

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 C₃ 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

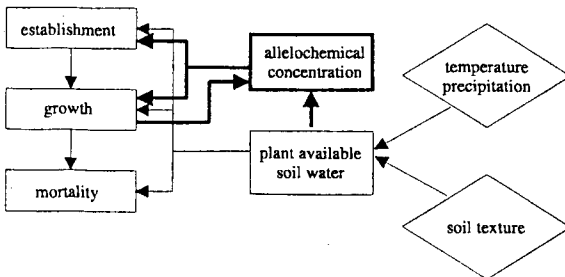


Fig. 1. ECOTONE model diagram showing the linkages between the soil water module, allelopathy, and the plant recruitment, growth and mortality components. Linkages new to this version of the model are shown in bold.

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)

	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>Native species</i>								
<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.

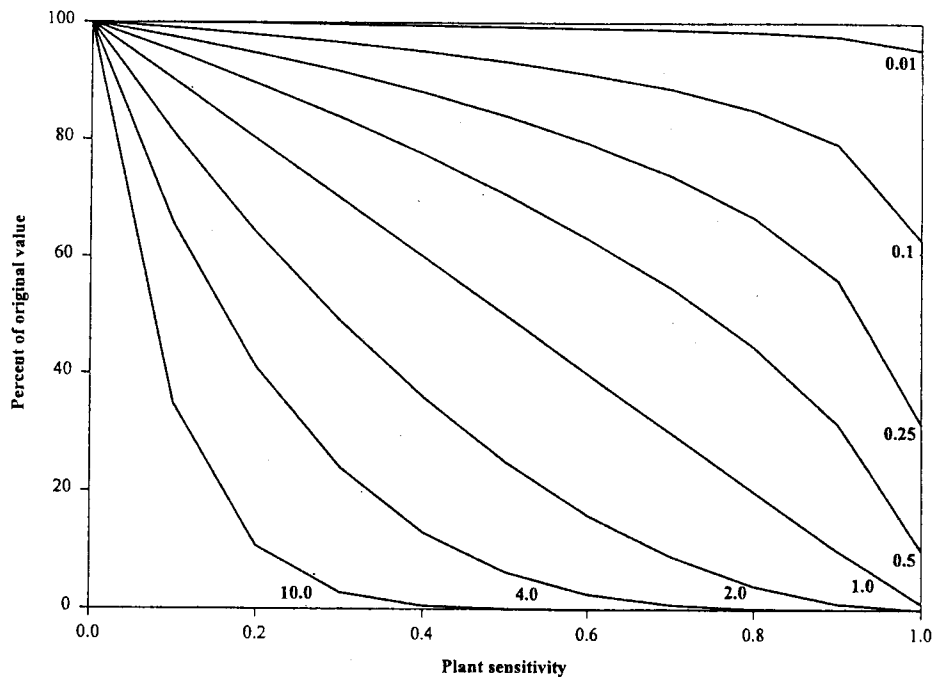


Fig. 2. Theoretical curves showing the reduction in growth or recruitment due to particular combinations of allelochemical concentration and plant sensitivity. Each line represents the indicated allelochemical concentration (in arbitrary units).

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).

