

## Modelling plant growth dynamics in sagebrush steppe communities affected by fire

R. Mata-González<sup>a,\*</sup>, R.G. Hunter<sup>a</sup>, C.L. Coldren<sup>a</sup>,  
T. McLendon<sup>a</sup>, M.W. Paschke<sup>b</sup>

<sup>a</sup>MWH Americas Inc., 1825 Sharp Point Drive, Suite 118, Fort Collins, CO 80523, USA

<sup>b</sup>Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University,  
Fort Collins, CO 80523, USA

Received 24 February 2006; received in revised form 25 July 2006; accepted 7 September 2006

Available online 31 October 2006

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### Abstract

The EDYS model was used to simulate plant production in burned and unburned communities dominated by *Bromus tectorum* at the US Army Yakima Training Centre, Washington. Model results were validated with 4 years of field data obtained in experiments designed specifically for this study. Subsequently, 50-year simulations of plant production were conducted with normal precipitation for the area and with no disturbances such as grazing or military training. Our simulations of plant production were not significantly different ( $p > 0.05$ ) from observed results of burned and unburned communities in 90% of the comparisons, indicating that EDYS adequately simulated the dynamics of this system. Long-term simulations indicated that annual species, primarily *B. tectorum*, dominated burned and unburned plant communities for 13–15 years, after which, annuals were replaced by perennials. *B. tectorum*, however, remained five years longer in the burned than in the unburned community, suggesting that fire favors the persistence of this species in invaded areas. Although *B. tectorum* dominated both plant communities during the initial simulation period, its production fluctuated greatly. The main perennials that replaced *B. tectorum* were *Chrysothamnus nauseosus*, *Artemisia tridentata*, and *Agropyron cristatum*. Our long-term modelling results are supported by previous field observations in which annual species are replaced by perennials in the absence of disturbances.

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**Keywords:** *Bromus tectorum*; Burning; Cheatgrass; Ecological modelling; EDYS; Invasive species

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\*Corresponding author. Tel.: +1 970 2122752; fax: +1 970 3779406.

E-mail address: [ricardo.mata-gonzalez@mwhglobal.com](mailto:ricardo.mata-gonzalez@mwhglobal.com) (R. Mata-González).

## 1. Introduction

The replacement of native perennial vegetation with near-monocultures of annual exotic grasses such as *Bromus tectorum* is troublesome because the original ecosystem functions are disrupted. For example, wildlife habitat provided by former perennial vegetation cannot be maintained under annual grassland vegetation, which threatens the survival of associated fauna (Brooks et al., 2004; Newbold, 2005). Invasion of exotic weeds is favoured in disturbed ecosystems, such as those subject to military training (Milchunas et al., 2000). The challenge of successful re-establishment of native plants is further complicated by variations in management that a site might be exposed to (Anderson and Ostler, 2002). Addressing this challenge requires multiple perspectives of ecological management.

The usefulness of field experimentation for the purposes of testing concepts and refining methodologies relative to control of invasive species is limited by the relatively short time periods in which they are conducted and the environmental conditions that occurred during the experimental period. Simulation modelling provides one method of addressing the limitations of field experiments. When combined with field experiments, simulation modelling is a powerful tool to evaluate the results of field experiments over longer periods of time and under many more variations of environmental factors than are practical with field experiments (Freckleton, 2004).

Successful simulation modelling is a two-step process. First, the simulation model must be able to adequately simulate the results of field experiments (Rykiel, 1996). Otherwise, there is little reason to have confidence in the results of the model relative to longer-term responses and variations in environmental factors. Once this validation process is accomplished, the second step of applying the model to longer-term responses and variations in environmental factors can be implemented (Freckleton, 2004).

The simulation model used in this study was the ecological dynamics simulation (EDYS) model. EDYS is a PC-based, mechanistic, spatially explicit, and temporally dynamic simulation model (Childress and McLendon, 1999; Childress et al., 1999a, b). It 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 in the USA (Childress and McLendon, 1999; Childress et al., 1999a, b, 2002; Price et al., 2004; Naumburg et al., 2005) and Australia (Ash and Walker, 1999).

EDYS was used to simulate plant community production in Yakima Training Centre (YTC), a US Army military training facility located in south-central Washington. This installation contains one of the largest remaining areas of shrub-steppe habitat in the state, but also contains large areas of land that have been invaded by *B. tectorum* (Gayaldo, 1996). This species has been recognized for decades as a serious invader, converting sagebrush-steppe to annual grassland in many areas in the western USA, but especially in the upper Great Basin and the Columbia Basin regions (Stewart and Hull, 1949; Klemmedson and Smith, 1964; Young and Evans, 1973; Knapp, 1996; Humphrey and Schupp, 2004). It is widely recognized that the dominance of *B. tectorum* increases fire frequency in invaded areas, which in turn, favors the establishment of this species by reducing competition with perennials (Pickford, 1932; Whisenant, 1990; Brooks et al., 2004; Mensing et al., 2006).

In this study, EDYS simulations were compared to the results of a 4-year field experiment conducted on areas dominated by *B. tectorum* to determine EDYS potential for simulating plant production on unburned areas and in areas that were burned the first year of the study. EDYS was then used to simulate plant production over a 50-year period on burned and unburned plant communities with precipitation conditions that are normal in the area and without disturbances such as grazing or military training.

## 2. Materials and methods

### 2.1. Description of EDYS

Details about EDYS can be found in several sources (Childress and McLendon, 1999; Childress et al., 1999a b, 2002). Here, we highlight some of its characteristics. EDYS is a mechanistic model that contains climatic, soil, hydrologic, plant, animal, stressor, spatial, landscape, and management modules. Climatic inputs can be historical or stochastically generated. The soil module is divided into layers, whose characteristics are site-specific for each application. The hydrologic module provides for infiltration and water movement through the soil profile according to the water retention capacity of soil layers and the amount of precipitation.

The plant module includes above- and belowground components for each species included in each user-defined application. EDYS includes a large number of species-specific ecophysiological variables. Examples include growth allocation (i.e., how much of the monthly primary production is allocated to each plant part), water use efficiency, tissue nitrogen concentration, initial root architecture, monthly phenology, maximum growth rate, seasonal growth rate, sensitivity to shading, and seed germination rate. Parameterization values for these variables are taken from the literature for the individual species and the geographical area of the modelling application when available, and for nearest ecological equivalent otherwise. Plant roots take water and nitrogen based on availability of these resources and root densities per soil layer. Plant uptake is dictated by seasonal demand and regulated by potential growth rate. Plant uptake is translated into plant growth depending on the efficiency of each species of converting resources (water and nitrogen) into biomass. Plant growth is simulated as production under optimal conditions, constrained by the actual availability of water and nitrogen and by the season. Plant growth is dynamic in relation to plant components (roots, trunk, stems, leaves, seeds, and standing dead), season, resource requirements (water, nutrients, sunlight), and stressors (e.g., herbivory, competition, fire, trampling, chemical contaminants).

The animal module consists of basic population parameters and diet attributes (preferences, utilization potential, competitive success) for each species (e.g., insects, rodent, native ungulates, livestock). The stressor module includes drought, nutrient availability, fire, herbivory, trampling (foot and vehicle), contaminants, shading, and competition (soil moisture, nutrients, food). The effect of fire is 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 spatial module allows growth of individual plants (e.g., trees) and distribution patterns (e.g., colonies, fire patterns, soil heterogeneity) to be explicitly represented in the simulations. The landscape module allows for multi-scale simulations: fine scale (1 m<sup>2</sup> or smaller), patches (e.g., 100 m<sup>2</sup>), communities (e.g., 1–10 ha), and landscapes and watersheds (1 km<sup>2</sup> and larger). Time intervals vary from

day (e.g., precipitation events, plant water demand, fire, herbivory) to month (e.g., species composition) to year and longer (e.g., climatic cycles).

## 2.2. Field experiment

YTC is a 1295 km<sup>2</sup> installation located in Yakima and Kittitas Counties of south-central Washington. 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*/*Agropyron spicatum* association (Gayaldo, 1996). However, large portions of land are now dominated by the exotic *B. tectorum*. The landscape selected for the field experiment was representative of the *B. tectorum* invaded areas and consisted of 4000 m<sup>2</sup> located at the eastern edge of Training Area 4, on an upper terrace of the Columbia River floodplain.

In April 2000, 10 × 10-m<sup>2</sup> study plots were located in representative areas of the study area to evaluate and monitor aboveground plant biomass for four years. Initial (pre-treatment) aboveground biomass was assessed in May 2000 by clipping at ground level inside ten randomly located quadrates of 0.5 m<sup>2</sup> per plot. Biomass was clipped by species, dried to constant mass, and weighed. Five plots were used to evaluate plant biomass without manipulating the existing vegetation (control plots). Five other plots were burned in July 2000 to evaluate plant biomass in the subsequent years following the prescribed fire. The burn was applied until late July due to dangerous fire conditions that forced a fire ban in the area. Fire was not repeated in subsequent years. Aboveground biomass was monitored (post-treatment) from 2001 to 2003 in June, with the same methods used in the initial biomass assessment. Care was taken to avoid clipping in the same place in subsequent years within the study plots.

## 2.3. EDYS application

EDYS was parameterized for the conditions of YTC. Cells of the same size as the field experiment plots were used in this application. Based on NRCS soils maps for the area, the soil series corresponding to the study area was Esqutzel Silt Loam. Physical data for the soil series were taken from the NRCS Soil Survey for Yakima County listed on the NRCS web site. Organic matter and soil nitrogen (total and available) data were compiled from soil profiles listed in Soil Survey Staff (1975).

In EDYS, initial values are entered for each of the soil variables. Values for each variable can change during a simulation run, depending on the dynamics of environmental conditions. For example, nitrogen content will vary on a daily basis because of (1) plant uptake, (2) release from decomposition and mineralization, (3) downward transport through infiltration of soil water, and (4) inputs from atmospheric deposition and nitrogen fixation.

A 50-year daily precipitation file for the landscape was obtained from existing precipitation data at Yakima Air Terminal/McAllister Field Airport (latitude 46°34'N, longitude 120°32'W). This set of data, whose annual totals are presented in Fig. 1, 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. Average monthly values for the period 1948–2003 are presented in Fig. 2.

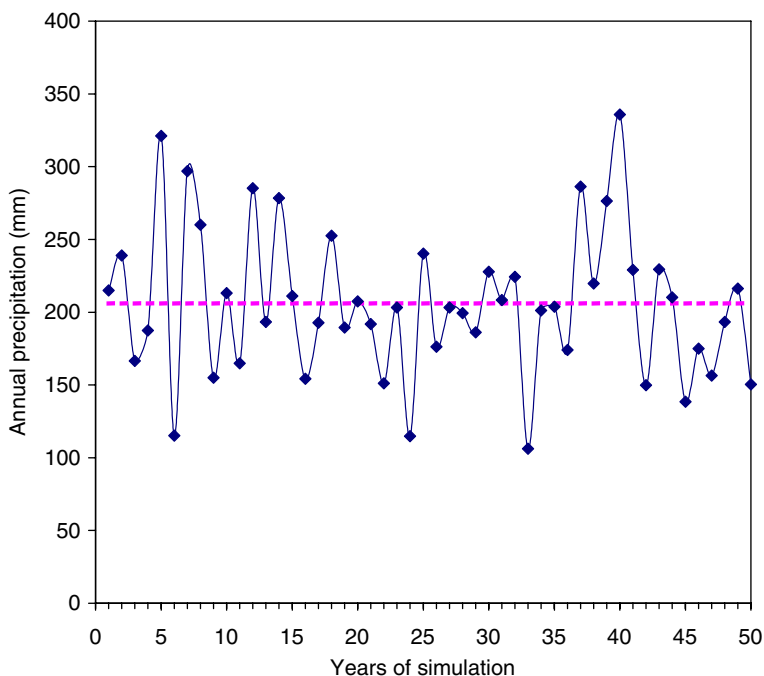


Fig. 1. Annual precipitation during the 50 years of the simulation period. The first 4 years correspond to actual precipitation at Yakima Training Centre during 2000–2003 and the following years correspond to precipitation registered in the site from 1948 to 1993. The horizontal bar indicates the annual mean during the 50-year simulation.

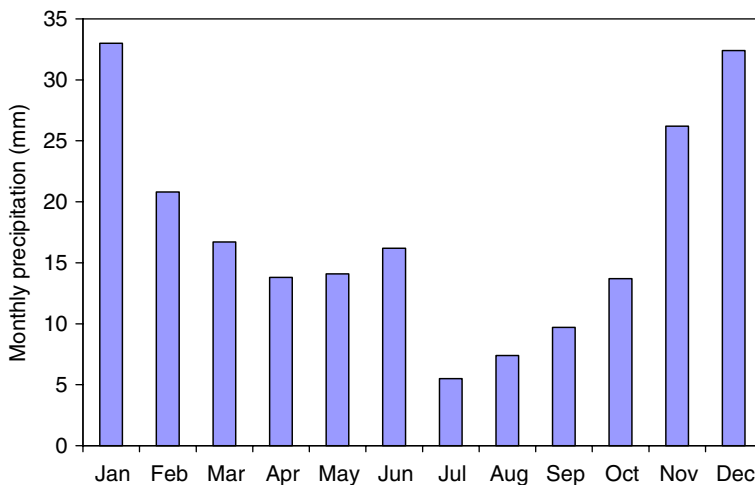


Fig. 2. Monthly precipitation at Yakima Training Centre averaged from 1948 to 2003.

Initial field data provided information on the plant species to be included in this application. A total of 49 species were found on the study area in 2000, including the plots used in this study and additional plots that were part of other studies. Most of the 49

Table 1  
Plant species included in the Yakima Training Centre application of EDYS

Species	Common name
<i>Achillea millefolium</i>	Yarrow
<i>Achnatherum hymenoides</i>	Indian ricegrass
<i>Acroptilon repens</i>	Russian knapweed
<i>Agropyron cristatum</i>	Crested wheatgrass
<i>Artemisia tridentata</i>	Big sagebrush
<i>Astragalus caricinus</i>	Buckwheat milkvetch
<i>Bromus tectorum</i>	Cheatgrass
<i>Centaurea diffusa</i>	Diffuse knapweed
<i>Chrysothamnus nauseosus</i>	Rubber rabbitbrush
<i>Elymus elymoides</i>	Squirreltail
<i>Erigeron pumilus</i>	Shaggy daisy
<i>Erodium cicutarium</i>	Storksbill
<i>Lepidium perfoliatum</i>	Pepperweed
<i>Oenothera pallida</i>	Evening primrose
<i>Pascopyrum smithii</i>	Western wheatgrass
<i>Phlox longifolia</i>	Longleaf phlox
<i>Poa secunda</i>	Sandberg bluegrass
<i>Pseudoroegneria spicata</i>	Bluebunch wheatgrass
<i>Sisymbrium altissimum</i>	Tumble mustard
<i>Stipa comata</i>	Needle-and-thread

species, however, had very low production. 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, two (*B. tectorum* and *Sisymbrium altissimum*) of the 20 species, constituted 80–100% of the total biomass in the experimental plots of this study. Despite this dominance, we assumed that the other species found in the plant community were present in the seedbank.

#### 2.4. Analysis of data for validation

The 95% confidence intervals for the biomass means by treatment, species, and year of both field observations and simulations were calculated and compared. If the confidence intervals overlapped, the means were not considered significantly different at the  $p$  value of 0.05.

### 3. Results

#### 3.1. Model validation with field data

*B. tectorum* and *S. altissimum* were, by far, the most important species of the experimental area. Initial biomass in 2000 represented the original conditions of the plots before applying the fire treatment, for which, production in control and burned plots were similar (Fig. 3). Biomass in 2001–2003 reflected the changes of burned and control plots. In the control plots, EDYS simulations were not different from field observations of total and *B. tectorum* biomass in 4 years of the study (Fig. 3 upper panel). The simulations, however,

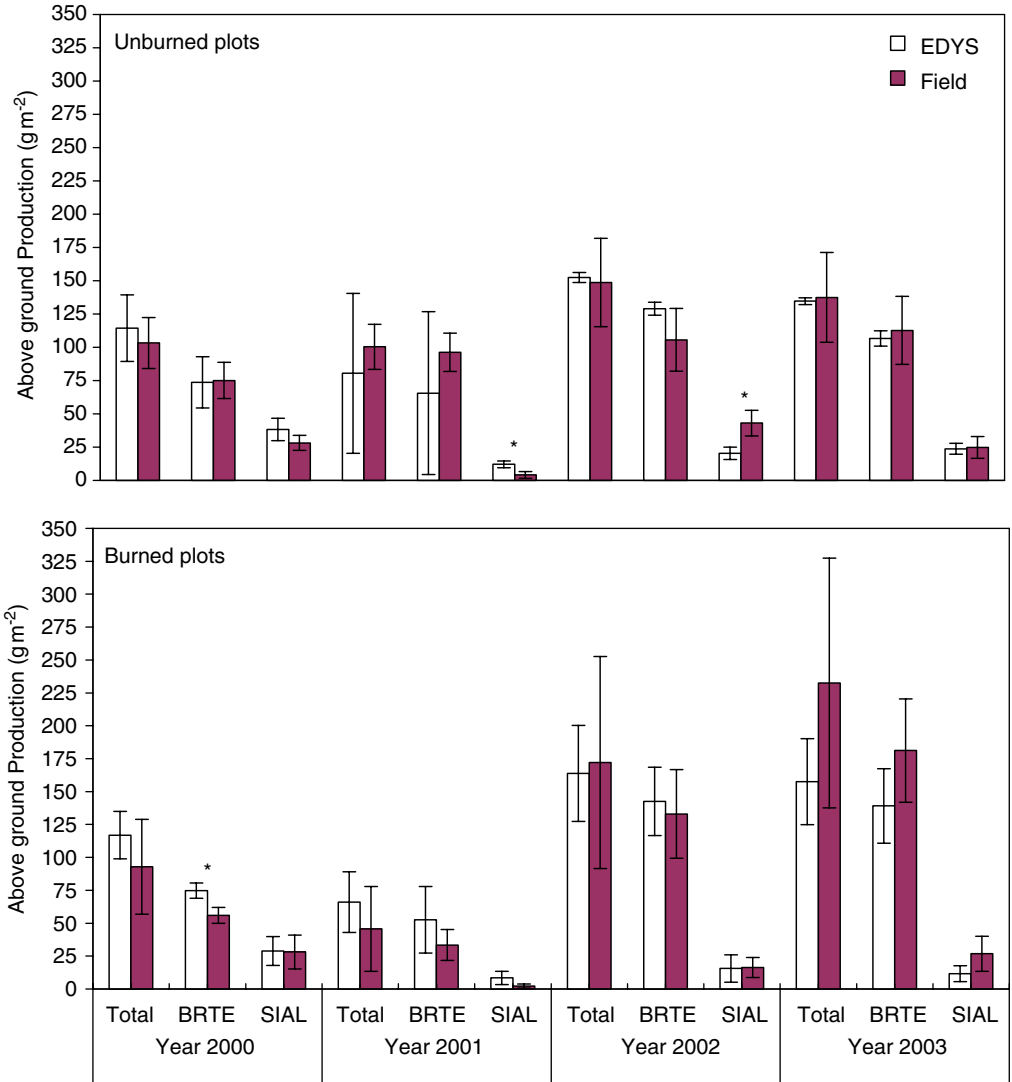


Fig. 3. Total, *Bromus tectorum*, and *Sisymbrium altissimum* biomass production in unburned (upper panel) and burned (lower panel) plots simulated by EDYS and sampled in the field for 4 years at Yakima Training Centre. Bars are means  $\pm$  95% confidence intervals. Significantly different means ( $p < 0.05$ ) are indicated by \*.

differed from field observations of *S. altissimum* in two of 4 years of the study. In the burned plots (Fig. 3 lower panel), EDYS simulations were not different from field sampling of total and *S. altissimum* biomass in 4 years of the study. Only in 1 year (2000), EDYS simulations differed from the field sampling of *B. tectorum*. Overall, in 21 out of 24 comparisons, simulations were not significantly different ( $p > 0.05$ ) from field data, indicating that in nearly 90% of the comparisons, the simulations were at least as accurate as the sampling techniques to represent the means of the population.

### 3.2. Long-term simulations

The 50-year simulations started with a plant community completely dominated by annuals (*B. tectorum* and *S. altissimum*), as observed in the field for the first 4 years. The control plots continued to be dominated by annuals for another 13 years (Fig. 4 upper panel). Production of *S. altissimum* was highest in year 1, then tended to decline to zero by year 9. *B. tectorum* showed large fluctuations in production. The maximum production of about 225 g m<sup>-2</sup> occurred in year 7, while 2 years later the production was about 20 g m<sup>-2</sup>. *B. tectorum*, however, was the dominant species in the plant community until year 12, finally disappearing from the community by year 15. As annuals decreased, perennials

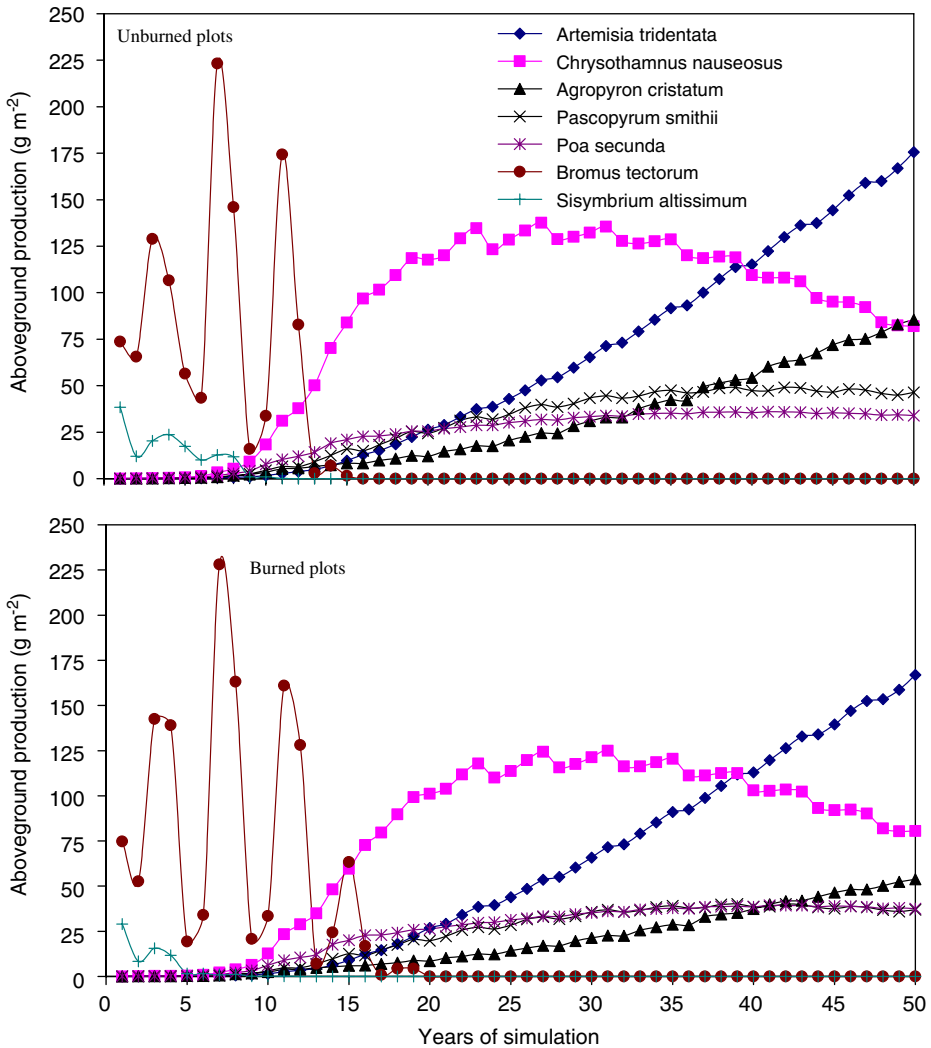


Fig. 4. Fifty-year EDYS simulations of plant production by species in unburned (upper panel) and burned (lower panel) plots.

started to gain dominance. By year 13, the dominant species was the shrub *Chrysothamnus nauseosus*, which remained dominant until year 39. Subsequently, another shrub, *A. tridentata*, became the dominant species and continued to dominate through year 50, but with significant presence of *C. nauseosus*. Although shrubs were the dominant species after the collapse of the annuals, perennial grasses also became a substantial part of the plant community. By the end of the simulation period the most productive grass was *Agropyron cristatum*, followed by *Pascopyrum smithii* and *Poa secunda*.

In the burned plots, as in the control plots, annuals dominated the plant community the first years of the simulation period, but tended to decrease after a decade, after which perennials started to gain dominance and finally replaced all annuals (Fig. 4 lower panel). *S. altissimum* lasted in the burned plots 4 years less than in the control plots. As in the control plots, *B. tectorum* showed large fluctuations in production before disappearing from the burned plant community. However, in the burned plots, the *B. tectorum* population dominated the plant community until year 15, 3 years longer than in the control plots and remained in the community until year 20, 5 years longer than in the control plots. The longer dominance of *B. tectorum* coincided with lower growth of *C. nauseosus* in the burned plots compared to those unburned. Over the 50-year simulation period, the general patterns of species replacement observed in the burned plots and in the control plots were similar. Burning merely extended the period of *B. tectorum* dominance by a few years.

#### 4. Discussion

According to Rykiel (1996), validation means that a model is acceptable for its intended use if the model outputs meet specified performance criteria. Rykiel (1996) proposed that an appropriate test to declare the validity of an ecological model would be that the model results and the observed results are not statistically different (based on 95% confidence intervals) at least 75% of the time. Our simulations met this criterion 90% of the time, indicating that the EDYS model produces adequate results and can be an effective tool in environmental management. However, *S. altissimum* biomass was not as well simulated as total or *B. tectorum* biomass. A limitation for the simulation of *S. altissimum* was the limited amount of reliable plant parameters available in the scientific literature to parameterize EDYS. In comparison, information on *B. tectorum* is abundant, facilitating the modelling process and producing higher accuracy. In general, field measurements had larger confidence intervals than simulated values. This was in part because in the simulation process it is assumed a level of plot homogeneity (soil characteristics) that does not occur in the actual field plots.

Validation centred in *B. tectorum* and *S. altissimum* because these were the major species during the validation period. Later in the long-term simulation, these species were replaced by perennials. Although the later successional perennial species were not part of the validation, their presence in the plant community as predicted by our model is supported by many literature reports in similar systems (Piemeisel, 1951; McLendon and Redente, 1991, 1992; Hosten and West, 1994; Allen-Diaz and Bartolome, 1998; Paschke et al., 2000). The fact that the originally minor species gained importance through the 50-year simulation period only attests to the dynamic nature of the system and the capacity of the EDYS model to simulate it.

Long-term simulations indicated that annual production of *B. tectorum* was highly variable. In a period of 2 years, production varied more than ten-fold. Similar fluctuation has been amply documented in field studies reporting the extreme dependence of this species to weather variations in comparison to perennial species (Hull and Pechanec, 1947; Hull, 1949; Stewart and Hull, 1949; Uresk et al., 1979). This makes *B. tectorum* an unreliable source of forage for herbivores in areas that have been invaded by this species.

In the long-term simulations, the populations of annuals disappeared from the community in both the unburned and the burned areas after 15–20 years. In the burned area, however, *B. tectorum* remained in the community longer than in the unburned area. This indicates that in the absence of disturbances native perennial species are more successful competitors than exotic annuals. This has been documented in a number of reports (Piemeisel, 1951; McLendon and Redente, 1991, 1992; Hosten and West, 1994; Paschke et al., 2000; Corbin and D'Antonio, 2004). Hosten and West (1994) reported a population of *B. tectorum* in Utah that dominated the plant community after a wildfire. This population, however, became totally replaced by perennials after 10 years under no fire conditions and several years of drought. Similarly, Piemeisel (1951) reported that *B. tectorum* became dominant in areas that were cleared for agriculture in south-central Idaho. Eleven years after the disturbance, however, the *B. tectorum* population started to decline, coinciding with the increase in the population of native perennial grasses. A similar pattern of displacement of *B. tectorum* by perennials was also reported by Allen-Diaz and Bartolome (1998).

The dominant species at the end of the simulation period were the native shrubs and grasses (*A. tridentata*, *C. nauseosus*, *P. smithii* and *P. secunda*) and the non-native grass *A. cristatum*, which was previously introduced in revegetation efforts to YTC (Gayaldo, 1996). Noticeable, the native grass *Psuedoroegneria spicata* did not recover at the end of the simulation, likely due to its low competitive ability in relation to more aggressive grasses such as *A. cristatum* (Robertson et al., 1966; Cox and Anderson, 2004).

Disturbance typically releases plant resources, which annuals more readily capitalize than perennials. As long as disturbance provides unusually high plant resources, annuals tend to dominate the plant community and conversely, as resources become limiting, annuals are less able to dominate (McLendon and Redente, 1991, 1992; Paschke et al., 2000). Despite its reputation for being an aggressive invader, *B. tectorum* has clear limitations to persist in a site with respect to perennials. An unusually dry spring can eliminate nearly all *B. tectorum* seedlings of the population, especially if most of the seedlings germinated in the winter due to good moisture conditions (Smith et al., 1997). Low nitrogen levels also represent a limitation for the success and dominance of *B. tectorum* (McLendon and Redente, 1991, 1992, 1994; Paschke et al., 2000).

Native perennial species are usually more resilient than *B. tectorum* and yet, *B. tectorum* has successfully invaded for decades large areas formerly dominated by perennials. It has been well documented that in many areas the success of *B. tectorum* has been due to the acceleration of fire frequencies, which is more deleterious to the perennial species than to *B. tectorum* (Pickford, 1932; Wright and Klemmedson, 1965; Whisenant, 1990; Melgoza and Nowak, 1991). This was clearly manifested in our long-term projections of the burned area where a single fire event lengthened the time *B. tectorum* dominated the plant community. Fire facilitated this effect by retarding the successional recovery of *C. nauseosus*, since this shrub was the species that first replaced *B. tectorum* as dominant. Therefore, if fires occur at least every 10 years in areas dominated by *B. tectorum* the

perennial species would have little opportunity for recovery and the site would be dominated by *B. tectorum* for decades. Unfortunately, the dominance of *B. tectorum* has shortened the fire frequency period in some areas from 60 to 100 years to less than 5 years (Whisenant, 1990).

Fire is an important factor to explain the invasive success of *B. tectorum* in many areas. However, there are places in which this species has dominated for years without the apparent mediation of fire (Tausch et al., 1994). *B. tectorum* is an aggressive competitor in its own right by depleting soil water and nutrients in the cool season, leaving little resources for perennials in the warm season. Another reason for the success and permanence of *B. tectorum* in invaded plant communities is the modification of the plant community. As a community turns from perennial-dominated to annual-dominated, the system becomes more pulse-driven with marked seasonal periods of high resources in the spring followed by periods of low resources in the summer (Booth et al., 2003a). Such a system is ideal for the continuous dominance of *B. tectorum* for its ability to rapidly acquire nutrients and water in the cool season. It has also been reported that in areas dominated by *B. tectorum*, available soil nitrogen is present in higher levels than in areas dominated by perennials (Booth et al., 2003b; Norton et al., 2004). This is beneficial for the long-term establishment of annuals as demonstrated by McLendon and Redente (1991, 1992) and Paschke et al. (2000).

EDYS simulations also indicated that, in the absence of disturbance, the re-establishment of annual species in the plant community is unlikely once the perennial species are well established. Evidence indicates that undisturbed and well-established plant communities are less likely to be invaded by exotic annuals (Davis et al., 2000; Corbin and D'Antonio, 2004; Humphrey and Schupp, 2004). Early reports indicated that *B. tectorum* invaded rangelands predominantly on areas that were severely disturbed by overgrazing or fire (Pickford, 1932; Stewart and Hull, 1949; Beatley, 1966). Recent reports also show that *B. tectorum* is more prone to dominate areas affected by disturbance (McLendon and Redente 1991, 1992; Paschke et al., 2000).

McLendon and Redente (1991, 1992) monitored vegetation dynamics after removal of vegetation and top 5 cm of soil by a bulldozer in northwestern Colorado. The disturbance favored the dominance by annuals, but perennial species started to re-gain dominance of the plant community after 3 years. EDYS simulations showed a much longer period of time for the recovery of perennial species in the absence of disturbance. In northwestern Colorado a significant (39%) part of the annual precipitation is received in the summer (May–August) (Tiedeman and Terwilliger, 1978). Higher precipitation in the summer would favor the re-establishment of perennial species that actively grow in the summer, making it more difficult for a winter annual to dominate the area. However, in sites such as south-central Washington where precipitation is concentrated in winter-spring and with lower proportion of precipitation in the summer (21% at YTC) *B. tectorum* would be more likely to dominate longer after disturbance. This relationship between seasonality of precipitation and persistence of *B. tectorum* in the community in the absence of disturbance was previously hypothesized by McLendon and Redente (1994).

The invasion and persistence of *B. tectorum* in former sagebrush-steppe areas has led to the assumption that new annual grasslands are stable states that cannot return to the former condition of the plant community (Miller et al., 1994). Our long-term simulation results and field observations (Hosten and West, 1994) show that such an assumption cannot be generalized. Populations of *B. tectorum* are not immune to natural stresses.

Native perennial species are, in effect, more resilient to stresses than this annual grass. In most cases, what prevents native species from re-gaining dominance in invaded plant communities is the recurrence of disturbances such as fire.

## Acknowledgements

Funding for this study was obtained through a grant (US Department of defence SERDP Programme Project No. SI-1145) to Colorado State University.

## References

- Allen-Diaz, B., Bartolome, J.W., 1998. Sagebrush-grass vegetation dynamics: comparing classical and state-transition models. *Ecol. Appl.* 8, 795–804.
- Anderson, D.C., Ostler, W.K., 2002. Revegetation of degraded lands at US Department of Energy and US Department of Defense installations: strategies and successes. *Arid Land Res. Manage.* 16, 197–212.
- Ash, A., Walker, L., 1999. Environmental Management of Military Lands. Constructing decision support tools to evaluate management alternatives. LWRRDC Project CTC19. Final Report, CSIRO Tropical Agriculture, Aitkenvale, Queensland, Australia.
- Beatley, J.C., 1966. Ecological status of introduced brome grass (*Bromus* spp.) in desert vegetation of Southern Nevada. *Ecology* 47, 548–554.
- Booth, M.S., Caldwell, M.M., Stark, J.M., 2003a. Overlapping resource use in three Great Basin species: implications for community invisibility and vegetation dynamics. *J. Ecol.* 91, 36–48.
- Booth, M.S., Stark, J.M., Caldwell, M.M., 2003b. Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub steppe ecosystem. *Biogeochemistry* 66, 311–330.
- Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688.
- Childress, W.M., McLendon, T., 1999. Simulation of multi-scale environmental impacts using the EDYS model. *Hydrol. Sci. Technol.* 15, 257–269.
- Childress, W.M., McLendon, T., Price, D.L., 1999a. A multiscale ecological model for allocation of training activities on US Army installations. In: Klopatek, J.M., Gardner, R.H. (Eds.), *Landscape Ecological Analysis: Issues and Applications*. Springer, New York, pp. 80–108.
- Childress, W.M., Price, D.L., Coldren, C.L., McLendon, T., 1999b. A Functional Description of the Ecological Dynamics Simulation (EDYS) Model, with Applications for Army and Other Federal Land Managers. USACERL Technical Report 99, US Army Corps of Engineers Research Laboratory, Champaign, IL.
- Childress, W.M., Coldren, C.L., McLendon, T., 2002. Applying a complex, general ecosystem model (EDYS) in large scale land management. *Ecol. Model.* 153, 97–108.
- Corbin, J.D., D'Antonio, C.M., 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* 85, 1273–1283.
- Cox, R.D., Anderson, V.J., 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *J. Range Manage.* 57, 203–210.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88, 528–534.
- Freckleton, R.P., 2004. The problems of prediction and scale in applied ecology: the example of fire as a management tool. *J. Appl. Ecol.* 41, 599–603.
- Gayaldo, P.F., 1996. Native Shrub-Steppe Restoration at the Yakima Training Centre, Yakima, Washington. MS Thesis, University of Washington, Seattle, Washington.
- Hosten, P.E., West, N.E., 1994. Cheatgrass dynamics following wildfire on a sagebrush semidesert site in Central Utah. In: Monsen, S.B., Kitchen, S.G. (Eds.), *Proceeding—Ecology and Management of Annual Rangelands*, Gen. Tec. Rep. INT-313, USDA Forest Service, Ogden, UT, pp. 56–62.
- Hull Jr., A.C., 1949. Growth periods and herbage production of cheatgrass and reseeded grasses in southwestern Idaho. *J. Range Manage.* 2, 183–186.
- Hull, A.C., Pechanec, J.F., 1947. Cheatgrass—a challenge to range research. *J. Forest.* 45, 555–564.
- Humphrey, L.D., Schupp, E.W., 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *J. Arid Environ.* 58, 405–422.

- Klemmedson, J.O., Smith, J.G., 1964. Cheatgrass (*Bromus tectorum* L.). Bot. Rev. 30, 226–262.
- Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert. Global Environ. Change 6, 37–52.
- McLendon, T., Redente, E.F., 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. Ecology 72, 2016–2024.
- McLendon, T., Redente, E.F., 1992. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. Oecologia 91, 312–317.
- McLendon, T., Redente, E.F., 1994. Role of nitrogen availability in the transition from annual dominated to perennial dominated seral communities. In: Monsen, S.B., Kitchen, S.G. (Eds.), Proceeding-Ecology and Management of Annual Rangelands. Gen. Tec. Rep. INT-313. USDA Forest Service, Ogden, UT, pp. 352–362.
- Melgoza, G., Nowak, R.S., 1991. Competition between cheatgrass and two native species after fire: implications from observations and measurements of root distribution. J. Range Manage. 44, 27–33.
- Mensing, S., Livingston, S., Barker, P., 2006. Long-term fire history in Great Basin sagebrush reconstructed from macroscopic charcoal in spring sediments, Newark Valley, Nevada. West. N. Am. Nat. 66, 64–77.
- Milchunas, D.G., Schulz, K.A., Shaw, R.B., 2000. Plant community structure in relation to long-term disturbance by mechanized military maneuvers in a semiarid region. Environ. Manage. 25, 525–539.
- Miller, R.F., Svejcar, T.J., West, N.E., 1994. Implications of livestock grazing in the Intermountain Sagebrush Region: plant composition. In: Vavra, M., Laycock, W.A., Pieper, R.D. (Eds.), Ecological Implications of Livestock Herbivory in the West. Society for Range Management. Denver, Colorado, pp. 101–146.
- Naumburg, E., Mata-Gonzalez, R., Hunter, R.G., McLendon, T., Martin, D.W., 2005. Phreatophytic vegetation and groundwater fluctuations: a review of current research and application of ecosystem response modeling with an emphasis on Great Basin vegetation. Environ. Manage. 35, 726–740.
- Newbold, T.A.S., 2005. Desert horned lizard (*Phrynosoma platyrhinos*) locomotor performance: the influence of cheatgrass (*Bromus tectorum*). Southwest. Nat. 50, 17–23.
- Norton, J.B., Monaco, T.A., Norton, J.M., Johnson, D.A., Jones, T.A., 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. J. Arid Environ. 57, 445–466.
- Paschke, M.W., McLendon, T., Redente, E.F., 2000. Nitrogen availability and old-field succession in a shortgrass steppe. Ecosystems 3, 144–158.
- Pickford, G.D., 1932. The influence of continued heavy grazing and promiscuous burning on spring-fall ranges in Utah. Ecology 13, 159–171.
- Pienseis, R.L., 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. Ecology 32, 53–72.
- Price, D.L., McLendon, T., Coldren, C.L., 2004. Application of an ecological model for the Cibola Creek Watershed. Water Quality Technical Notes Collection. ERDC WQTN-CS-04. US Army Engineer Research and Development Center, Vicksburg, MS.
- Robertson, J.H., Eckert Jr., R.E., Bleak, A.T., 1966. Responses of grasses seeded in an *Artemisia tridentata* habitat in Nevada. Ecology 47, 187–194.
- Rykiel Jr., E.J., 1996. Testing ecological models: the meaning of validation. Ecol. Model. 90, 229–244.
- Smith, S.D., Monson, R.K., Anderson, J.E., 1997. Physiological Ecology of North American Desert Plants. Springer, Berlin, Germany.
- Soil Survey Staff, 1975. Soil Taxonomy. US Department of Agriculture Handbook No. 436, Soil Conservation Service, Washington, DC.
- Stewart, G., Hull, A.C., 1949. Cheatgrass (*Bromus tectorum* L.)—an ecologic intruder in southern Idaho. Ecology 30, 58–74.
- Tausch, R.J., Svejcar, T., Burkhardt, J.W., 1994. Patterns of annual grass dominance on Anaho Island: implications for Great Basin vegetation management. In: Monsen, S.B., Kitchen S.G. (Eds.), Proceeding—Ecology and Management of Annual Rangelands. Gen. Tec. Rep. INT-313, USDA Forest Service, Ogden, Utah, pp. 120–125.
- Tiedeman, J.A., Terwilliger Jr., C., 1978. Phyto-edaphic Classification of the Piceance Basin, Range Science Series No. 31. Colorado State University, Fort Collins, CO.
- Uresk, D.W., Cline, J.F., Rickard, W.H., 1979. Growth rates of a cheatgrass community and some associated factors. J. Range Manage. 32, 168–170.
- Whisenant, S.G., 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur, E.D., Romney, E.M., Smith, S.D., Tueller, P.T. (Eds.), Proceedings of a

Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management, Gen. Tech. Rep. INT-276, USDA Forest Service, Ogden, Utah, pp. 4–10.

Wright, H.A., Klemmedson, J.O., 1965. Effect of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. *Ecology* 46, 680–688.

Young, J.A., Evans, R.A., 1973. Downy brome—intruder in the plant succession of big sagebrush communities in the Great Basin. *J. Range Manage.* 26, 410–415.