

Climatic variability alters the outcome of long-term community assembly

Andrew S. MacDougall^{1*}, Scott D. Wilson¹ and Jonathan D. Bakker²

¹Department of Biology, University of Regina, Regina, Saskatchewan, Canada, S4S 0A2; and ²College of Forest Resources, University of Washington, Box 354115, Seattle, Washington, 98195–4115, USA

Summary

1. We used seed additions to test experimentally whether long-term community assembly unfolds consistently (deterministic model) or whether different outcomes are possible depending on variations in climate and the presence of exotic dominants (stochastic model). The experiment was conducted in homogeneous semi-arid grassland on the northern Great Plains of North America. Native grass seed additions in each of 3 years (1994–96) were combined factorially with repeated selective herbicide applications to reduce the cover of the extant dominant, a Eurasian C₃ grass (*Agropyron cristatum*). We assessed whether composition converged or diverged among treatments between 1996 and 2004.

2. The outcome of long-term community assembly varied by establishment year, in association with significant variations in monthly growing-season precipitation from 68-year averages during the years when seed was added. In 2004, the added native C₄ grass *Bouteloua gracilis* dominated plots sprayed and seeded in 1994 and 1995, resisting re-invasion and having significantly higher plot diversity. In contrast, plots sown in 1996 – one of the driest years on record – reverted to the exotic C₃ grass. Seeded but unsprayed plots maintained their pre-treatment dominance by exotic grass. Rainfall variability was also associated with the extent of exotic grass cover and bare soil in unsprayed plots, and natural recruitment by native species from nearby prairie.

3. Establishment success varied significantly among the added species. All seeded grasses, other than *B. gracilis*, were mostly absent by 2004. The failure of these native C₃ species to establish appears consistent with deterministic assembly models where local abiotic conditions filter out unsuitable species.

4. Synthesis. Our results indicate that stochastic and deterministic processes operate simultaneously to influence community assembly, depending on interactions among climate, seed availability, species identity and disturbance during the initial stages of establishment. Multiple assembly trajectories developed, but the assembled communities did not include all the added species. Conversion of degraded grassland back to native-dominated grassland was possible, but only with the removal of the exotic dominant and seed additions during years that were suitably wet for establishment. Once formed, however, the assembled native community resisted re-invasion. This suggests that native grassland restoration will depend on establishment measures as intense as those used during initial cultivation almost a century earlier.

Key-words: climate variability, community assembly, competition, invasion, northern Great Plains, recruitment limitation, restoration, succession

Introduction

There are two contrasting models of community assembly within homogeneous environments (Weiher & Keddy 1995; Tofts & Silvertown 2002; Walker & Wilson 2002; Bell 2005).

*Correspondence author. Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada, N1G 2W1. E-mail: amacdo02@uoguelph.ca

Deterministic models predict repeatable successional trajectories driven by trait differences, regardless of the order of establishment (Diamond 1975; Keddy 1992; Diaz *et al.* 1998; Grime 2001). Stochastic models predict non-repeatable successional trajectories driven by dispersal limitation, order of establishment or abundance feedbacks, with outcomes often determined by which species arrive first and in what abundance (Harper 1977; Chesson & Case 1986; Gilpin *et al.* 1986; Zobel 1992; Hubbell 2001; Tofts & Silvertown 2002;

MacDougall & Turkington 2004; Del Moral & Lacher 2005). Testing these alternatives can be limited by the short duration of assembly experiments, where transient dynamics predominate initially (Tilman 1988; Milchunas & Lauenroth 1995), and by temporal variability, where the intensity of limiting factors fluctuates among years (Adler *et al.* 2006; Adler & Levine 2007; Wilson 2007). In the latter case, the direction of community assembly can only be determined by repeating an experiment over multiple years and assessing variation in establishment success.

Here, we compare deterministic vs. stochastic models of community assembly using seed additions tracked over 9–11 years in an experiment repeated over 3 years. Our study site is environmentally homogeneous and dominated by an exotic grass at the start of the experiment. We asked whether all experimental treatments converged to the same composition and abundance over time, or whether alternative communities developed. Deterministic models predict that recovery by the exotic dominant should occur eventually, based on the assumption that its high abundance reflects site suitability and competitive superiority. Stochastic models predict that recovery should be resisted once individuals have established successfully, regardless of their taxonomic or functional identity (e.g. Sale 1977).

Many assembly experiments are initiated in unoccupied habitats and thus only examine size–symmetric interactions among the added species. However, size–asymmetric interactions (seedlings establishing amongst adults) are also important; many plant communities have been shown to be permeable and unsaturated with species (Turnbull *et al.* 2000). Therefore, the trajectory of assembly in later-successional communities may be controlled by dispersal limitation rather than by competition. We used selective herbicide applications to create areas where the abundance of the exotic grasses was greatly reduced, allowing us to examine the internal sorting among the added species over time and their resistance to re-invasion by the exotic dominant. Areas where herbicide was not applied allowed us to examine establishment success within the existing exotic community. Similarly, our long-term data allowed us to examine patterns of natural recruitment. Low diversity in short-term experimental plots is often interpreted as indicative of competitive resistance (i.e. deterministic control of diversity), but may actually reflect poor dispersal (i.e. stochastic control of diversity). Therefore, we tested whether the establishment of non-seeded species was dependent on community type (native or exotic cover).

Methods

STUDY AREA

We worked in an old field located in the Grasslands National Park of south-western Saskatchewan, Canada (49°22' N, 107°53' W; the 'tableland' site described in Bakker *et al.* 2003). The site is homogeneous in environment and vegetative cover. The soils are brown Chernozemic clay loams greater than 1 m in depth (Bakker *et al.* 2003; MacDougall & Wilson, unpubl. data). The old field was cultivated



Fig. 1. A plot (3 × 10 m) sown in 1994 and dominated by the C₄ native grass *Bouteloua gracilis*. The matrix vegetation is the introduced grass *Agropyron cristatum*, which was planted in the 1950s (Photo: S. Wilson, 2003).

from the early 1900s until 1951, when it was sown with *Agropyron cristatum*, an exotic C₃ perennial tussock grass that continues to dominate all untreated areas of the field (Fig. 1). Richness is low relative to native vegetation (Christian & Wilson 1999). Nearby (< 1 km), uncultivated areas support native mixed-grass prairie species (e.g. *Bouteloua gracilis*, *Stipa comata* and *Selaginella densa*). Annual rainfall in the region averages < 350 mm, based on 68 years of data from the weather station in Val Marie, Saskatchewan (c. 10 km to the west; <http://www.climate.weatheroffice.ec.gc.ca/index.html>), with approximately half falling from May to July. Annual growing-season temperatures average 15.9 °C.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSES

In 1994, 240 plots (3 × 10 m) were established within the *A. cristatum* field (Fig. 1). Eighty plots were assigned randomly to each of the three seed-addition years: 1994, 1995 or 1996.

The experiment was originally designed to test the relative effects of seeding method and *A. cristatum* control on restoration success, using four seed-addition treatments (none, hay gathered from native prairie, broadcast seed, and seed drilling) and three control treatments (none, herbicide, and mulching using wheat straw or sawdust). The experiment used a complete factorial design with 10 replicates per treatment, with results described previously (Bakker *et al.* 2003; Wilson & Partel 2003). For this study, we re-sampled the plots 9–11 years after plot establishment and considered only a subset of the initial treatments. We focused on the effects of seed addition via broadcasting and on the herbicide treatment. All other treatment types had either no impact on recruitment or control (e.g. mulching) or comparatively low germination, which suggested methodological limitations (hay, drilling). In total, we used 12 treatment combinations for this study [3 establishment years × 2 seeding treatments (broadcast, none) × 2 herbicide treatments (applied, not applied) × 10 replicates per treatment].

Herbicide (glyphosate) was applied using a combination of methods that increased in intensity over time in an attempt to eliminate *A. cristatum*. In 1994, the plots were sprayed (1.1 kg ha⁻¹)

in early May, when *A. cristatum* is growing but the native grasses are dormant. In subsequent years (1995–98), herbicide was applied in May and June using a tractor-mounted wick 10 cm above ground level. The wick applied herbicide to the taller *A. cristatum* but not the shorter native grasses. Herbicide was applied selectively to *A. cristatum* through 2003 for half of the plots seeded in 1994. This allowed us to compare persistence and invasion resistance by the added grasses, with and without the continuous suppression of *A. cristatum*.

The seed mixture contained up to four native grass species each year. The sowing density and species composition of the mixture was determined by seed availability from suppliers. The relative proportions in the mixture are also comparable to the relative per cent covers of the grasses in nearby native prairie (Bakker & Wilson, unpubl. data), thereby providing a crude surrogate for natural levels of seed output (e.g. MacDougall & Turkington 2006). The seed mixture in 1994 contained *B. gracilis*, *S. comata* and *Koeleria cristata* (seed densities per m² were 3670, 130 and 1910, respectively). The seed mixture in 1995 and 1996 contained *B. gracilis*, *S. comata*, *Agropyron dasystachyum* and *Agropyron smithii* (seed densities per m² were 3670, 210, 250 and 190, respectively, in 1995; 3670, 150, 150 and 150, respectively, in 1996). Seed was added in late May each year when soils were still moist from snowmelt. Plots were lightly tilled before addition to improve seed contact with bare soil.

Per cent cover of all vascular plant species, as well as lichens, were sampled in randomly placed 1 m × 0.5 m subplots in August of 1996, 1997 and 2004 using a modified Daubenmire scale (Bakker *et al.* 2003). Because the surveys in 1996 and 1997 used three subplots per plot, compared to only one subplot per plot in 2004, we randomly selected one of the three subplots from the 1996 and 1997 surveys for our comparisons. For natural recruitment, species accumulation was determined by contrasting the identity and richness of species surveyed in 1996 and 1997 vs. 2004. All vegetation data were arcsine-transformed to improve normality (Zar 1999). The individual and combined impacts of herbicide, seed addition and establishment year on the cover of each species were analysed using repeated-measures ANOVA and Tukey's tests (Von Ende 2001). Statistical analyses were conducted using JMP (SAS Institute Inc., Belmont, CA, USA).

We determined how weather conditions during the 11 years of this study related to long-term trends by examining the 68-year climate record for temperature and precipitation from 1936 to 2004. Inter-annual variability of temperature and precipitation were determined using the relative maxima [(max_{year} – mean_{year})/mean_{year}] and relative minima [(mean_{year} – min_{year})/mean_{year}] (Knapp & Smith 2001). To determine the relationship between monthly climate conditions during the experiment and long-term climatic averages, we calculated 95% confidence intervals (CIs) around the 68-year means for each month and assessed whether the monthly measures fell within those limits. We included climate conditions prior to the start of the experiment (1993) because there can be carry-over effects of climate on establishment from one year to the next in semi-arid systems (Adler & Levine 2007). We focused only on the growing season (March–October).

Results

Two distinct community types were evident in 2004, 9–11 years after the seed additions: those dominated by the exotic *A. cristatum* established in the 1950s, and those dominated by the native C₄ grass *B. gracilis* established in the 1990s (Fig. 1). Dominance by one or the other was contingent on significant interactions between the year of seed addition

Table 1. Interactions between the year of seed addition (1994, 1995, 1996) and herbicide spraying (until 1998) on the cover of *Bouteloua gracilis* and *Agropyron cristatum* in 2004 (Full model: *B. gracilis* $F_{5,54} = 13.9$, $P < 0.0001$; *A. cristatum* $F_{5,54} = 46.6$; $P < 0.0001$)

Source	d.f.	F	P
<i>B. gracilis</i> cover			
Year	2	9.6	0.0003
Spray	1	21.5	< 0.0001
Year × spray	2	8.5	0.0007
<i>A. cristatum</i> cover			
Year	2	46.2	< 0.0001
Spray	1	73.4	< 0.0001
Year × spray	2	19.2	< 0.0001

and whether herbicide was applied (Table 1). Tukey's tests revealed that plots seeded in 1995 and herbicide-treated, and to a lesser degree in 1994, had significantly higher *B. gracilis* cover and significantly lower *A. cristatum* cover compared to herbicide-treated but unseeded plots (Table 1; Fig. 2). In contrast, plots herbicide-treated and seeded in 1996 reverted back to *A. cristatum* dominance within 1 year (Fig. 2). There was no significant effect of any treatment variable on the cover of bare soil in any of the three establishment years ($F_{4,329} = 0.52$, $P = 0.72$).

Of the added native grasses, only *B. gracilis* established consistently. In 2004, the four other grasses – all C₃ species – had < 1% cover (*K. cristata*, *S. comata*) or did not persist at all (*A. dasystachyum*, *A. smithii*).

By 2004, there was no significant difference in *B. gracilis* cover between the 1994 seeded plots that were herbicide-treated until 1998 vs. those herbicide-treated until 2003 [$F_{2,359} = 2.0$; $P = 0.15$; 1997 mean = 18.4 (SE 2.7); 2003 mean = 23.1 (SE = 7.4)]. There was also no difference in *A. cristatum* cover between these plots [$F_{2,359} = 0.8$; $P = 0.46$; mean = 13.0 (SE = 1.8) and 6.7 (SE = 1.8), respectively]. Both results indicate that the success of *B. gracilis* establishment and *A. cristatum* control were not dependent on the continual application of herbicide. Total species richness, however, was significantly higher in plots treated with herbicide until 2003 ($F_{2,359} = 8.9$, $P = 0.003$) because of the persistence of native annual species that disappeared from plots only treated until 1998.

The establishment success of *B. gracilis* was associated with variations in climate conditions in the spring and summer of the establishment years (Table 2). In the year of highest establishment (1995), monthly rainfall averages exceeded the 95% CIs in every month from April until October except May (Table 2). Based on the 68-year climate data, 1995 had the fifth wettest June on record and the total rainfall for the 1995 growing season (362.4 mm) was the sixth highest (68-year mean = 284.8 mm; maximum = 608 mm; minimum = 113 mm). In the year of lowest establishment (1996), monthly rainfall averages fell below the 95% CIs in every month from April to August except May (Table 2). Total rainfall for this period (221 mm) was the tenth lowest on record. There were no

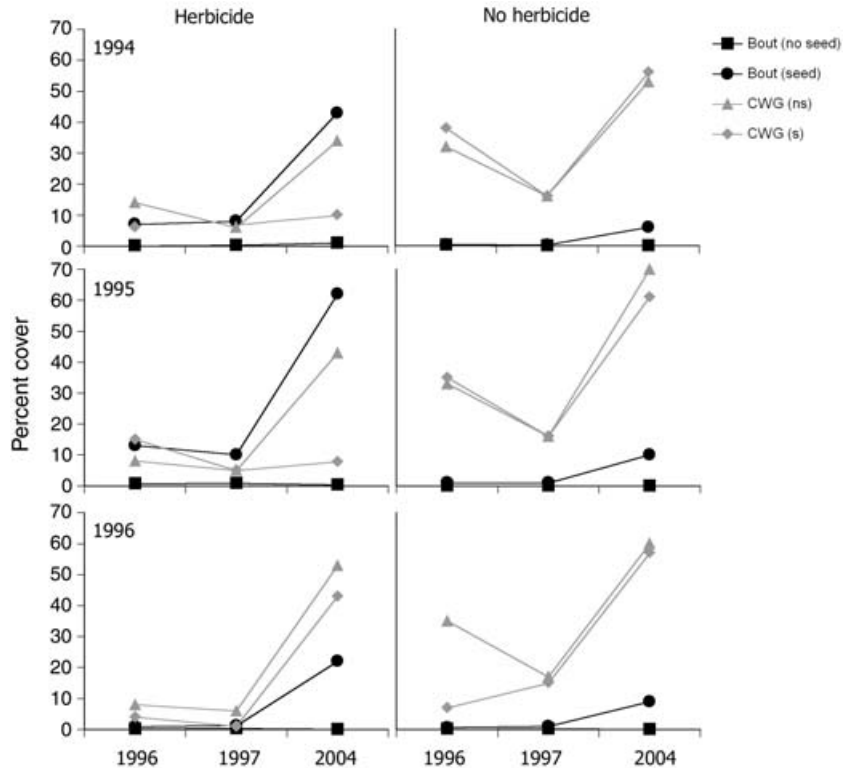


Fig. 2. Changes in mean percentage cover per plot for the native grass *Bouteloua gracilis* (Bout) and the introduced grass *Agropyron cristatum* (crested wheatgrass, CWG) in 1996, 1997 and 2004 in plots with and without herbicide application. Seed addition years were 1994, 1995 and 1996. Errors bars are excluded for clarity.

Table 2. Long-term monthly temperature (°C) and precipitation (mm) averages for the 68-year period of data available near the study site for the years prior to (1993) and during (1994, 1995, 1996) plot establishment, and for the three survey years (1996, 1997, 2004). Winter data (November–February) are not included. Bold = above the 95% CI; italics = below the 95% CI

	Mean	1993	1994	1995	1996	1997	2004
68-year temperature							
March	-4	0	1.3	-4	-8	-4	-1
April	4.6	6	6	<i>1.1</i>	<i>4</i>	<i>3</i>	6
May	10.8	12	12	<i>10</i>	<i>8</i>	<i>10</i>	<i>8</i>
June	15.3	15	15	16	16	17	<i>12</i>
July	18.7	<i>15</i>	19	<i>17</i>	19	18	<i>17</i>
August	17.8	<i>15</i>	18	17	19	18	<i>15</i>
September	12	<i>10</i>	14	<i>11</i>	<i>11</i>	14	<i>11</i>
October	5.2	5	6	5	-	5	<i>4</i>
68-year precipitation							
March	18.2	18	2	17	21	38	9
April	22.8	<i>10</i>	20	50	<i>10</i>	40	<i>3</i>
May	42.5	5	61	<i>24</i>	43	46	131
June	63.9	83	97	104	38	96	<i>46</i>
July	46.7	172	<i>17</i>	75	<i>14</i>	32	83
August	32	113	20	45	<i>15</i>	40	40
September	23.3	32	<i>4</i>	37	82	<i>13</i>	<i>23</i>
October	15.7	20	29	46	-	17	<i>8</i>

obvious differences in spring or summer temperature averages among the three establishment years.

There was no significant difference in the cover of added species in the sprayed but unseeded plots (i.e. natural recruitment) vs. the seeded but unsprayed plots in the three establishment years (Tukey's test), indicating that the exotic grass and dispersal limitation both influence native grass recruitment in these fields (Fig. 3).

The cover of *A. cristatum* in the untreated and unseeded control plots varied significantly by survey year ($F_{2,239} = 8.54$, $P = 0.0002$). This reflected low *A. cristatum* cover in 1997. Plot diversity and the per cent cover of bare soil both responded positively to these changes (Table 3) (diversity: $F_{2,329} = 46.7$, $P < 0.0001$; bare soil: $F_{2,329} = 28.0$, $P < 0.0001$). Increases in diversity were mostly the result of the presence of annuals such as *Polygonum aviculare*, *Lepidium densiflorum* and *Erigeron*

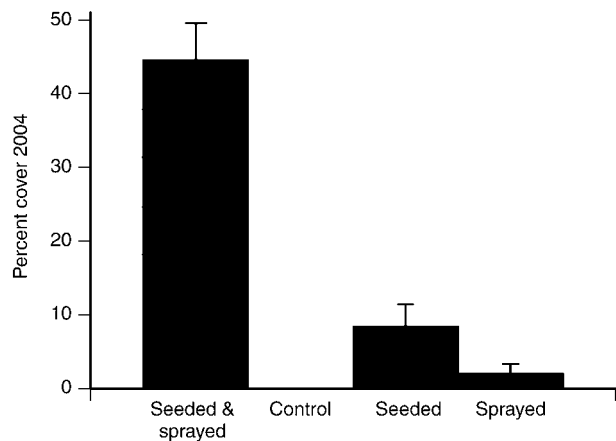


Fig. 3. Mean cover of *Bouteloua gracilis* in 2004, for the four different treatment combinations averaged over the 3 years of establishment. Note the lack of significant difference in recruitment between the seeded but unsprayed plots vs. the sprayed but unseeded plots; the latter demonstrates natural recruitment from nearby native prairie. No recruitment was recorded in the control plots. Error bars = 1 SE.

canadensis, which were absent in other years. The cause of decreased *A. cristatum* cover appeared to be the dry conditions of the previous growing season, based on significant increases in dead standing litter in 1997 compared to 1996 [$t = 13.89$, $P < 0.0001$; 1997 mean cover per plot: 50.7%; 1996 mean: 36.3% (Bakker & Wilson, unpubl. data)]. There may also have been a connection between reduced *A. cristatum* cover and the cold and wet spring of 1997 (Table 2), although spring conditions in 1995 – the year of highest establishment by *B. gracilis* – were similarly cold and wet.

Table 3. Variation in mean percent cover and diversity in the control plots (unseeded and no herbicide application) during the three survey years. Plot sizes are 1 m × 0.5 m (SE = 1)

	1996	1997	2004
<i>Agropyron cristatum</i>	30.2 [1.6]	15.9 [0.3]	59.7 [3.0]
Bare soil	23.6 [3.1]	31.9 [3.2]	3.0 [0.9]
Diversity	3.6 [0.2]	4.9 [0.2]	2.6 [0.1]

Not all subordinate species followed the trend of increased cover in association with reductions in *A. cristatum*. Like *A. cristatum*, some native forbs and shrubs also had significantly lower cover in 1997 compared to 1996 and 2004 (Table 4), suggesting that their above-ground activity is limited more by climate than by *A. cristatum* cover. Others showed no response, or increased significantly and consistently in the untreated plots from 1996 to 2004 (Table 4).

The climatic variability experienced during this study (Table 2) typifies the long-term weather patterns of this region, where both precipitation and temperature fluctuate widely from year to year (Fig. 4a,b). The annual averages of these two measures have remained largely unchanged over the past 68 years. There were also no significant changes in mean monthly temperature and precipitation in most months since 1938, nor has inter-annual variation changed significantly (Fig. 4a,b). There were, however, several notable exceptions. On average, there have been significant precipitation increases in May (Fig. 4c) and significant temperature increases in March (Fig. 4d). Variability in temperature has decreased in May and July [$F_{1,58} = 4.59$, $P = 0.036$ (May); $F_{1,60} = 6.13$, $P = 0.016$ (July)], while July also showed significant decreases in rainfall variability ($F_{1,60} = 4.36$, $P = 0.04$).

Table 4. Patterns of natural recruitment within the treatment plots for the three years of seed addition (1994–96). F - and P -values derive from ANOVA comparisons of herbicide, year of seed addition and survey year. ‘Increaseers’ are species that increased significantly from 1996 to 2004; ‘decreaseers’ did the opposite. Letters indicate significant differences in per cent cover among the years of seed addition (Tukey’s test), as observed during the 2004 survey. Species not listed showed no significant treatment responses or were too infrequent to analyse ($n = 21$ species). ‘Control’ refers to unseeded and unsprayed plots.

Species	Description	F	P	Year of seed addition		
				1994	1995	1996
Sprayed plot increaseers						
<i>Antennaria aprica</i>	Native perennial forb	8.6	0.0002	b	a	c
<i>Achillea millifolium</i>	Native perennial forb	5.9	0.003	a	b	b
<i>Ratibida columnifera</i>	Native perennial forb	5.6	0.004	b	a	c
<i>Astragalus lotiflorus</i>	Native perennial forb	3.5	0.03	b	a	b
<i>Plantago patagonica</i>	Native annual forb	3.1	0.04	a	a	b
<i>Sphaeralcea coccinea</i>	Native perennial forb	7.3	0.007	a	a	a
Control plot increaseers						
<i>Selaginella densa</i>	Native perennial cryptogam	8.4	0.0003	a	a	b
<i>Artemisia frigida</i>	Native perennial shrub	4.3	0.01	a	b	a
Sprayed plot decreaseers						
<i>Erigeron canadensis</i>	Native annual forb	8.1	0.0004	a	a	a
<i>Lepidium densiflorum</i>	Native annual forb	8.8	< 0.0001	a	a	a

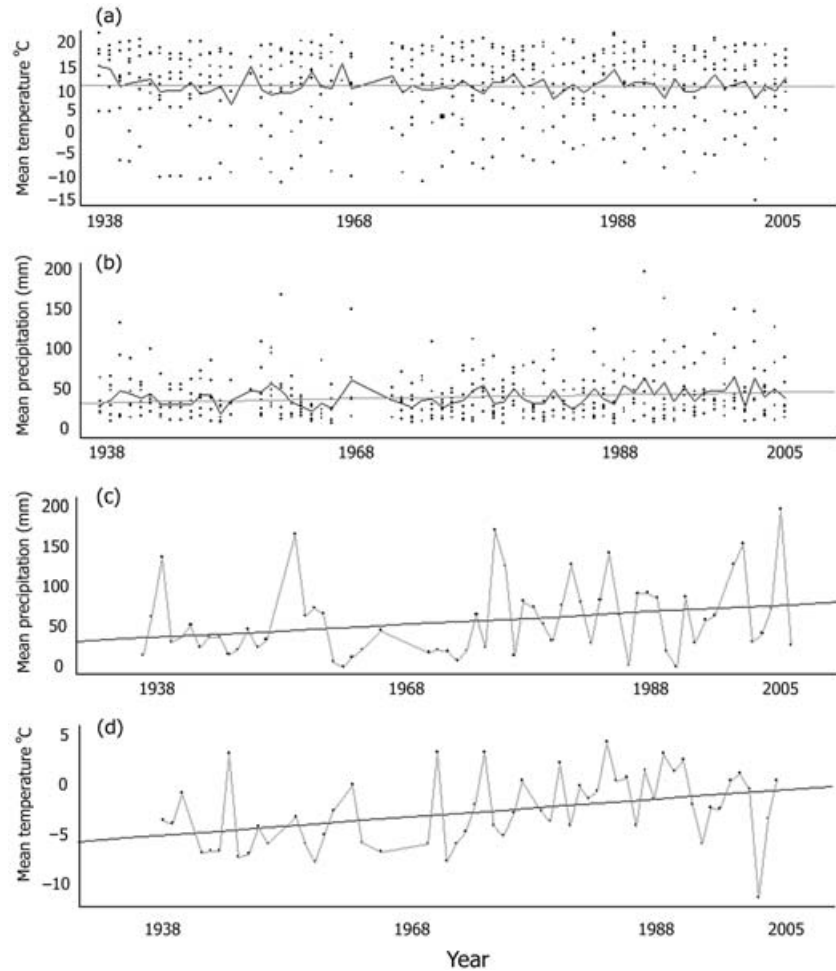


Fig. 4. Long-term climate data from southwestern Saskatchewan, 1938–2005. (a) Mean monthly temperatures (°C) for March–August inclusive, showing inter-annual fluctuations around the fitted trend line ($F_{1,430} = 0.01$, $P = 0.9$). (b) Mean monthly precipitation (mm) for March–August inclusive, showing inter-annual fluctuations around the fitted trend line ($F_{1,410} = 6.19$, $P = 0.013$). (c) Mean monthly precipitation (mm) for May, showing significant increases since 1938 ($F_{1,60} = 4.73$, $P = 0.033$). (d) Mean monthly temperature (°C) for March, showing significant increases since 1938 ($F_{1,55} = 9.51$, $P = 0.003$).

Discussion

Our results provide support for both the stochastic and deterministic models of community assembly. Different dominance hierarchies formed within a single environment, based on differences in inter-annual climate and on control of the extant vegetation. However, not all possible communities developed because of establishment failure by the added native C_3 grasses. These results were only detectable by repeating the experiment for multiple years and following the outcomes for over a decade. Evidence for stochastic assembly often derives from early successional communities, where wide variation in seed availability at fine scales can lead to different communities, at least initially (e.g. Tilman 2004; Del Moral & Lacher 2005; Walker *et al.* 2006). Here, our species are associated with later-successional semi-arid prairie, yet the outcome was similar. After seeding, two communities formed repeatedly: one mostly dominated by a native C_4 perennial grass (*B. gracilis*), which is assumed to have been abundant prior to cultivation; the other dominated by the exotic C_3 perennial grass (*A. cristatum*), which was planted widely during the 1950s.

The most critical stage of assembly was establishment. Whether seedlings persisted was determined by the year that seed was added, an effect associated with high rainfall in

spring and early summer. It was also dependent on disturbance. Dominance by *B. gracilis* only occurred when *A. cristatum* was treated with herbicide. However, these plots were resistant to re-invasion by *A. cristatum* and continued to maintain higher plot diversity up to 11 years after the start of the experiment. When *B. gracilis* failed to establish, *A. cristatum* was again dominant by the following year.

The establishment failure of the four added native C_3 grasses, by contrast, is consistent with deterministic assembly models where local abiotic or competitive conditions filter out unsuitable species (Keddy 1992; Holdaway & Sparrow 2006), although the identity of these filters is unclear. One possibility is the effect of intense competition by the functionally similar exotic C_3 grass, where large or identical overlaps in resource cause the displacement of the inferior competitors. The two species that failed to recruit in any plot, *A. smithii* and *A. dasystachyum*, are phylogenetic congeners of *A. cristatum* (Westover & Rogler 1941). However, recruitment failure by these species also occurred in sprayed plots dominated by *B. gracilis*, and this result did not vary with establishment year. Another possibility is that low seed density constrained plant establishment – the four native C_3 grasses had substantially fewer added seeds than *B. gracilis*. However, a companion study using the same experimental design at a nearby bottom-land site, with nearly identical seed densities, found that the

native C₃ grasses established in higher numbers than *B. gracilis* despite lower seed density (Bakker & Wilson 2004). *A. dasystachyum* eventually dominated the herbicide-treated plots. Given these considerations, the most likely explanation for recruitment failure appears to be site suitability rather than competition or seed density, with the native C₄ grass more capable of persisting on the moisture-limited tableland. Furthermore, it appears that *A. cristatum* is much better adapted to establishment in moisture-limited situations than its native congeners (Westover & Rogler 1941).

The evidence that both stochastic and deterministic processes influenced assembly suggests that they operate simultaneously (Weiher & Keddy 1995; Temperton & Hobbs 2004). Therefore, despite strong evidence for stochasticity, assembly was not a pure lottery where the first individuals to arrive were most likely to persist regardless of their identity (Fagerstrom 1988). Rather, our results suggest that abiotic filters deterministically constrain the demographic performance of certain species (e.g. C₃ native grasses) based on their functional traits (Wilson 1999). The establishment difficulties of the C₃ grasses in all years suggest that these filters are associated with the exposed location of the tableland (e.g. limited snow accumulation, high wind exposure), which may be relatively insensitive to annual climatic variation.

However, species that overcome these filters appear capable of dominating depending on seasonal vagaries in climate and disturbance during establishment (Fattorini & Halle 2004). This observation contradicts more deterministic-based assembly models, where the winner of competition is predicted to be independent of initial conditions (Tilman 1982; Wedin & Tilman 1993). It is probably no coincidence that supporting evidence for fine-scale deterministic models comes from highly productive systems where competition predominates (Wilson 2007). In our system, both recruitment success and dominant plant cover, with its assumed connection to above- and below-ground resource availability (Grime 2001), varied widely from year to year, as is typical of semi-arid systems (Ewing & Menke 1983; Figueroa & Davy 1991; Briggs & Knapp 1995; Holmgren *et al.* 2006; Adler & Levine 2007; Houlahan *et al.* 2007). Therefore, community assembly in less productive systems could be more prone to stochastic outcomes.

The exact combination of climatic triggers that determined recruitment success was unclear. The success of the 1995 and, to a lesser degree, 1994 establishment years – when precipitation levels at the time of seed addition were above average – suggests that precipitation-based limitations supersede the limiting effects of higher dominant cover, and that these filters are also associated with higher rainfall. This suggests that moisture availability and the intensity of competition may be inversely correlated (Wiens 1977; Tielbörger & Kadmon 2000), with the intensity of competition highest when moisture is scarcest despite lower cover.

The occurrence of multiple assembly trajectories raises questions about the underlying causes of exotic dominance in this system. Exotic dominance has often been attributed to competitive superiority. Hypotheses explaining competitive superiority by exotics in adaptively unfamiliar habitats are

numerous, and include enemy escape (Blossey & Notzold 1995), the switch from native to exotic herbivores (Parker *et al.* 2006), altered below-ground mutualisms (Klironomos 2002; Callaway *et al.* 2005) and phylogenetic novelty (Strauss *et al.* 2006). Although the causal mechanism for *A. cristatum* dominance is clouded because of aggressive breeding programmes during its introduction (Westover & Rogler 1941), the prediction is the same: dominance should occur by its trait-based competitive superiority, so that no alternative assembly trajectories develop.

In spite of this, we observed alternative trajectories. The implication is that site history may be more important for dominance by *A. cristatum* than is suggested by its widespread distribution and abundance, in line with stochastic assembly models. The extreme measures we used to establish *B. gracilis* in the *A. cristatum* field (seed additions and repeated herbicide application) are presumably similar in intensity to the extreme measures taken decades earlier to establish *A. cristatum* in native prairie (e.g. repeated ploughing, the massive and repeated addition of seed). These similarities raise the question of whether communities constructed in this way subsequently persist by inertia, rather than by competitive superiority (Milchunas & Lauenroth 1995). Under this inertia scenario, dominance following establishment is maintained by feedbacks among high and persistent propagule pressure, low disturbance once ploughing ceases and limited recruitment space. If few competitive differences exist between the displaced and planted dominant, there is no mechanism for re-invasion by the former unless similarly intense disturbance events occur in association with high seed inputs. Our results support this possibility, given the on-going persistence of our constructed communities within the exotic matrix for over a decade after establishment, and despite presumably being inundated annually by *A. cristatum* seed (Fig. 1). The possibility of competitive inertia among invasive and displaced species in grasslands is contrary to other studies, including work on *A. cristatum* (Waldron *et al.* 2005), but has been observed elsewhere in North America (Seabloom *et al.* 2003; MacDougall & Turkington 2005).

There was a net decrease in total plot diversity with time – a reflection of the reduction or disappearance of annual species that initially flourished following the herbicide applications. However, as these species disappeared, others slowly accumulated. This gradual accumulation, mostly by perennial native forbs and shrubs, indicates that seeds are dispersing from nearby native prairie and, given the significantly higher numbers in the herbicide-treated plots, that competition slows the rate by which this occurs. However, even though species are accumulating more slowly in unsprayed plots, these exotic swards were not impenetrable. The latter point may be consistent with emerging evidence that *A. cristatum* is invasive in native prairie but, once dominant, can also be significantly inhibited by intra-specific competition that lowers its growth rate and fitness (Hansen & Wilson 2006). Strong intra-specific suppression, interacting with inter-annual abiotic variability, might increase recruitment opportunities for other species in this system over time, as long as their propagule supply is not limiting.

Our long-term climate data indicate significant increases in temperature and precipitation early in the growing season and reduced climatic variability in May and July, with inter-annual climatic variability remaining largely unchanged. These observations are not the predicted outcomes of climate change in North American grasslands (Karl *et al.* 1995; Easterling *et al.* 2000). The impact of a warmer, wetter and less variable climate during parts of the growing season is unclear. Both spring and early summer are critical periods for growth and reproduction by most native and exotic prairie plants (Lauenroth & Sala 1992; Knapp & Smith 2001). Therefore, all species may be affected positively by warmer and wetter conditions. Reduced rainfall variability should also favour all species by increasing the water content in the soil, compared to patterns of water availability in regions with intense but episodic rainfall events (Fay *et al.* 2003). However, these changes might benefit *A. cristatum* in particular. This species initiates shoot growth several weeks earlier than native grasses (including its native congeners) and produces significantly more above-ground biomass than any co-occurring grass species. This latter trait presumably increases its moisture demands during the summer because of higher evapotranspiration, so that increased rainfall combined with higher soil moisture would further support its growth and reproduction at this time. If true, the implication is that climate changes over the past half-century have contributed to the invasion success of *A. cristatum*.

In conclusion, the widespread dominance of *A. cristatum* on the northern Great Plains, combined with the failure of many eradication programmes, suggests that the conversion from native prairie may be permanent. Interest in reversing this trend extends beyond the preservation of native prairie flora. Conversion of prairie to exotic grassland is associated with altered net primary productivity (Alward *et al.* 1999), reduced drought and over-grazing tolerance (Alward *et al.* 1999), weakened resistance to further invasions (Zavaleta & Hulvey 2004) and reduced soil carbon sequestration (Christian & Wilson 1999), suggesting that prairie restoration has the potential to slow, or even reverse, these functional transformations.

Our results suggest that the conversion of native prairie to exotic grassland need not be permanent. We confirmed that *A. cristatum* was difficult to eradicate, requiring multiple herbicide applications. We also confirmed that native grasses are difficult to re-establish: some species failed completely, and some years were unsuitable for recruitment. However, in certain years, it was possible to assemble a native-dominated community that resisted re-invasion by *A. cristatum*. This result was only detectable with our experimental design and with long-term monitoring. Restoration success required repeated seed additions to take advantage of climate-mediated recruitment windows, together with persistent efforts to reduce exotic grass cover. These treatments were intensive but the outcome agrees with emerging non-deterministic perspectives on assembly, where dominance by largely similar species can be shaped by factors such as abundance feedbacks, disturbance, habitat size, seed inputs or climatic fluctuations (e.g. Hubbell 2001; Seabloom *et al.* 2003; MacDougall & Turkington 2004; Orrock

& Fletcher 2005; Adler *et al.* 2006; DiVittorio *et al.* 2007). More work will be required to scale these assembly efforts beyond the plot level, but our work suggests its feasibility.

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Received 14 May 2007; accepted 23 October 2007

Handling Editor: Scott Collins