Invasibility of a mesic grassland depends on the time-scale of fluctuating resources

By: Sally E. Koerner, Meghan L. Avolio, Cynthia C. Chang, Jesse Gray, David L. Hoover, and Melinda D. Smith

Abstract:

1. Global change is increasing the frequency and magnitude of resource fluctuations (pulses) at multiple time-scales. According to the fluctuating resource availability hypothesis (FRAH), susceptibility of an ecosystem to invasion (i.e. invasibility) is expected to increase whenever resource supply exceeds that which is utilized by native communities. Thus, global change has the potential to increase invasibility around the world.
2. Here, we test the FRAH by adding seeds of a target invader grass species to a long-term climate change experiment manipulating precipitation pulse size in tallgrass prairie in Kansas, USA.
3. Our experimental work yielded three important findings. First, contrary to predictions of the FRAH, invasibility was *reduced* with short time-scale resource pulses (intra-annual time-scale). Secondly, we found evidence to suggest that at inter-annual time-scales, the FRAH is supported. Wet years resulted in an increase in the number of established seedlings as well as the number of seedlings that persisted to the end of the season. Finally, we found that invasibility was positively related to native community richness and the density of individuals in the community suggesting that native communities facilitate establishment of invader species. Perhaps more importantly, results from this 10-year invasion study also show that resource availability drives invasion and that the biotic filters of plant community structure and diversity are secondary.
4. *Synthesis*. Our findings suggest that intensification of precipitation regimes may enhance resistance to invasion at intra-annual time-scales, but will have opposing effects if precipitation regimes include more wet years.

Article:

Introduction

The role of resources in determining ecosystem invasibility has long been recognized (Elton 1958; Huston 1994) and continues to be a focus of invasion research (Blumenthal *et al.* 2009; Parepa, Fischer & Bossdorf 2013; Eskelinen & Harrison 2014; Houseman, Foster & Brassil 2014). The fluctuating resource availability hypothesis [FRAH; also known as the fluctuating resource hypothesis (FRH)] (Davis, Grime & Thompson 2000) states that plant invasions are enhanced when resources exceed that which can be used by the native community. Consequently, ecosystem invasibility is expected to vary as amounts of unused resources fluctuate, with increases in the frequency and magnitude of resource pulses enhancing invasion success (Davis, Grime & Thompson 2000; Shea & Chesson 2002). This theory also predicts that ecosystems characterized by substantial pulses of resource availability will be more susceptible to invasions than those with more stable (continuous) resource supply rates (Rejmánek 1989; Parepa, Fischer & Bossdorf 2013). Anthropogenic activities are affecting resource levels (e.g. increased N inputs), as well as temporal patterns of availability (e.g. altered precipitation patterns; IPCC 2007, 2012, Smith, Knapp & Collins 2009). Thus, in addition to direct movement of propagules, humans may increase invasibility by altering historic templates of resource availability in ecosystems (Stachowicz *et al.* 2002; Bradley, Wilcove & Oppenheimer 2010; Jimenez *et al.* 2011). However, the time-scale over which pulses in resource availability must occur to enhance invasion is poorly resolved (Rejmánek 1989; Parepa, Fischer & Bossdorf 2013).

Over the past few decades, precipitation regimes have become more variable both intra-annually (within a year) and interannually (between years) due to climate change (Min *et al.* 2011; Smith 2011; Coumou & Rahmstorf 2012). These trends are projected to continue in the future, with an increase in event size, more frequent extreme rainfall events and longer dry periods expected within years (Kendon *et al.* 2014), while wet and dry years are forecast to intensify and extend in duration spanning multiple years (IPCC 2012). Interannual variability in precipitation (i.e. wet vs. dry years) is recognized as important in influencing invasion (Davis *et al.* 1999; Hobbs & Mooney 1991; Dukes & Mooney 1999), yet it is unknown how altered precipitation patterns (larger but fewer events) at intra-annual time-scales may affect invasibility.

To address this fundamental knowledge gap, we conducted a decade-long invasion study within the context of a novel, long-term climate change experiment – the Rainfall Manipulation Plots (RaMPs; Fay *et al.* 2000, 2011; Knapp *et al.* 2002). The RaMPs experiment, established in 1998 in a mesic, native grassland ecosystem, is the first and longest running field experiment to impose altered intra-annual precipitation variability (Fay *et al.* 2011). The altered precipitation treatment increases growing season rain event size while decreasing event frequency, relative to ambient patterns. This results in more variable within-season soil moisture regimes, driven by a greater number of large rainfall events and increased fluctuations between high and low soil water availability (Fay *et al.* 2011). A key strength of this experiment is that there is no difference in total growing season rainfall between ambient and altered rainfall treatments for any year, and thus, alterations in precipitation patterns and soil moisture variability are not confounded by changes in total precipitation inputs. This allowed us, for the first time, to

rigorously assess how precipitation resource pulses on an intra-annual time-scale may impact invasibility.

Invasibility is a product of propagule supply, traits of the invading species, characteristics of the native community and environmental conditions (Lonsdale 1999). Because the focus of our study was on how changing environmental conditions will interact with a naturally heterogeneous native community to affect invasion, we controlled for propagule supply and invader traits by adding a known and constant number of seeds of a focal invader, a perennial C_3 grass, *Bromus inermis*. This exotic species is a regionally successful invader of grasslands (Fink & Wilson 2011), and although not present in the immediate RaMPs area, *B. inermis* is an indicator species of disturbance at the site (Gibson, Seastedt & Briggs 1993) as are many of the exotic species found in the region. From 2004 to 2013, *B. inermis* seeds were added to RaMPs plots at the beginning of each growing season. We quantified two critical stages of the invasion process (Levine & D'Antonio 1999) that could be strongly influenced by resource pulses at an intra-annual time-scale – seedling establishment (number of seedlings observed ~1 month after seed addition) and seedling persistence (number of seedlings present ~3 months after seed addition). As predicted by FRAH, we hypothesized that (i) the altered rainfall would increase both invader establishment and persistence, by increasing the size of resource pulses (fewer, but larger rainfall events). Because the invasion study was conducted over a 10-year period, we were able to concurrently assess the importance of intra-annual variation in rainfall and years with high precipitation amounts that occur as part of interannual variation in precipitation on invader establishment and persistence. We hypothesized that (ii) increased intra-annual variability in precipitation would be as or more important than natural patterns of interannual precipitation. These potential abiotic determinants of invasion success were then compared with previously identified biotic attributes of the native plant community, including species richness, densities of individuals, light availability at the soil surface (as a proxy of canopy cover) and abundance of the dominant species, shown to affect invasion in many ecosystems (Naeem *et al*. 2000; Stohlgren, Barnett & Kartesz 2003; Smith *et al*. 2004; Chang & Smith 2012). We hypothesized that (iii) invasibility would be controlled primarily by abiotic resource pulses (either intra-annual or wet years), rather than mediated through native plant community dynamics.

Materials and methods

Study site and ramps experiment

Konza Prairie Biological Station (Konza) is a 3487-ha native unploughed tallgrass prairie Long-Term Ecological Research (LTER) site located in the Flint Hills of north-eastern Kansas (39°05′ N, 96°35′ W). Perennial C_4 grasses including *Andropogon gerardii* and *Sorghastrum nutans* dominate the plant community and account for the majority of herbaceous primary productivity (Knapp *et al*. 1998), while plant species diversity is generally a function of the richness and relative abundance of subdominant forb species (Collins & Glenn 1991). The climate is temperate with mean monthly air temperature in July of 27 °C. Annual precipitation is highly variable, averaging 835 mm/year, with approximately 75% falling as rain during the May–September growing season. Variation from average precipitation patterns is common, both in yearly totals and seasonal distribution (Hayden 1998).

We utilized a long-term climate change experiment – the RaMPs – for this study. The RaMPs are located at Konza Prairie in ungrazed, intact lowland prairie that is burned annually in late March. The dominant plant species in the plots include *A. gerardii*, *S. nutans* and *Panicum virgatum*, all rhizomatous, warm-season, C_4 tall grasses. Dominant perennial forbs include *Solidago canadensis*, *Aster ericoides* and *Solidago missouriensis*. Productivity in the RaMPs has averaged 725 g m^{-2} to date with approximately 25% of the productivity being derived from forbs (A. K. Knapp, unpublished data).

A set of twelve fixed-location rainout shelters, arranged in three blocks, was established in 1998. The shelters exclude and collect natural rainfall inputs from the plots. The collected rainfall is either applied to mimic ambient rainfall patterns ($n = 6$ shelters), or it is applied as an altered treatment with fewer and larger rainfall events ($n = 6$ shelters) without altering total growing season precipitation amount. Fay *et al*. (2000) provide details on shelter design and efficacy. Ramp roofs over both rainfall treatments (control and altered) decrease photosynthetic active radiation by 22%, with no effect on temperature (Fay *et al*. 2000). Nested within each rainout shelter is a warming treatment plot (each 2 × 2 m), in which infrared heating lamps are used year round and increase growing season temperature by ~1 °C (see Fay *et al*. 2011 for details).

Invasion experiment

We conducted the invasion experiment within the context of the RaMPs experiment from 2004 to 2013. Under each shelter, two 2 × 2 m plots (one control, one warmed) were utilized for the study. In each plot, we added seeds of *B. inermis* (100 in 2004 & 2006 or 200 in all other years) to two 0.10-m^2 subplots in ~mid-May of each year (excluding 2009). The exact dates of seed addition were 16 May 2004, 12 May 2005, 16 May 2006, 12 May 2007, 20 May 2008, 22 May 2010, 1 June 2011, 11 June 2012 and 11 May 2013. Seedling establishment and persistence were monitored throughout the growing season in each subplot. Seedlings were counted and marked with a toothpick within each 0.10-m^2 subplot. We define seedling establishment as the number of live seedlings present ~1 month after seeds were added (mid-June). The exact dates seedling establishment surveys were conducted were 10 June 2004, 18 June 2005, 15 June 2006, 18 June 2007, 19 June 2008, 25 June 2010, 14 June 2011, 28 June 2012 and 10 June 2013. We define seedling persistence as the number of live individuals of *B. inermis* present ~3 months after seeds were added (mid- to late August). The exact dates seedling persistence surveys were conducted were 20 August 2004, 20 August 2005, 26 August 2006, 5 September 2007, 22 August 2008, 21 August 2010, 23 August 2011, 12 August 2012 and 17 August 2013. Invader seedlings were completely removed from each subplot at the end of each growing season to prevent cumulative effects of invasion over time. Although seed dormancy is possible (2–14 years; Howard 1996), annual spring burning removed any seedlings that had established that season from previous years seeds. In addition, the lack of a linear increase through time strongly suggests there was no build-up of the seed bank from previous year's seeds.

Water additions to all plots were recorded throughout the growing season each year. Volumetric soil water content was measured continuously throughout the growing season within each 2 × 2 m plot in each ramp. Thirty-cm time-domain reflectometry (TDR) probes (Campbell Scientific, Inc., Logan, UT, USA) were buried 0.50 m from the edge of each plot at a 45° angle to sample 0–15 cm soil depth. Soil temperature was measured with thermocouples at 5 cm depth

in each of the four quadrants of a plot in three ambient and three altered plots. These sensors were recorded in 30-min intervals using a Campbell CR10X data logger (Campbell Scientific, Inc.).

Photosynthetically active radiation (PAR) was measured within 1 week of the establishment and persistence seedling counts each year in each plot using a LP-80 AccuPAR Ceptometer (Decagon Devices, Inc., Pullman, WA, USA). Light availability was expressed as the ratio of light at the soil surface to light above the canopy. Total number of individuals of all species was measured in each of the invasion subplots in early June and again in mid-August of each year. In addition to providing an estimate of stem density, this also allowed us to calculate plant community richness and abundance of the dominant species.

Statistical analyses

We defined the establishment period (~1 month) as the time from which seeds were added (~mid-May) to the day that seedling establishment was counted (~mid-June). We define the persistence period (~2 months) as the day after the establishment period ended to the day seedling persistence was counted (mid- to late August). Because seeds were added at different times within a 4-week window during the study, the establishment and persistence periods differed slightly for each year. Mean daily soil moisture was calculated for each establishment and persistence period in a given year, and the coefficient of variation (CV) of mean daily soil moisture was calculated for that same time period. Seedling establishment and persistence were calculated as the number of seedlings counted divided by the total number of seeds added (100 in 2004 & 2006 or 200 in all other years).

Table 1. Effects of precipitation and warming treatments on soil moisture availability

Variable	d.f.	Establishment		Persistence	
		F-value	*P*-value	*F*-value	*P*-value
Soil moisture					
Precip	1, 10	0.27	0.615	0.00	0.965
Heat	1, 170	0.10	0.749	0.27	0.604
Year	8, 170	67.09	< 0.001	114.71	< 0.001
P × H	1, 170	1.63	0.204	1.60	0.208
P × Yr	8, 170	7.70	< 0.001	5.20	< 0.001
H × Yr	8, 170	0.75	0.647	0.43	0.899
P × H × Yr	8, 170	0.60	0.777	0.57	0.802
Soil moisture variability (CV)					
Precip	1, 10	7.56	0.021	8.75	0.014
Heat	1, 170	2.68	0.103	1.14	0.287
Year	8, 170	149.46	< 0.001	40.51	< 0.001
P × H	1, 170	0.73	0.395	0.64	0.423
P × Yr	8, 170	29.05	< 0.001	16.68	< 0.001
H × Yr	8, 170	1.26	0.268	1.53	0.150
P × H × Yr	8, 170	0.39	0.923	1.22	0.290

Effects of precipitation treatment (precip, P), warming treatment (heat, H) and year (year, Yr) on mean daily soil moisture and the coefficient of variation (CV) of mean daily soil moisture for the establishment (~1 month – mid-May to mid-June) and persistence period (~2 month – mid-June to mid-August). Statistical tests were performed using repeated-measures mixed-model anovas.

Effects of the RaMPs precipitation treatment on precipitation event size were tested using mixed-model anovas. Effects of precipitation and warming treatments on mean daily soil moisture and CV of mean daily soil moisture (log-transformed) were tested using repeated-measures mixed-model anovas. Finally, effects of precipitation and warming treatments on numbers of established and persisting seedlings (square-root-transformed) were tested using repeated-measures mixed-model anovas. In all cases, when main effects were significant, differences between treatments were tested using least significant difference tests. Because warming was not a focus of this study and the warming treatment did not significantly affect either mean soil moisture or variability (Table 1) nor did it affect invader establishment or persistence (Table 2), only results from the precipitation treatment are presented.

Table 2. Effects of precipitation and warming treatments on establishment and persistence of the focal invader, *Bromus inermis*

Variable	d.f.	Establishment		Persistence	
		F-value	*P*-value	*F*-value	*P*-value
Precip	1, 10	3.88	0.077	0.57	0.469
Heat	1, 170	0.21	0.651	3.08	0.081
Year	8, 170	45.97	< 0.001	33.89	< 0.001
P × H	1, 170	0.06	0.804	0.02	0.877
P × Yr	8, 170	2.27	0.025	2.13	0.061
H × Yr	8, 170	0.26	0.978	0.47	0.908
P × H × Yr	8, 170	0.20	0.995	0.60	0.785

Effects of precipitation treatment (precip, P), warming treatment (heat, H) and year (year, Yr) on square-root-transformed seedling establishment (~1 month – mid-May to mid-June) and persistence (~2 month – mid-June to mid-August). Statistical tests were performed using repeated-measures mixed-model anovas.

To determine the relative importance of abiotic and biotic variables on seedling establishment and persistence of the invader, we used structural equation modelling (path analysis) to test for both direct and indirect effects of biotic and abiotic factors (Shipley 2002). A single *a priori* model was developed for both seedling establishment and persistence based on knowledge of what variables may be important to invasion success (Fig. 1). Possible variables included precipitation, soil moisture, soil moisture variability, community richness, stem density, abundance of dominant species and light availability. For the persistence model, establishment number was also included. The number of seedlings, CV of mean daily soil moisture, light availability at the soil surface, species richness, stem density and abundance of the dominant species were transformed to correct for non-normal distributions. All years of data (except 2008 in the establishment model and 2011 in the persistence model given that no stem density data were recorded) were included in the analyses. All models were a good fit to the data, according the χ^2 statistic with $P > 0.05$ (Grace 2006). Structural equation model analyses were conducted using amos v7 (SPSS, Chicago, IL, USA).
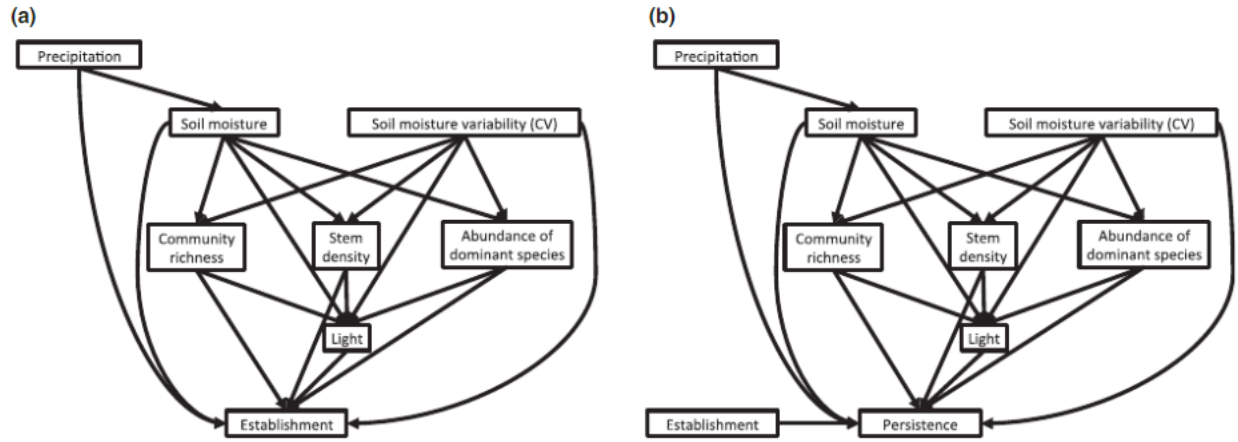
Figure 1. *A priori* structural equation models used to evaluate invader seedling establishment (a) and persistence (b).
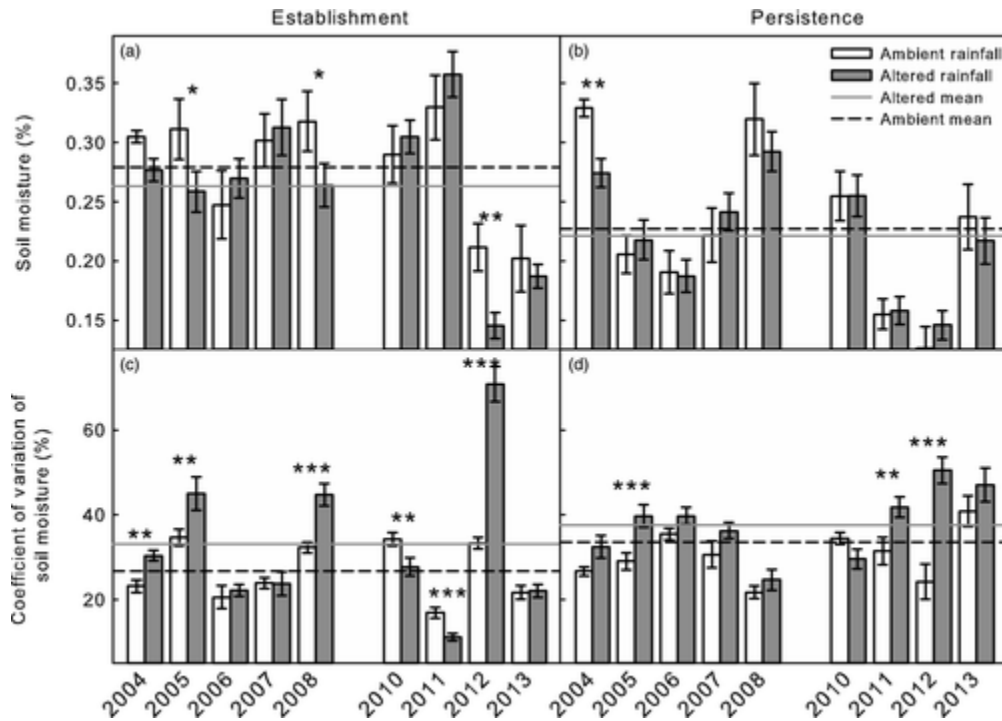

Figure 2. Soil moisture & coefficient of variation (CV) of soil moisture during the establishment & persistence periods. Soil moisture properties were measured from 0 to 15 cm depth. Shown are establishment (a) and persistence (b) mean soil moisture, and establishment (c) and persistence (d) soil moisture CV for the ambient (white) and the altered (grey) precipitation treatments. CV was calculated each year for the establishment and persistence time periods of that year from mean daily soil moisture values in each treatment. For both mean and CV of soil moisture, the establishment time period was defined by the day invader seeds were added to the day the seeds were counted for establishment (~1 month), while the persistence time period was defined by the day invader seeds were added to the day the seeds were counted for survival (~3 months). P-values are from repeated-measures mixed-model anovas (Table 1) on soil moisture and the log-transformed CV of soil moisture data (*$P < 0.1$; **$P < 0.05$; ***$P < 0.01$).

Results

Soil moisture and soil moisture variability were significantly impacted by year alone and by the precipitation treatment by year interaction (Fig. 2; Table 1). Soil moisture variability was increased significantly during the establishment period by the altered precipitation treatment in 6 of the 9 years and 3 of 9 years in the persistence period (Fig. 2c,d; Table 1). This resulted from significantly larger rainfall event size and decreased number of events in the altered precipitation treatment for both the establishment and persistence periods (Fig. 3a,b; Table S1 in Supporting Information). In contrast, the altered precipitation treatment significantly decreased average soil moisture content in 3 out of 9 years during the establishment period but only 1 year during the persistence period (Fig. 2a,b; Table 1). This reduction in mean soil moisture likely resulted from an increase in the length of the dry periods between rainfall events during the establishment and persistence periods (Fig. S1, Table S2).
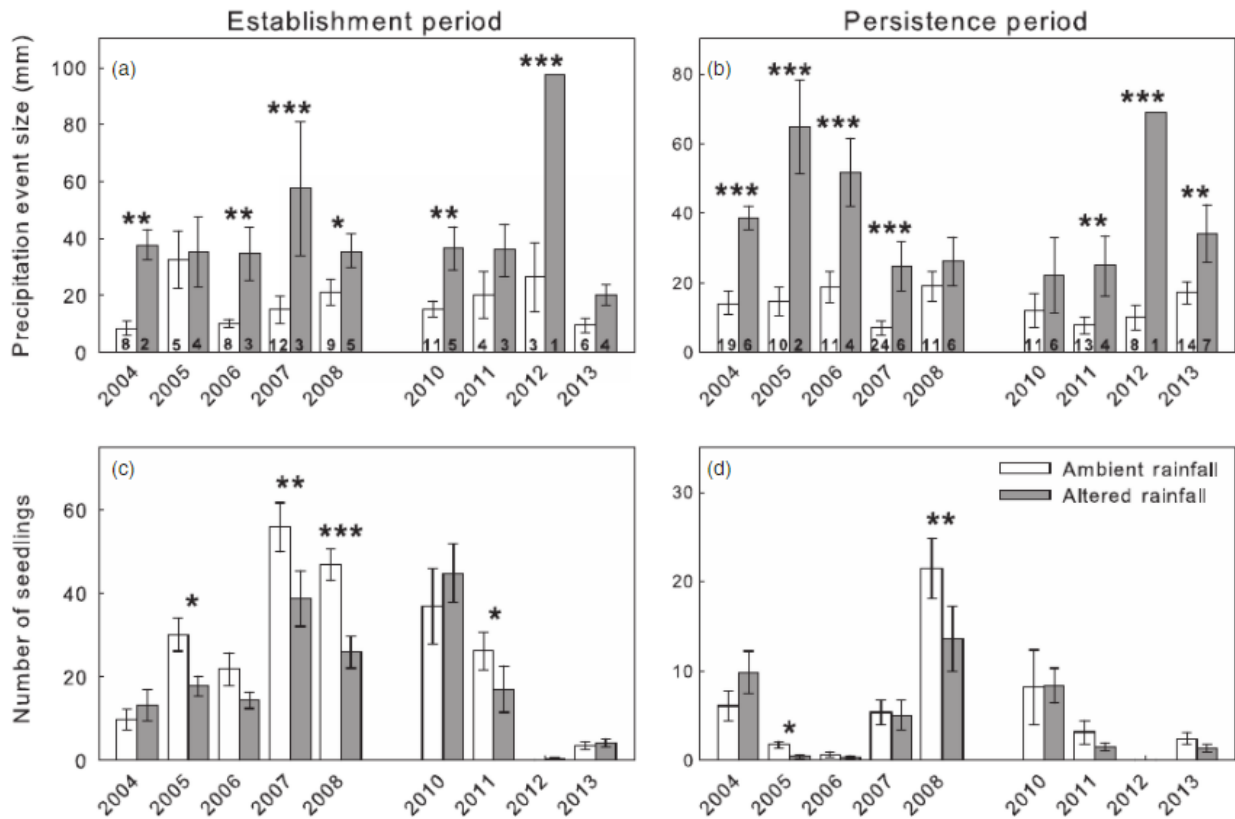

Figure 3. Rainfall treatment effects on mean precipitation event size and invasion. The effect of precipitation treatment (ambient = white; altered = dark grey) on mean precipitation event size (a and b) and the percentage of seedlings of *Bromus inermis* (c and d) during the establishment (~15 May to 15 June; a and c) and the persistence (~15 June to 15 August; b and d) periods. (top) Numbers within each bar refers to the number of precipitation events that occurred during the establishment or persistence periods. The altered rainfall treatment significantly increased event size (Table S1) while decreasing the number of events. *P*-values are from mixed-model anovas (*$P < 0.1$; **$P < 0.05$; ***$P < 0.01$). (bottom) The altered rainfall treatment decreased invader establishment and persistence in certain years. *P*-values are from repeated-measures mixed-model anovas on the square-root-transformed seedling count data (Table 2; *$P < 0.1$; **$P < 0.05$; ***$P < 0.01$).

The altered precipitation treatment decreased invasion success in some but not all years (Fig. 3c,d; Table 2). Seedling establishment decreased in 4 out of 9 years, and seedling persistence decreased in 2 of 9 years. Seedling persistence was significantly and negatively correlated with both CV of soil moisture and the maximum length of consecutive dry days

(Fig. 4). However, year was the strongest predictor of both establishment and persistence (Table 2). Growing season precipitation and mean daily soil moisture during the establishment and persistence periods were positively correlated with seedling establishment and persistence, respectively (Fig. 5), with slightly stronger correlations observed with mean daily soil moisture.
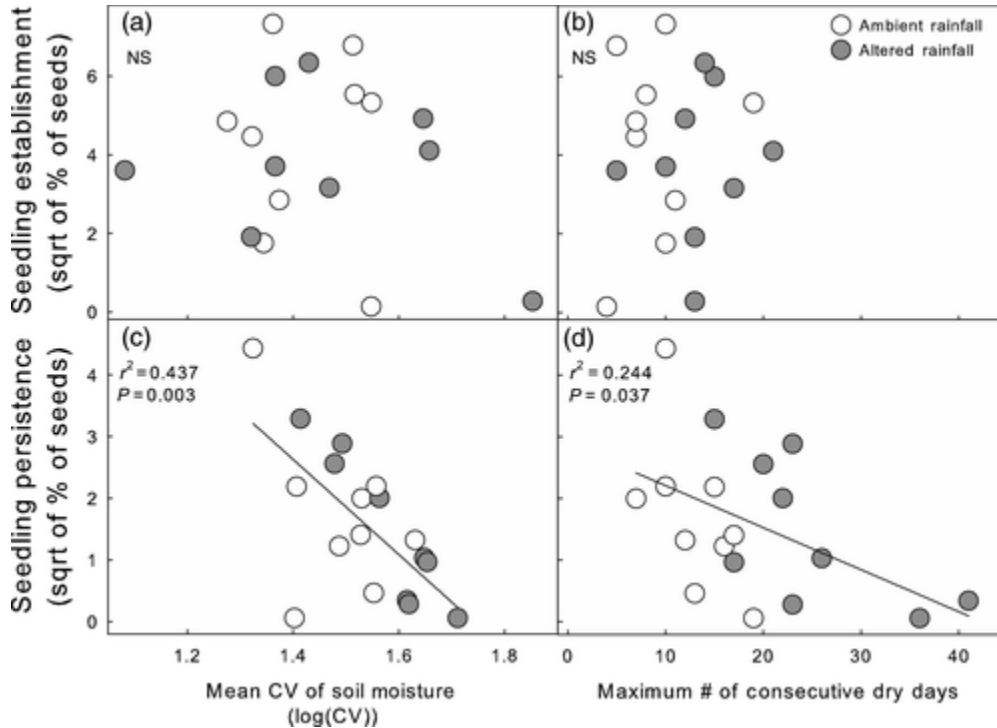

Figure 4. Effects of intra-annual variation in rainfall on invasibility of native tallgrass prairie. The square root of the mean number of seedlings that established (a and b) and persisted (c and d) relative to the coefficient of variation (CV) of soil moisture (0–15 cm) and the maximum consecutive number of dry days. For seedling establishment, CV of soil moisture and maximum dry days were calculated based on the establishment period (1 week before seed addition to ~1 month after seed addition). For seedling persistence, these metrics were calculated based on the entire growing season (establishment + persistence periods; persistence period was ~2 month after the establishment period). Regression lines are shown with corresponding statistics in the upper left corner of each graph. N.S. = not significant.

Using structural equation modelling, we found that seedling establishment was significantly and directly impacted by measures of water availability and native community stem density (Fig. 6a). Precipitation and soil moisture were positively correlated with seedling establishment while soil moisture variability was negatively correlated with seedling establishment. The native plant community stem density was positively correlated with seedling establishment. Soil moisture also indirectly affected establishment positively via stem density. Seedling persistence was significantly and directly impacted by seedling establishment, measures of soil moisture availability and native plant community richness (Fig. 6b). Seedling establishment had the strongest correlation and a positive correlation with seedling persistence. Soil moisture also was positively correlated with seedling persistence while soil moisture variability was negatively correlated with persistence of invader seedlings. Finally, native plant community richness was positively correlated with seedling persistence.
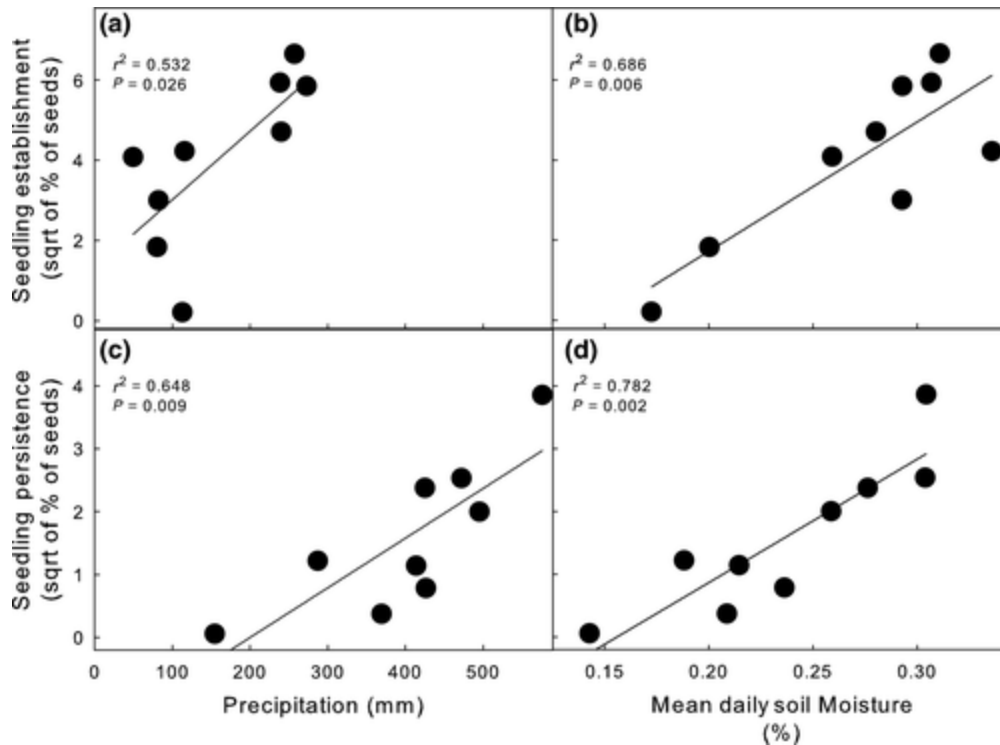
Figure 5. Effects of interannual variability in rainfall on invasibility of native tallgrass prairie. The square root of the mean number of seedlings that established (a and b) and persisted (c and d) relative to precipitation amount or mean soil moisture (0–15 cm). For seedling establishment, precipitation amount and mean soil moisture were calculated based on the establishment period (1 week before seed addition to ~1 month after seed addition). For seedling persistence, precipitation amount and soil moisture were calculated based on the entire growing season (establishment + persistence periods; persistence period was ~2 month after the establishment period). Regression lines are shown with corres-ponding statistics in the upper left corner of each graph.
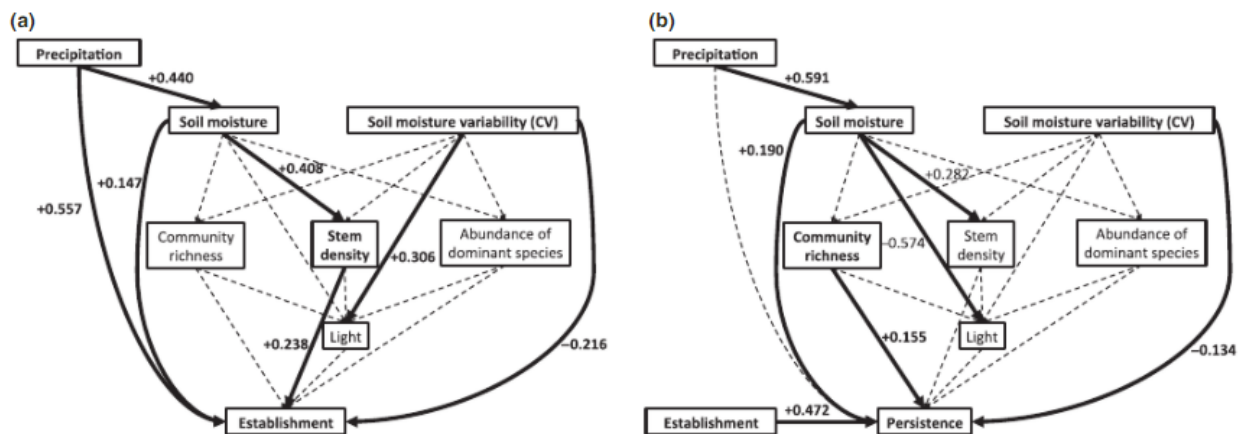

Figure 6. Direct and indirect effects of abiotic and biotic factors on invasibility. Structural equation models examining relationships between abiotic (precipitation, soil moisture and soil moisture variability) and biotic (community richness, stem density, abundance of the dominant species and light availability) factors on establishment (a) and persistence (b) of *Bromus inermis* seedlings in native tallgrass prairie. Black solid lines are significant pathways ($P < 0.05$). Precipitation, soil moisture, soil moisture variability and stem density significantly explained variation in seedling establishment ($\chi^2 = 9.093$; d.f. = 5; $P = 0.105$). Seedling establishment, soil moisture, soil moisture variability and community richness significantly explained variation seen in seedling persistence ($\chi^2 = 7.537$; d.f. = 5; $P = 0.184$).

Discussion

Contrary to predictions of the FRAH (Davis, Grime & Thompson 2000), larger pulses in rainfall at the intra-annual time-scale did not increase invasion success, during either the establishment or persistence periods. Further, in the years where establishment or persistence of the invader was significantly different between the precipitation treatments, it was consistently *lower* for the altered precipitation treatment. Thus, it appears that the extended periods of low soil moisture resulting from longer periods between rainfall events impacted invasibility more than an increased number of large precipitation pulses creating soil moisture pulses during the growing season. However, precipitation amount and mean soil moisture over an entire growing season explained a significant amount of variation in invader establishment and persistence. Due to the long-term, repeated addition of the target invader seeds, our experiment captured a broad range of growing season rainfall amounts allowing us to determine the importance of time-scale for fluctuating resources. Here, we show that for plants, a pulse must be an entire wet summer rather than discrete rainfall events within a summer.

In addition, the attributes of the native plant community also could have large effects on invasion success (Lonsdale 1999; Naeem *et al*. 2000; Stohlgren, Barnett & Kartesz 2003; Fink & Wilson 2011; Chang & Smith 2012). Thus, we used structural equation modelling to examine how abiotic variables as well as plant community richness, total density of individuals (stems or ramets), light availability and dominance affected invader establishment and persistence over time. We found that more diverse and dense native communities had higher invasibility, with the total density of individuals positively related to establishment and plant species richness positively related to persistence. This could be because factors that favour high species diversity or high numbers of individuals also increase invasion success (Tilman 2004), or because the native community facilitates seedling success by alleviating stressful conditions (e.g. high temperatures or decreased soil moisture) present when native community cover is low (Stohlgren, Barnett & Kartesz 2003; Cleland *et al*. 2004; Chang & Smith 2012). Thus, rather than having negative and strong effects on invasion success as predicted by the biotic resistance hypothesis (Levine & D'Antonio 1999; Naeem *et al*. 2000), diverse and higher density communities also had higher invader success. This correlation effect was, in part, enhanced by increased soil moisture, which appeared to act indirectly on invader establishment by increasing the density of individuals in the community. Nonetheless, while the plant community did influence invasibility during establishment, community characteristics were secondary to abiotic controls on invasion.

Among these abiotic controls, precipitation amount during the establishment period was the strongest driver of invader establishment. More importantly, increased seedling success due to high rainfall or soil moisture during the establishment period was a strong predictor of survivorship and invasion success over longer time periods, as evidenced by the direct effect of establishment on persistence (i.e. direct path between the two phases of invasion). Thus, high rainfall years particularly during the establishment period, even if infrequent, could be a key driver of long-term invasion dynamics, as it may only take one pulse resource year in which invader establishment is high to promote persistence.

Our experimental work yielded two important findings. First, we found that invasibility in mesic grasslands is impacted by the time-scale of fluctuating resources. Invasibility was *reduced* with short time-scale resource pulses (intra-annual increases in precipitation event size), which is contrary to predictions of the FRAH. FRAH has become a cornerstone of invasion biology and is often cited as a key mechanism behind increases in invasibility, yet experimental tests of its predictions in which mean resource availability is held constant and only variability is increased are still rare. Here, we show that FRAH is not supported for soil moisture pulses that occur at an interannual time-scale. However, we found evidence to suggest that at interannual time-scales, the FRAH is supported. Increased interannual variability in precipitation would yield more dry years as well as more wet years, and we found that invasion success was *enhanced* in years with high resource availability. Wet years resulted in a twofold increase in the number of established seedlings, and a threefold increase in the number of seedlings that persisted to the end of the season. Secondly, we found that invasibility was positively related to native community richness and the density of individuals in the community. This adds to the body of the literature suggesting that biotic resistance is often not supported for native communities, but instead, native communities often facilitate establishment of invader species (Levine, Adler & Yelenik 2004; Smith *et al*. 2004; Zabin & Altieri 2007; Bulleri & Benedetti-Cecchi 2008). We show that across natural gradients of community richness and stem density, environmental conditions that promote richness and denser number of individual plants also promote invasibility. Perhaps more importantly, results from this 10-year invasion study also show that resource availability drives invasion and that the biotic filters of plant community structure and diversity are secondary.

Global change is altering both the abiotic and biotic filters that potential invaders encounter on both short- and long-term scales. Here, we provide evidence that increased frequency of precipitation pulses at shorter time-scales decreases invasions, suggesting that predicted changes in intra-annual precipitation (Coumou & Rahmstorf 2012) may enhance resistance to invasion. However, we also show, as others have (Hobbs & Mooney 1991; Hobbs, Yates & Mooney 2007), that years of high precipitation enhance invader seedling establishment and persistence. Increased interannual variability in precipitation is also forecast with climate change, yielding more dry and wet years (IPCC 2012). We show that a single wet year, even if infrequent, has the potential to promote invasion, producing a self-sustaining viable invader population. Thus, the net effect of future alterations in precipitation regimes, and resulting resource fluctuations at short and long time-scales, needs to be assessed to forecast how ecosystem invasibility will change in the future.

Acknowledgements

Data accessibility

The species composition, light, soil moisture and precipitation data used in this manuscript are currently available through the ramps website (http://www.konza.ksu.edu/ramps/data.html). Invasion data will be made publically available through the same website within 1 month of publication.

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1 **Supporting Information**

2 **Table S1.** Effect of precipitation treatment on rainfall event size through time. Effects of

3 precipitation treatment (Precip, P) and year (Year, Yr) on precipitation event size for the

4 establishment (~1 month – mid-May to mid-June) and persistence periods (~2 month – mid-June

5 to mid-August). Statistical tests were performed using mixed model ANOVAs.

|	Establishment			Persistence		
	df	F-value	P-value	df	F-value	P-value
Precip	1, 78	47.67	<0.001	1, 145	77.53	<0.001
Year	8, 78	3.55	0.002	8, 145	4.28	<0.001
P*Yr	8, 78	2.31	0.028	8, 145	2.81	0.006

6

7

8   **Table S2.** Effect of precipitation treatment on length of dry period through time. Effects of

9   precipitation treatment (Precip, P) and year (Year, Yr) on the average length of dry periods (days

10   between rainfall events) for the establishment (~1 month – mid-May to mid-June) and

11   persistence periods (~2 month – mid-June to mid-August). Statistical tests were performed using

12   mixed model ANOVAs.

	Establishment			Persistence		
	df	F-value	P-value	df	F-value	P-value
Precip	1, 59	18.48	<0.001	1, 130	118.74	<0.001
Year	8, 59	2.21	0.040	8, 130	8.25	<0.001
PxYr	8, 59	1.00	0.446	8, 130	4.84	<0.001

13

14
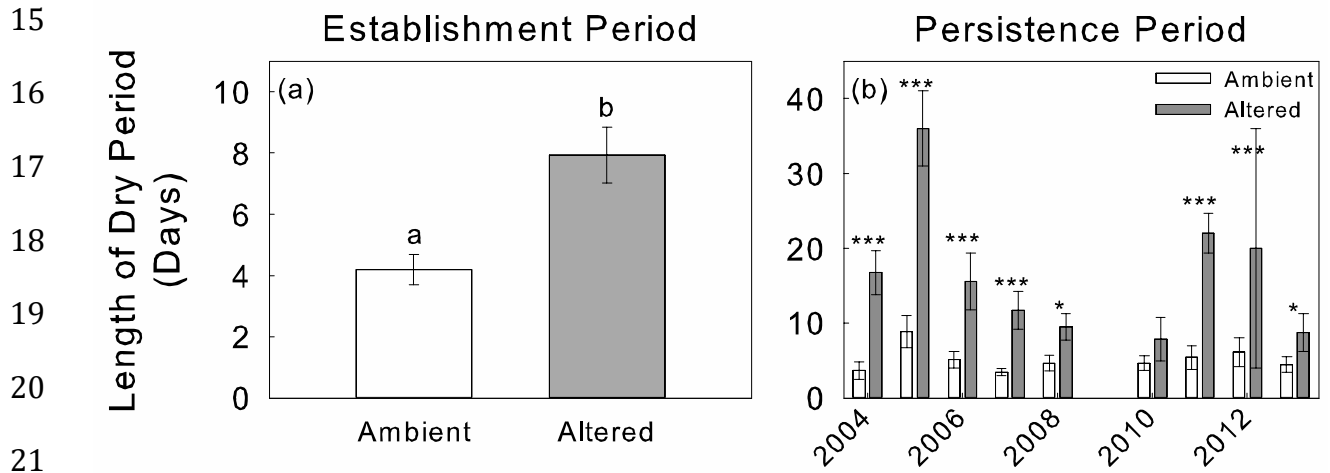
Fig. S1. Effect of rainfall treatment on length of dry periods. The effect of precipitation treatment (ambient = white; altered = dark grey) on length of dry periods (days between rainfall events) for the (a) establishment (~15 May – 15 June) and (b) persistence (~15 June – 15 August) periods. (a) The altered precipitation treatment significantly increased the length of dry periods during the establishment phase (Table S2). Letters denote significant differences between treatments (p-value <0.05). (b) The altered precipitation treatment significantly increased the length of dry period in eight out of nine years during the persistence period. P-values are from mixed model ANOVAs (* = p-value <0.1; ** = p-value < 0.05; *** = p-value < 0.01).