Final report for CIPM

Testing models of succession for restoration of montane communities invaded by cheatgrass

(awarded 2004)

Helen Ivy Rowe
Cynthia S. Brown

Submitted June 24, 2005

Abstract:
It is estimated that 40,000,000 ha of rangelands in the United States, once dominated by perennial bunchgrasses and shrubs, are now infested with cheatgrass (*Bromus tectorum*). Its early life cycle enables cheatgrass to dominate plant communities by depleting nutrients and water in the winter and early spring months when natives are dormant, and ending its life cycle early, providing abundant fuel for fire. We must develop effective methods for the control of cheatgrass and restoration of the sites that it invades to conserve biological diversity and ecosystem functioning. Here we test the facilitation, tolerance and inhibition models of succession when applied to the restoration of cheatgrass dominated montane plant communities. The models explain different interactions among early- and late-successional species that ultimately allow late-successional species to dominate, as is our goal for restoration. This field experiment was conducted to evaluate the models through the performance of late-successional species when grown alone, planted simultaneously with early-successional species, and planted one year after early-successional species. The facilitation model for restoration would be supported if late-successional species established better when seeded together with or subsequent to early-successional species. The tolerance model would be supported if late-successional species established equally well when seeded with or without early-successional species. However, because we seeded into the existing native community, tolerance cannot be distinguished from facilitation in this study. The inhibition model would be supported if late-successional species established better when seeded alone than when seeded with early-successional species. In our experiment, there were no differences among treatments in the first year.

Introduction:
It is estimated that 40,000,000 ha of rangelands in the United States, once dominated by perennial bunchgrasses and shrubs, are now infested with cheatgrass (*Bromus tectorum* L.) (DiTomaso, 2000), an annual grass introduced from Eurasia (Klemmedson, 1964). Approximately 20% of the sagebrush-steppe vegetation zone in the Western U.S. is dominated by cheatgrass to the point where the establishment of native perennial species is nearly impossible (Knapp, 1996). It is estimated that cheatgrass and other rangeland weeds together result in economic losses of $2 billion annually in the U.S. (DiTomaso, 2000). Cheatgrass is the most ubiquitous weed in steppe vegetation in Western North America (Mack, 1981).

The success of cheatgrass as an invading species in the Western U.S. is largely attributed to its winter annual lifecycle (Hulbert, 1955). Fall-germinated seedlings of cheatgrass spend winter in a semi-dormant state and grow rapidly in the spring as conditions become favorable (Hulbert, 1955; Mitich, 1999; Stewart and Hull, 1949). This early growth allows cheatgrass to gain a competitive advantage over slower growing native perennial species as cheatgrass completes its lifecycle by early summer (Hulbert, 1955). The resulting accumulation of fine fuels from senescent cheatgrass often results in fires that further reduce native species abundance, and increase cheatgrass dominance (Smith and Knapp, 2001; Dakheel, Radosevich, and Barbour, 1993; McLendon and Redente, 1991; Rasmussen, 1995; Kay and Evans, 1965; Ball, Wysocki, and Chastain, 1996; Peloquin and Hiebert, 1999; Paschke, McLendon, and Redente, 2000).

A relatively new term, "ecological bridge", describing the use of early-successional species as an intermediate step to ameliorate site conditions for late-successional species has been recently applied to the restoration of weed dominated landscapes (Hardy and Palazzo, 2002). This bridging concept assumes facilitation (Connell and Slatyer, 1977) to be the predominant model at work. Yet Connell and Slatyer (1977) described three models of succession. In all models, disturbance opens a space and colonizers with early-successional traits establish on the site. The models differ in how late-successional species become established. With facilitation, early-successional species create conditions favorable for establishment of late-successional species. In both the tolerance and inhibition models, late-successional species do not require amelioration of the site by other species. In the tolerance model, late-successional species establish later than early species because of their life history traits, but will eventually dominate due to their superior competitive abilities. The early species on this site will neither increase nor decrease the rates of recruitment or growth of other species. The inhibition model describes conditions by which the early colonizer inhibits establishment of other species. The early colonizer must die or be damaged in order for other species to establish (Connell and Slatyer, 1977). By testing which successional model applies to the restoration of weed-dominated communities, we can evaluate the appropriateness of the "ecological bridge" concept.

The ultimate goal of the proposed research is to establish a critical understanding of and practical methods for restoring cheatgrass invaded montane communities to native late-successional, perennial grass and shrub-dominated communities. This research will test the ecological theory of successional and restoration approach of "bridging" by applying different combinations of late- and early-successional native seed mixes to a cheatgrass dominated site.

Methods:

Description: An experiment was conducted to evaluate the performance of early-successional (ES) and late-successional (LS) species mixtures grown alone, planted simultaneous (LE), or planted sequentially (LSES). In the sequential trial the LS mixture was added during the second year to plots planted the first year with the ES mixture (LSES) and to a non-seeded plot as a control (LSNS) treatment. The following table describes alternative hypothesis for testing which model of succession dominates in this sub-alpine system (Table 1). The experiment was located at an elevation of about 2,378 m on a mixed for south facing slope in Rocky Mountain National Park (RMNP). *Helianthus pumilus*, *Eriogonum umbelatum*, *Chrysothamnus viscidiflorus*, *Purshia tridentata*, *Muhlenbergia montana*, *Hesperostipa comata* comprise much of the natural vegetation on this slope with scattered *Pinus ponderosa*. Cheatgrass invasion on this site is patchy, ranging from no cheatgrass in some areas, to high dominance (70-80 % cover) in others.

Table 1: Test emergence and establishment of late-successional species

Hypothesis	**Interpretation**	**Restoration implications**
LS>LE, LSNS>LSES	Inhibition	Plant LS seeds alone
LS=LE	Tolerance or facilitation by established ES species	Plant LS seeds with ES species or alone.
LSNS=LSES	Tolerance or facilitation by established ES species	Plant LS species alone or into established ES communities.
LS<LE	Same year facilitation	Plant LS seeds with ES species, “ecological bridge” concept validated.
LSNS<LSES	Next year facilitation	Better to plant LS seeds into established ES community than into bare soil, “ecological bridge” concept validated.

Experimental design: A complete block design was used to control for environmental gradients; there were 72 1.5 m^2 plots and 12 blocks with one replicate of each of the 6 treatments (LS, LE, ES, NS, LSNS, LSES) in each block. We selected block locations to minimize differences in soil type, cheatgrass and soil cover among plots within blocks. Treatment plots were chosen according to cheatgrass cover estimates (between 55-70%) to minimize variation.

Disturbance treatment: Secondary succession describes the changes in community composition after a disturbance event. In order to diminish cheatgrass competition and create an opening similar to that found after a disturbance, cheatgrass was removed to ≤ 5% cover in April 2004 with glyphosate (Roundup®), applied at a rate of 0.55 kg/ha with a CO_2 pressurized backpack sprayer (Whitson & Koch 1998). Native plants were protected from spray.

Seed mixes: Seed mixes were comprised of grasses, forbs, and shrubs. Seeding rates of a nearby RMNP restoration project (646 seeds m^2) were followed. The two-year seeding treatments (LSES and LSNS) followed an additive design. In the first year LSES was seeded with the ES mixture at the 646 seeds m^2 rate and the LSNS was not seeded. In the second year both treatments were seeded with the LS mixture at the same 646 seeds m^2 rate. We do not compare the multi-year seeding treatments to the one-year treatments.

Seeds were collected within one mile of the field site in the same drainage basin at elevations of approximately 2,377-2,743 m (7800 – 9000 ft).

We characterized late-successional species as perennial and long-lived; our late-successional mixture included two shrubs (*Artemisia frigida* Willd. [fringed sage] and *Prunus virginiana* L [chokecherry], two forbs (*Aster laevis* L [smooth blue aster], and *Eriogonum umbellatum* Torr. [sulfur-flower buckwheat]), and two grasses (*Muhlenbergia montana* (Nutt.) Hitchc. [mountain muhly] and *Hesperostipa comata* (Trin. & Rupr.) Barkworth [needle and thread]). Early successional species were shorter lived perennials and annuals and included no shrubs, five forbs (*Lappula redowskii* (Hornem.) [flatspine stickseed], *Helianthus pumilus* Nutt. [little sunflower], *Chenopodium atrovirens* Rydb. [pinyon goosefoot], *Polygonum douglasii* Greene [Douglas' knotweed] and *Heterotheca villosa* (Pursh) Shinners [hairy false goldenaster] and one grass *Elymus elymoides* (Raf.) Swezey [squirreltail]). Germination and dormancy (tetrazolium) tests (Association of Official Seed Analysts , 2003; Fulbright, Redente, and Hargis, 1982; Redente, Ogle, and Hargis, 1982) were conducted on a subsample of all collected seeds.

Existing plant cover:
In order to monitor whether the removal of cheatgrass and seed mixture treatments affected existing community composition, cover was estimated. Diversity was calculated based on cover estimates using the Shannon-Wiener function (Krebs, 1999) such that:

$$H' = \sum_{i=1}^{s} (p_i)(\log_2 p_i),$$

where H' = information content of sample (bits/individual) = index of species diversity

s = number of species

p_i = proportion of total sample belonging to the *i*th species(Anonymous, 1999)

Existing species in the community were classified into early- and late-successional plant species. Annuals were placed in the early-successional category and perennials in the late-successional category. If a plant species was categorized as annual and biennial, it was placed in the early-successional category. On the other hand, plant species that could be biennial or perennial were placed in the late-successional category. The single native annual, biennial, or perennial plant species, *Bahia dissecta*, was categorized as late successional, as was the biennial native, *Erigeron flagellaris*. The biennial non-native, *Cerastium fontana*, was placed in the early-successional category (http://plants.usda.gov/). Of the 16 early-successional species, only four are native and five are sometimes biennial. Cheatgrass was not included in the early-successional species category for diversity analyses, except where indicated. All 41 late-successional species are native; four of these are sometimes biennial.

Monitoring Treatment effects: Seedling densities and ocular estimates of plant cover were made in July and August 2004 and will be repeated at the same times in 2005. Pre-treatment baseline estimates of plant cover were taken in August 2003. Annual aboveground biomass will be collected, dried and weighed at the end of the experiment in August 2005.

Analysis:

The experimental design is a complete factorial with two factors: (1) 6 seed mixes (LS, LE, LSNS, ESNS, ES, NS) and (2) 12 blocks. Pre-treatment cover estimates were compared using ANOVA to verify that no prior treatment differences existed using SAS version 9.1 (SAS Institute, Inc., SAS OnlineDoc®, Cary, NC, 1999). A repeated measures design was used to evaluate cover and diversity differences between treatment plots over time using Procedure Mixed, SAS version 9.1 (SAS Institute, Inc., SAS OnlineDoc®, Cary, NC, 1999). Cover data was arcsine transformed and diversity indices were log transformed to meet assumptions of normality and homogeneity of variance. Seedling data was log transformed to meet assumptions of normality and homogeneity of variance and to minimize outlier effects.

Results

Seeding treatment differences:

In the summer of 2004, no significant differences in late successional seed establishment was found amongst treatments (Fig. 1). There is an outlier in the early-late successional seeding treatment with a high number (13) of *A. frigida* seedlings. The high establishment may have been from increased seed rain from mature *A. frigida* near the plot. Without this sample, there is still no difference among treatments.

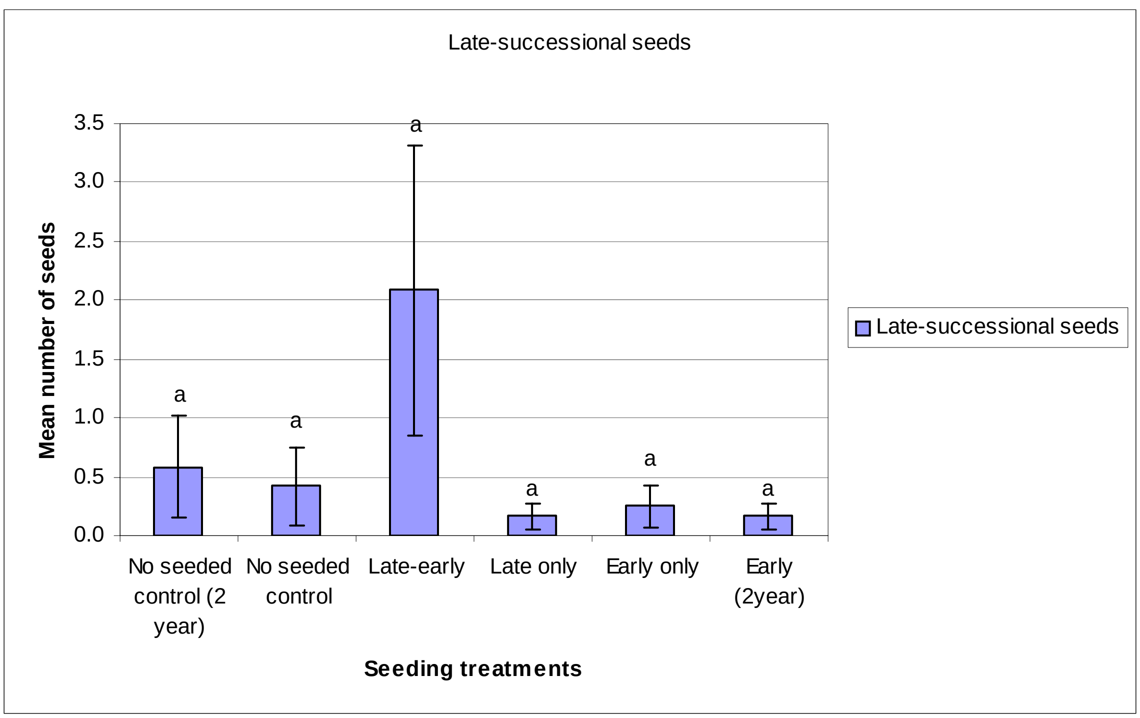

Figure 1: Mean establishment of seeded species by late-successional categories. Error bars represent one standard error of the mean.

Existing plant community:

No cover or diversity differences were found among treatment plots prior to treatment application. Existing plant cover and diversity did not change with treatment, but both indices showed significant changes with time. Diversity of early successional plants increased (Fig. 2), but their coverage did not change (Fig. 3) over the two growing seasons. Both diversity and cover of late successional plants increased with time (Figs. 2&3). Cheatgrass decreased after 2003 due to the Roundup treatment applied in spring of 2004 (Fig. 3).

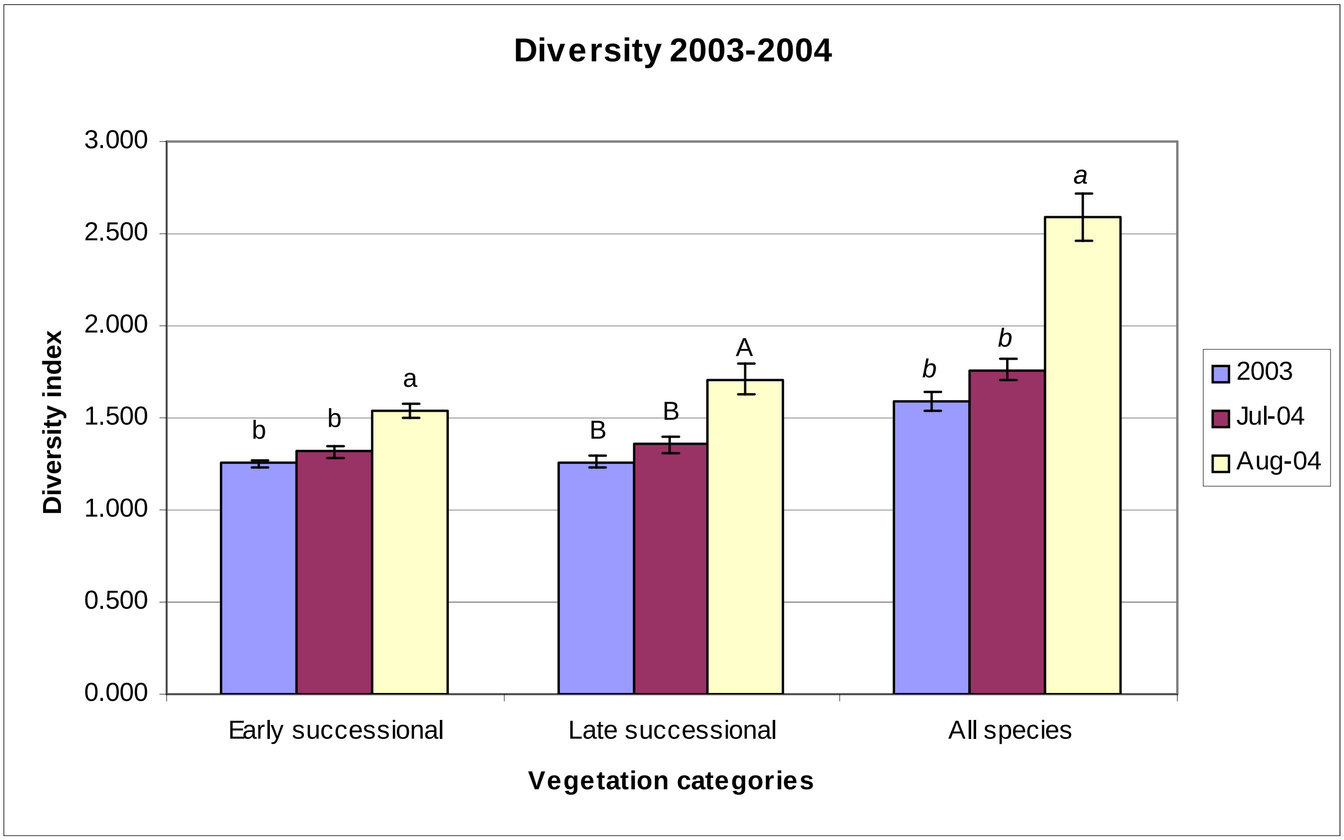

Figure 2: Mean diversity indices by plant successional category over time. Error bars represent one standard error of the mean. Lower and upper cases and italics distinguish separate statistical analyses.

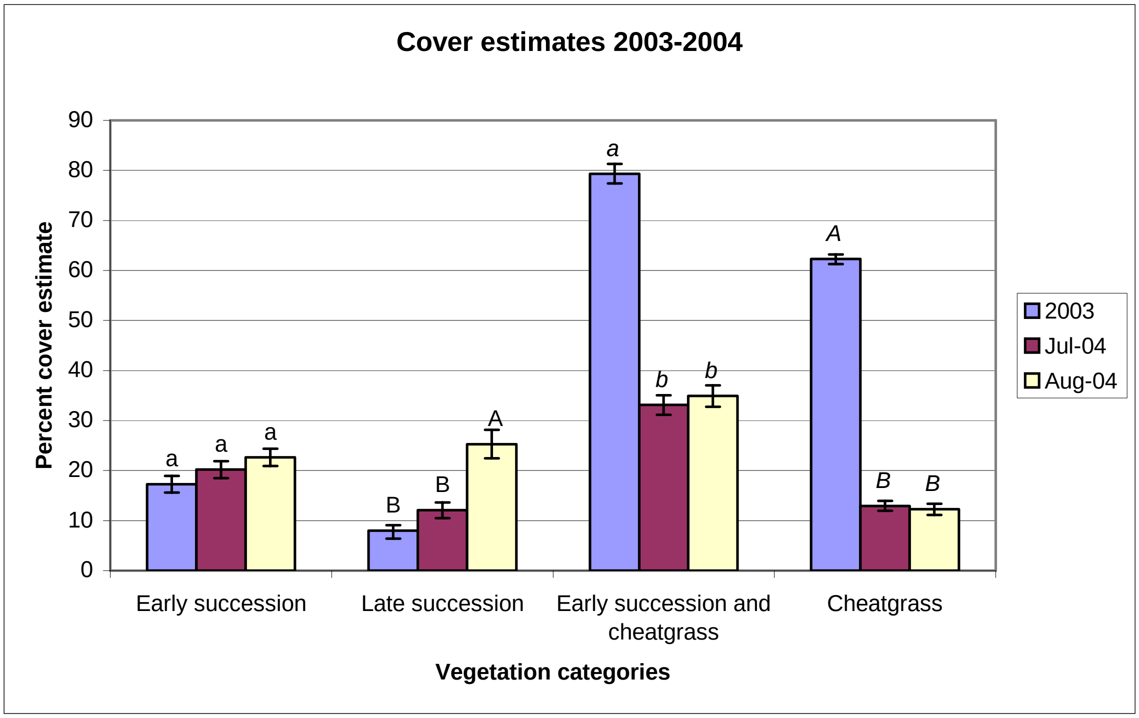

Figure 3: Mean percent cover by plant successional category over time. Error bars represent one standard error of the mean. Lower and upper cases and italics distinguish separate statistical analyses.

Seed testing:
Seeds collected for the experiment ranged from 32 to 94 percent viability and most performed well in greenhouse experiments (Table 2).

Table 2: Germination and dormancy test results on collected seed

			Total viability		
Plant Species	Year collected/Year planted	Treatment	Percent viability	s.e.m.	Greenhouse germination
Artemisia frigida	2003/2003	15-25	72.44	0.089	high
		P, 15-25	69.54	0.022	
Aster laevis	2003/2003	15-25	93.68	0.005	high
Chenopodium atrovirens	2003/2003	20-30	32**	-	high
		P, 20-30	-	-	
Chrysothamnus viscidiflorus	2003/2003	20-30	39.59	0.031	high
Elymus elymoides	2003/2003	15-25	90.96	0.033	high
		P, 15-25	92.96	0.033	
Eriogonum umbellatum	2003/2003	20-30	43**	-	low
		P, 20-30	-	-	
Helianthus pumilus	2003/2003	5-20	35.13	0.197	n/a

		P, 5-20	20.52	0.122	
Hesperostipa comata	2003/2003	G, D, 15-25	54.50	0.022	n/a
		P, 15-25	74.00	0.022	
Heterotheca villosa	2003/2003	15-25	83.31	0.060	n/a
		P, 15-25	80.95	0.025	
Lappula occidentalis	2003/2003	15-25	74.60	0.078	high
		P, 15-25	76.25	0.025	
Muhlenbergia montana	2003/2003	K, 20-30	27.50	0.064	high
Polygonum douglasii	2003/2003	C, 20-30	70.82	0.037	low
		20-30	76**	-	
Prunus virginiana	2003/2003	MP	-	-	n/a
Artemisia frigida	2003/2004	15-25	91.68	0.019	fair
Aster laevis	2003/2003	15-25	84.41	0.03	n/a
Chrysothamnus viscidiflorus	2003/2004	n/a***	-	-	high
Eriogonum umbellatum	2004/2004	P, 20-30	90.15	0.03	n/a
Hesperostipa comata	2004/2004	G, D, 15-25	69.36	0.01	n/a
Muhlenbergia montana	2004/2004	K, 20-30	88.63	0.03	n/a
Prunus virginiana	2004/2004	n/a	-	-	n/a

P=prechill
G=gibberellic acid
D=dark treatment
K=Potassium nitrate
C=removed outer seed layer
MP=3 month moist stratification at 5C

*with difficulty
DP=Dry cold storage

**Germination tests were extremely low. This percent viability is the result of one TZ test.

***Cv germinated well in a 2005 greenhouse experiment, so more germination tests were not required. Af seemed to have have lower germination rates in the same study, so was retested.

Discussion

Because there were no differences between seeded and unseeded treatments, it appears that ambient seed rain is as effective as the seeding treatments for establishing late-successional species. Whether seeded or not seeded, based on our hypotheses, the first year data indicate that either facilitation or tolerance models of succession may apply in this system. One may conclude that the tolerance model predominates if one considers only seedling establishment; there were no significant differences amongst late-successional seedlings establishment amongst treatments. However, one must also consider that plots were not cleared of early successional cover before adding the seed mixtures, thus established early-successional species in the plots may have contributed to the establishment of late-successional species. In this case it is impossible to distinguish between tolerance and facilitation.

The cheatgrass control treatment appeared to result in a release from competition and consequent increase in diversity and cover of existing late successional species. Early successional diversity appears to follow the same trend, though early-successional cover did not increase over time.

We hope that higher germination and establishment rates in 2005 will help elucidate differences amongst seeding mixtures and allow for some stronger conclusions about the ecological bridge approach to restoring weed-dominated landscapes.

Final budget

The $5000 CIPM grant was spent on student stipend for graduate student, Helen Rowe, for her full-time work on this project June, July, and August 2004.

Literature Cited

Association of Official Seed Analysts (AOSA). Rules for testing seeds. 2003.

Ball, D.A., D.J. Wysocki, and T.G. Chastain. 1996. Nitrogen application timing effects on downy brome (*Bromus tectorum*) and winter wheat (*Triticum aestivum*) growth and yield. Weed Technology **10**:305-310.

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist **111**:1119-1144.

Dakheel, A.J., S.R. Radosevich, and M.G. Barbour . 1993. Effect of nitrogen and phosphorus on growth and interference between *Bromus-tectorum* and *Taeniatherum-asperum*. Weed Research **33**:415-422.

DiTomaso, J.M.. 2000. Invasive weeds in rangelands: Species, impacts, and management. Weed Science **48**:255-265.

Fulbright, Timothy E., Redente, Edward F., and Hargis, Norman E. Volume II: Grasses and Grasslike Plants. Growing Colorado plants from seed: A state of the art. 1982. U.S. Dept. Int. Fish Wildl. Serv.

Hardy, Susan E. and Palazzo, Antonio J. Report on the workshop on new grass germplasms and invasive weed control. 2002. Fort Carson and the US Air Force Academy, Colorado Springs, CO, US Corps of Engineers.

Hulbert, L.C. 1955. Ecological studies of *Bromus-tectorum* and other annual bromegrasses. Ecological Monographs **25**:181-213.

Kay, B.L. and R.A. Evans. 1965. Effects of fertilization on a mixed stand of cheatgrass and intermediate wheatgrass. Journal of Range Management **18**:7-11.

Klemmedson, J.O. 1964. Cheatgrass (*Bromus-Tectorum*-L. C.). Botanical Review **30**:226-262.

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

Krebs, C.J. 1999. Ecological Methodology. Second edition. Addison Wesley Longman, New York.

Mack, R.N.. 1981. Invasion of *Bromus-tectorum* L into Western North-America - an ecological chronicle. Agro-Ecosystems **7**:145-165.

McLendon, T. and E.F. Redente. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. Ecology **76**:2016-2024.

Mitich, L.W.. 1999. Downy brome, *Bromus tectorum* L. Weed Technology **13**:665-668.

Paschke, M.W., T. McLendon, and E.F. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. Ecosystems **3**:144-158.

Peloquin, R.L. and R.D. Hiebert. 1999. The effects of black locust (*Robinia pseudoacacia* L.) on species diversity and composition of black oak savanna/woodland communities. Natural Areas Journal **19**:121-131.

Rasmussen, P.E.. 1995. Effects of fertilizer and stubble burning on downy brome competition in winter-wheat. Communications in Soil Science and Plant Analysis **26**:951-960.

Redente, E. F., Ogle, P. R., and Hargis, N. E. Growing Colorado plants from seed: a state of the art. Vol III: Forbs. U.S. Dept. Int. Fish Wildl. Serv.

Smith, M.D. and A.K. Knapp. 2001. Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. Int. J. Plant Sci. **162**:785-792.

Stewart, G. and A.C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.)-- an ecologic intruder in southern idaho. Ecology **30**:58-74.