stuefer and Hutchings 1994; Alpert 1996; Wijesinghe and Hutchings 1997; Kembell and Marshall 1995), enables clonal species to exploit patchy resources (Alpert and Mooney 1986; Wijesinghe and Hutchings 1997; Ikegami et al. 2008), ameliorate environmental stress (Amsberry et al. 2000; Pennings and Callaway 2000), and reduce the impacts of competition and herbivory (Hartnett and Bazzaz 1985; Schmid et al. 1988).

Despite the preponderance of clonal growth among successful invaders, few experimental studies have explored the functional role of clonality in the course of exotic invasions (Puth and Post 2005; but see Meyer and Schmid 1999; Maurer and Zedler 2002; Price et al. 2002). Where examined, clonal growth most often facilitated the proliferation of exotic species invading stressful environments, including wetlands (Amsberry et al. 2000) but its role in supporting invasions of other plant communities is less clear (Pennings and Callaway 2000).

We focused our experiments on examining the role of clonal growth in exotic plants invasions of native prairies. Using smooth brome (*Bromus inermis* Leyss.), a Eurasian perennial that has successfully invaded prairie ecosystems across the Great Plains (Cully et al. 2003; Otfinowski et al. 2007), we designed a field experiment to examine the importance and environmental contexts of clonal integration among invading plants. We focused our experiment along the margins of invading clones,

where interspecific interactions between the invader and the native prairie community most likely contribute to resource heterogeneity (Caraco and Kelly 1991) and hypothesized that physiological integration would most benefit ramets invading low resource environments.

Methods

Research was conducted in Riding Mountain National Park, MB, Canada. The park occupies an area of 2,978 km² in Western Canada, 225 km northwest of Winnipeg (49° 53' 04" N–97° 08' 47" W) and consists of large areas of rolling upland (550–640 m), underlain by glacial tills (Lang 1974). The region is characterized by mean annual precipitation of 450–500 mm and a growing season of 168–173 days; mean temperatures range between –18°C in January and 18°C in July (Leeson et al. 2005). The park lies in the Mixedwood Section of the Boreal Forest Region (Rowe 1972) and protects areas of rough fescue prairie, threatened in western Canada as a result of grazing, cultivation, and invasions by exotic species (Trottier 1986).

To examine the role of physiological integration in the proliferation of smooth brome, we randomly selected 20 clones invading prairies in each of two areas of Riding Mountain National Park. Prairies in the park have been recently invaded by smooth brome, which continues to compromise their function and biodiversity, transforming diverse plant communities into virtual monocultures (Otfinowski et al. 2007). Although invading clones of smooth brome forms dense, circular patches (5–15 m in diameter), the genetic structure of these remains unresolved. The two study areas were situated approximately 50 km apart; soils at the more western Bob Hill prairie were more xeric and lower in mineral nitrogen than the centrally located Strathclair prairie [moisture (0–20 cm, July 2005) $7.5 \pm 3.7\%$ vs. $9.5 \pm 4.2\%$, $F_{1,100} = 9.2$, $P = 0.0031$; mineral nitrogen (0–15 cm; July 2005): NH_4^+ , 5.3 ± 0.4 mg/kg vs. 9.1 ± 0.4 mg/kg, $F_{1,38} = 37.4$, $P < 0.0001$; NO_3^- , 0.60 ± 0.1 mg/kg vs. 2.1 ± 0.2 mg/kg, $F_{1,38} = 40.7$, $P < 0.0001$].

We examined the importance and the environmental contexts that favour physiological integration among smooth brome ramets invading prairies by manipulating belowground rhizomes and the levels of

soil nitrogen. Based on a factorial design, we divided each clone into three pie-shaped sections and randomly assigned one of two rhizome treatments, three nitrogen treatments, and a control to each (Fig. 1). Rhizomes, located 5–15 cm below the soil surface (R. Otfinowski, pers. obs.), were left intact or severed using plastic lawn edging (0.15 × 1.6 m), installed into narrow, semi-circular trenches along the margins of invading clones. Severing connections is a standard method of investigating the importance of clonal integration (Kelly 1995). Despite its potential to traumatize plants and allow entry of pathogens (Kelly 1995), many field studies have found no effect of severing on plants, suggesting that potential artefacts are limited (Hartnett and Bazzaz 1983; Alpert 1991; Evans 1992; Pennings and Callaway 2000; Peltzer 2002). We did not observe any sudden death of ramets or increased incidence of disease following severing.

Starting in May 2004, we broadcast glucose (40% C) and ammonium nitrate fertilizer (34-0-0) inside the circular treatment areas (diameter =

0.91 cm) to manipulate the levels of soil nitrogen available to invading ramets. Annual rate of glucose ($300 \text{ gCm}^{-2} \text{ year}^{-1}$) was split among three applications (May, June, July; 2004, 2005) and corresponded to the calculated amount of carbon required to immobilize most mineral nitrogen within 10 cm of the soil surface; application of fertilizer ($11 \text{ gNm}^{-2} \text{ year}^{-1}$) were also split (May, June, 2004, 2005) and corresponded with the amount of mineral nitrogen immobilized in the glucose treatments. Carbon amendments to soils stimulate microbial immobilization of available nitrogen (Recous and Mary 1990) and can reduce the competitiveness of exotic invaders (Blumenthal et al. 2003; Perry et al. 2004). In separate trials, additions of glucose ($300 \text{ gCm}^{-2} \text{ year}^{-1}$) decreased soil concentrations of nitrate more than ammonium. In 2005, soil nitrate (0–15 cm) declined 25–59% ($2.4 \pm 0.2 \text{ mg/kg}$ (control; annual mean ± 1 S.E.) vs. $1.4 \pm 0.1 \text{ mg/kg}$, $F_{1,99} = 33.1$, $P < 0.0001$), compared with 4–9% for ammonium (9.7 ± 0.5 vs. 9.1 ± 0.5 , $F_{1,99} = 1.5$, $P = 0.2275$).

Impacts of rhizome and nitrogen manipulations on smooth brome invasion were measured following two growing seasons. The density and mass of all ramets were measured inside $50 \times 50 \text{ cm}$ quadrats centred inside each treatment area. Ramets were clipped at the soil surface, air dried (48 h, 60°C), and weighed. We determined the encroachment of clones by comparing the position of invading ramets at the beginning and at the end of the experiment.

Statistical analysis

We used two-way analysis of variance (ANOVA), blocked by individual clones, to examine the response of smooth brome to rhizome and nitrogen manipulations. All data were log transformed to improve the homogeneity of variance (Zar 1999). Data were pooled where no significant differences were found between the two study sites. Linear models were implemented using Data Desk 6.2 (Data Description Inc., Ithaca NY).

Results

Severing clonal connections reduced the mass of smooth brome shoots invading native prairies and

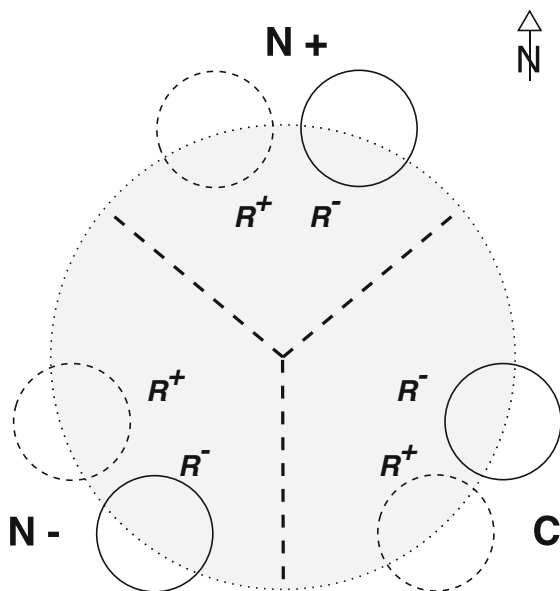


Fig. 1 Manipulation of soil nitrogen and rhizomes along the margins smooth brome (*Bromus inermis*) clones invading northern fescue prairies in Riding Mountain National Park, MB, Canada. Each clone was divided into three sections and each randomly assigned the following treatments: intact rhizome (R+), severed rhizome (R-), nitrogen immobilized (N-), nitrogen unmanipulated (C), nitrogen added (N+). Circles represent treatment areas (diameter = 0.91 cm)

was exacerbated by the immobilization of soil nutrients with glucose. Reducing soil nitrogen decreased the biomass of shoots disconnected from parent plants, but had no effect on those with intact rhizomes (Fig. 2a; Table 1). Clonal connections were equally important in the maintenance of smooth brome density, and for all levels of nitrogen, the density of brome shoots declined following the severing of rhizomes (Fig. 2b; Table 1). Physiological integration remained important in the horizontal proliferation of smooth brome clones, but its effect was site specific. Among the two study areas, sharing of resources with mother clones inhibited the encroachment of ramets invading Bob Hill prairie in the western part of the Park, an area lower in mineral soil nitrogen (Fig. 2c–d, Table 1).

Discussion

Our observations demonstrate the importance of physiological integration in the proliferation of smooth brome clones invading native prairies. Underground rhizomes, connecting ramets with

mother clones, maintained the biomass and density of invading ramets and were, as predicted, key to the proliferation of smooth brome into resource poor environments. Physiological integration between vegetatively connected ramets often facilitates the colonization of environments where parts of the clone experience contrasting conditions. Coastal dunes, deserts, and wetlands are often dominated by clonal perennials, whose vegetative connections permit the “homogenization” of patchy resources and the amelioration of environmental stress (Alpert 1996; Pennings and Callaway 2000; Ikegami et al. 2008). Translocation between ramets supported the encroachment of smooth brome into adjacent prairies; however, sharing of resources with the mother clone inhibited the proliferation of ramets invading a nutrient-poor prairie. While integration among ramets most often entails transport of resources towards younger ramets (Alpert 1991), competition among sibling ramets can reduce their growth in heterogeneous environments (Hellström et al. 2006). Others have suggested that suppression of proliferation in low nutrient environments may reduce intraramet competition for scarce resources and facilitate the

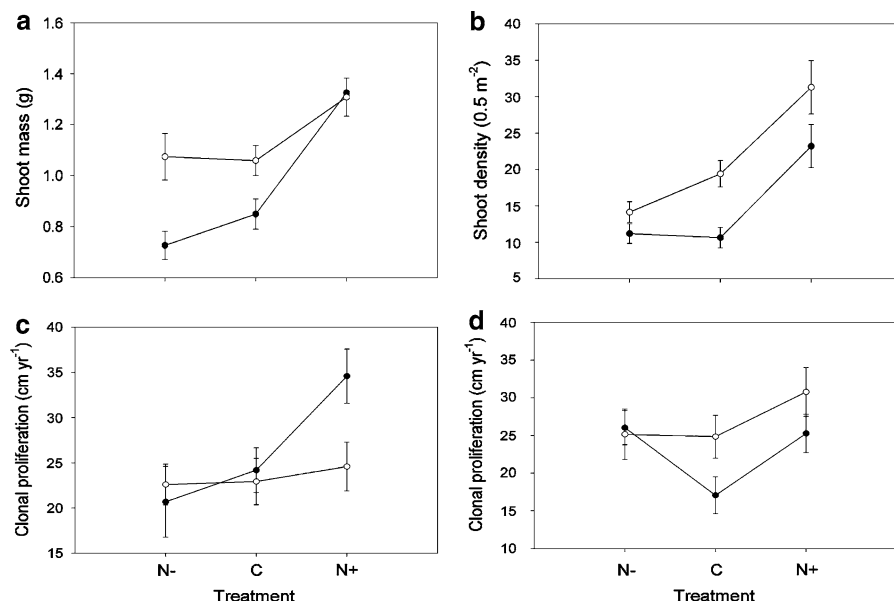


Fig. 2 Impacts of soil nitrogen addition (N+) and immobilization (N-) on the biomass, density, and horizontal proliferation of smooth brome (*Bromus inermis*) ramets invading two northern fescue prairies in Riding Mountain National Park, MB, Canada. Ramets along the margins of invading clones were either left intact (open symbols) or severed from parent clones (closed

symbols; $n = 40$, error bars = ± 1 S.E.). Illustrations of shoot mass (a) and density (b) represent the combined measurements from two study areas; those of clonal proliferation represent separate measurements from Bob Hill (c) and Strathclair (d) prairies, located in the western and central areas of the Park, respectively (see text for details)

Table 1 Two-way ANOVA testing the effect of soil nitrogen addition and immobilization on the biomass, density, and horizontal proliferation of smooth brome (*Bromus inermis*) invading a two northern fescue prairies in Riding Mountain

Effect	Shoot mass			Shoot density			Encroachment (Bob Hill)			Encroachment (Strathclair)		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Sever	18.18	1.195	<0.0001	21.90	1.195	<0.0001	0.08	1.95	0.7729	0.90	1.95	0.3461
Nitrogen	37.58	2.195	<0.0001	27.52	2.195	<0.0001	3.25	2.95	0.0432	3.12	2.95	0.0488
Sever × nitrogen	6.57	2.195	<0.0017	1.87	2.195	0.1563	4.53	2.95	0.0132	0.65	2.95	0.5264

Ramets along the margins of invading clones were either left intact or severed from parent clones

formation of monoclonal patches (Schmid and Bazzaz 1987). The observed increase in the proliferation of severed ramets invading a low-nutrient prairie illustrates the potential of clonal invaders to rapidly dominate nutrient enriched areas (Sutherland and Stillman 1988). Increasing concerns about the impacts of atmospheric nitrogen deposition (Porter and Johnson 2007) emphasize the importance of environmental context in the proliferation of clonal invaders and stress their threat to low-nutrient environments (Soukupová 1992, Brooks 2003, Porter and Johnson 2007).

Our observations illustrate the importance of vegetative connections in the proliferation of exotic plants invading native prairies. Although several previous authors have accorded greater importance to clonal integration in resource-limited environments, its role in interspecific interactions remains unresolved. For example, Amsberry et al. (2000) and Pennings and Callaway (2000) reported that clonal connections did not affect the growth of plants penetrating dense marsh communities, and Peltzer (2002) did not observe a significant decrease in the growth of severed *Populus tremuloides* ramets invading a native prairie. In contrast, by manipulating the composition of plant communities neighbouring *Solidago canadensis*, Hartnett and Bazzaz (1985) demonstrated the importance of physiological integration in ameliorating impacts of interspecific interactions. It remains unresolved whether more intense interactions between smooth brome and its neighbours could inhibit or reverse the observed integration (Kelly 1995; Hellström et al. 2006) and how other factors, including intraspecific competition between ramets (Bullock et al. 1994), the spatio-temporal heterogeneity of resources (Gough et al. 2002), and the age and length of clonal connections

National Park, MB, Canada. Analyses of ramet biomass and density were combined for two study areas, while those of clonal proliferation were separated. The *F*-values and their significance levels are shown

(Schmid and Bazzaz 1987; Bullock et al. 1994) affect its importance during invasions. These questions deserve further investigation.

The persistence of clonal connections remains key to understanding the impact of physiological integration on the invasiveness of exotic plants. Our observations illustrate that smooth brome ramets remain physiologically integrated along clone edges, a distance of at least 0.5 m from the clone margin, and based on the observed rate of clonal advance (~24 cm/year), those 2–3 years old remain active in supporting the vegetative advance of invading clones. In other herbaceous species, physiological integration often encompasses at least 4 or 5 rooted ramets (Noble and Marshall 1983; Headley et al. 1988; Birch and Hutchings 1999), but its maintenance may be contingent on the net contribution of connected ramets to the genet's growth (Kelly 1995). As a result, disintegration of clonal connections is predicted whenever the growth of daughter ramets does not compensate for the physiological demands of the older parts of the clone (Caraco and Kelly 1991).

Conceptual models of exotic plant invasion are characterized by several discrete steps, including dispersal, establishment, and proliferation (Kolar and Lodge 2001; Puth and Post 2005). Successful invasion requires that an exotic species be superior to the native species it displaces in at least one or all these stages. Even though exotic plants often possess traits that distinguish them from the native species they displace (Andersen 1995; Rejmánek and Richardson 1996; Kolar and Lodge 2001; but see Thompson et al. 1995; Acosta et al. 2006), successful invaders represent a variety of plant families and possess a wide range of life forms and breeding systems (Crawley 1987). Although our results demonstrate that clonal growth facilitates the proliferation of

smooth brome invading native prairies and may help explain the success of clonal invaders in other regions (Andersen 1995; Pyšek 1997; Reichard and Hamilton 1997; Acosta et al. 2006; Cadotte et al. 2006), many questions related to the success of clonal invaders remain unanswered. For example, clonal growth remains a common trait among native species in many plant communities (Kelly 1995; Pyšek 1997), and other factors, including ramet longevity, the persistence of clonal connections, and the spatio-temporal extent of physiological integration (Schmid and Bazzaz 1987; Jonsdottir and Watson 1997; Tamm et al. 2002), deserve further investigation. To our knowledge, no studies have explored these hypotheses in the context of differences between exotic invaders and the native plants they displace.

The preponderance of vegetative reproduction among successful invaders requires an understanding of the ecological contexts and the extent of physiological integration among invading species and the extent of physiological integration among invading ramets. Our results demonstrate that physiological integration maintains the biomass and density of smooth brome ramets invading native prairies and that its importance is greatest in low resource environments. The observed integration suggests several methods of managing clonal invaders. For example, applications of herbicide along the margins of invading clones could capitalize on the translocation of resources between the mother clone and establishing ramets and help slow or stop their proliferation (Brej 2001), while mowing the margins of invading clones could facilitate the potential disintegration of connections between the damaged ramets and the mother clone (Caraco and Kelly 1991; Meyer and Schmid 1999; Hellström et al. 2006). Our results suggest that due to their increased dependence on clonal subsidy, ramets in resource poor environments would be most vulnerable to such manipulations.

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