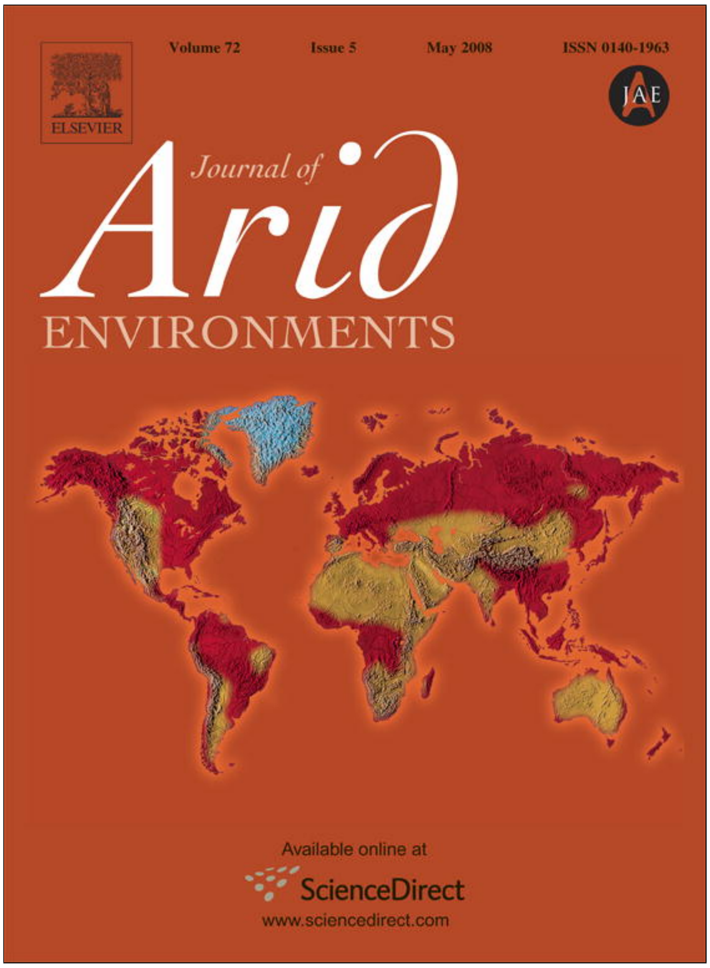

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A comparison of modeled and measured impacts of resource manipulations for control of *Bromus tectorum* in sagebrush steppe

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Abstract

The EDYS (ecological dynamics simulation) model was used to simulate vegetation growth resulting from different experimental treatments for *Bromus tectorum* control at Yakima Training Center, Washington. The treatments tested in the field for 4 years were seeding, sucrose application, and a combination of seeding and sucrose application. These treatments included burning to favor their implementation. A control plant community with no manipulations was also monitored in the study. The simulations of plant production were not significantly different from the observed field results in 90% of the comparisons, supporting the validity of the model. In long-term simulations, the population of *B. tectorum* ceased to dominate the plant community in about 12 years regardless of the treatments. Subsequently, the successional patterns were affected by the treatments. The control and sucrose treatments produced similar successional trends dominated mainly by shrubs (*Artemisia tridentata* and *Chrysothamnus nauseosus*). In contrast, both seeding treatments, including the one with sucrose, produced successional trends dominated by grasses, which reflected the seed mix composition. Seeding had more lasting effects than sucrose application. However, the seeded species only started to dominate the seeded areas when the dominance of *B. tectorum* was reduced. The long-term simulations provided projections that were difficult to envision solely based on the results of the 4-year field experiment.

Keywords: Annual grass; EDYS; Exotic grass; Invasive plants; Seeding; Succession; Sucrose application

1. Introduction

Invasion by exotic species causes major environmental and economic damage to managed and natural ecosystems in the world (Pimentel et al., 2005; Zavaleta et al., 2001). Invasion of exotic weeds is favored in disturbed ecosystems, including those subject to military training (Milchunas et al., 2000). Annual species tend

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to replace perennials in areas under heavy tank training in part because annuals can complete their life cycle in a short period of time, thus having more chance to reproduce without being destroyed (Johnson, 1982).

Bromus tectorum L. is an exotic annual grass introduced to North America from Eurasia that has converted large areas of sagebrush steppe to annual grassland in many areas of western USA, but especially in the upper Great Basin and the Columbia Basin regions (Humphrey and Schupp, 2004; Klemmedson and Smith, 1964; Knapp, 1996; Stewart and Hull, 1949; Young and Evans, 1973). The replacement of native perennial vegetation with near-monocultures of annual grass is troublesome because the original functions of the system are unsustainable. For example, the wildlife habitat provided by former perennial vegetation is not maintained under the new annual grassland vegetation conditions, which threatens the survival of associated fauna (Billings, 1994; Brooks et al., 2004; Newbold, 2005).

Studies have reported that *B. tectorum* dominance is favored by ecological disturbance and surges in plant resources (McLendon and Redente, 1991, 1992; Paschke et al., 2000). Increase in soil available nitrogen in disturbed areas prolongs the period of time that *B. tectorum* dominates a plant community and slows the process of recovery of native perennial vegetation. On the contrary, reduction of available nitrogen favors the recovery of the perennial vegetation at the expense of *B. tectorum* because perennials are better adapted to survive in low fertility soils (McLendon and Redente, 1991, 1992; Paschke et al., 2000; Young et al., 1997). Therefore, lowering soil nitrogen in disturbed lands can be an effective manner of controlling the exotic annual *B. tectorum* while favoring the recovery of native perennial-dominated vegetation (Paschke et al., 2000). Lowering soil nitrogen can be done by applying labile carbon sources to tie up nitrogen in soil microbial biomass. Some common carbon sources are sucrose and sawdust, but sucrose has proven more successful (Corbin and D'Antonio, 2004; Paschke et al., 2000).

A direct means of favoring the recovery of perennial vegetation and controlling *B. tectorum* on an invaded site is sowing seeds of perennials with the expectation that well-established perennial vegetation can better resist a further invasion. However, in dense stands of *B. tectorum*, elimination of this annual grass may be necessary to achieve success in perennial revegetation (Klomp and Hull, 1972). Fire can be used to eliminate the dense cover of *B. tectorum* and prepare the ground for seeding (Hull and Stewart, 1948; Robocker et al., 1965), although recurrent fires may favor this annual grass by reducing the competition with perennials (Mata-González et al., 2007; Pickford, 1932; Whisenant, 1990).

Field experiments are necessary to test effects and methods related to the control of invasive species, but are limited by their temporal and spatial extent. However, results of field experiments are commonly used to predict the complexity of ecological systems at temporal scales much larger than those at which the experimental results were obtained. To avoid the risk of extrapolation, the results of field experiments should be used in conjunction with long-term observational data sets or with ecological modeling that projects the temporal or spatial scope of the results observed in the field (Freckleton, 2004).

The EDYS (ecological dynamics simulation) model is a PC-based, mechanistic, spatially explicit, and temporally dynamic simulation model that simulates changes in soil, water, plant, animal, and landscape components resulting from natural and anthropogenic ecological stressors (Childress et al., 2002). EDYS has been applied to a wide variety of ecosystems, management scenarios, and disturbance regimes (Ash and Walker, 1999; Childress and McLendon, 1999; Childress et al., 1999a, b, 2002; Mata-González et al., 2007; Naumburg et al., 2005).

The objective of this study was to assess the effectiveness of the EDYS model to simulate the impact of (1) sucrose application, (2) seeding, and (3) a combination of sucrose application and seeding as methods of control of *B. tectorum*. EDYS simulations were compared with empirically derived data and the model was subsequently used to project long-term impacts of the methods of control.

2. Materials and methods

2.1. Study site and field experimental treatments

The methods of control were tested and monitored in the field for 4 years at an area, part of the US Army's Yakima Training Center (YTC), invaded by *B. tectorum*. YTC is a 1295 km^2 area located in the Yakima and Kittitas counties of eastern Washington. This region has a long-term annual average precipitation of 206 mm.

Table 1
Species name, functional group, and life form of the plants included in EDYS simulations

Species	Functional group	Life form	Application in seeding mix ($kg\,ha^{-1}$, pure live seed)
Achillea millefolium L.	Forb	Perennial	1.6
Achnatherum hymenoides (Roemer & J.A. Shultes) Barkworth	Grass	Perennial	1.5
Acroptilon repens (L.) DC.	Forb	Perennial	NA
Agropyron cristatum (L.) Gaertn.	Grass	Perennial	6.7
Artemisia tridentata Nutt.	Shrub	Perennial	NA
Astragalus caricinus (M.E. Jones) Barneby	Forb	Perennial	NA
Bromus tectorum L.	Grass	Annual	NA
Centaurea diffusa Lam.	Forb	Annual/perennial	NA
Chrysothamnus nauseosus (Pall.) Britt	Shrub	Perennial	NA
Elymus elymoides (Raf.) Swezey	Grass	Perennial	NA
Erigeron pumilus Nutt.	Forb	Perennial	NA
Erodium cicutarium (L.) L'Hér. ex Ait.	Forb	Annual	NA
Lepidium perfoliatum L.	Forb	Annual	NA
Oenothera pallida Lindl.	Forb	Biennial	NA
Pascopyrum smithii (Rydb.) A. Löve	Grass	Perennial	1.7
Phlox longifolia Nutt.	Forb	Perennial	NA
Poa secunda J. Presl	Grass	Perennial	0.7
Pseudoroegneria spicata (Pursh) A. Löve	Grass	Perennial	7.4
Sisymbrium altissimum L.	Forb	Annual	NA
Stipa comata Trin. & Rupr.	Grass	Perennial	NA

The fourth column indicates the species and the amounts of seed that were used in the seeding mix simulation. Some species of the experimental seed mix were substituted by other species in the simulation (see explanation in text). NA indicates a species that was not used in the seeding mix.

YTC is one of the largest remaining pieces of shrub-steppe habitat in the state. The native vegetation of the area is mainly characterized by the *Artemisia tridentata* Nutt. ssp. *wyomingensis*/*Pseudoroegneria spicata* (Pursh) A. Löve association (Gayaldo, 1996). However, large portions of land are now dominated by the exotic *B. tectorum*.

The experimental design comprised 10-m × 10-m plots located on a uniform substrate on an upper terrace of the Columbia River floodplain. The treatments were randomly arranged in five blocks. Before treatment establishment, aboveground biomass by species was assessed in all plots in May 2000 by clipping plants at ground level inside 10 randomly located quadrats of $0.5\,m^2$. The treatments were (1) control, the vegetation in the plots was not altered, (2) the plots were burned and seeded, (3) the plots were burned and had sucrose applied, and (4) the plots were burned, had sucrose applied, and were seeded. Burning was used in all treatments, except in the control, with the objective of clearing the ground to facilitate the application of treatments. Burning took place on late July 2000. Seeds were sown in late September 2000 by hand broadcast and seeding rate and mixtures were based on standard practices employed by resource management personnel at the installation (Table 1). A second seeding was conducted in December 2001 due to poor initial seedling recruitment. Sucrose was hand broadcast at a rate of $1600\,kg\,C\,ha^{-1}\,year^{-1}$ in three increments (fall, winter, and early spring of 2000–2003) to provide a temporally uniform immobilization of available nitrogen during periods of growth by winter annuals. Soil available nitrogen was monitored using bimonthly incubations of ion-exchange resin bags (Binkley and Matson, 1983) to assess the effectiveness of sucrose applications (Paschke et al., 2000). Post-treatment aboveground biomass was assessed in June of 2001–2003 following same procedure as the 2000 pre-treatment assessment.

2.2. Modeled projections

The EDYS model has been described by Childress and McLendon (1999), Childress et al. (1999a, b, 2002), Naumburg et al. (2005), and Mata-González et al. (2007). EDYS modeling was applied to the study area by using cells of the same size as the field experiment to simulate each field plot. Therefore, simulations had also replications for statistical analysis. The 4-year results of the experiment were used to validate and adjust the model. After that, the model was run for 50 years for assessment of long-term impacts.

EDYS was parameterized for the study area. A 50-year daily precipitation file for the landscape was created using existing precipitation data from Yakima Air Terminal/McAllister Field Airport (latitude 46°34′N, longitude 120°32′W). This set of data was used for the 50-year simulation. The first 4 years of precipitation corresponded to the actual precipitation registered during years 2000–2003, with which we validated the model. For years 5–50, precipitation corresponded to that of years 1948–1993. The 50-year mean annual precipitation was 206 mm.

The Esqutzel Silt Loam soil series corresponded to the study area and its data was used for the EDYS simulation. Physical data for the soil series were taken from the US Department of Agriculture's Natural Resource Conservation Service (USDA-NRCS) Soil Survey for Yakima County listed on the USDA-NRCS web site. Organic matter and soil nitrogen (total and available) data were compiled from soil profiles listed in Soil Survey Staff (1975). A uniform elevation throughout the area was assumed because impacts of the treatments were analyzed on a small scale.

The biomass assessment in 2000 indicated that a total of 49 plant species were present in the experimental plots, although most of these 49 species occurred in very low amounts. The 20 plant species with the highest production were chosen for this application (Table 1) and the rest of the species with minor production were grouped with ecologically similar species. However, only two (*B. tectorum* and *Sisymbrium altissimum* L.) of the 20 species constituted 80–100% of the total biomass in the experimental plots of this study. We assumed that all the species that were included in the simulation were present in the seedbank.

The effect of fire was simulated by establishing the fire intensity, based on the amount of fuel available, and the proportion of plant components and seed bank that are affected by fire. The fuel load for this calculation was defined as the sum of the litter plus the non-trunk aboveground biomass of all herbaceous species. Fire was simulated only once, on July 2000 as occurred in the field. In EDYS, the user selects when the burn is to take place (month, year) and how often the prescribed fire will occur (e.g., every 4 years).

To simulate seeding, a given amount of seed was added to the seedbank in each cell where seeding was to take place according to the seed mix specifications (Table 1) and to the seeding schedule. Three species of the seed mix were not part of the set of species selected for the simulation. Therefore, for simulation purposes we substituted these three species with similar species of the simulation set. *Agropyron fragile* (Roth) P. Candargy was substituted with *Agropyron cristatum* (L.) Gaertn. since *A. fragile* is sometimes considered a subspecies of *A. cristatum. Agropyron intermedium* (Host) Barkworth & D.R. Dewey was substituted with *Pascopyrum smithii* (Rydb.) A. Löve because both are cool season species that have in common rhizomatous growth. *P. spicata* (Pursh) A. Löve ssp. *inermis* (Scribn. & J.G. Sm.) A. Löve was substituted with *P. spicata.* Seeding was simulated on the dates that it was applied in the field.

The purpose of the sucrose treatment was to reduce nitrogen availability in the soils of the study plots. To simulate the impact, we reduced the amount of soil available nitrogen during 1 month after the sucrose application as has been observed in the field (Reever Morghan and Seastedt, 1999). The simulation of sucrose application was done at the same intervals as in the field applications. The reduction of soil available nitrogen in the simulation followed the actual reductions observed in the field.

2.3. Statistical analysis

Confidence intervals (95%) for the biomass means of field and simulation data obtained during 2000–2003 were calculated and compared. If the confidence intervals overlapped, the determinations of field and simulated means were considered not significantly different at $P<0.05$. Confidence intervals were also used to compare the simulated long-term outcome of the treatments on the main species. For this, we selected results of years 25 and 50 to provide snapshots at the middle and end of the simulation period.

3. Results

The most common species found in the treatment plots over the 4 years of the field experiment were *B. tectorum* and *S. altissimum*. Observed and simulated production of these species and total production by treatment and year are shown in Fig. 1. EDYS simulations closely followed the variations in plant production observed in the field. In 43 out of 48 direct comparisons, the 95% confidence intervals of the simulated and the observed production overlapped, indicating that in 90% of the cases the simulations were at least as accurate ($P<0.05$) as the sampling techniques to represent the means of the population. The confidence intervals of observed and simulated biomass did not overlap in five comparisons. Four of these comparisons were related to the biomass of *S. altissimum* and one to the biomass of *B. tectorum*.

In the long-term simulations, *B. tectorum* dominated the plant community in all the treatments for the first 12 years, after which, this species tended to decline and finally disappeared from the community (Fig. 2). However, during these years, the production of *B. tectorum* fluctuated largely. *S. altissimum* was the other major species early in the simulation years, but it disappeared from the control community in 9 years (Fig. 2A) and from the other three communities in 5 or less years (Fig. 2B–D).

In the control plots, the first perennial species to gain dominance was the shrub *Chrysothamnus nauseosus* (Pall.) Britt and it remained dominant until year 39, when was replaced by the late-seral shrub, *A. tridentata*, until the end of the simulation period (Fig. 2A). Perennial grasses were slower than shrubs to become major species in the community, but at the end of the simulation period, *A. cristatum* was as productive as *C. nauseosus*, and second only to *A. tridentata*.

In the burned and seeded plots, the most productive species after the decline of the annuals was the grass *P. smithii* (Fig. 2B). By the end of the simulation period, *A. cristatum* was as productive as *P. smithii*, followed closely by *Achnatherum hymenoides* (Roemer & J.A. Shultes) Barkworth. Therefore, the main species that dominated this community were grasses, in contrast to the shrub-dominated control community.

In plots that were burned and supplied with sucrose (Fig. 2C), the long-term dynamics of species replacement were similar to those observed in the control plots (Fig. 2A). The most common perennial species were shrubs. In the plots that were burned, supplied with sucrose, and seeded the main perennial species were grasses (Fig. 2D), resembling the vegetation trends obtained in the burned and seeded plots (Fig. 2B). *P. smithii* dominated the plant community after the collapse of the annuals and until year 36 and subsequently, *A. cristatum* became the dominant species.

In general, control and sucrose treatments had similar effects in the simulated production at years 25 and 50 (Fig. 3A and B). However, sucrose application produced higher biomass of *A. cristatum* with respect to control on years 25 and 50. Likewise, both of the seeding treatments, i.e., with and without sucrose, produced similar results in general, but seeding with sucrose resulted in lower production of *A. hymenoides* than seeding alone.

4. Discussion

Overall, our simulations of plant production were not statistically different from the observed results in 90% of the comparisons. Rykiel (1996) suggested that an ecological model would be correctly validated if the simulation outputs and the observed results are not significantly different ($P<0.05$) at least 75% of the time for the most important variables. Therefore, EDYS outputs adequately simulated the field conditions, corroborating the utility of this model in environmental management.

Total biomass was always correctly simulated, whereas *S. altissimum* biomass was the less correctly simulated. *B. tectorum* biomass was correctly simulated in all but one of the 16 comparisons. The reason for the lower accuracy in *S. altissimum* simulations was the lower availability of reliable species parameters. The EDYS model relies heavily on individual species parameters to estimate plant growth and competition among species. These parameters are preferentially obtained from literature values adequate for the specific study area of the EDYS application. Therefore, the more literature information that exists about a given species, the more reliable parameters can be used in the modeling process. There is much more literature information on *B. tectorum* than on *S. altissimum* and this was reflected in the accuracy of the simulations.

Our validation was focused on *B. tectorum* and *S. altissimum* because these were the most important species during the 4 years of the validation period. Later in the long-term simulation these species were replaced by perennials and although the later successional perennial species were not part of the validation, their presence in the plant community as predicted here is supported by abundant reports in similar systems (Allen-Diaz and Bartolome, 1998; Hironaka and Tisdale, 1963; Hosten and West, 1994; McLendon and Redente, 1991, 1992;

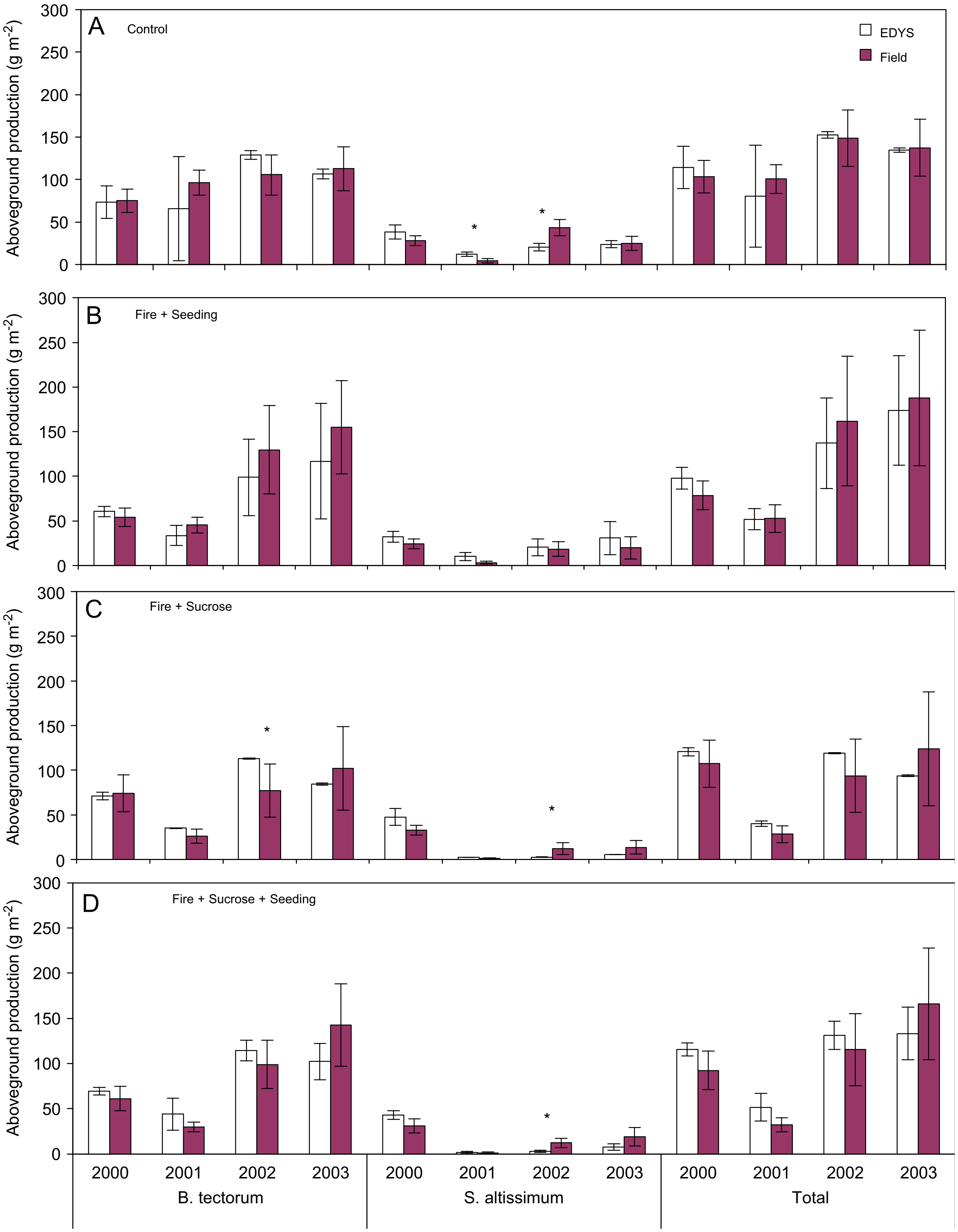

Fig. 1. Field-observed and EDYS-simulated aboveground biomass production (total, *Bromus tectorum* and *Sisymbrium altissimum*) under different treatments: (A) control, (B) fire + seeding, (C) fire + sucrose, and (D) fire + sucrose + seeding during 4 years at Yakima Training Center, Washington. Bars are means ± 95% confidence intervals. Significantly different means ($P < 0.05$) are indicated by asterisks (*).

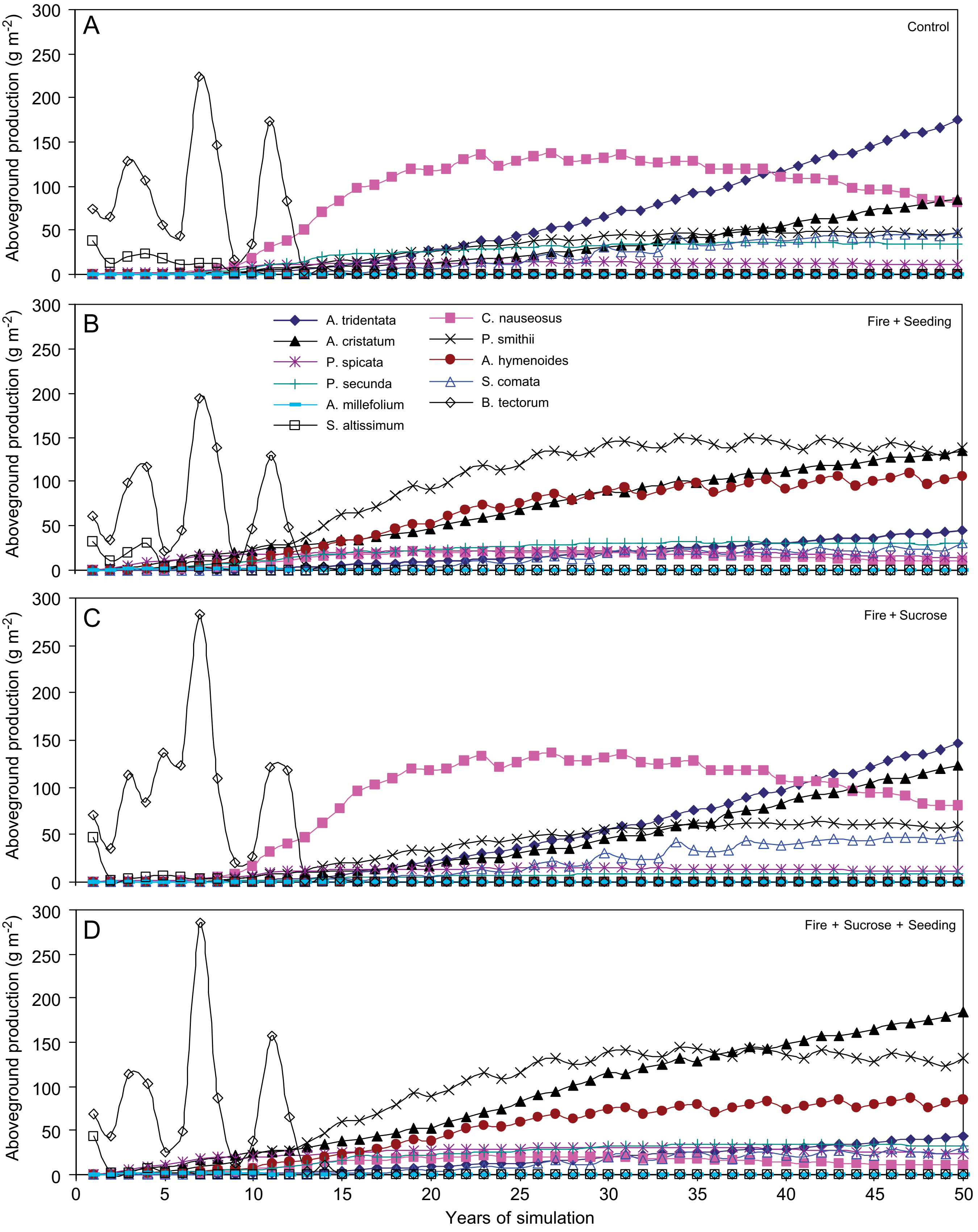

Fig. 2. Fifty-year EDYS simulations of aboveground biomass production by species under different treatments: (A) control, (B) fire + seeding, (C) fire + sucrose, and (D) fire + sucrose + seeding at Yakima Training Center, Washington.

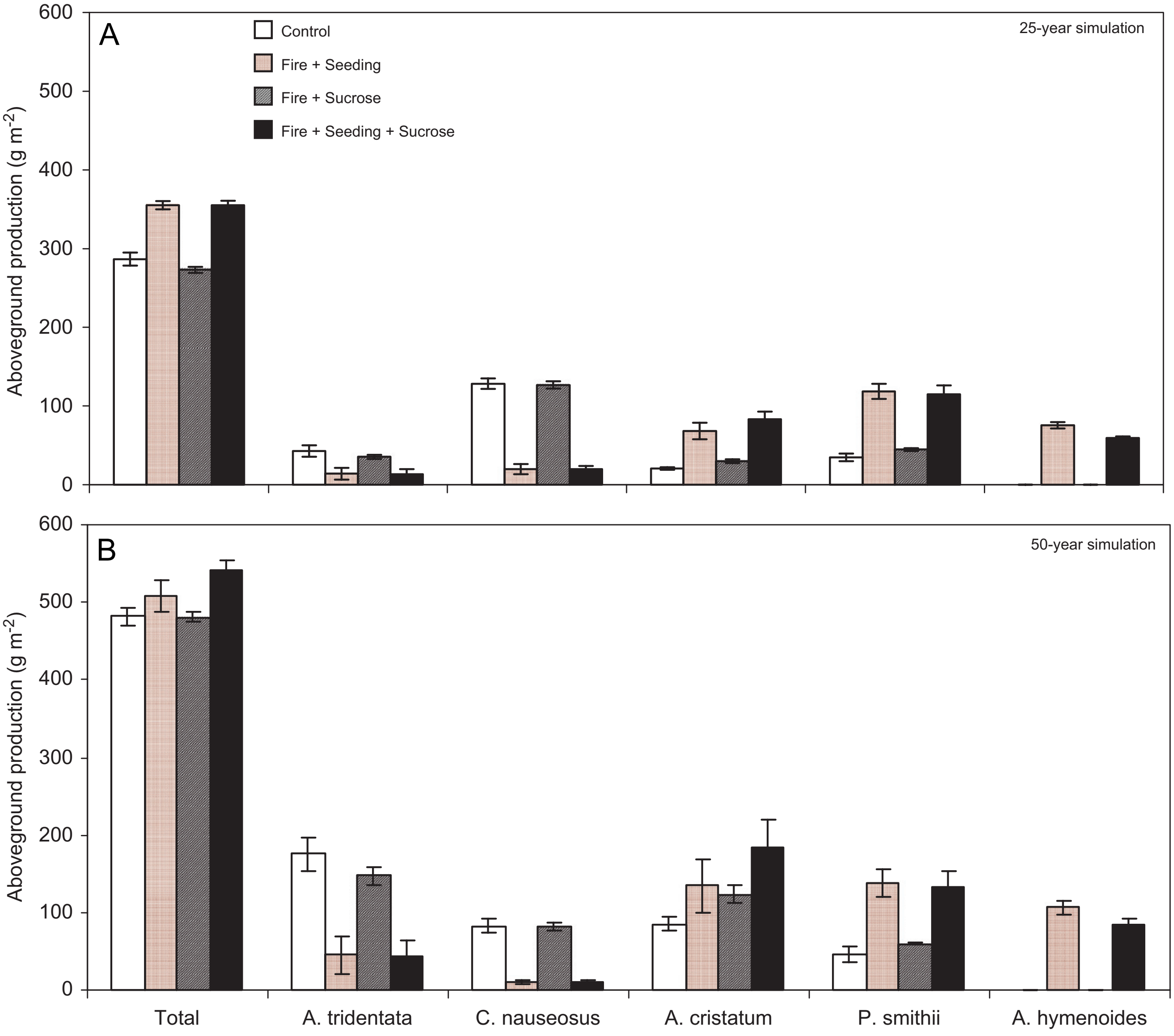

Fig. 3. Simulated aboveground biomass production of main plant species at years (A) 25 and (B) 50 of the simulation period under different treatments at Yakima Training Center, Washington. Bars are means ± 95% confidence intervals.

Paschke et al., 2000; Piemeisel, 1951). In the control treatment, the recovery and dominance by native shrubs that we observed in long-term simulations is in agreement with the recovery periods of *A. tridentata* observed in other areas (Lesica et al., 2007; Watts and Wambolt, 1996). However, we did not find reports for our specific study area, which somewhat precluded a better long-term validation.

In the long-term simulations, all the treatments showed a similar trend in the population of *B. tectorum*. This species dominated the community during the initial 12-year period, but with extreme fluctuations in plant production. Fluctuations of this type have been previously documented (Hull, 1949; Stewart and Hull, 1949) and are due to the extreme dependence of this species to weather conditions. Following this 12-year period, *B. tectorum* became negligible in the plant community while perennials started to increase. The treatments did not affect the successional pattern of *B. tectorum*. Rather, our simulations fitted the pattern observed in field studies where *B. tectorum* ceases to dominate a disturbed plant community as plant resources become limiting, at which point perennial species start to regain dominance due to their adaptation to survive under limiting soil nutrients and water (Allen and Knight, 1984; Hironaka and Tisdale, 1963; Hosten and West, 1994;

Klemmedson and Smith, 1964; McLendon and Redente, 1991, 1992; Paschke et al., 2000; Piemeisel, 1951). Our simulations also predicted that the population of *S. altissimum* would decline in a shorter period of time than the population of *B. tectorum*, which is in agreement with the successional trends observed by Piemeisel (1951) in southcentral Idaho.

A problem with some annual invasive plants such as *B. tectorum* is that their dominance favors some types of disturbance such as fire, which in turn favors the perpetuation of the invasion by inhibiting the recovery of native perennials (Brooks et al., 2004; Pickford, 1932; Whisenant, 1990). Other types of disturbance such as heavy grazing (Klemmedson and Smith, 1964; Pickford, 1932) or military training (Johnson, 1982; Milchunas et al., 2000) also tend to perpetuate the dominance of annuals because the populations of perennials are more likely to be negatively affected by these activities.

In our field study, the sucrose treatment reduced the growth of *B. tectorum* compared to the control in 2001, but not in the other 3 years. Thus, the sucrose effect was not as pronounced as in previous studies (McLendon and Redente, 1992; Paschke et al., 2000). In long-term simulations, the sucrose and control treatments resulted in similar trends, with *C. nauseosus* initially replacing *B. tectorum* as the dominant species and with *A. tridentata* gaining dominance at the end of the 50-year simulation. Therefore, the sucrose application did not have appreciable long-term effects in the general successional trend. Sucrose increases the C:N ratio in the soil, promoting the increase in the population of heterotrophic microorganisms and a consequent higher use and immobilization of soil nitrogen (McLendon and Redente, 1992). This effect, however, is of short duration. Reever Morghan and Seastedt (1999) reported that sucrose (applied at $200\,\mathrm{g\,m^{-2}}$) reduced soil available nitrogen up to 1 month after the application, but by the second month the sucrose effect was no longer observed. Therefore, if sucrose is to aid in promoting the long-term recovery of perennial species, it should be applied repeatedly to have a continuous effect on nitrogen availability. Alternatively, more detailed research could help to improve the fine-tuning of timing of application with respect to phenological stages.

The two seeding treatments (with and without sucrose) produced similar successional trends, with grasses dominating the plant community in the long term. This was in sharp contrast to the control and sucrose treatments in which shrubs dominated the long-term succession. A close analysis of the simulation results demonstrated, however, that sucrose had some long-term effects reflected mainly in individual species. Sucrose application promoted the production of *A. cristatum* and inhibited that of *A. hymenoides*, but this effect was not manifested in the 4 years of the field observations. The reasons for the differential long-term simulated effect of sucrose on *A. cristatum* and *A. hymenoides* are not clear.

The effect of seeding was not manifested during the 4 years of the experiment, but until the population of annuals ceased to dominate the plant community in the long-term simulations. This is in agreement with Klomp and Hull (1972), who found that seeding in areas invaded by *B. tectorum* was successful only when this species was eliminated. Similarly, Allen and Knight (1984) concluded that the successional growth of native perennials in a disturbed area in Wyoming was inhibited by the population of annuals. *B. tectorum* is a successful invader in part because it effectively uses soil water during the winter and spring, depleting the soil water reserves for the summer and reducing the possibilities of growth for perennials (Harris, 1967).

Without the long-term simulation results, we would have to conclude, based on the field experiment, that seeding was of limited value. Instead, the simulations indicated that seeding could lead to a plant community dominated in the long term by the seeded species. Newman and Redente (2001) reported that after 20 years of seeding a disturbed area of northwestern Colorado, the composition of the plant community reflected the composition of the original seed mix used. They also found that the seeded plant community was stable and resisted the invasion by weeds, which has been also reported by Blumenthal et al. (2005). Newman and Redente (2001) recommended long-term monitoring for revegetated areas because short-term results can be misleading.

Because of the difficulty to obtain funding for long-term monitoring of revegetation studies it is recommended the use of modeling for predicting long-term effects (Freckleton, 2004). A limitation of long-term simulations is the difficulty to obtain data for validation over multi-decade experiments that reflect succession dynamics in arid and semi-arid environments. In this study we support our long-term simulations with literature information from similar systems, although we lacked specific information for our study area.

5. Conclusions

The simulated results of plant production were not significantly different from the observed field data in 90% of the comparisons. In the 4-year experiments, seeding and sucrose application had limited effect on vegetation growth and control of *B. tectorum*. In the long-term projections, the sucrose treatment and the control produced similar successional trends, with shrubs dominating the plant community at the end of the simulation period. In contrast, both of the seeding treatments resulted in plant communities dominated by grasses and reflecting the seed mix composition at the end of the long-term simulation period. Sucrose application is less likely to have long-term effects than seeding. Seeding is an attractive method to modify the long-term composition of the plant community. However, the displacement of exotic annuals by the seeded species would not occur if the conditions that favor the prosperity of the annuals do not disappear or if the conditions that favor the seeded perennials do not improve.

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