

Modeling invasive weeds in grasslands: the role of allelopathy in *Acroptilon repens* invasion

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Abstract

We used an individual plant-based simulation model (ECOTONE) to evaluate the importance of allelopathy and soil texture to the invasion of semiarid grasslands by the non-native perennial C_3 forb *Acroptilon repens*. We also assessed the sensitivity of model results to the negative effects of allelochemicals on recruitment and growth of perennial grasses. ECOTONE simulates the recruitment, growth, and mortality of individual plants on a small plot (0.12 m²) through time at an annual time step. A daily time step, multi-layer model of soil water dynamics (SOILWAT) was incorporated into ECOTONE to represent competition for soil water on a finer temporal scale. The model was parameterized for a shortgrass community in eastern Colorado, USA, using data available from the literature. Experimental simulations examined the effects of four soil textures and a range of levels of plant sensitivity to allelochemicals on the aboveground biomass of *A. repens* and of native perennial grasses. Simulation results showed that *A. repens* dominated the aboveground biomass on a plot only if native species were affected by allelopathic interactions. At moderate levels of plant sensitivity, *A. repens* became dominant faster and reached a higher proportion of the total biomass on fine- than on coarse-textured soils. Community composition and rate of *A. repens* dominance were more affected by the sensitivity of plant growth to allelochemicals than the sensitivity of species recruitment. Allelopathic interactions were an important component of the invasion dynamics of this perennial invasive weed, and further field investigations are warranted. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Gap dynamics; Individual-based simulation model; Invasive perennial weed; Shortgrass steppe; Soil texture

1. Introduction

Introduced invasive weeds are a serious problem in grasslands globally (Baker, 1986). These

species can have adverse economic impacts by reducing crop yields or the quality of grazing lands and can have negative ecological impacts including reducing biodiversity, endangering rare communities and altering processes such as nutrient cycling (Vitousek, 1990; Young and Longland, 1996; Higgins et al., 1999; Stohlgren et al., 1999). At least 57 000 km² of public rangelands in

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the western United States have been invaded by noxious weeds. The total geographic range of these species has quadrupled from 1985 to 1995 (Westbrooks, 1998). Introduced perennial species are particularly important, as they have the capability to dominate native vegetation for extended periods of time.

There are a number of factors that influence invasion dynamics, including life history traits of native and exotic species, and physical characteristics of the site, such as soil texture and climate. We have a limited understanding of the relative importance of these different processes and environmental conditions on invasion dynamics. Most studies of invasive perennials have focused exclusively on management methods and have met with limited success (Donald, 1990; Fay, 1991; Rosenthal et al., 1991; Benz et al., 1999). A broader understanding of the ecological processes underlying the invasion and spread of exotic perennial weeds can contribute to our understanding of plant ecology as well as improve our ability to control and eliminate weed infestations (Cousens and Mortimer, 1995; Sheley et al., 1996, 1999).

An ecological approach that integrates process-based research with ecological simulation models provides a powerful alternative to traditional weed management research (Higgins and Richardson, 1996). Such an approach has several advantages, (1) it can be used to identify the importance of different processes as well as their interactions; (2) it can provide a predictive tool; and (3) it can assess the sensitivity of invasion dynamics to changes in ecological processes caused by global climate change or by alterations in local disturbance patterns. This type of comprehensive ecologically-based approach has been used successfully to assess the importance of disturbances in structuring shortgrass steppe communities (Coffin and Lauenroth, 1990; Coffin et al., 1998), and has great potential to improve our understanding of weed invasions. Our goal was to assess the relative importance of different ecological processes and their interactions with soil texture on the invasion dynamics of one invasive perennial weed in the shortgrass steppe community of eastern Colorado.

Invasion by knapweed species has caused particularly severe problems in North American grasslands. At least 15 species of knapweed have been introduced to the western US and Canada, primarily from Eurasia (Whitson et al., 1996). Four have become serious problems in western grasslands, *Centaurea solstitialis* L., *Centaurea diffusa* Lam., *Centaurea maculosa* Lam., and *Acroptilon repens* (L.) DC. These species reduce forage quality, increase soil erosion and reduce wildlife populations (Roché and Roché, 1988). Within the western US and Canada, *C. solstitialis* covers about 38 000 km², *C. diffusa* about 13 000 km², *C. maculosa* about 29 000 km², and *A. repens* about 6000 km² (Howery and Ruyle, 1997). Although it covers the least total area, *A. repens*, which has the longest lifespan (> 75 year), is the most likely to form dense monocultures with associated large losses of native biodiversity (Watson and Renney, 1974; Roché and Roché, 1988). We chose to focus our analyses on the invasion dynamics of this species.

The aggressive vegetative spread and potential for dominance of *A. repens* have been attributed to effects of water-soluble allelochemicals produced in its roots and leaves (Stevens, 1986; Stevens and Merrill, 1985; Kelsey and Bedunah, 1989). Other exotic perennial species are known to release allelochemicals into the soil (Baker, 1986; Wardle et al., 1998), with negative impacts on the growth and recruitment of surrounding species that can lead to loss of biomass and reduction in abundance of perennial grasses through time (Fletcher and Renney, 1963; Beck and Hanson, 1989; Whitson, 1999). Although allelopathic effects have been demonstrated frequently in the laboratory, it is difficult to assess the importance of those effects in the field because of confounding ecological processes, particularly resource competition (Wardle et al., 1998).

In Colorado, *A. repens* does not always form dense monocultures; instead, a mixture of *A. repens* and native grasses can persist for many years. Dominance of *A. repens* appears to be related to soil texture: it tends to dominate on fine-textured soils, while on coarser soils, it forms a persistent mixture with other species (K.G. Beck, unpublished observations). Soil texture may

be an important determinant of allelopathic interactions (Rice, 1984). In semi-arid environments, such as Colorado grasslands, sites with fine-textured soils typically have higher evaporation rates near the surface and lower infiltration rates than sites with coarse-textured soils (Noy-Meir, 1973). High evaporation would concentrate allelochemicals in the soil, and low infiltration would prevent allelochemicals from leaching out of the rooting zone of the dominant perennial grasses on sites with fine soils. Other allelopathic species of semi-arid environments have been found to be more toxic on fine than on coarse soils (del Moral and Muller, 1970; Inderjit and Dakshini, 1994). Thus, we hypothesized that the observed relationship between *A. repens* dominance and soil texture is due to allelopathy. Furthermore, we predict that allelopathic effects lead to a greater reduction in growth and recruitment of native species on fine- than on coarse-textured soils.

Our specific objectives were to investigate, (1) the effect of allelopathy on the biomass and time to dominance of *A. repens* in a perennial grass-dominated community; (2) the relationship between soil texture and allelopathic effects at the community level; and (3) the relative importance of the negative effects of allelochemicals on recruitment versus growth of perennial grasses for the invasion dynamics of *A. repens*. Our approach was to use an individual-based simulation model to control the levels of plant sensitivity to allelochemical concentration for both growth and recruitment, and to examine the effects of varying levels of plant sensitivity on community dynamics for sites with different soil textures.

2. Methods

2.1. Site description

Our model was parameterized for the Central Plains Experimental Range (CPER) in northeastern Colorado, USA (40°49'N, 107°47'W, 1660 m ASL). The CPER is administered by the United States Department of Agriculture — Agricultural Research Service, and is a Long-Term Ecological Research Site funded by the National Science

Foundation. Long-term (52 year) annual precipitation is 321 mm (S.D. = 98 mm) and mean monthly temperatures range from -5°C in January to 22°C in July (Lauenroth and Milchunas, 1991; Lauenroth and Sala, 1992). The shortgrass vegetation is dominated by perennial C_4 grasses, particularly *Bouteloua gracilis*, but other C_3 and C_4 annual and perennial grasses and forbs, dwarf shrubs and succulents are common (Lauenroth and Milchunas, 1991). Introduced species make up about 15% of the CPER flora (Kotanen et al., 1998). The topography is relatively flat, with gentle slopes between upland and lowland areas. The CPER contains soils of a wide range of textures, from fine clay and clay loam to coarse sandy loam (Yonker et al., 1988).

2.2. Characteristics of *A. repens*

A. repens was introduced to the western US in contaminated alfalfa seed during the early 1900s (Rogers, 1928; Watson, 1980). It has since become widely distributed and is a problem weed throughout the region (Maddox et al., 1985). As well as suppressing the growth of crop species, *A. repens* is unpalatable as forage and poisonous to horses (Watson, 1980; Roché and Roché, 1991). This species does not colonize new sites efficiently because of low production of viable seed and poor dispersal mechanisms (Selleck, 1964; Watson, 1980; Roché and Roché, 1988).

Once it becomes established, *A. repens* is highly competitive and spreads aggressively from horizontal buds on the root system (Frazier, 1944; Watson, 1980). Under favorable conditions, seedlings can spread 2.0 m radially and 1.2 m vertically during the first growing season (28 week), and at least 3.7 m radially and 3.2 m vertically after 72 week (the end of the second growing season; Frazier, 1944). It can form dense patches with 100–300 shoots per m^2 (Watson, 1980). This species is highly persistent, with infestations known to have lasted > 75 year (Watson, 1980).

Both roots and leaves of *A. repens* have been found to produce chemicals inhibitory to the germination and growth of other species (Kelsey and Bedunah, 1989). A polyacetylene extracted from

A. repens roots was shown to inhibit root growth in several test species (*Lactuca sativa*, *Medicago sativa*, *Echinochloa crus-galli* and *Panicum miliaceum*) by 30% at concentrations comparable to those found in the soil surrounding *A. repens* plants (Stevens, 1986). Grant, 2000 found that *A. repens* roots inhibited both germination and growth in several perennial grasses. Soil from *A. repens*-infested sites reduced both shoot height and total biomass of *Lycopersicon esculentum* and *Hordeum vulgare*. Fletcher and Renney (1963) found leaf extracts to be more inhibitory than extracts of other plant parts. Aqueous extracts of *A. repens* leaves inhibited germination of *Agropyron smithii* and *Bromus marginatus* at high levels, although lower concentrations stimulated germination (Beck and Hanson, 1989). *Agropyron smithii* germination was suppressed but not eliminated by aqueous extracts of *A. repens*, while *Bromus inermis* germination was not affected (Whitson, 1999).

2.3. Simulation model description

We used an individual-based gap dynamics model (ECOTONE) to evaluate the importance of allelopathy to the invasion success of *A. repens*. ECOTONE was developed for arid and semiarid grasslands and shrublands and is described in Peters and Herrick (2001). Modifications for simulating allelopathy are described here. ECOTONE was based on STEPPE, a model used extensively to simulate shortgrass steppe commu-

nities of eastern Colorado (Coffin and Lauenroth, 1990, 1994). Similar to gap dynamics models of forests (JABOWA, Botkin et al., 1972; FORET, Shugart, 1984), ECOTONE simulates recruitment, growth, and mortality of each plant on a small plot at an annual timestep (Fig. 1).

Recruitment and mortality both have stochastic elements. The probability of recruitment for each species is determined by the availability of its seeds relative to those of other species (Coffin and Lauenroth, 1994). Mortality for each plant depends upon species-specific longevity (e.g. annuals can only live 1 year). For perennial species, slow growth constraints also determine mortality, production insufficient new biomass to support maintenance or growth results in a higher probability of plant mortality (Shugart, 1984). Disturbances were not included in the current set of simulations because we lack sufficient knowledge of the effects of disturbance on *A. repens* growth and allelopathic effects.

Plant growth is a deterministic process based on competition for resources. Because light and nitrogen are important less frequently than soil water in semiarid grasslands (Noy-Meir, 1973; Lauenroth et al., 1978), we only simulated competition for soil water. The amount of water available to each plant at each depth within the soil profile is determined by the proportion of total root biomass at that depth during the time of year when its roots were actively growing. Active root growth is calculated based on temperature response for different physiologies (C_3 or C_4). Biomass increment for each plant in each year is calculated using the species-specific water-use efficiency (g biomass/g water) and the total amount of water available to the plant across all soil layers and days in the year.

Plant available soil water is simulated by incorporating a daily time step, multi-layer soil water model into ECOTONE (Fig. 1; SOILWAT, Parton, 1978; Sala et al., 1992). Simulated daily information on soil water processes, including losses to interception, evaporation, and transpiration, and soil water content by depth, is used to calculate annual soil water availability in each soil layer. Weather conditions are simulated using a first-order Markov model, which generates daily weather

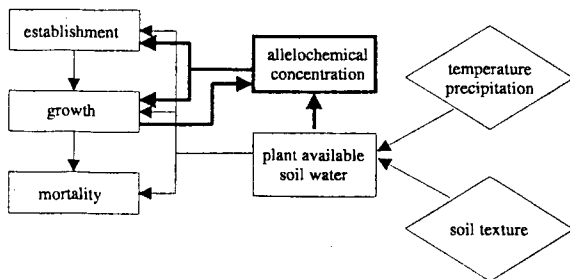


Fig. 1. ECOTONE model diagram showing the linkages between the soil water module, allelopathy, and the plant recruitment, growth and mortality components. Linkages new to this version of the model are shown in bold.

with characteristics similar to historical weather at the CPER (Lauenroth et al., 1994).

2.4. Simulation of allelopathy

Allelopathy is incorporated as effects on growth and recruitment in ECOTONE (Fig. 1). Allelochemical exudation was assumed to be a constant fraction of the total *A. repens* live biomass on an individual plot in each year. Total live biomass is used because both roots and leaves of *A. repens* have been found to produce allelochemicals (Kelsey and Bedunah, 1989; Stevens, 1986, 1991). Although litter may be another source of allelochemicals, we assumed it was negligible compared with live biomass. We also assumed that annual precipitation was the major environmental determinant of allelochemical concentration on a plot.

$$\frac{\text{concentration}}{\text{plot}} = \left(\frac{A. \text{repens biomass/plot} \times \text{allelochemical production/plot}}{\text{annual precipitation} - \text{annual evaporation/plot}} \right) \quad (1)$$

where *A. repens* biomass is the total live above- and below-ground biomass on a plot for that year, allelochemical production is a constant describing the quantity of allelochemicals produced per unit biomass, annual precipitation is the total amount of precipitation received in that year, and annual evaporation is simulated by ECOTONE and summed over all soil layers for a plot. Allelochemical concentration was assumed to be constant throughout the soil profile in a particular year. While no time-decay is explicitly included, allelochemicals are not carried over from year-to-year. Allelochemical concentration is multiplied by the annual growth of each plant and weighted by a constant related to the sensitivity of that species to allelochemicals:

$$\text{growth}_{\text{allel}} = \text{growth}_{\text{resource}}(1 - g)^{\text{concentration}} \quad (2)$$

where $\text{growth}_{\text{allel}}$ is the final growth increment once negative allelopathic interactions have been included, $\text{growth}_{\text{resource}}$ is the biomass increment

calculated by ECOTONE based on water availability, and g is a species-specific growth sensitivity parameter describing the negative effect of allelochemicals on plant growth. The probability of recruitment by a species was modified using a similar equation, but based on a species-specific recruitment sensitivity parameter r and the recruitment probability calculated based on plant success in that year:

$$\text{recruitment}_{\text{allel}} = \text{recruitment}_{\text{resource}}(1 - r)^{\text{concentration}} \quad (3)$$

This functional form results in a percentage reduction in growth or recruitment per unit of allelochemical concentration that is proportional to the value of the sensitivity parameter (Fig. 2). At low levels, even species with high sensitivities are little affected, while at high concentrations, even species that are not very sensitive have reduced growth or recruitment. This form of relationship is commonly seen in laboratory studies of allelopathy (e.g. Einhellig, 1999; Oleszek et al., 1999). A similar curve was found for the effect of an *A. repens* polyacetylene on root growth of *L. sativa* (Stevens, 1991).

2.5. Model parameterization

Fifteen species were simulated; this set represents the range of life history traits of the > 300 species found in shortgrass steppe communities (Table 1). Species parameters were derived from published modeling experiments whenever possible (Coffin and Lauenroth, 1990; Peters and Herrick, 2001). Not all parameters are shown; only those most important to this study. Recruitment is determined by two parameters, SDECOF and VEGGROW. The first, SDECOF, determines the relative seed availability for that species, and the second specifies the probability of growth from rhizomes (e.g. *C. heliophila*) or tap roots (*Sphaeralcea coccinea*). AGEMAX is the maximum lifespan in years and is used to calculate mortality. Photosynthetic pathway determines the values for temperature response used in calculating active root growth, minimum growth rate, which sets the slow growth constraints, and water use

Table 1
Species parameters used in ECOTONE (Peters and Herrick, 2001)

Native species	Probability of seedling establishment SDECOF	Clonal growth CLONTYP	Probability of vegetative regrowth VEGGROW	Lifespan (per year) AGEMAX	Photosynthetic pathway ^a	Maximum growth rate GRORAT ^a	Maximum biomass (g per plant) FULBIO ^a	Depth of maximum root biomass (cm) ³ RTDEPTH ^c
<i>Perennial graminoids</i>								
<i>Bouteloua gracilis</i>	0.090	Present	0.0	NA ^d	C ₄	0.474	36.3	15
<i>Aristida purpurea</i> var. <i>longiseta</i>	0.105	Absent	0.0	25	C ₄	0.474	9.2	30
<i>Carex heliophila</i>	0.090	Present	0.5	25	C ₃	0.474	7.2	30
<i>Sitanion hystrix</i>	0.125	Absent	0.0	10	C ₃	0.474	9.2	20
<i>Schedonardus paniculatus</i>	0.030	Absent	0.0	10	C ₄	0.474	9.2	20
<i>Perennial forbs</i>								
<i>Sphaeralcea coccinea</i>	0.030	Present	0.5	35	C ₃	0.474	5.1	30
<i>Picrodendropsis oppositifolia</i>	0.010	Absent	0.0	35	C ₄	0.474	2.1	20
<i>Machaeranthera tanacetifolia</i>	0.065	Absent	0.0	10	C ₄	0.737	1.3	20
<i>Gaura coccinea</i>	0.030	Absent	0.0	10	C ₃	0.737	1.3	20
<i>Shrubs</i>								
<i>Chrysothamnus nauseosus</i>	0.010	Absent	0.0	35	C ₃	0.474	59.2	40
<i>Gutierrezia sarothrae</i>	0.010	Absent	0.0	10	C ₃	0.737	6.4	25
<i>Annual grasses and forbs</i>								
<i>Vulpia octoflora</i>		Absent	0.0	1	C ₃	0.947	1.3	15
<i>Chenopodium album</i>		Absent	0.0	1	C ₄	0.947	1.3	15
<i>Lepidium densiflorum</i>		Absent	0.0	1	C ₃	0.947	1.3	15

Table 1 (Continued)

	Probability of seedling establishment SDECOF	Clonal growth CLONTYP	Probability of vegetative regrowth VEGGROW	Lifespan (per year) AGEMAX	Photosynthetic pathway ^a	Maximum growth rate GRORAT ^a	Maximum biomass (g per plant) FULBIO ^a	Depth of maximum root biomass (cm) ^b RTDEPTH ^c
<i>Non-native species</i>								
<i>Perennial forb</i>								
<i>Acroptilon repens</i>		Present ^b	0.8 ^b	NA ^{b,d}	C ₃ ^b	0.474	12.0 ^b	30

^a These parameters are from Coffin and Lauenroth (1990) for native species.

^b Values for *A. repens* are from Watson (1980). Unavailable parameter values were based on those for *S. coccinea*.

^c Root distributions are from Sun et al. (1997).

^d NA, indeterminate lifespan.

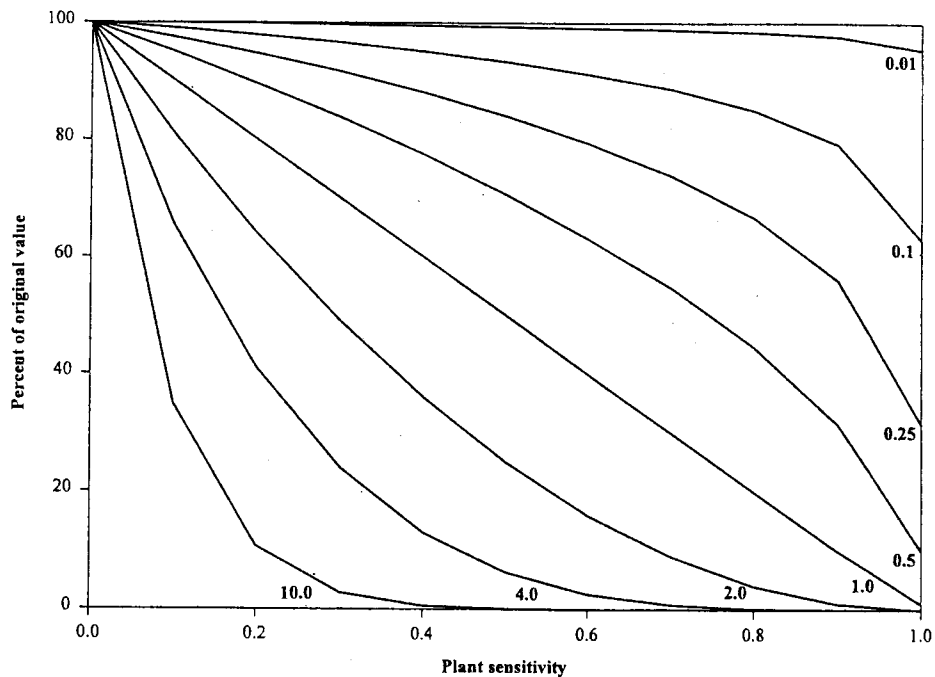


Fig. 2. Theoretical curves showing the reduction in growth or recruitment due to particular combinations of allelochemical concentration and plant sensitivity. Each line represents the indicated allelochemical concentration (in arbitrary units).

efficiency, used to calculate biomass increment (Larcher, 1995). Maximum relative growth rate (GRORAT) and maximum biomass (FULBIO) determine the upper bounds of the annual biomass increment.

Root biomass distributions by depth for each species were required in order to initialize seedling biomass and simulate growth response to soil water availability; these parameters were obtained using similar species from Sun et al. (1997). Root distribution is described by two parameters, the depth at which maximum root biomass occurs and the maximum depth at which roots were found. For these simulations, the depth of maximum biomass was species-specific (RTDEPTH), while the maximum rooting depth for all species was assumed to be 100 cm, the deepest layer in the soil profile.

Parameter values for *A. repens* were derived from the literature whenever possible; other estimates were derived from the values for similar perennial forbs (Table 1). Major differences between *A. repens* and native perennial forbs (e.g.

S. coccinea) include lifespan, maximum biomass and probability of vegetative spread. *A. repens* was assumed to have no autotoxic effects, since little is known about this aspect of *A. repens* allelopathy.

Driving variables include climate and soil characteristics. Climate parameters were derived from historical weather data from the CPER over the past 45 years. Daily values for precipitation and minimum and maximum temperature were used to calculate the probability of precipitation and the temperature covariance of temperature; these values were then used in a first-order Markov model to generate long sequences of daily weather with characteristics similar to that observed at the CPER (Parton, 1978; Lauenroth et al., 1994). The other climate parameters used were monthly values for cloud cover, windspeed and relative humidity. Soil layer structure was adapted from Lane (1995; 5–10 cm, 5–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–60 cm, 60–80 cm, 80–100 cm).

2.6. Simulation experiments

We used ECOTONE to simulate *A. repens* invasion at the CPER on single plots of one of four soil textures (USDA, 1993), clay (58% clay, 22% sand), clay loam (34% clay, 32% sand), loam (18% clay, 43% sand) and loamy sand (6% clay, 82% sand). Soil texture was assumed to be constant through the soil profile. For the first experiment, growth sensitivity was equal to recruitment sensitivity for all species (this value was termed 'plant sensitivity' for convenience), and spanned the range of allowable values (0–0.9 by 0.1 intervals). Because the actual sensitivity of each species to the allelochemicals is unknown, we simulated a range of sensitivities and assumed that all species had the same response during a particular run. Thus, a total of 40 different simulations were conducted (four soil textures \times ten plant sensitivities). Each simulation was conducted on 25 independent plots, and the results averaged across plots (within years) since this is a stochastic model (Shugart, 1984). This experiment allowed us to examine both the importance of allelopathic effects to *A. repens* biomass and time to dominance as well as the interaction between soil texture and allelopathic effects.

For the second simulation experiment, growth and recruitment sensitivities were varied individually over the allowable range, for a total of 400 simulations (four soil textures \times ten growth sensitivities \times ten recruitment sensitivities). Each simulation was again repeated for 25 independent plots. This experiment separated the effects of allelopathic impacts on growth and recruitment so we could assess the importance of each demographic process to the success of *A. repens*.

For clarity of presentation, we combined model output into five functional groups as indicated in Table 1, four groups of native species and *A. repens*. Since perennial grasses are the dominant species in the shortgrass steppe, *A. repens* biomass was compared with perennial grass biomass as an index of invasion success. We chose two values to efficiently summarize the model output. The first was the biomass of *A. repens* or perennial grasses as a percentage of the total biomass during the last 50 years of the simulation, which represents

the time at which the average of the 25 initially bare plots has reached a pseudo-equilibrium (sensu Shugart, 1984). The second value was the time at which *A. repens* reached a higher total aboveground biomass than perennial grasses (time of *A. repens* dominance).

3. Results

3.1. Model verification

ECOTONE was verified for native shortgrass steppe communities by conducting simulations without allelopathic effects. On these simulated plots, *B. gracilis* was the most abundant species, with total aboveground biomass from 123 g/m² on clay soils to 172 g/m² on loam soils. These results are consistent with data from the CPER, where biomass in grass-dominated areas is 150–200 g/m², and coarse soils support the greatest biomass (Lauenroth and Milchunas, 1991). Perennial grass biomass on the CPER ranges from 72 g/m² on clay loam soils to 150 g/m² on sandy loam soils (Liang et al., 1989), which corresponds well to the simulated perennial grass biomass of 92–172 g/m². Species in other functional groups made up a minor 12 component of the simulated vegetation, similar to field data.

ECOTONE was also verified for *A. repens*-dominated communities. While no long-term data on *A. repens* invasions are available, short-term sampling at two sites in Colorado found that this species made up 63% of the total cover within stands on clay loam soils (K.G. Beck, unpub. data). This is comparable to our simulation results with low levels of plant sensitivity on clay loam soils, where *A. repens* made up 54% of the aboveground biomass. Simulations without allelopathic effects had only 11% *A. repens* biomass, much lower than observed values.

3.2. Allelopathic simulations

Dominance of perennial grasses was a function of soil texture when plant sensitivity to allelochemicals was low (<0.2 ; Fig. 3). Perennial grasses dominated aboveground biomass on all

soils simulated for the first 30 year. Perennial grasses maintained dominance throughout the 250-year simulation on coarse-textured soils (Fig. 3c and d). On the finest-textured soil, *A. repens* rapidly increased to dominate aboveground biomass within 30 year (Fig. 3a). Perennial grasses and *A. repens* were codominant on plots with clay loam soils beginning 90 year after the start of the simulation (Fig. 3b). In each case, the perennial grass functional group was primarily composed of *B. gracilis* (>70% of the perennial grass biomass). Annuals, shrubs and perennial forbs other than *A. repens* made up less than 10% of the total biomass. Because of the very low proportion of these species groups, they will not be considered further. The results in Fig. 3 illustrate the time course of the model output; only the two summary statistics will be presented for the remaining simulations.

The percentage biomass of perennial grasses averaged over the last 50 year of each simulation decreased with increasing plant sensitivity to alle-

lochemical concentration (Fig. 4a), while the percentage of *A. repens* biomass increased (Fig. 4b). Finer-textured soils (clay and clay loam) had lower proportions of perennial grasses and more *A. repens* than coarser soils, particularly at moderate levels of plant sensitivity (0.1–0.3). The greatest range of responses among soils was found at a plant sensitivity of 0.2. At high plant sensitivities (>0.6), invasion success was no longer related to soil texture since no perennial grass biomass was found on any plot.

The length of time needed for *A. repens* to become the dominant species was strongly related to the sensitivity to allelochemicals of the native vegetation (Fig. 5). If allelochemical effects were not included in a simulation (i.e. plant sensitivity = 0), biomass remained dominated by perennial grasses throughout the 250-year simulations. At low to moderate levels of sensitivity (0.1–0.3), *A. repens* became dominant over perennial grasses (had a greater aboveground biomass) only on plots with fine-textured soils. *A. repens* dominated

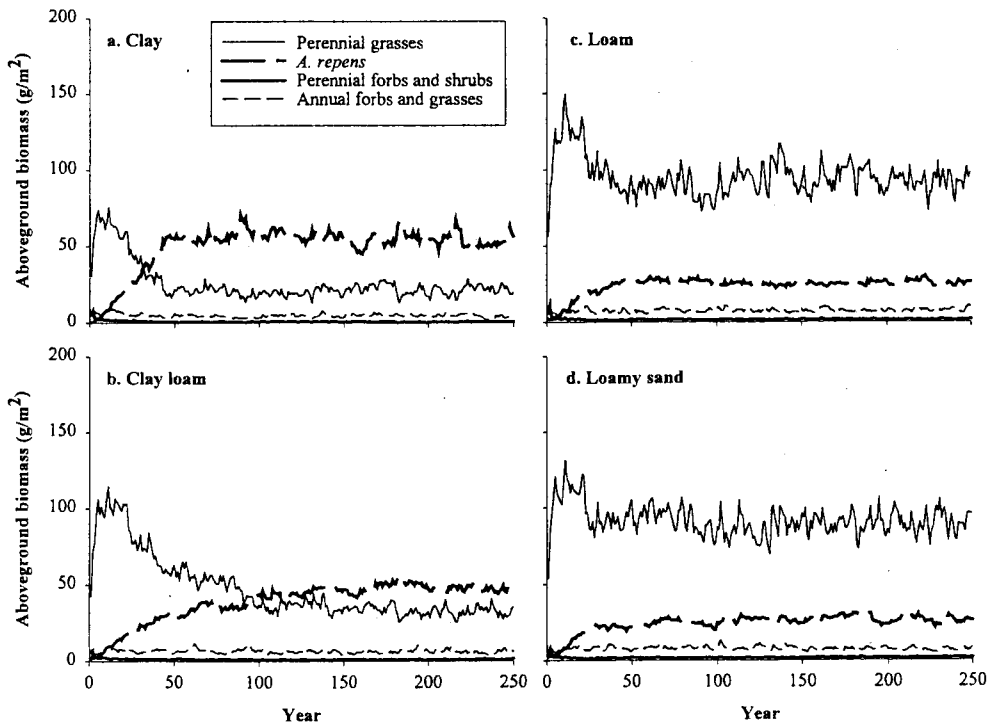


Fig. 3. Mean aboveground biomass by functional group for four soil textures with a plant sensitivity to allelochemicals of 0.2.

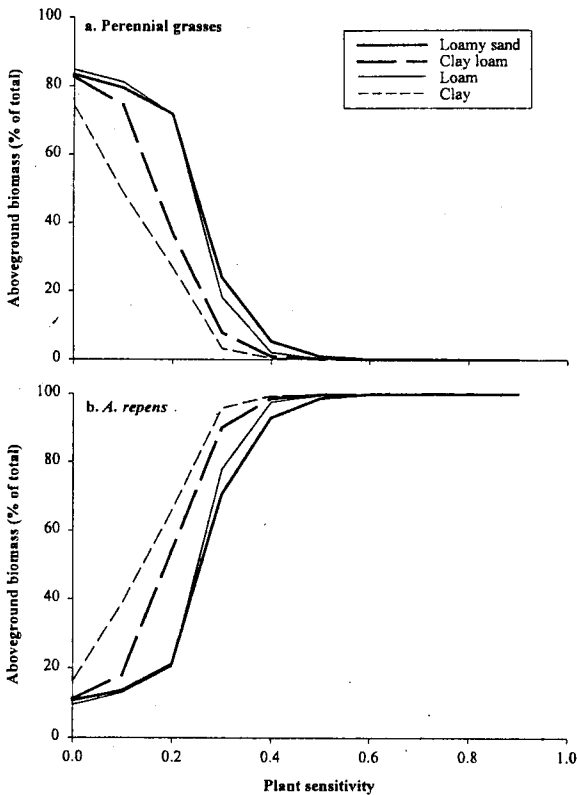


Fig. 4. Mean percentage aboveground biomass of (a) perennial grasses and (b) *A. repens* from the last 50 years of simulations varying soil texture and plant sensitivities to allelochemicals.

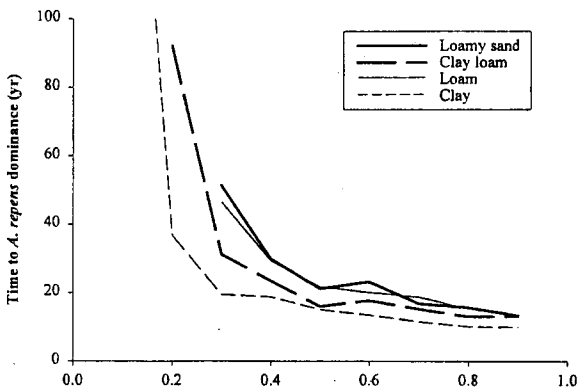


Fig. 5. Time to *A. repens* dominance from simulations using different soil textures and plant sensitivities to allelochemicals.

the aboveground biomass on all soil textures when plant sensitivities were moderate (0.3–0.6), but dominance occurred most rapidly on fine-text-

tured soils. The time to dominance was unrelated to soil texture at very high sensitivities (> 0.6); *A. repens* became the dominant species within 25 year on all plots.

When varied individually, growth and recruitment sensitivities to allelochemicals affected the percentage of perennial grass biomass in different ways (Fig. 6). Only the results for loam soils are presented here; results for the other three soil textures followed similar patterns. Changes in the growth sensitivity parameter (g) had the largest effect on proportion of perennial grasses. When $g = 0$, the proportion of aboveground biomass comprised of perennial grasses changed from 85 to 57% along the range of the recruitment sensitivity parameter (r) from 0 to 1. When $r = 0$, the change in percentage of perennial grass biomass was much greater (from 40 to 85%) along the range of possible values for g . Likewise, complete exclusion of perennial grasses was reached at lower values of g (0.2) than of r (0.5).

The length of time required for *A. repens* to reach dominance was more closely related to growth than to recruitment sensitivity (Fig. 7).

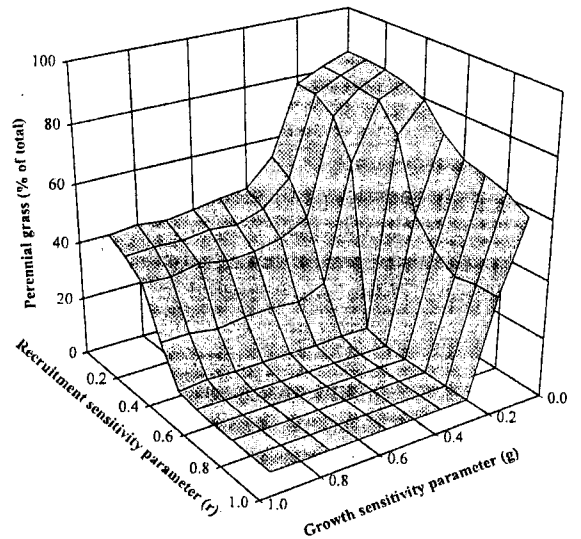


Fig. 6. Mean percentage aboveground biomass of perennial grasses from the last 50 years of simulations using loam soils and a range of both growth and recruitment sensitivities to allelochemicals.

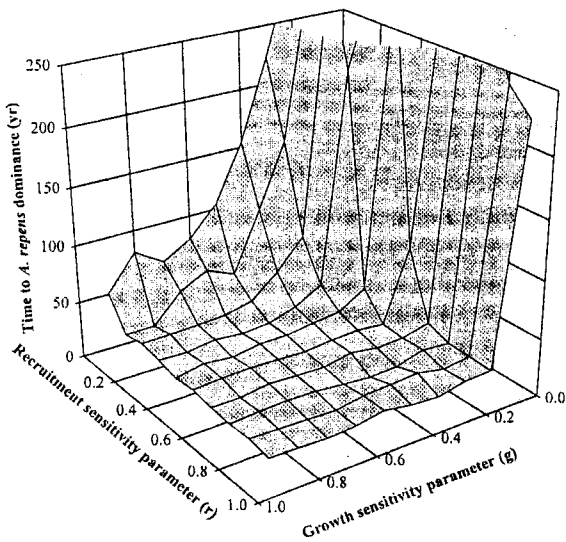


Fig. 7. Time to *A. repens* dominance from simulations using loam soils and a range of both growth and recruitment sensitivities to allelochemicals.

When $g = 0$, *A. repens* did not become dominant even after 250 years when levels of r were low to moderate (< 0.8), and even when $r = 0.9$, the time to dominance was 221 year. However, when $r = 0$, *A. repens* dominated even at moderate values of g (> 0.3), and when $g = 0.9$, *A. repens* became the dominant species after only 51 year.

4. Discussion

The incorporation of allelopathy into ECOTONE produced complex results despite the simplicity of this component of the model formulation. While we expected that *A. repens* would be more successful when other species were sensitive to allelochemicals, the form of the relationship (Fig. 4) was not predictable from the model formulation (Fig. 2). The plant response curves are very different shapes than the theoretical curves. In addition, the same allelopathy parameters were used for all soil types, so that the differences between soil textures are not an artifact of the model parameterization.

Previous studies have shown that *A. repens* reduces growth and reproduction of other species

under greenhouse conditions and in field experiments, but little effort has been made to demonstrate the importance of allelopathy to the success of this species in multispecies communities (Selleck, 1964; Watson, 1980; Kelsey and Bedunah, 1989; Grant, 2000). Simulation results most closely matched observed community composition when plant sensitivity was low (0.2), and were very different from field results when allelopathic effects were not included. This sensitivity value is similar to the 30% reduction in growth and recruitment seen in greenhouse and field studies of *A. repens* allelopathy (Stevens, 1986; Grant, 2000).

The faster dominance and higher proportion of total biomass by *A. repens* on fine- compared with coarse-textured soils in our simulations agrees with field observations (K.G. Beck, unpublished data). Pure stands of *A. repens* are more prevalent on fine-textured soils throughout Colorado, while mixed stands of *A. repens* and perennial grasses are more often observed on coarse-textured soils. Further support comes from a study showing a decline in *A. repens* density at irrigated sites over a 7-year period (Selleck, 1964). This decline appeared to be caused by increased competition from perennial grasses due to a reduction in allelochemical concentration caused by dilution or leaching. This relationship between soil texture and the importance of allelopathic interactions has been observed in other species of semi-arid regions (del Moral and Muller, 1970; Inderjit and Dakshini, 1994). Additional confirmation comes from a laboratory comparison of the retention of *Medicago sativa* toxins in a fine sandy loam and a silty clay loam, which demonstrated that allelopathic chemicals moved through the coarse soil faster, and required less water for complete leaching (Jennings and Nelson, 1998).

Allelochemicals have been observed to affect both growth and recruitment of sensitive species under laboratory conditions, but it is difficult to separate these effects in the field (Rice, 1984; Whitson, 1999). Even though growth and recruitment effects were coded identically in the model and a similar range of sensitivity parameters was used, simulation results showed that the effect of allelochemicals on growth was more important

than effects on recruitment to community composition and invasion dynamics. Growth sensitivity may have had such a large effect on community properties because it also affects plant mortality, a plant that grows too slowly for several years is subject to high mortality rates. Recruitment sensitivity affects only the establishment probability for each species and does not cause this type of feedback within the model.

Our results show the utility of using an individual-based simulation model to elucidate the mechanisms underlying patterns observed in the field, thereby generating hypotheses for further experimental testing. The use of modeling as an approach for studying allelopathy is particularly helpful, since allelopathy is only one of many stresses on plants, and may be indistinguishable from resource competition under field conditions (Inderjit and del Moral, 1997; Einhellig, 1999). Simulation modeling allowed us to investigate the important processes individually, something that would be impossible in the field.

New laboratory and field studies can be designed to complement these simulation results. Using simulation results to guide further experimentation has proven to be effective in increasing our understanding of grassland ecology (e.g. Coffin and Lauenroth, 1990, 1994). Simulation modeling is particularly effective at revealing which processes and parameters are not well-understood. Knowledge is lacking in two important areas for the understanding of *A. repens* allelopathy. Variation in the sensitivity of most native species to allelochemicals is not well-known (Grant, 2000), and little is known about potential autotoxic effects of *A. repens* on itself, since it appears that this species may inhibit its own growth in the field (K.G. Beck, unpublished data).

The results of these simulation experiments can be used to prioritize management efforts for *A. repens* in the shortgrass steppe of Colorado. Since allelopathic effects were shown to be important for the success of this species, management efforts should be directed towards sites that contain species sensitive to *A. repens* allelo-

chemicals. Communities composed of relatively insensitive species should have lower management priorities. Similarly, management of *A. repens* should be targeted towards sites with fine-textured soils, since *A. repens* had the fastest invasion rate and most complete dominance on these sites.

5. Conclusions

Our ecologically-based simulation approach allowed us to examine the complex interactions between soil texture, allelopathic effects on growth and recruitment, and invasion success of *A. repens*. Model results from simulations incorporating moderate levels of allelopathy (plant sensitivity of approximately 0.2) were most similar to observed community compositions in the shortgrass steppe community of Colorado. Allelopathic interactions contribute to the invasion success of *A. repens*, and can help explain the distribution of *A. repens* with respect to soil texture that has been seen in the field. Allelopathy has a greater impact on fine- than coarse-textured soils, leading to faster invasion rates and more complete *A. repens* dominance on these sites. The correspondence between simulated and observed patterns demonstrates that simulation modeling is an effective tool for synthesis of our understanding of the ecology of this species and potentially other invasive perennial weeds; moreover, it allows us to formulate ecologically-based management plans. Gap models have been successfully used in other ecosystems, especially forests. Our results show that this modeling approach is also useful in studying invasive species.

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