Twenty-five years of sagebrush steppe plant community development following seed addition

Timothy B. Hoelzle, Jayne L. Jonas and Mark W. Paschke*

Forest and Rangeland Stewardship Department, Colorado State University, 1472 Campus Delivery, Fort Collins, CO 80523-1472, USA

Summary

1. Plant community succession has been a major area of study over the past century with recent research focusing on the importance of initial colonisers following disturbance. Seed addition can accelerate ecosystem regeneration and is a method commonly used by land managers to restore disturbed lands. However, few studies have examined the effects of seeding treatments on long-term community composition.

2. A study was established in 1984 in the Piceance Basin of northwest Colorado to examine how various revegetation seed mixes affect plant community development following disturbance. The site was surveyed again in 2008 and 2009 to assess long-term community development.

3. Initial seed mix resulted in significant differences in plant community composition after 25 years. Seeding with native and exotic early-seral species resulted in a community with significantly more exotic species and mid-seral shrubs, while seeding with native late-seral species resulted in a community dominated by perennial grasses. Additionally, an unseeded control resulted in a vegetation community dominated by both perennial grasses and mid-seral shrubs, but community composition at the species level was considerably different from that of the seeded treatments. However, the plant community composition of each of the three treatments was significantly different from an adjacent undisturbed reference area, which was dominated by the late-seral shrub, *Artemisia tridentata*, and perennial grasses.

4. *Synthesis and applications.* Our results illustrate how initial colonisers (seed mix) can strongly affect subsequent community assemblage after 25 years of development. Restoration ecologists should give considerable thought to the species used in a restoration seed mix to ensure the success of restoration designs and to create the desired community assembly and associated ecosystem services.

Key-words: *Artemisia tridentata*, community assembly, initial colonisers, long-term experiment, Piceance Basin, plant succession, restoration ecology, revegetation seed mix

Introduction

Global ecosystems are facing rapid degradation, resulting in dramatic habitat transformations and a reduction in key ecosystem services, including wild plant- and animal-based foods, erosion control and water purification (Millennium Ecosystem Assessment 2005). Restoration of these degraded lands is paramount in improving vital ecosystem services and requires a thorough understanding of the processes and patterns regulating ecosystem progression (Temperton & Hobbs 2004). Theories of succession and community assembly attempt to explain plant community development following disturbance by examining the resulting sequence of communities (seral stages) and are among the core concepts of restoration ecology (Young 2000).

Early successional theories, first posited by Clements (1916), hypothesised that plants characteristic of early-seral environments are gradually replaced by more competitive later-seral species. However, recent studies by applied ecologists suggest that non-equilibrium dynamics prevail (Wallington, Hobbs & Moore 2005), especially at smaller spatial scales where initial colonisers have been shown to have a strong influence on future community composition (Belyea & Lancaster 1999; Temperton & Hobbs 2004; Fukami *et al.* 2005). The order and timing of the arrival of species is something that is often manipulated in a restoration setting. Research focused in this area is critical in developing our knowledge of how species included in restoration seed mixes can affect plant community development and, subsequently, the success of restoration

*Correspondence author. E-mail: mark.paschke@colostate.edu

designs. A long-standing dilemma in ecological restoration is whether to plant late-seral species to speed up recovery or plant early-seral species to mimic natural successional processes. Seeding native early-seral species to disturbed lands has been shown to prevent the establishment and development of invasive annual species (Beyers 2004; Young *et al.* 2009; Herron 2010). However, incorporating late-seral species, which are often dispersal limited, as components of restoration seed mixes has been shown to expedite the recovery process of degraded lands (Kleijn 2003; Yoshida 2007; Cole *et al.* 2011).

The field of restoration ecology can not only improve degraded lands but also test theories of ecosystem succession by examining community responses to direct manipulations of ecosystem function and structure (Bradshaw 1987). By manipulating ecosystem processes, such as propagule dispersal (Quinn & Robinson 1987; Stevenson, McLendon & Redente 2000; Foster & Tilman 2003), practitioners can alter the rate and trajectory of ecosystem recovery while improving our understanding of the constraints to ecosystem development. On sites of low species richness or where seed bank and propagule sources are limited, seed addition can be a useful method to accelerate ecosystem succession (Palmer, Ambrose & Poff 1997). For example, a study examining the succession of abandoned agricultural lands in the Netherlands found that seeding with both early- and late-seral species resulted in dominance of the former after 3 years of community development (Kleijn, Joenje & Kropff 1997), while a study testing seed addition along a chronosequence of succession found early-seral species could only successfully establish early in succession (Kleijn 2003). Similarly, addition of late-seral propagules to a disturbed sagebrush steppe ecosystem resulted in greater production of late-seral grass and shrub species and decreased the contribution by early-seral components, while addition of early-seral propagules produced a plant community similar to that of an unseeded control (Stevenson, McLendon & Redente 2000).

Our aim was to revisit the Stevenson, McLendon & Redente's (2000) study site to examine how early- and late-seral seed mixtures control plant community development relative to unseeded control treatments and a late-seral reference community. Although most experiments of this nature occur over short time periods (Callahan 1984; Inouye & Tilman 1995; Lake 2001; Hobbie *et al.* 2003), this study revisited an experiment that began in the mid 1980s to understand how common restoration practices affect plant communities after 25 years of development. We hypothesised that seeding with late-seral species would result in a community that more closely resembled the species composition of the adjacent reference community, while seeding with early-seral species (native and introduced) would result in a community that more closely resembled the species composition of the unseeded control.

Materials and methods

SITE DESCRIPTION

The study site is located 65 km northwest of Rifle, Colorado, USA, in the Piceance Basin (UTM 12 S 722198 4420302) at an elevation of 2030 m. The climate is semi-arid, with mean annual temperature of 8·7 °C and mean annual precipitation of 326 mm (period of record = 1970–2000), with approximately half occurring as snowfall (High Plains Regional Climate Center 2010). The main soil type is Yamac loams (fine-loamy mixed, Borollic Camborthids) (United States Department of Agriculture 1982), supporting a vegetation community dominated by *Artemisia tridentata* ssp. *wyomingensis* Beetle and Young Wyoming big sagebrush, with an understorey dominated by perennial grasses *Hesperostipa comata* needle and thread, *Koeleria macrantha* prairie junegrass, *Pascopyrum smithii* western wheatgrass and *Pseudoroegneria spicata* bluebunch wheatgrass and the succulent *Opuntia polyacantha* Haw. plains pricklypear (Redente *et al.* 1985).

EXPERIMENTAL DESIGN

In August 1984, research blocks were established, fenced to exclude cattle grazing, and a disturbance, similar to that of proposed resource extraction activity (oil shale mining), was conducted within the *A. tridentata* community. All vegetation and the top 5 cm of soil were removed from the site, and the next 25 cm of soil was thoroughly mixed. The disturbance resulted in a reduction of >90% of the soil seed bank (Carpenter *et al.* 1990). Following the disturbance, four blocks of treatment plots were established in a split-block design, where each block consisted of six 500-m^2 treatment plots. The first treatment level was fumigation (fumigated or not fumigated), and the second treatment level was seed mix (early-seral, late-seral or unseeded control). Species and naming authorities included in each seeding treatment are provided in Table 1. Treatments were randomly assigned to plots within blocks. The purpose of soil fumigation was to assess the impact of soil organism removal on plant community development. However, in the current study, fumigation treatments were pooled across seeding treatments because there were no longer discernable effects of fumigation in the plant community data. Additionally, an undisturbed reference plot was left intact immediately adjacent to each block. These reference plots were of equal size to the treatment plots; however, they were not randomly located within each block because of the logistics of plot setup using heavy machinery.

TREATMENTS

In September 1984, fumigation plots were surrounded with a 2-cm-thick plywood sidewall to a depth of 55 cm and covered with plastic tarpaulins. Plots were injected with the soil fumigant, methyl bromide, at a rate of 90 kg ha^{-1} for a 24-hour period to ensure even and adequate exposure (Stevenson, McLendon & Redente 2000).

Early- and late-seral seed mixes (native and introduced species) were applied to specified plots in October–November 1984 (Table 1). Direct observations of colonising and mature communities at this site guided species selection for the early- and late-seral seed mixes, respectively. The early-seral seed mix included exotic annual species common to the site: *Bassia scoparia* burningbush, *Bromus tectorum* cheatgrass and *Salsola tragus* prickly Russian thistle, in an effort to better understand the vegetation dynamics associated with invasive species present in this area.

All species were hand broadcast seeded and lightly raked into the soil to cover the seeds. In addition to seeding, 150 *A. tridentata* seedlings (6 months old) were hand transplanted to the late-seral treatment plots to further encourage establishment of this species (Stevenson, McLendon & Redente 2000).

Table 1. Seed mixtures used in replicated seeding treatments in the Piceance Basin of northwest Colorado, USA. Seed was applied following disturbance in the fall of 1984 to examine the effect of initial propagule availability on long-term community composition

Seed Mix	Life-form	Scientific name	Common name	Seeding rate	
				kg PLS ha^{-1}	# PLS m^{-2}†
Early-seral	Grass	*Bromus tectorum* L.	Cheatgrass*	0·78	34
	Grass	*Elymus elymoides* (Raf.) Swezey	Squirreltail	2·37	100
	Grass	*Hordeum jubatum* L.	Foxtail barley	0·05	2
	Forb	*Bassia scoparia* (L.) A.J. Scott	Burning bush*	0·32	38
	Forb	*Erigeron engelmannii* A. Nelson	Engelmann's fleabane	0·01	4
	Forb	*Packera multilobata* W.A. Weber and A. Löve	Lobeleaf groundsel	0·02	3
	Forb	*Salsola tragus* L.	Prickly Russian thistle*	1·40	309
	Forb	*Sphaeralcea coccinea* (Nutt.) Rydb.	Scarlet globemallow	0·91	100
	Shrub	*Chrysothamnus viscidiflorus* (Hook.) Nutt.	Yellow rabbitbrush	0·01	2
	Shrub	*Ericameria nauseosa* G.L. Nesom and Baird	Rubber rabbitbrush	0·38	34
	Shrub	*Gutierrezia sarothrae* (Pursh) Britton and Rusby	Broom snakeweed	0·06	3
Late-seral	Grass	*Achnatherum hymenoides* (Roem. and Schult.) Barkworth	Indian ricegrass	0·32	11
	Grass	*Elymus lanceolatus* (Scribn. and J.G. Sm.)	Thickspike wheatgrass	0·29	9
	Grass	*Hesperostipa comata* (Trin. and Rupr.) Barkworth	Needle and thread	2·57	78
	Grass	*Koeleria macrantha* (Ledeb.) Schult.	Prairie Junegrass	0·26	133
	Grass	*Pascopyrum smithii* (Rydb.) A. Löve	Western wheatgrass	0·12	3
	Grass	*Poa secunda* J. Presl	Sandberg bluegrass	0·59	136
	Grass	*Pseudoroegneria spicata* (Pursh) A. Löve	Bluebunch wheatgrass	0·65	18
	Forb	*Astragalus purshii* Douglas ex Hook.	Woollypod milkvetch	0·01	1
	Forb	*Phlox hoodii* Richardson	Spiny phlox	0·01	1
	Forb	*Trifolium gymnocarpon* Nutt.	Hollyleaf clover	0·01	1
	Shrub	*Artemisia tridentata* Nutt.‡	Big sagebrush	0·50	260
	Shrub	*Krascheninnikovia lanata* (Pursh) A. Meeuse and Smit	Winterfat	2·40	59

*Indicates exotic species.
†# PLS m^{-2} is estimated based on species averages for numbers of seeds per unit weight.
‡Six-month-old seedlings transplanted in addition to seeding.

VEGETATION ESTIMATION

Vegetation sampling occurred during the summers of 2008 and 2009. Sampling was conducted twice during the growing season in an effort to capture the peak biomass of both cool and warm season plant species (Lauenroth *et al.* 1986). During each sampling period, eight 0·5-m^2 quadrats were randomly placed within each treatment, control and reference plot. Current-year above-ground biomass was harvested to ground level, separated by species and collected. For woody perennials, only the current-year biomass was collected. Vegetation was then dried to constant mass at 55 °C and weighed. Total annual above-ground production for each species was estimated by using the greater of the two mass values within each year.

DATA ANALYSIS

Relative values for plant production (relative biomass) were used to reduce heterogeneity because of variation in abiotic variables, such as precipitation totals and timing (Doerr, Redente & Reeves 1984). Relative biomass was determined by dividing mean species production values by the mean total plant production for that year. When necessary, values were transformed to satisfy the assumptions of normality and heterogeneity of variance using natural log, power or square root transformations. Vegetation composition by life-form (grass, forb and shrub) and life-history (annual, biennial and perennial) were analysed by use of repeated measures two-way restricted maximum likelihood (REML) analysis with a split-block design (fumigation as the whole plot and seeding as the subplot) and block as a random variable with the MIXED procedure of SAS statistical software, version 9.2 (SAS Institute, Cary, NC, USA). Tukey's studentized range test

(HSD) was used to explore differences among treatment means. As no differences were observed between the fumigated and non-fumigated treatments, fumigation plots were pooled across seeding treatments for further analyses.

A comparison of species composition was used to examine differences across the seeding treatments, control and reference using non-metric multidimensional scaling (NMS) based on Sorensen distances (McCune & Grace 2002) with 50 iterations of the real data and 250 runs in PC-Ord version 6 (McCune & Medford 2011). To test for differences in species composition between treatments, NMS axes scores for plots were analysed using repeated measures randomized complete block MANOVA and contrast statements and permutation *P*-value adjustment procedures were used to make pairwise comparisons with the GLM procedure (SAS Institute). Using ordination scores to assess treatment effects on community composition (Kourtev, Ehrenfeld & Haggblom 2002; Kluber, Smith & Myrold 2011) was chosen over procedures using the dissimilarity matrix due limitations associated with analysis of complex experimental designs (i.e. both random and repeated measures) in these approaches.

Results

Perennial grasses and mid-seral shrubs dominated all plots after 25 years of community development (Tables 2 and 3). The early-seral seeded (ES) treatment was similar to the unseeded control, and both were significantly different from the late-seral seeded (LS) treatment and reference (Fig. 1). The LS treatment and reference differed from each other. Together axes 1 and 2 of NMS analysis accounted for 73·4% of the

Table 2. Mean and standard error of species composition (% of total biomass) by major species and functional groups in 2008 for study plots that received various seed mixtures in 1984. Major species were determined as any species > 5% of total biomass among treatments or years. Seed mixture treatments were addition of early-seral seed, an unseeded control, addition of late-seral seed and an undisturbed reference. Means followed by different letters within rows indicate significant differences (*P* < 0·05) using Tukey's HSD

		Early-seral		Control		Late-seral		Reference	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Alyssum alyssoides	A F*	5·3b	0·8	4·5a	0·8	2·7ab	0·6	1·3b	0·5
Bromus tectorum	A G	11·4a	3·7	9·2ab	2·9	4·3bc	1·4	1·2c	0·8
Castilleja angustifolia	P F	0·0	0·0	0·3	0·3	0·0	0·0	0·0	0·0
Linum lewisii	P F	4·1	1·6	3·1	1·6	2·8	1·3	0·0	0·0
Melilotus officinalis	P F	0·5	0·4	0·2	0·1	0·0	0·0	0·0	0·0
Phlox hoodii	P F	0·0b	0·0	0·0b	0·0	0·1b	0·1	7·2a	5·4
Sphaeralcea coccinea	P F	1·7	0·8	3·4	1·2	2·9	0·9	0·5	0·4
Agropyron cristatum	P G	4·0ab	2·0	20·3a	7·8	2·4b	2·0	2·3ab	2·2
Elymus lanceolatus	P G	0·9	0·9	1·9	1·4	7·6	4·8	1·8	1·7
Hesperostipa comata	P G	8·4b	2·1	12·2b	2·7	24·5a	4·1	6·4b	1·9
Koeleria macrantha	P G	2·7b	1·6	1·6b	0·8	1·8b	0·7	9·0a	1·9
Pascopyrum smithii	P G	6·3b	3·3	7·4b	1·7	20·8a	4·6	11·5ab	1·6
Poa fendleriana	P G	0·0	0·0	0·0	0·0	0·1	0·1	2·6	2·6
Poa secunda	P G	2·8b	1·8	1·5b	0·5	3·6ab	0·8	13·5a	3·5
Pseudoroegneria spicata	P G	0·0	0·0	0·3	0·3	2·4	1·4	0·0	0·0
Artemisia tridentata	P S	7·0b	2·3	6·1b	1·2	6·8b	2·6	26·8a	8·8
Chrysothmnus viscidiflorus	P S	13·0a	3·1	2·1b	1·5	1·0b	0·7	0·4b	0·1
Ericameria nauseosa	P S	22·4a	5·0	13·5ab	3·0	3·9b	1·8	0·0c	0·0
Annual forb		5·9a	0·8	6·9a	1·1	3·5ab	0·5	0·9b	0·6
Annual grass		11·4a	3·7	9·2ab	3·0	4·3bc	1·4	1·2c	0·8
Perennial forb		11·1	2·4	9·0	2·4	9·1	2·7	14·6	7·1
Perennial grass		28·9b	4·8	52·9a	6·5	71·2a	4·2	55·3a	7·1
Mid-seral shrub		35·4a	4·2	15·8b	2·7	4·9c	2·3	0·4c	0·1
Late-seral shrub		7·0b	2·3	6·2b	1·2	6·8b	2·6	27·2a	8·7

*Life-form and life-history for each species are indicated as A, Annual; P, Perennial; F, Forb; G, Grass; S, Shrub.

variability in species composition between treatments. Early- and late-seral seeded species were the most dominant group of species within the early- and late-seral seeded treatments, respectively (Fig. 2). Additionally, the ES treatment was most similar to the control treatment, and the LS treatment was most similar to the reference in terms of early- and late-seral species composition (Fig. 2).

Perennial grass abundance was greatest in the LS treatment and lowest in the ES treatment (Tables 2 and 3). Differences can be attributed to increased production of *Elymus lanceolatus* thickspike wheatgrass, *H. comata* and *P. smithii* in the LS treatment, while increased perennial grasses in the unseeded control can mainly be attributed to the exotic perennial grass *Agropyron cristatum* L. Gaertn. crested wheatgrass (Tables 2 and 3). In both 2008 and 2009, mid-seral shrub composition was greatest in the ES treatment, while the unseeded control had more mid-seral shrub production than the LS treatment or reference (Tables 2 and 3). These differences can be attributed to *Ericameria nauseosa* rubber rabbitbrush and *Chrysothamnus viscidiflorus* yellow rabbitbrush in the ES treatment and *E. nauseosa* in the unseeded control (Tables 2 and 3).

Exotic species abundance was greater in the ES and unseeded treatments relative to the LS treatment, with both ES and LS treatments having similar relative biomass of exotics as the reference (Fig. 3). Differences in exotic species were mainly due to the increased contribution of *A. cristatum* and *B. tectorum* (Tables 2 and 3). *Artemisia tridentata*, the dominant late-seral shrub found in this system, was more abundant in the reference than seeded treatments in 2008 and 2009 but was significantly lower in the unseeded control relative to the ES treatment in 2009 (Tables 2 and 3).

Discussion

Initial results (1991) from this experiment were previously reported by Stevenson, McLendon & Redente (2000). These findings showed that after 7 years of development, seeding with late-seral species (LS treatment) accelerated community succession, while seeding with early-seral species (ES treatment) resulted in a community similar to that of the unseeded control. Specifically, production of perennial grasses and the late-seral shrub, *A. tridentata*, was greater on the LS treatment, while the production of annual grasses, annual forbs and the mid-seral shrubs, *C. viscidiflorus*, *E. nauseosa* and *Gutierrezia sarothrae* broom snakeweed, was greater on the unseeded and ES treatments (Stevenson, McLendon & Redente 2000).

These trends continued to be seen after 25 years of ecosystem development, where the two different seeding treatments resulted in considerably different species assemblages (Fig. 1), providing long-term evidence that initial colonisers (seeded

Table 3. Mean and standard error of species composition (% of total biomass) by major species and functional groups in 2009 for study plots that received various seed mixtures in 1984. Major species were determined as any species > 5% of total biomass among treatments or years. Seed mixture treatments were addition of early-seral seed, an unseeded control, addition of late-seral seed and an undisturbed reference. Means followed by different letters within rows indicate significant differences ($P < 0.05$) using Tukey's HSD

		Early-seral		Control		Late-seral		Reference	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Alyssum alyssoides	A F*	4·2a	1·3	2·8a	1·0	2·0a	0·6	0·2b	0·1
Bromus tectorum	A G	4·5a	1·6	5·3a	3·4	1·9ab	0·7	0·2b	0·1
Castilleja angustifolia	P F	0·0	0·0	5·6	4·4	0·0	0·0	0·0	0·0
Linum lewisii	P F	3·4ab	1·8	4·2ab	2·1	7·0a	2·9	0·0b	0·0
Melilotus officinalis	P F	8·3	5·4	3·9	2·7	0·0	0·0	0·0	0·0
Phlox hoodii	P F	0·0b	0·0	0·3b	0·3	0·1b	0·1	5·7a	3·0
Sphaeralcea coccinea	P F	5·6	1·9	6·6	2·7	2·6	0·9	1·0	0·4
Agropyron cristatum	P G	8·1	3·3	17·2	10·0	3·3	1·4	6·8	4·4
Elymus lanceolatus	P G	0·4b	0·3	1·2b	0·6	17·1a	4·3	4·2b	1·3
Hesperostipa comata	P G	5·6	1·3	7·7	2·7	15·1	4·1	4·5	2·0
Koeleria macrantha	P G	0·3b	0·3	1·7b	0·8	0·6b	0·3	4·6a	1·0
Pascopyrum smithii	P G	3·3b	2·4	6·5b	1·8	16·9a	2·3	2·5b	0·3
Poa fendleriana	P G	5·1ab	3·7	1·2ab	0·5	0·1b	0·1	10·0a	4·3
Poa secunda	P G	0·2ab	0·1	0·1b	0·0	0·2ab	0·1	0·7a	0·5
Pseudoroegneria spicata	P G	1·9	1·9	5·6	2·7	13·0	3·4	5·4	5·0
Artemisia tridentata	P S	17·6b	4·1	6·3b	2·0	7·5bc	1·8	40·6a	7·2
Chrysothmnus viscidiflorus	P S	7·7a	1·5	2·4b	1·5	1·1b	0·5	0·2b	0·2
Ericameria nauseosa	P S	15·6a	2·8	8·4ab	2·5	1·8bc	0·7	1·0c	0·7
Annual forb		12·7	4·9	7·6	2·9	2·5	0·6	0·5	0·2
Annual grass		4·3	1·5	5·3	3·4	1·9	0·7	0·2	0·1
Perennial forb		12·6	3·7	19·0	5·8	13·2	3·3	12·1	3·3
Perennial grass		27·7c	6·8	51ab	9·9	72·2a	3·2	42·1bc	5·6
Mid-seral shrub		23·3a	2·4	10·8b	3·0	2·8bc	0·7	1·5c	0·9
Late-seral shrub		17·3b	4·0	6·3b	2·0	7·5b	1·8	43·7a	5·5

*Life-form and life-history for each species are indicated as A, Annual; P, Perennial; F, Forb; G, Grass; S, Shrub.
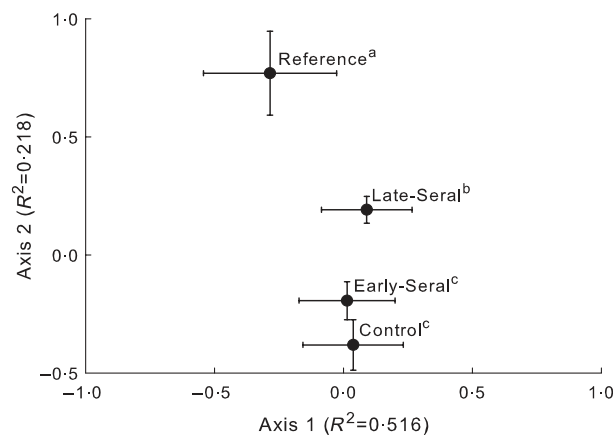

Fig. 1. Mean and standard error of axes scores from non-metric multidimensional scaling analysis of plant species composition in 2008 and 2009. Treatments were an unseeded control, addition of early-seral seed, addition of late-seral seed and an undisturbed reference. The final ordination resulted in a 3-dimensional solution; the two axes accounting for the greatest proportion of variance in the distance matrix are shown. Different letters indicate significant differences ($P < 0.05$) among treatments based on MANOVA with all three axes scores.

species) can impact the trajectory of ecosystem development. Although the ES, unseeded and LS treatments each contained major components of a typical mid-successional community at this site (McLendon & Redente 1990, 1991), the structure of the dominant vegetation varied across treatments. Mid-seral shrub and exotic species composition were significantly greater in the ES and unseeded treatments compared with the LS treatment, while perennial grasses dominated the LS treatment (Tables 2 and 3; Fig. 3). Differences in species and community composition observed in this study suggest that the dominant life-forms of these two assemblies occupy similar niches in this ecosystem, where dominant perennial grasses can limit the establishment of mid-seral shrubs and *vice versa* (Drake 1991; Laycock 1991). Previous research has observed the relationships among these functional groups in the western US, where dense understorey of perennial grass precludes seedling establishment of mid-seral shrubs (Young & Evans 1974), while rapid resprouting of rabbitbrush species can preclude the establishment of competitors (West 1999). Increased abundance of shrubs may result in improved wildlife habitat for common and endangered species (Olson *et al.* 2000; Watters *et al.* 2002), while greater abundance of perennial grasses may increase forage availability for large herbivores (Hodgson *et al.* 1991; Bisigato *et al.* 2005) and decrease potential for soil erosion (Dear & Roggero 2003). Additionally, establishment of diverse native plant communities has been found to limit the contribution of persistent exotic species (Lonsdale 1999; Naeem *et al.* 2000), such as *B. tectorum* and *A. cristatum* in this region (Eckert & Evans 1963).
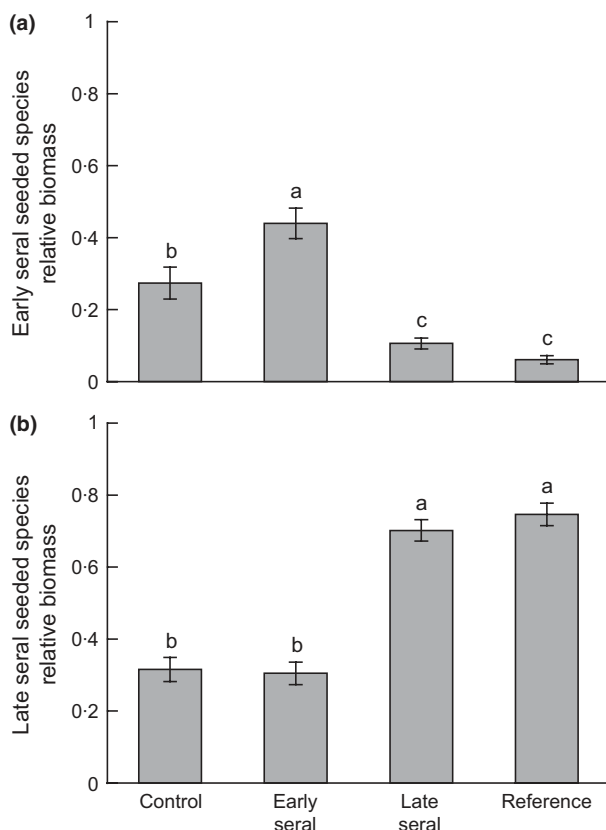
Fig. 2. Mean and standard error of (a) early- and (b) late-seral seeded species relative biomass. Data from 2008 to 2009 were averaged for each treatment because the year x treatment interaction was not significant ($P > 0.05$). Treatments were an unseeded control, addition of early-seral seed, addition of late-seral seed and an undisturbed reference. Different letters indicate significant differences ($P < 0.05$) among treatments based on Tukey's HSD.
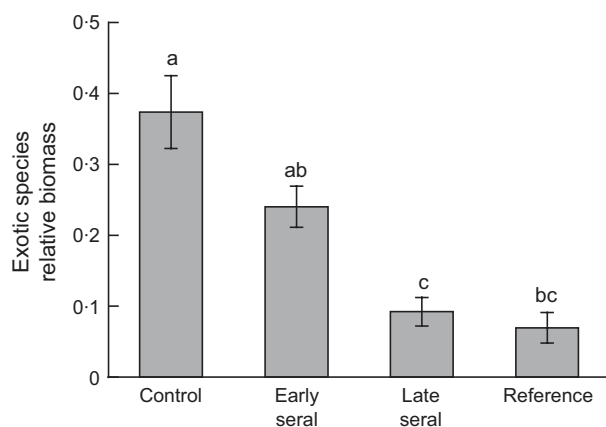

Fig. 3. Mean and standard error of exotic species relative biomass across 2008 and 2009. Treatments were an unseeded control, addition of early-seral seed, addition of late-seral seed and an undisturbed reference. Different letters indicate significant differences ($P < 0.05$) among treatments based on Tukey's HSD.

Plant community assembly theory places a strong emphasis on the controls of plant colonisation, establishment and persistence in community development (Young, Chase & Huddle-

ston 2001). Community assembly has been shown to converge along functional groups but diverge along species composition, illustrating that initial species establishment can control future community assemblage by inhibiting establishment of species with similar niches (Lulow 2004; Fukami *et al.* 2005). In this study, we found perennial grasses constituted $> 50\%$ of above-ground production in both the LS and unseeded treatments, but there were significant differences in species composition (Tables 2 and 3). Native perennial grasses, *E. lanceolatus*, *H. comata* and *P. smithii*, dominated the LS treatment, while the introduced perennial grass, *A. cristatum,* which was not seeded in this study, was more abundant in the unseeded control (Tables 2 and 3). *Agropyron cristatum* was historically seeded as a reclamation species in this region and, once established, is able to persist for decades (Eckert & Evans 1963; Bowles 2011). The differences between the LS and unseeded treatments demonstrate convergence in plant composition among functional group, but divergence in species composition during secondary succession. We observed another example of this type of divergence in the species composition of mid-seral shrubs, which were a major component of both the ES and unseeded treatments. The ES treatment consisted of both *E. nauseosa* and *C. viscidiflorus* (both seeded in the ES treatment), while mid-seral shrub composition in the unseeded and LS treatments was dominated by *E. nauseosa* only (Tables 2 and 3).

After 25 years, the species present in the ES or LS seed mixes dominated the plots receiving the respective seed treatments (Fig. 2). This relationship was even more pronounced in the LS treatment compared with the ES treatment, indicating that seeding with late-seral species may have a greater effect on long-term community development. Additionally, the unseeded control had similar composition as the ES seeded treatment, while the LS treatment was more similar to the reference plots than either the ES or unseeded control treatments (Fig. 2). This shows that seeding with the appropriate late-seral species can facilitate community development towards the reference conditions better than either seeding with early-seral species or not applying seed. However, there could be some instances where seeding with native early-seral species might be effective in precluding the establishment of undesirable invasive species. It should be noted that in our study, the exotic and highly invasive *B. tectorum* was part of the ES seed mix. Restoration practitioners historically considered *B. tectorum* as simply an early-seral component of ecosystems in this region. Research has shown that this species can have significant effects on ecological succession through early season growth, increased fire frequency and altered nutrient dynamics (Knapp 1996; Chambers *et al.* 2007; Wainwright, Wolkovich & Cleland 2012) and may have further retarded successional processes in this study than would have been observed if only native early-seral species had been included in the seed mix.

It is also important to note that even though the LS treatment was most similar to the reference community, there were still considerable differences (Fig. 1), which indicate that more successional development of the LS plots will be needed before they become ecologically similar to the reference condition.

Although late-seral shrub (i.e. *A. tridentata*) development was initially greatest in the LS treatment (Stevenson, McLendon & Redente 2000), this was no longer observed after 25 years of development, even though this species was both seeded and transplanted to the LS treatment. In our first year of data collection, *A. tridentata* composition was similar across all treatments (Table 2), but in the second year of the study, significantly more *A. tridentata* was observed in the ES treatment compared with the control (Table 3). This indicates that recruitment and development of *A. tridentata* can occur in areas where a propagule source is available and may be aided by microsites provided by similar life-forms (i.e. mid-seral shrubs) (Callaway 1992; Owens, Wallace & Archer1995).

Understanding the factors controlling community development is critical to the field of restoration ecology (Bradshaw 1987; Palmer, Ambrose & Poff 1997; Young 2000). Recognising these factors can guide management prescriptions, lead to the development of more accurate descriptions of reference conditions and improve chances for meeting restoration goals (Young, Chase & Huddleston 2001). Understanding mechanisms of change not only adds to our knowledge of how ecosystems develop but can also lead to improved ecosystem management, providing an opportunity to use management objectives to guide the trajectory of ecosystem recovery towards self-regulating vegetation communities that provide desired ecosystem services (George, Brown & Clawson1992; Mayer & Rietkerk 2004; Temperton & Hobbs 2004; Quetier, Thebault & Lavorel 2007; Johnstone *et al.* 2010). Studies, such as this one, that assess long-term community development are especially important for developing successful restoration designs, as this information allows us to understand how initial restoration actions impact the long-term dynamics of plant community development. The results of this study demonstrate how initial colonisers or seeded species can exhibit a strong effect on long-term plant community composition and that seeding with late-seral species following a severe disturbance can produce a plant community more similar to reference conditions after 25 years of development, compared with seeding with early-seral species or not adding seed. Natural resource managers should consider both the desired long-term community composition and any immediate goals (e.g. excluding non-native or invasive species during initial colonisation) when using seed addition as a part of any ecological restoration goals and plans. A greater understanding of the mechanisms involved with propagule arrival time and establishment on subsequent community assembly is critical to refining successional theories and devising successful restoration programmes and should be a focus of future research on the ecology of disturbed lands.

Acknowledgements

References

Belyea, L.R. & Lancaster, J. (1999) Assembly rules within a contingent ecology. *Oikos*, **86**, 402–416.

Beyers, J.L. (2004) Postfire seeding for erosion control: effectiveness and impacts on native plant communities. *Conservation Biology*, **18**, 947–956.

Bisigato, A.J., Bertiller, M.B., Ares, J.O. & Pazos, G.E. (2005) Effect of grazing on plant patterns in arid ecosystems of Patagonia Monte. *Ecography*, **28**, 561–572.

Bowles, B. (2011) *Development of a Sagebrush Steppe Plant Community 33 years After Surface Disturbance.* MS thesis, Colorado State University, Fort Collins.

Bradshaw, A.D. (1987) The reclamation of derelict land and the ecology of ecosystems. *Restoration Ecology: A Synthetic Approach to Ecological Research* (eds W.R. Jordan III, M.E. Gilpin & J.D. Aber), pp. 53–74. Cambridge University Press, New York.

Callahan, J.T. (1984) Long-term ecological research. *BioScience*, **34**, 363–367.

Callaway, R.M. (1992) Effect of shrubs on recruitment of Quercus-douglasii and Quercus-lobata in California. *Ecology*, **73**, 2118–2128.

Carpenter, A.T., Moore, J.C, Redente, E.F. & Stark, J.C. (1990) Plant community dynamics in a semiarid ecosystem in relation to nutrient addition following a major disturbance. *Plant and Soil*, **126**, 91–99.

Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E. & Whittaker, A. (2007) What makes Great Basin sagebrush ecosystems invasible by Bromus tectorum? *Ecological Monographs*, **77**, 117–145.

Clements, F.E. (1916) *Plant Succession; an Analysis of the Development of Vegetation.* Carnegie Institution of Washington, Washington, D.C.

Cole, R.J., Holl, K.D., Keene, C.L. & Zahawl, R.A. (2011) Direct seeding of late-successional trees to restore tropical montane forest. *Forest Ecology and Management*, **261**, 1590–1597.

Dear, B.S. & Roggero, P.P. (2003) The present and potential role of perennial grass monocultures and mixtures with annual legumes in Italian and Southern Australian farming systems. *New Perennial Legumes for Sustainable Agriculture* (ed. S.J. Bennett), pp. 131–158. University of Western Australia Press, Crawley.

Doerr, T.B., Redente, E.F. & Reeves, F.B. (1984) Effects of soil disturbance on plant succession and levels of mycorrhizal fungi in a sagebrush-grassland community. *Journal of Range Management*, **37**, 135–139.

Drake, J.A. (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist*, **137**, 1–26.

Eckert, R.E. & Evans, R.A. (1963) Responses of downy brome and crested wheatgrass to nitrogen and phosphorus in nutrient solution. *Weeds*, **11**, 170–174.

Foster, B.L. & Tilman, D. (2003) Seed limitation and the regulation of community structure in oak savanna grassland. *Journal of Ecology*, **91**, 999–1007.

Fukami, T., Bezemer, T.M., Mortimer, S.R. & van der Putten, W.H. (2005) Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, **8**, 1283–1290.

George, M.R., Brown, J.R. & Clawson, W.J. (1992) Application of nonequilibrium ecology to management of Mediterranean grasslands. *Journal of Range Management*, **45**, 436–440.

Herron, C.M. (2010) *Using Native Annual Plants to Suppress Weedy Invasive Species in Post-Fire Habitats.* MS thesis, Colorado State University, Fort Collins.

High Plains Regional Climate Center. (2010). Rifle, CO (057031). URL http://www.hprcc.unl.edu/cgi-bin/cli_perl_lib/cliMAIN.pl?co7031 [accessed 5 July 2010].

Hobbie, J.E., Carpenter, S.R., Grimm, N.B., Gosz, J.R. & Seastedt, T.R. (2003) The US long term ecological research program. *BioScience*, **53**, 21–32.

Hodgson, J., Forbes, T.D.A., Armstrong, R.H., Beattie, M.M. & Hunter, E.A. (1991) Comparative studies of the ingestive behaviour and herbage intake of sheep and cattle grazing indigenous hill plant communities. *Journal of Applied Ecology*, **28**, 205–227.

Inouye, R.S. & Tilman, D. (1995) Convergence and divergence of old-field vegetation after 11 year of nitrogen addition. *Ecology*, **76**, 1872–1887.

Johnstone, J.F., Hollingsworth, T.N., Chapin, F.S. & Mack, M.C. (2010) Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, **16**, 1281–1295.

Kleijn, D. (2003) Can establishment characteristics explain the poor colonization success of late successional grassland species on ex-arable land? *Restoration Ecology*, **11**, 131–138.

Kleijn, D., Joenje, W. & Kropff, M.J. (1997) Patterns in species composition of arable field boundary vegetation. *Acta Botanica Neerlandica*, **46**, 175–192.

Kluber, L.A., Smith, J.E. & Myrold, D.D. (2011) Distinctive fungal and bacterial communities are associated with mats formed by ectomycorrhizal fungi. *Soil Biology & Biochemistry*, **42**, 1042–1050.

Knapp, P.A. (1996) Cheatgrass dominance (*Bromus tectorum* L.) in the Great Basin Desert: history, persistence, and influences to human activities. *Global Environmental Change*, **6**, 37–52.

Kourtev, P.S., Ehrenfeld, J.G. & Haggblom, M. (2002) Exotic plant species alter the microbial community structure and function in the soil. *Ecology*, **83**, 3152–3166.

Lake, P.S. (2001) On the maturing of restoration: linking ecological research and restoration. *Ecological Restoration and Management*, **2**, 110–115.

Lauenroth, W.K., Hunt, H.W., Swift, D.M. & Singh, J.S. (1986) Estimating aboveground net primary production in grasslands – a simulation approach. *Ecological Modelling*, **33**, 297–314.

Laycock, W.A. (1991) Stable states and thresholds of range condition on North-American rangelands – a viewpoint. *Journal of Range Management*, **44**, 427–433.

Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.

Lulow, M.E. (2004) *Restoration in California's Inland Grasslands: the Role of Priority Effects and Management Strategies in Establishing Native Communities and the Ability of Native Grasses to Resist Invasion by Non-Native Grasses.* PhD dissertation, University of California, Davis.

Mayer, A.L. & Rietkerk, M. (2004) The dynamic regime concept for ecosystem management and restoration. *BioScience*, **54**, 1013–1020.

McCune, B. & Grace, J. (2002) *Analysis of Ecological Communities.* MJM Software, Gleneden Beach, Oregon.

McCune, B. & Medford, M.J. (2011) *PC-ORD. Multivariate Analysis of Ecogical Data. Version 6.* MJM Software, Gleneden Beach, Oregon.

McLendon, T. & Redente, E.F. (1990) Succession patterns following soil disturbance in a sagebrush steppe community. *Oecologia*, **85**, 293–300.

McLendon, T. & Redente, E.F. (1991) Nitrogen and phosphorus effects on secondary succession dynamics on a semiarid sagebrush site. *Ecology*, **72**, 2016–2024.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Synthesis.* Island Press, Washington, DC.

Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. & Gale, S. (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, **91**, 97–108.

Olson, R.A., Gores, J.K., Booth, D.T. & Schuman, G.E. (2000) Suitability of shrub establishment on Wyoming mined lands reclaimed for wildlife habitat. *Western North American Naturalist*, **60**, 77–92.

Owens, M.K., Wallace, R.B. & Archer, S.R. (1995) Landscape and microsite influences on shrub recruitment in a disturbed semi-arid Quercus-Juniperus woodland. *Oikos*, **74**, 493–502.

Palmer, M.A., Ambrose, R.F. & Poff, N.L. (1997) Ecological theory and community restoration ecology. *Restoration Ecology*, **5**, 291–300.

Quetier, F., Thebault, A. & Lavorel, S. (2007) Plant traits in a state and transition framework as markers of ecosystem response to land-use change. *Ecological Monographs*, **77**, 33–52.

Quinn, J.F. & Robinson, G.R. (1987) The effects of experimental subdivision on flowering plant diversity in a California annual grassland. *Journal of Ecology*, **75**, 837–855.

Redente, E.F., Cook, C.W., Stark, J.M. & Simmons, C.L. (1985) *Semiarid Ecosystem Development as a Function of Resource Processing and Allocation.* Progress Report for DOE (DE-A502-T5EY04018). Range Science Department, Colorado State University, Fort Collins, Colorado, USA.

Stevenson, B.A., McLendon, T. & Redente, E.F. (2000) Effects of soil fumigation and seeding regimes on secondary succession in a semiarid shrubland. *Arid Soil Research and Rehabilitation*, **14**, 87–99.

Temperton, V.M. & Hobbs, R.J. (2004) Assembly rules and restoration ecology bridging the gap between theory and practice. *Assembly Rules and Restoration Ecology* (eds V.M. Temperton, R.J. Hobbs, T. Nuttle & S. Halle), pp. 34–54. Island Press, Washington, DC.

United States Department of Agriculture (1982) *Soil survey of Rio Blanco County area, Colorado.* US Department of Agriculture, Soil Conservation Service, Washington, DC.

Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2012) Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *Journal of Applied Ecology*, **49**, 234–241.

Wallington, T.J., Hobbs, R.J. & Moore, S.A. (2005) Implications of current ecological thinking for biodiversity conservation: a review of the salient issues. *Ecology and Society*, **10**, 15.

Watters, M.E., Mclash, T.L., Aldridge, C.L. & Brigham, R.M. (2002) The effect of vegetation structure on predation of artificial Greater Sage-Grouse nests. *Ecoscience*, **9**, 314–319.

West, N.E. (1999) Synecology and disturbance regimes of sagebrush steppe ecosystems. *Sagebrush Steppe Ecosystems Symposium* (eds P.G. Entwistle, A.M. DeBolt, J.H. Kaltenecker & K. Steenhof), pp. 15–26. Bureau of Land Management, Boise State University, Boise, ID.

Yoshida, H. (2007) Seeding on slopes in Japan for natural restoration. *Landscape Ecological Applications in Man-Influenced Areas: Linking Man and Nature Systems* (eds S-K. Hong, N. Nakagoshi, B. Fu & Y. Morimoto), pp. 311–328. Spring, Dordrecht, The Netherlands.

Young, T.P. (2000) Restoration ecology and conservation biology. *Biological Conservation*, **92**, 73–83.

Young, T.P., Chase, J.M. & Huddleston, R.T. (2001) Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration*, **19**, 5–18.

Young, J.A. & Evans, R.A. (1974) Population dynamics of green rabbitbrush in disturbed sagebrush communities. *Journal of Range Management*, **27**, 127–132.

Young, S.L., Barney, J.N., Kyser, G.B., Jones, T.S. & DiTomaso, J.M. (2009) Functionally similar species confer greater resistance to invasion: implications for grassland restoration. *Restoration Ecology*, **17**, 884–892.