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Similarity between grassland vegetation and seed bank shifts with altered precipitation and clipping, but not warming

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Abstract: Similarity between seed bank and aboveground vegetation is frequently studied in order to better understand how community composition is affected by factors such as disturbance and succession. Grassland plant communities are known to be sensitive to shifts in precipitation and increases in temperature associated with climate change, but we do not know if and how these factors interact to affect the similarity between seed bank and aboveground vegetation. Also unknown is how the impact of grazing, the dominant land-use in grasslands, will interact with climatic conditions to affect similarity. We manipulated precipitation and temperature, and cut vegetation (as a proxy for grazing) at a grassland site for three years. Percent cover of aboveground vegetation was estimated in the third year, and compared with persistent seed bank samples taken in the year prior from the same plots. Similarity increased with reduced precipitation, was unresponsive to warming, and decreased with clipping. The aboveground community responded strongly to the treatments, while the seed bank community did less so, suggesting similarity responses were largely driven by changes in aboveground vegetation. Because of the importance of the seed bank in vegetation regeneration, understanding the relationship between seed bank and aboveground vegetation will improve our understanding of plant community dynamics under climate change and varied management (grazing) intensities.

Nomenclature: USDA, NRCS. 2011. The PLANTS Database (http://plants.usda.gov, 14 April 2011). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Abbreviations: ISA–Indicator Species Analysis; OTC–Open Top Chamber.

Introduction

The seed bank, defined as all viable seeds contained in the soil of a given area (Harper 1977), holds a record of previous vegetation, as well as potential permutations for future plant communities. Similarity between the aboveground vegetation and seed bank for a given community can be affected by factors such as disturbance and succession, and is frequently studied in order to better understand the mechanisms controlling plant community composition (Hopfensperger 2007). In grasslands, both aboveground community (Walther 2004) and seed bank composition (Walck et al. 2011) have been shown to respond to shifts in precipitation and increases in temperature associated with climate change, as well as to the dominant land use in grasslands: grazing (Diaz et al. 2007, Milchunas and Lauenroth 1993, McIntyre et al. 1999, McIntyre and Lavorel 2001, Saatkamp et al. 2010). However, we do not know how the effects of precipitation, warming, and grazing on aboveground vegetation and seed bank interact to affect similarity between these components.

Identifying changes in similarity between aboveground vegetation and the seed bank (hereafter referred to as "similarity") is important because the extent of similarity can indicate the potential for a seed bank to maintain and restore the aboveground community after disturbance, with increased potential for restoration from a seed bank that more closely mirrors vegetation (Valko et al. 2011). On average, grasslands generally have higher similarity than wetlands or forests (Hopfensperger 2007), and thus have great potential to restore the aboveground community after disturbance. However, similarity varies widely among grasslands (Bossuyt and Honnay 2008), with similarity generally higher in established grasslands or extreme growing conditions (Hopfensperger 2007), and communities dominated by annuals (Ungar and Woodell 1996, Peco et al. 1998).

Temperature increases and changes to precipitation associated with recent and future climate change can be expected to impact similarity via impacts on both the aboveground community (Walther 2004) and seed bank (Walck et al. 2011). The effects of warming and altered precipitation on aboveground vegetation are increasingly well documented (Wu et al. 2011), but a variety of factors related to plant regeneration from seed, such as seed dormancy, viability and germination (Lloret et al. 2004, Lloret et al. 2005, Walck et al. 2011) and including seed bank composition itself (Saatkamp et al. 2010) can also be highly sensitive to climatic conditions. However, it has also been demonstrated that climatic effects on regeneration processes from seed, such as those of precipitation on germination, are relatively weak compared to local environmental conditions, like soil type (Petru and Tielborger 2008).

Studies have shown precipitation to have variable effects on similarity over small time scales (Caballero et al. 2008, Gonzalez and Ghermandi 2008). However, we know of no study that has specifically monitored the effect of manipulated temperature on similarity. However, highly species-specific responses of seed viability (Ooi et al. 2009), germination (Saatkamp et al. 2011), and seedling success (Lloret et al. 2004) to warming suggest potential ramifications for the plant community, and thus similarity.

Grazing affects a suite of both aboveground vegetation and seed bank measures that can contribute to changes in similarity, including composition of the vegetation and seed bank community (Diaz et al. 2007, Milchunas and Lauenroth 1993, McIntyre et al. 1999, McIntyre and Lavorel 2001, Saatkamp et al. 2010). Studies have also been performed to specifically evaluate changes to similarity with grazing. Although similarity is generally thought to increase after a disturbance such as grazing (Ungar and Woodell 1996) as seeds in the soil can be the source for subsequent regeneration, grazing has also been shown to decrease similarity (Peco et al. 1998, Osem et al. 2006). Yet another study (Peco et al. 1998) showed no effect of grazing on similarity. These variable results among studies have been attributed to differences in grazing regimes, environmental conditions and vegetation characteristics among sites (Osem et al. 2006).

Interactive effects between grazing and climatic conditions have been shown to affect above ground vegetation differently than if applied independently (Klein 2004). Seed bank composition has also been shown to respond to the interactive effects of slope and grazing (Ortega et al. 1997). However, Peco et al. (1998) found no interactive effects between grazing and altitude or topography on similarity. No study has manipulated grazing and climatic conditions simultaneously to determine how they may interact to affect similarity.

We ask whether similarity between aboveground vegetation and seed bank composition in our grassland system responds to the climatic factors of altered precipitation and warming, and disturbance (clipping, as a proxy for grazing), as well as whether these factors have interactive effects on similarity. Unlike studies manipulating the effect of only one factor on similarity, we will be able to investigate and compare the relative impacts of multiple factors on similarity within a single grassland site.

Methods

Study site

This study was conducted at the University of Alberta Research Station near Kinsella, Alberta, Canada (53°85'0"N; 111°83'30"W). The area has a continental climate with average annual temperature of 2.8 °C and precipitation of 431.3 mm (Environment Canada, unpublished data). The study area is part of the Aspen Parkland natural sub-region and includes a mosaic of trembling aspen (*Populus tremuloides*) groves and rough fescue (*Festuca hallii*) grassland (Sims 2000). The study site was a 40 m × 100 m field on an east-facing slope, consisting of diverse native grassland dominated by *Festuca hallii, Hesperostipa curtiseta* and *Elymus trachycaulus,* as well as many perennial forbs. The site is used for cattle grazing, though grazing was ceased for the duration of the experiment. Soils are thin Orthic Black Chernozems developed from glacial till (Howitt 1988., Soil Classification Working Group 1998).

Experimental design and treatments

In May 2007, we initiated a three year manipulative experiment to determine the effects of warming (control, warmed), precipitation (reduced, ambient, added), and clipping (none, moderate, severe), on an array of grassland responses, including similarity between seed bank and aboveground composition. We used a randomized complete block design, with each of the 18 treatment combinations occurring once in each of five replicate blocks, for a total of 90 plots, each approximately 4 m^2.

Plots received either ambient, reduced (approximately 60% less), or added (approximately 60% more) precipitation. Rain-out shelters, 60-120 cm tall wood frames with plastic tops, were installed over all plots (Dura-Film Super 4™ 6-mil polyethylene film; AT Plastics, Edmonton, Alberta, Canada; see Appendix, Fig. 1 for photo). Although the shelters themselves may have some effect on micro-environmental conditions, we installed sham shelters over the control plots to maintain consistency in these conditions between treatments. The reduced precipitation treatment had small slits in the plastic that allowed approximately 40% of rainfall to reach the ground; water not falling through the plastic was collected in tanks using a gutter system. The added and ambient precipitation treatments had larger slits and holes to allow complete rainfall entry but control for any unintended effects of the structure itself. To increase precipitation but not affect the timing of rainfall within the added plots, water collected from reduced precipitation plots was redistributed by hand to adjacent added precipitation plots within 48 hours after rainfall. Rainout shelters were installed in 2007, although the added precipitation treatment was first implemented in 2008.

Plots were either left uncut, or cut in midsummer (June 15-30) to a stubble height of 7 cm (moderate intensity) or 3 cm (severe intensity) above ground, corresponding to approximately 35% and 56% of standing annual biomass, respectively. Vegetation was cut with a mower set at the corresponding height, except for the central 50 cm by 50 cm permanent sampling area, which was cut by hand to limit disturbance. Cut biomass was determined by sorting out any litter from the live biomass, drying, and weighing.

Half the plots were warmed by approximately 3 °C using fibreglass open-top chambers (OTCs; Sunlite-HP, Solar Components Corporation/Kalwall Corporation, Manchester, NH, USA). The OTC design has previously been used to increase air temperatures by 2-4 °C. OTCs were 2 m in diameter and 40 cm high, with sides positioned at a 60° angle to the ground (Marion et al. 1997). OTCs and rain-out shelters were installed in spring (May) of each year and removed in mid-October.

Two Davis Rain Collector II buckets (Davis Instruments, Hayward, CA, USA) measured ambient precipitation. Air temperature 25 cm above ground was recorded in two blocks (36 plots) every half hour using Onset HOBO Pendant Temperature data loggers (Onset Computer Corporation, Bourne, MA, USA). Photosynthetically active radiation (PAR, μmol photos/m^2/s) was measured above the shelter, and below the vegetation canopy, during the first year of the experiment, in August 2007, before most of the sham treatments were set up, using Decagon AccuPAR PAR-80 light metre. Light penetration (%) was determined by dividing PAR readings from below the vegetation canopy by PAR above the shelter, and multiplying by 100.

Aboveground vegetation

Vegetation sampling in each plot was concentrated within the central 50 cm by 50 cm sampling area. Plant cover (%) by species was estimated mid-month in May, June, July, and August of 2009. Every July, aboveground shoot biomass was cut from an independent 0.10 m^2 (10 cm by 100 cm) microplot. Harvested biomass was sorted to litter and live biomass, with the latter dried and weighed. To determine total live biomass per plot, biomass measures from the initial clipping treatments and final biomass harvest were combined, and presented as g/m^2.

Seed bank

Seed bank composition in each plot was sampled in 2008 from soil with the litter layer removed. To sample the persistent seed bank, those species which retain their seed bank for more than 12 months (Thompson and Grime 1979), rather than the transient seed bank, it is recommended to sample when species germinating in the spring have begun to develop but no fresh seeds have been dispersed (Csontos 2007). We sampled in mid-July, near the ideal time (end of June) suggested for seed bank sampling in our climate (Milberg 1992, Milberg and Persson 1994).

Within each plot, one 7 cm diameter sample of 15 cm depth was taken using a soil auger, of which half was subsampled, and one 5 cm diameter sleeve core of 20 cm depth was taken using a root corer. Thus, the total volume of soil sampled per plot was approximately 680 cm^3. Soil was successively washed through two sieves (6 mm and 0.212 mm mesh) to remove coarse (plant shoots, roots and soil invertebrates) and fine debris (TerHeerdt et al. 1996); this sieve size has been used to capture grassland seeds and likely captures the majority of seeds, but we acknowledge that some smaller seeds may have passed through and escaped detection. Remaining coarse debris was visually inspected for seeds. The remaining soil containing seeds was spread in a thin layer over 3 cm of sterilized seedling starter mix in 25 cm × 25 cm greenhouse trays. Three control trays filled with only the seedling starter mix were used to identify any seed contamination within the greenhouse. Trays were exposed to supplemental heat and lighting, watered every two to three days, and randomly rearranged biweekly. Emerging seedlings were counted and removed as they became identifiable, with unidentifiable seedlings transplanted into pots and grown until identifiable. After five months, germination ceased and the top layer of the tray was raked; seedling assessment continued until no germination was evident at seven months.

Similarity

We used the Bray-Curtis quantitative measure C_N (Magurran 1988) to determine similarity between 2008 seed bank composition and monthly standing vegetation in 2009 for each plot, as vegetation composition is influenced by previous year persistent seed bank (Caballero et al. 2008). This is a quantitative similarity measure and thus incorporates both species presence/absence and abundance. Relative abundances of seed bank and vegetation were used by converting to percentages prior to calculation of similarity. Similarity is calculated as $C_N = 2jN/(aN + bN)$, where aN is the total vegetation cover of each plot, bN is the total number of seeds in each plot (both 100 in this case), and jN is the sum of the lower of the two abundances (vegetation cover or seed number) for species occurring both in the seed bank and aboveground in each plot.

Statistical analysis

To determine unintended effects of the rain-out shelters on air temperature, we compared growing season (May-August) air temperatures in 2009 at mid-afternoon (1:30 PM) in the reduced and ambient precipitation plots, under control temperature and clipping conditions. Similarly, we compared light penetration in 2007 in the reduced and ambient precipitation plots, under control temperature and clipping conditions. For both air temperature and light penetration, means were compared using an independent samples t-test, in PASW Statistics 18, Release Version 18.0.0 (SPSS, Inc., 2009, Chicago, IL, www.spss.com).

Fixed effects of the treatments on similarity were assessed using a linear mixed model with restricted maximum likelihood estimation, and precipitation, clipping, and warming as categorical fixed factors, and block as a random factor, using PASW Statistics 18. Similarity was square-root transformed prior to analysis.

Shifts in similarity could be due to changes in the composition of the seed bank or the aboveground community. To parse out these roles, we measured responses of the seed bank and aboveground community to the treatments. To describe these community responses, we performed Unconstrained Non-metric Multidimensional Scaling (NMDS) ordinations using the Bray-Curtis distance measure on the 2008

Table 1. Relative abundance by species (%) across all treatments in the seed bank for 2008 and aboveground vegetation for 2009.

Plant species	Seed bank	Vegetation
Achillea millefolium L.	-	0.07
Allium textile A. Nels. & J.F. Macbr.	-	0.02
Androsace septentrionalis L.	17.54	0.02
Artemisia frigida Willd.	60.26	8.80
Antennaria parvifolia Nutt.	-	0.03
Astragalus flexuosus Dougl. Ex G. Don	1.59	4.53
Avenula hookeri (Scribn.) Holub	-	0.07
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	-	3.72
Campanula rotundifolia L.	0.15	-
Carex stenophylla Wohl. ssp. Eleocharis (bailey) Hult.	2.38	21.31
Chenopodium album L.	0.01	-
Cirsium arvense (L.) Scop.	0.02	-
Comandra umbellata (L.) Nutt.	-	2.09
Crepis tectorum L.	1.67	0.02
Elymus trachycaulus (link.) Gould ex Skinners ssp. Trachycalus	0.28	17.55
Epilobium glaberrimum Barbey	0.80	-
Erigeron caespitose Vent.	-	1.07
Erysimum inconspicuous (S. Wats.) MacM	0.26	0.16
Festuca hallii (Vasey) Piper	1.77	6.08
Gaillardia aristata Pursh	-	-
Geum triflorum Pursh	-	0.03
Gnaphalium palustre Nutt.	0.02	-
Hesperostipa curtiseta (A.S. Hitchc.) Barkworth	3.86	20.64
Heterotheca villosa (Pursh) Shinners var. hispida	-	0.30
Koeleria macrantha (Ledeb.) J.A.	1.42	0.22
Lygodesmia juncea (Pursh) D. Don ex Hook	-	0.11
Muhlenbergia cuspidata (Tarr. Ex Hook) Rydb.	-	0.03
Oxytropis campestris (L.) DC.	1.10	0.36
Poa pratensis L.	0.40	0.04
Potentilla bipinnatifida (Pursh) D. Don ex Hook	2.31	0.29
Potentilla concinna Richards.	0.85	0.47
Pulsatilla patens (L.) P. Mill. ssp. multifida (Pritz.) Zamels	2.02	6.75
Rosa arkansana Porter	-	0.28
Selaginella densa Rydb.	-	0.04
Solidago missouriensis Nutt.	-	4.35
Sphaeralcea coccinea (Nutt.) Rydb.	-	0.15
Taraxacum officinale G.H. Weber ex Wiggers	0.13	0.05
Thermopsis rhombifolia (Nutt. ex Pursh) Nutt. ex Richards.	-	0.27
Tragopogon dubius Scop.	-	0.04
Urtica dioica L.	0.17	-

seed bank and 2009 aboveground community (McCune and Mefford 2006). Multi-Response Permutation Procedures (MRPP) were conducted for each treatment to determine treatment effects on community composition. Ordinations were performed using PC-ORD Version 5.10 (McCune 2002)). We used Indicator Species Analysis (ISA) to identify individual species underlying compositional differences in response to the main treatments (Dufrene and Legendre 1997).

Results

Treatment effects

Rainout shelters reduced precipitation in relation to ambient conditions by 64.7 ± 2.4% in 2008 and 59.9 ± 1.4% (mean ± 1SE) in 2009, with corresponding increases in precipitation within the added precipitation treatment. Clipping removed 57.4 ± 5.5 g/m^3 (moderate clipping) and 76.7 ± 6.2 g/m^3 (severe clipping) in 2008, corresponding to 39% and 56% of total biomass. In 2009, clipping removed 74.8 ± 10.8 g/m^3 (moderate) and 99.3 ± 16.3 g/m^3 (severe), 32% and 56% removal of total biomass, respectively. On average, growing season (May-August) air temperatures at mid-afternoon (1:30 PM) were 3.1 ± 0.15 °C greater in warmed plots than control plots in 2008, and 4.2 ± 0.16 °C greater in 2009.

There was no difference between air temperature in the ambient (23.6 ± 0.4 °C) and reduced (23.6 ± 0.428 °C) precipitation treatments (t_{190} = 0.106, p = 0.92). There was also no difference between light penetration in ambient (20.0 ± 2.13%) and reduced (22.1 ± 4.84%) precipitation treatments (t_8 = 0.423, p = 0.68).

Table 2. Mixed model analysis of effects of precipitation, clipping, and warming on similarity between 2008 seed bank and 2009 aboveground vegetation.

Source of variation	Similarity	
	$F_{,df}$	P
Precipitation	$5.342_{2,146}$	0.036
Cutting	$9.411_{2,147}$	0.047
Warming	$0.031_{1,146}$	0.725
Warming * Cutting	$0.424_{2,146}$	0.735
Warming * Precipitation	$2.459_{2,146}$	0.315
Cutting * Precipitation	$0.692_{4,145}$	0.871
Warming * Cutting * Precipitation	$.302_{4,146}$	0.914

Aboveground vegetation

Visual inspection of the NMDS ordination of 2009 aboveground vegetation (Appendix, Fig.2), along with MRPP analysis, indicated that precipitation ($p < 0.001$, Appendix, Table 1) and clipping ($p < 0.001$; Appendix, Table 1) affected aboveground community composition, but temperature did not. Pair-wise contrasts were significant for all levels of precipitation and clipping (Appendix, Table 1). The ISA analysis identified one indicator species: *Astragalus flexuosus* (added precipitation, p = 0.04).

Seed bank

Both visual inspection of the resulting ordination from the seed bank data and the MRPP analysis indicated that only precipitation affected seed bank community composition ($p < 0.05$; Appendix, Table 1, Fig. 2). Pair-wise analysis revealed that this change in seed bank community composition was driven by differences between the added and reduced precipitation treatment (p = 0.02; Appendix, Table 1). No species were associated with particular treatments in the ISA.

Similarity

Total species richness was one-third lower in the seed bank (22 species) than in aboveground vegetation (33 species). Six species present in the seed bank were not found in the aboveground vegetation, while 17 species present in the vegetation were not detected in the seed bank (Table 1). Similarity between the seed bank and aboveground vegetation as a response to treatments followed a similar pattern across all months, so we present July (peak biomass and richness) results only. Reduced precipitation increased similarity between the seed bank and aboveground vegetation (p = 0.04; Table 2, Fig. 1), and severe clipping decreased similarity (p = 0.05; Fig. 1). Warming had no effect on similarity (p = 0.73; Fig. 1). There were no interactions between any of the three treatments (Table 2).

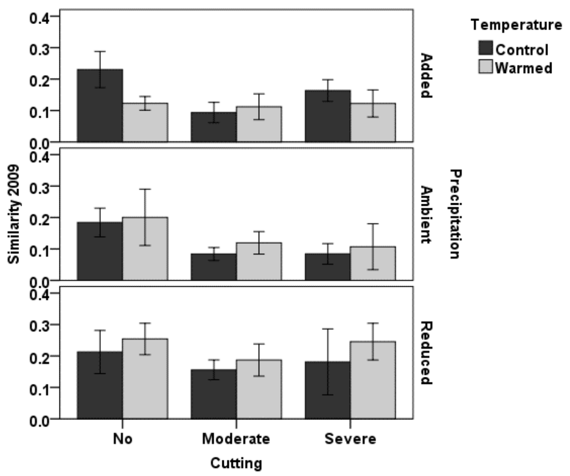

Figure 1. Effect of precipitation, clipping, and warming on similarity between 2008 seed bank and 2009 aboveground vegetation. Bars are 1±SE

Discussion

Warming, precipitation, and clipping have not previously been jointly investigated for their effects on similarity between the seed bank and aboveground vegetation; indeed, warming has not been tested independently for effects on similarity. We found that the response of similarity was dependent on treatment, with both clipping and precipitation, but not warming, affecting similarity on a short timescale. The magnitude and direction of response varied with treatment, with clipping decreasing similarity and reduced precipitation increasing similarity. There were no interactions between any of the factors, suggesting that the seed bank responded independently to the different factors.

As seed bank composition, density, and richness, were unaffected by clipping, changes to similarity probably reflected changes in the aboveground vegetation. Clipping may be expected to increase similarity, as germination success typically increases following release from dense plant cover (Kitajima and Tilman 1996, Peco et al. 1998). However, direct mechanical harm to seedlings and alteration of micro-environmental conditions that limit seed generation, such as may have occurred with our clipping treatment, are known to decrease similarity (Bakker and Devries 1992). Alternatively, grazing-adapted adult plants that use vegetative propagation to maintain dominance in the community, rather than seedlings emerging from the seed bank, may have been able to fill any gaps caused by clipping (simulated grazing), subsequently decreasing similarity.

The increase in similarity in response to reduced precipitation is consistent with the observed pattern of increased similarity in communities subject to extreme growing conditions (Henderson et al. 1988, Peco et al. 1998, Gul and Weber 2001). Because both the seed bank and aboveground vegetation responded to the reduced precipitation treatment, the change in similarity could reflect changes to the aboveground vegetation, the seed bank, or both. Annual and biennial species that colonize under extreme conditions, such as reduced precipitation, rely on seed banks, unlike perennial species that rely primarily on vegetative reproduction (Henderson et al. 1988). As well, formation of soil seed banks has been found to vary, in terms of species contributing seed and numbers of seed, with decreased predictability of rainfall in aid systems (Venable 2007, Angert 2009).

We found no response of similarity to increased precipitation. No other studies have specifically evaluated the effect of added precipitation on similarity. However, it has been demonstrated that seed bank expression in aboveground vegetation increases during wet years (Gutierrez and Meserve 2003, Caballero et al. 2008), likely because of increased moisture necessary for seed bank germination (Clauss and Venable 2000). In contrast, the well-established continuous cover of perennial grasses and forbs in our grassland may benefit from increased resources such as soil moisture, and thereby restrict seed bank germination or survival of seedlings via competition (Buckland et al. 2001, Osem et al. 2006).

Both our measures of the seed bank and aboveground community, as well as the similarity between them, were unresponsive to warming. A certain threshold treatment value can be necessary before similarity is affected (Wellstein et al. 2007) and it may be that more prolonged warming or a greater increase in temperature would affect similarity. Consistent with our findings, other studies have found that both the seed bank (Akinola et al. 1998) and aboveground community (Grime et al. 2008) can be unresponsive to warming.

Seed bank density was unaffected by the treatments, and thus was not found to contribute to changes in similarity. The average density we found of 6,923 seeds/m^2 (Appendix, Fig. 3) is similar to that previously identified within fescue prairie seed banks (Willms and Quinton 1995). Seed density is a function of soil volume, and the volume of soil recommended for seed bank studies varies. Our sample volume (681 cm^3) was above that suggested by Hayashi and Numata (1971) and Roberts (1981), but below the recommendation of others (Oomes and Ham 1983, Thompson et al. 1997). Rather than providing an exhaustive description of the seed bank, our intent was to document changes in similarity between the seed bank and above ground vegetation. Sampling intensity does not appear to be a constraint in the current study given that we found rapid responses in similarity to the treatments over the study period. This is consistent with the finding of Caballero et al. (2008) where the relationship between seed bank and aboveground vegetation was closely linked on a short time scale, from one to three years.

The seed bank showed a lack of response to both warming and clipping treatments. Other studies have reported delayed responses of seed bank composition compared to responses of aboveground vegetation, with little effects from short-term manipulation of warming and precipitation (Akinola et al. 1998), or grazing and mowing (Peco et al. 1998). Composition of the seed bank community did, however, respond to short-term manipulation of precipitation. Changes in similarity due to precipitation found here are likely attributable to both changes in the seed bank and the aboveground vegetation, as only the reduced and added precipitation treatments differed in aboveground community, but seed bank similarity differed between the reduced and ambient treatments. Changes in soil moisture can affect seed longevity in the soil (Bekker et al. 1998). For example, the species *Pulsatilla patens* comprised 2% of seed bank abundance, and was indicative of reduced precipitation, which in turn may have contributed to the increase in seed bank similarity under those conditions.

Although we conclude that changes in aboveground vegetation were generally responsible for the similarity response, especially for clipping, we cannot discern from our study whether changes in similarity are due to changes in germination and establishment of new plants, or changes in the abundance of pre-existing plant species. For example, it is possible that those species that have high presence in the seed bank are those that also increase in size or cover with reduced precipitation. Additionally, small changes in abundance of the most common species in the seed bank and vegetation (Table 1) would have the most profound effect on the similarity index, and may be primarily responsible for observed changes in similarity.

We found that within our grassland site, similarity responded over the short-term to precipitation manipulation and clipping, with responses largely driven by changes to the aboveground community, rather than the seed bank. Site characteristics such as domination by perennial plant cover and adaption to grazing may help explain our findings. We recommend more studies be conducted manipulating multiple factors in a single experimental design, in order to compare the relative impact of various factors on similarity, and better understand variable responses of similarity across systems. Grasslands are increasingly under the pressures of climate change and grazing from larger herds, and this information will aid us in understanding any subsequent plant community shifts. As the seed bank can harbour species not expressed in aboveground vegetation, and as regeneration from seed is largely responsible for the introduction of plant species (Grubb 1977), changes in the relationship between the seed bank and aboveground vegetation are important in understanding plant community dynamics.

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References

Angert, A.L. 2009. The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *Proc. Nat. Acad. Sci. U.S.A.* 106: 19693-19698.

Akinola, M.O., K. Thompson and S.M. Buckland. 1998. Soil seed bank of an upland calcareous grassland after 6 years of climate and management manipulations. *J. Appl. Ecol*. 35: 544-552.

Bakker, J.P. and Y. Devries. 1992. Germination and early establishment of lower salt-marsh species in grazed and mown saltmarsh. *J. Veg. Sci*. 3: 247-252.

Bekker, R.M., M.J.M. Oomes and J.P. Bakker. 1998. The impact of groundwater level on soil seed bank survival. *Seed Sci. Res.* 8: 399-404.

Bossuyt, B. and O. Honnay. 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *J. Veg. Sci.* 9: 875-884.

Buckland, S.M., K. Thompson, J.G. Hodgson and J.P. Grime. 2001. Grassland invasions: Effects of manipulations of climate and management. *J. Appl. Ecol*. 38: 301-309.

Caballero, I., J.M. Olano, J. Loidi and A. Escudero. 2008. A model for small-scale seed bank and standing vegetation connection along time. *Oikos* 117: 1788-1795.

Clauss, M.J. and D.L. Venable. 2000. Seed germination in desert annuals: An empirical test of adaptive bet hedging. *Amer. Nat*. 155: 168-186.

Csontos, P. 2007. Seed banks: Ecological definitions and sampling considerations. *Community Ecol.* 8: 75-85.

Diaz, S., S. Lavorel, S. McIntyre, V. Falczuk, F. Casanoves, D.G. Milchunas, C. Skarpe, G. Rusch, M. Sternberg, I. Noy-Meir, J. Landsberg, W. Zhang, H. Clark and B.D. Campbell. 2007. Plant trait responses to grazing - a global synthesis. *Global Change Biol.* 13: 313-341.

Dufrene, M. and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol. Monogr.* 67: 345-366.

Gonzalez, S. and L. Ghermandi. 2008. Postfire seed bank dynamics in semiarid grasslands. *Plant Ecol.* 199: 175-185.

Grime, J.P., J.D. Fridley, A.P. Askew, K. Thompson, J.G. Hodgson and C.R. Bennett. 2008. Long-term resistance to simulated climate change in an infertile grassland. *P.N.A.S.* 105: 10028-10032.

Grubb, P.J. 1977. Maintenance of species-richness in plant communities - importance of regeneration niche. *Biol. Rev. Cam. Phil. Soc*. 52: 107-145.

Gul, B. and D.J. Weber. 2001. Seed bank dynamics in a Great Basin salt playa. *J. Arid Env*. 49: 785-794.

Gutierrez, J.R. and P.L. Meserve. 2003. El nino effects on soil seed bank dynamics in North-Central Chile. *Oecologia.* 134: 511-517.

Harper, J.L. 1977. *Population Biology of Plants.* Academic Press. London.

Hayashi, I. and M. Numata. 1971. Viable buried-seed population in the *Miscanthus* and *Zoysia* type grasslands in Japan - ecological studies on the buried-seed population in the soil related to plant succession. *Jap. J. Ecol*. 20: 10.

Henderson, C.B., K.E. Petersen and R.A. Redak. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. *J. Ecol*. 76: 717-728.

Hopfensperger, K.N. 2007. A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos.* 116: 1438-1448.

Howitt, R.W. 1988. Soil survey of the county of beaver. Alberta soil survey report No. 47. Alberta Research Council Open File Rep. 1987-4.

Kitajima, K. and D. Tilman. 1996. Seed banks and seedling establishment on an experimental productivity gradient. *Oikos* 76: 381-391.

Klein, J.A., G., Harte, and X. Zhao. 2004. Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecol. Lett.* 7: 1170-1179.

Lloret, F., J. Penuelas and M. Estiarte. 2004. Experimental evidence of reduced diversity of seedlings due to climate modification in a mediterranean-type community. *Global Change Biol.* 10: 248-258.

Lloret, F., J. Penuelas and M. Estiarte. 2005. Effects of vegetation canopy and climate on seedling establishment in mediterranean shrubland. *J. Veg. Sci.* 16: 67-76.

Magurran, A.E. 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, N J.

Marion, G.M., G.H.R. Henry, D.W. Freckman, J. Johnstone, G. Jones, M.H. Jones, E. Levesque, U. Molau, P. Molgaard, A.N. Parsons, J. Svoboda and R.A. Virginia. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biol*. 3: 20-32.

McCune, B., J.B. Grace, and J.P. Grime. 2002. *Analysis of Ecological Communities*. MjM Software Design, Oregon, USA.

McCune, B. and M.J. Mefford. 2006. Pc-Ord multivariate analysis of ecological data. MjM Software Gleneden Beach. Oregon, USA.

McIntyre, S. and S. Lavorel. 2001. Livestock grazing in subtropical pastures: Steps in the analysis of attribute response and plant functional types. *J. Ecol.* 89: 209-226.

McIntyre, S., Lavorel, S., Landsberg, J. and Forbes, T.D.A. 1999. Disturbance response in vegetation: towards a global perspective on functional traits. *J. Veg. Sci.* 10: 621-630.

Milberg, P. 1992. Seed bank in a 35-year-old experiment with different treatments of a seminatural grassland. *Acta Oecol*. 13: 743-752.

Milberg, P. and T.S. Persson. 1994. Soil seed bank and species recruitment in road verge grassland vegetation. *Ann. Bot. Fenn.* 31: 155-162.

Milchunas, D.G. and W.K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soil over a global range of environments. *Ecol. Monogr.* 63: 327-366.

Ooi, M.K.J., T.D. Auld and A.J. Denham. 2009. Climate change and bet-hedging: Interactions between increased soil temperatures and seed bank persistence. *Global Change Biol*. 15: 2375-2386.

Oomes, M.J.M. and M. Ham. 1983. Some methods of determining the seed bank. *Acta Bot. Neerl.* 32: 244-244.

Ortega, M., C. Levassor and B. Peco. 1997. Seasonal dynamics of mediterranean pasture seed banks along environmental gradients. *J. Biogeogr*. 24: 177-195.

Osem, Y., A. Perevolotsky and J. Kigel. 2006. Similarity between seed bank and vegetation in a semi-arid annual plant community: The role of productivity and grazing. *J. Veg. Sci.* 17: 29-36.

Peco, B., M. Ortega and C. Levassor. 1998. Similarity between seed bank and vegetation in Mediterranean grassland: A predictive model. *J. Veg. Sci*. 9: 815-828.

Petru, M. and K. Tielborger. 2008. Germination behaviour of annual plants under changing climatic conditions: Separating local and regional environmental effects. *Oecologia* 155: 717-728.

Roberts, H.A. 1981. Seed banks in soils. *Adv. Appl. Biol*. 6: 1-55.

Saatkamp, A., C. Romermann and T. Dutoit. 2010. Plant functional traits show non-linear response to grazing. *Fol. Geo.* 45: 239-252.

Saatkamp, A., L. Affre, T. Baumberger, P.J. Dumas, A. Gasmi, S. Gachet and F. Arene. 2011. Soil depth detection by seeds and diurnally fluctuating temperatures: Different dynamics in 10 annual plants. *Pl. Soil.* 349: 331-340.

Sims, P.L., and P.G. Risser. 2000. Grasslands. *North American Terrestrial Vegetation*, Second edition. Cambridge University Press, Cambridge.

Soil Classification Working Group. 1998. Canadian system of soil classification. Agriculture and Agri-food Canada, Ottawa, Ontario.

TerHeerdt, G.N.J., G.L. Verweij, R.M. Bekker and J.P. Bakker. 1996. An improved method for seed-bank analysis: Seedling emergence after removing the soil by sieving. *Func. Ecol.* 10: 144-151.

Thompson, K., Bakker, JP and Bekker, R M. 1997. *Soil Seed Banks of North-West Europe: Methodology, Density and Longevity.* Cambridge University Press, Cambridge.

Thompson, K. and J.P. Grime. 1979. Seasonal-variation in the seed banks of herbaceous species in 10 contrasting habitats. *J. Ecol.* 67: 893-921.

Ungar, I.A. and S.R.J. Woodell. 1996. Similarity of seed banks to aboveground vegetation in grazed and ungrazed salt marsh communities on the Gower Peninsula, South Wales. *Int. J. Plant Sci.* 157: 746-749.

Valkó, O., P. Török, B. Tóthmérész and G. Matus. 2011. Restoration potential in seed banks of acidic fen and dry-mesophilous meadows: Can restoration be based on local seed banks? *Rest. Ecol.* 19: 9-15.

Venable, D.L. 2007. Bet hedging in a guild of desert annuals. *Ecology* 88: 1086-1090.

Walck, J.L., S.N. Hidayati, K.W. Dixon, K. Thompson and P. Poschlod. 2011. Climate change and plant regeneration from seed. *Global Change Biol.* 17: 2145-2161.

Walther, G.R. 2004. Plants in a warmer world. *Persp. Plant Ecol. Evol. Syst.* 6: 169-185.

Wellstein, C., A. Otte and R. Waldhardt. 2007. Seed bank diversity in mesic grasslands in relation to vegetation type, management and site conditions. *J. Veg. Sci.* 18: 153-162.

Willms, W.D. and D.A. Quinton. 1995. Grazing effects on germinable seeds on the fescue prairie. *J. Range Manage.* 48: 423-430.

Wu, Z., P. Dijkstra, G.W. Koch, J. Penuelas and B.A. Hungate. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Global Change Biol.* 17: 927-942.

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Appendix

Table 1. Results of Multi-Response Permutation Procedures (MRPP) comparisons of precipitation, cutting and warming on seed bank and aboveground vegetation composition.

Figure 1. Rainout shelter design.

Figure 2. Precipitation and cutting treatments overlaid on NMS ordination of aboveground plant community.

Figure 3. Effect of precipitation, cutting, and warming on 2008 total seed bank density.

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