

Ecosystem Impacts of Exotic Plants Can Feed Back to Increase Invasion in Western US Rangelands

By Valerie T. Eviner, Sarah A. Hoskinson, and Christine V. Hawkes

nvasive, nonnative plant species have become one of the most pressing rangeland management issues. In the western United States (the 17 US states from North Dakota, south to Texas, and west to the Pacific coast), 51 million hectares of rangeland are now dominated by invasive plants considered to be noxious weeds.¹ In over two-thirds of western rangelands, nonnative annual grasses account for 50-85% of vascular plant cover.² Invasive plants have large negative impacts on the prevalence and diversity of native species, and many decrease livestock production through decreases in forage quantity and/or quality (Table 1). Invasive species on US rangelands have an estimated annual cost of US\$2 billion³ due to lost production and costs of control efforts. There are also hidden costs associated with invasive species in the form of degraded ecosystem services—key functions provided by ecosystems that benefit humans (e.g., water provisioning, flood control, erosion control, carbon storage, nutrient supply, climate regulation). In some cases, invasive species change ecosystem processes in ways that are self-reinforcing, making the system more suitable for the invader than for the previous inhabitants, in what is known as a positive feedback loop. The combination of degraded ecosystem properties and positive feedbacks can make invasive plant control and rangeland restoration much more challenging because in these cases, it is not sufficient to simply remove the invaders. The ecosystem impacts of invasive species can persist long after the plants have been removed, and when this occurs, the system can remain vulnerable to reinvasion until the ecosystem effects are mitigated or reversed. We review the ecosystem impacts of the current major rangeland invaders in the western United States, discuss the potential for these ecosystem changes to further promote invasion through positive feedbacks, and suggest strategies to address persistent ecosystem effects in order to enhance invasive

plant control and restoration of native (or otherwise desirable) plant communities.

Ecosystem Impacts of Plant Invasions

Most of the major rangeland invaders in the western United States have large impacts on at least some aspects of ecosystem function, ranging from forage productivity to soil and water quality¹ (Table 1). Invasive plants in western rangelands typically reduce livestock production by 30-75% (however, not all invasive plants are detrimental to livestock production, and the effects of a given invader can be beneficial to some livestock species but detrimental to others; Table 1). Although forage quality and production are the most immediate concerns for ranchers, invasive species can also change many other ecosystem characteristics that can negatively impact both the ranch itself and the surrounding areas that rely on ecosystem services provided by rangelands. These ecosystem services include regulation of water flow and quality, soil fertility, soil carbon storage, and wildlife habitat. Water use by yellow starthistle, for example, can remove 15-25% of annual precipitation, decreasing soil water availability for other plants and ultimately reducing downstream water flow. In California's Sacramento River watershed alone, the costs of lost water associated with yellow starthistle amount to US\$16-75 million annually.4 Medusahead has been shown to decrease soil carbon stores, which can have major implications for those seeking credits for carbon sequestration on rangelands. Goatgrass, cheatgrass, medusahead, and spotted knapweed can reduce nitrogen recycling rates, thus potentially limiting rangeland productivity because nitrogen is the most commonly limiting nutrient to plant growth in these systems. Even when invaders do not alter the total amount of soil resources, they can change the timing of resource availability, restricting which plant species have access to soil resources.⁵

Table 1: Effects of major invasive plants in western US rangelands. Empty cells indicate that data were unreported for these properties (either because they are unmeasured, or because differences that are not statistically different tend not to get reported). Citations provide specific references (see web appendix), and much of this information is reviewed in DiTomaso (2000), Ehrenfeld (2003), and Duncan and Clark (2005)

Cidin (2000)										
Invader and its coverage in hectares across 17 western US states	Plant productivity	Costs or economic losses	Diversity/ composition	Water availability and quality	Carbon	Nitrogen availability and litter turnover	Soil microbes	Disturbance regime	Other	References
Barbed goatgrass	Decreases productivity	40-75% decrease in	Can often form			Decreases decomposi-	Alters soil microbial		Increases soil aggregation	Batten et al. 2005
(Aegilops triuncialis), data on area	on nonser- pentine soils; on	livestock productivity	monotypic stands; decreases			tion com- pared to serpentine	community composi- tion		Gopher activity concentrated	Batten et al. 2006
covered not available	serpentine, increases		diversity particularly			natives. Decreases			in patches dominated by goatgrass	Batten et al. 2008
	compared to serpen-		tine soils, which had			nitrogen stored in microbial				Canals et al. 2005
	tine natives		been a refuge for native			biomass				Drenovsky and Batten 2007
										Eviner and Chapin 2005
										Jacobsen 1929
										Malmstrom et al. 2009
Canadian thistle (<i>Cirsium</i> <i>arvense</i>), 2.86 million ha		Decreases livestock carrying capacity by 42%, can injure livestock	Decreases plant diversity						Allelochemicals	Pritekel et al. 2006

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	References	Belnap and Phillips 2001 Bolton et al	Boxell and Drohan	Hall et al. 2009	Hawkes et al. 2006	Hooker et al. 2008	McHenry and Murphy 1985	Ponzetti et al. 2007	Rimer and Evans 2006	Rowe and Brown 2008	Sperry et al. 2006	Whisenant 1989	Wolfe and Klironomos 2005	Zouhar 2003
	Other	Palatable and used extensively by livestock	wildlife: some use as forage, others do not	Decrease in wildlife that rely on shrub habitat										
	Disturbance regime	Changes fire return interval from 60–100 years to 5 years												
	Soil microbes	Decreases arbuscular mycorrhizal fungal abun-	dance and diversity	arbuscular mycorrhi-	zal com- munity in soil	Shifts soil	tungal composi- tion and	pathogens	Direction of effects	particular microbes	on native	COLUMNIC		
	Nitrogen availability and litter turnover	Decreases nitrogen fixation by soil crusts	on plant- available	with site and duration of	invasion; range of 50% de-	crease to increase in	net nitrogen mineraliza- tion.	Increases	total nitrogen in most sites					
	Carbon	Alters distribution of soil carbon (disrupts islands of	fertility) Increases	carbon pools										
	Water availability and quality	Increase or no change in soil moisture Decreases	water illilitä- tion											
	Diversity/ composition	Can facilitate other invasives (medusa-	head) Decreases	perennial grasses and	snrubs (through fire)	Decreases	biological soil crusts							
	Costs or economic losses	\$20 million per year in firefighting costs												
inued	Plant productivity	Changes from patchy vegetation to	continuous	or de- creased	due to 10-fold variation in	productivity year to	year (vs. natives, which have	more reliable	production)					
Table 1. Continued	Invader and its coverage in hectares across 17 western US states	Cheatgrass (Bromus tectorum), 22.68 million ha												

Nitrogen
availability Carbon and litter Soil storage turnover microbes
soil carbon soil nitrogen, nitrogen
mineraliza- tion, and
nitrification
High silica content
leads to slow decomposi-

	References	Rees et al.	Blair et al. 2005	Broz et al. 2007	Carey et al.	2004	Hook et al. 2004	Lacey et al. 1989	Marler et al. 1999a, b	Mummey and Rillig 2006	Pearson 2009	Sheley et al. 1998
	Other	Allelopathy suspected	Decreases elk use	Allergen	mixed evidence	Alters spider	community, increases	density by 46- to 74-fold, with 89-fold	increase in invertebrate	predation by spiders		
	Disturbance regime		Reduces fire frequency									
	Soil microbes		Changes fungal and	arbuscular mycorrhi-	communi-	ties,	arbuscular mycorrhi-	zal fungal diversity	and hyphal length,	mixed ef- fects on quantity of	arbuscular mycorrhi- zae	
	Nitrogen availability and litter turnover		Varied effects,	tends to decrease	nitrogen availability							
	Carbon		Impact depends on	site: often no effect,	some sites,	decreased at	alis alio					
	Water availability and quality		Decreases	infiltration, increases	to increased	sedimenta-						
	Diversity/ composition		Decreases	diversity	cryptogamic crusts.	which are	important for soil	stability, nitrogen fixation, and	moisture retention			
	Costs or economic losses	Decreases livestock carrying capacity by 38%	\$42 million per year in	Montana (for C. maculosa,	and C.	diffusa)	Interferes with livestock	access to more desirable	forage, leads to 63%	reduction in livestock capacity		
inued	Plant productivity	Even at low densities, can decrease forage production by 23%	Decreases grass	productivity 60-90%								
Table 1. Continued	Invader and its coverage in hectares across 17 western US states	Musk thistle (<i>Carduus</i> <i>nutans</i>), 1.89 million ha	Spotted knap- weed	(Centaurea maculosa,	C. sroebel, 2.12 million ha							

Table 1. Continued	inued									
Invader and its coverage in hectares across 17 western US states	Plant productivity	Costs or economic losses	Diversity/ composition	Water availability and quality	Carbon	Nitrogen availability and litter turnover	Soil microbes	Disturbance regime	Other	References
Yellow starthistle (Centaurea solstitialis), 5.98 million ha	Lowers productivity	US\$12.5 million per year in management costs	Decreases plant diversity	Decreases soil moisture by drawing down the equivalent of			Changes microbial community composi-tion			Batten et al. 2006 Enloe 2002 Gerlach
		US\$16-75 million per year due to water loss in Sacramento River watershed, California		15–25% of annual pre- cipitation.						2004 Jetter et al. 2003 Malmstrom et al. 2009
		Toxic to horses		In Siskiyou County,						
		Lowers forage crude protein, but good forage for goats and sheep in early stages		California, water loss is more than 100,000 m³ per year						
. 1										

References available online at www.srmjournals.org.

Some ecosystem impacts of invasive species may be rapidly reversible upon removal of the invader. For example, decreased soil water availability caused by high plant transpiration rates should reverse quickly once the invasive plant is removed. In contrast, many invader-induced ecosystem effects can persist even after invasive removal, a concept known as legacy effects. For species that alter soil properties such as soil structure, water infiltration, water holding capacity, carbon storage, nitrogen availability, and so forth, it may take from months to decades to reverse these changes even with active management. Extensive erosion of topsoil in invaded systems, for example, can take decades to centuries to reverse via soil formation processes and the gradual buildup of organic matter by the restored plant community.

Understanding the ecosystem impacts of key invasive plants in western US rangelands can be difficult because even for a given species, ecosystem effects are often not constant but vary with site conditions, invader prevalence, and duration of the invasion.^{5,7,8} Continued research into the context-dependence of invasive species effects will help us better predict which sites will be most impacted by a particular invader, which ecosystem processes will need to be restored at a given site, and how these ecosystem effects change over time—giving us critical tools for prioritizing our eradication and restoration efforts.

Feedback Effects of Plant Invasions

Although the ecosystem effects of invasive plants are a concern in their own right, invaders can also change the soil conditions to such an extent that the new conditions alter which plant species can grow successfully at that site. Feedback effects, where a change in plant composition alters conditions that can further alter the plant community, can be either positive or negative. In a positive feedback, the effects of invasive plants on ecosystem properties will further promote the persistence and growth of the invader. In a negative feedback, changes to the ecosystem caused by invasive plants promote other species and thereby limit abundance of the invader. Feedbacks are typically mediated through changes in soil biota, microenvironment, disturbance regime, and/or the soil physical or chemical environment.

In general, feedbacks play an important role in community dynamics. In native communities, negative feedbacks are most common, and can decrease plant biomass by an average of 37%. Invasive plants are less likely to have negative feedbacks and are more likely to alter soils in ways that increase their own prevalence and biomass (by an average of 43%). In some cases, a given invasive plant alters the soil to benefit other invaders, as well as itself. For example, cheatgrass invasion can make a system more vulnerable to medusahead, and medusahead can increase the prevalence of exotic forbs (Table 1).

Positive feedbacks are common for a number of invasive species in western US rangelands, making their control a greater challenge (Table 2). Many of these invasive plants alter soil biota in ways that favor themselves, or inhibit natives more strongly than themselves. For example, Italian thistle decreases densities of symbiotic arbuscular mycorrhizal fungi, which limits the growth of native forb species. Black mustard displays a different type of feedback strategy; it inhibits native grasses by increasing consumption of the native species by small mammals. The effects of this feedback extend up to 30 m away from mustard patches. Rangeland invaders also generate feedbacks through changes in the fire regime (cheatgrass), changes in soil nitrogen availability (cheatgrass), and addition of allelochemicals (knapweed) that inhibit growth of other plant species (Table 2). Native communities may also resist invasion by altering soils in ways that suppress the growth of invasive species.¹³

The study of feedbacks created by invasive species is still a relatively new field, and although it is clear that feedbacks can play an important role in invasions, not all invader-induced ecosystem changes will feed back to benefit invaders. Just as the ecosystem impacts of invaders can be context-dependent, the strength and direction (positive or negative) of feedbacks can also vary with environmental conditions, the amount of time that the invader has been present, and with which plant species are interacting.

Management Considerations

Removing an invasive species through burning, grazing, or herbicide is a common and necessary starting point, but in some cases, successful management requires disruption of invader-induced soil changes, which can persist for weeks to decades after the invasive plant has been removed.⁶ Without management to reverse the effects of invasive species on soils, the system can often remain susceptible to reinvasion. Because plant-soil feedbacks operate through many mechanisms, there is no easy, one-size-fits-all management plan. Some of the common management practices that have the potential to alter plant-soil feedbacks in favor of native and other desirable species include selecting plants for restoration that can reverse the ecosystem impacts of invasive species, manipulating soil microbes, and adding carbon and charcoal to soil (described below and in Table 3). For these practices to be successful, we must identify the mechanisms driving the feedbacks and select the approaches that have the greatest likelihood of interfering with those specific mechanisms. These tools have been effective in controlling some invaders under specific conditions, but also have failed to work or even increased the prevalence of invaders (Table 3). Mitigating feedbacks is a relatively new approach, and a close collaboration is required between managers and researchers in order to rapidly fine-tune these tools for effective management of invaders.

Selection of Intermediate Plant Species for Restoration

Although restoration often aims to reestablish the preinvaded plant community, this may not be an immediately feasible goal if invader-induced feedbacks are strong enough to prevent the original native species from persisting long

Table 2. Feedbacks	impacting invasive	plants in western US range	lands	
Invader, study location	What does the invader change?	How do these changes affect native vs. invasive species?	What does this mean for managing the invader?	References
Barbed goatgrass (Aegilops triuncialis), California	Changes soil microbial community composition on serpentine soils	Decreases growth and flowering time of <i>Lasthenia</i> californica (native forb)	Need to alter soil community for successful restoration of this native species	Batten et al. 2008
Crested wheatgrass (Agropyron cristatum), Great Plains region	Changes soil biota	Increases its own growth and decreases growth of some native forbs (also increases growth of the invasive <i>Bromus inermis</i>)	Consider planting native species that are relatively insensitive to soils altered by the invader	Jordan et al. 2008
Black mustard (<i>Brassica nigra</i>), California	Increases consumption of the native Nassella pulchra by native small mammals	Curtails establishment of N. pulchra within 30 m of B. nigra patches	May not be able to reestablish <i>N. pulcha</i> close to <i>B. nigra</i>	Orrock et al. 2008
Smooth brome (Bromus inermis), Great Plains region	Changes soil biota	Increases its own growth and decreases some native forbs (also increases growth of the invasive <i>Euphorbia</i>)	Consider planting native species that are relatively insensitive to soils altered by the invader	Jordan et al. 2008
Cheatgrass (<i>Bromus</i> tectorum), Great Basin	Increases fire frequency	Decreases survival of native perennials	Must decrease fire frequency for restoration of perennials	Knick and Rotenberry 1997
Cheatgrass (<i>Bromus</i> tectorum), Utah	Increases soil nitrate deep in the soil profile through leaching from litter, inhibition of nitrogen supply from soil crusts	Natives cannot access this deep-soil nitrogen source	Need to restore surface soil nitrogen availability for reestablishment of natives	Sperry et al. 2006
Italian thistle (Carduus pycnocephalus), California	arduus densities nativ enocephalus), califi ifornia pycr in so		If species that do not maintain AMF communities invade an area, it may be difficult to restore the area soils without AMF and nonnative soils If species that do not maintain AMF communities invade an area, it may be difficult to restore the area to a native community that is reliant on AMF, potential for use of native AMF inoculum	
Knapweed (Centaurea maculosa	Releases allelochemicals	Decreases growth of some native species, but species	Centaurea maculosa and C. diffusa may exclude	Blair et al. 2005
and <i>C. diffusa</i>), Intermountain West		may be able to evolve resistance to allelochemicals over the long term	native species when they invade a new area, but plants that have been exposed to these invaders	Callway and Aschehoug 2000
			for a long time may be less affected	Callaway and Vivanco 2007
				Thorpe et al. 2009

Table 2. Continued				
Invader, study location	What does the invader change?	How do these changes affect native vs. invasive species?	What does this mean for managing the invader?	References
Spotted knapweed (Centaurea	Alters AMF function	Enhances ability for C. maculosa to competitively	Further study is needed, may need to suppress or	Carey et al. 2004
maculosa), Montana		suppress Festuca idahoen- sis (native bunchgrass); C. maculosa parasitizes F. idahoensis through AMF, increasing invader growth 87–168% in presence of AMF	alter AMF community	Marler et al. 1999a, b
Leafy spurge (Euphorbia esula), Great Plains region	Changes soil biota	Decreases growth of native forbs, as well as other invaders	Consider planting native species that are relatively insensitive to soils altered by the invader	Jordan et al. 2008
	cular mycorrhizal fung online at www.srmjou			

enough to alter soil conditions. Instead, a multistage successional approach can be employed by initially planting species that are more tolerant of the invaded soil conditions. Once these initial plantings ameliorate the invaded soil conditions, the native community that is ultimately desired can be seeded in (Tables 2 and 3). This approach is similar to agricultural use of cover crops to disrupt pathogen cycles, increase soil fertility, and build up organic matter. In Australian grasslands, a specific grass species is used to reduce high levels of soil nitrate created by invasive species, which prevents reinvasion (Table 3). To prevent spotted knapweed reinvasion after weed control measures, plant species are being tested for resistance to knapweed's allelochemicals (Table 3). The establishment of these resistant species can prevent knapweed from reinvading and eventually facilitate the establishment of native species that are susceptible to allelochemicals.

Soil Microbial Communities as a Tool for Restoration

Soil biota can strongly affect plant success, but their manipulation is not straightforward and our understanding of these interactions is still rudimentary. Two groups that are often targeted in restoration efforts are mycorrhizal fungi and biological soil crusts (Table 3). Mycorrhizal fungi are available as a commercial inoculum, but this is primarily a tool for severely degraded sites that have little to no soil biota remaining. In systems where native plants have a stronger benefit from local mycorrhizas than do invasive plants, a local native mycorrhizal inoculum may be useful if it can be obtained. Biological soil crusts have been used as a tool to enhance native seed germination at the expense of

invasive plants and can additionally increase nitrogen availability and soil stability in degraded ecosystems. Attempts to reestablish crusts at large scales using cultured, pelleted algae have had limited success (Table 3).

Carbon Additions to Decrease Soil Nitrogen

To manage invasive species that increase nutrient availability, carbon additions (e.g., sawdust, sugar) have sometimes been used with the goal of tying up excess soil nitrogen in microbial biomass by stimulating microbial growth. Although this approach can be successful in reducing some invasive species (e.g., diffuse knapweed), its effectiveness in reducing soil nitrogen availability and controlling invasives is variable (Table 3; also see article by Alpert in this issue).

Activated Carbon to Mitigate Allelochemicals

Activated carbon, also known as activated charcoal, is often used for chemical purification and pollutant removal from water and air because of its ability to efficiently sequester organic compounds on its highly porous surface area. In soils, the effects of activated carbon are not completely understood, but it is believed to play a large role in binding allelochemicals, removing them from the soil solution, and reducing their effects on native plants. The native grass Festuca idahoensis, when grown with spotted knapweed, grew 85% larger with activated carbon than without (Table 3). A single application of activated carbon combined with native seed additions in ex-arable fields also reversed dominance from invasives such as cheatgrass and diffuse knapweed to natives (largely bluebunch wheatgrass). Allelochemicals generally are short-lived in the soil (hours to days),14 suggesting that activated carbon may be most

Table 3. Some potential management practices for disrupting positive plant-soil feedbacks created by invasive species

Management option	Successful management	Management limitations/ failures	References
Successional	Use of species that can	The ability of species to	Herron et al. 2001
approach: rather than directly planting in	decrease soil-available nitrate, making restoration sites more	decrease soil nitrate may fluctuate seasonally, creating	Prober et al. 2005
desired plant community, initially plant species that	resistant to reinvasion and more conducive to the persistence of desirable species	windows of opportunities for invaders	Prober and Lunt 2009
can make system more amenable to	Use of species that are	Few species are resistant to	Alford et al. 2008
native reestablishment	resistant to allelochemicals (currently being tested)	allelochemicals at all life stages, so diversity of restored community may be limited initially	Perry et al. 2005
	Use of species minimally	Untested, based on studies	Jordan et al. 2008
	impacted by invader effects on soil microbial community	that suggest that invader effects on soil microbes limit reestablishment of some natives	Vogelsang and Bever 2009
Application of commercial mycorrhizal inocula	Can increase productivity and survival of target species, reduce invasive plant fitness, and increase soil aggregation	Can also decrease target species, increase invasive species, reduce soil carbon	Reviewed in Schwartz et al. 2006
Reestablishment of	Can increase soil stabilization,	Mass culturing and pelletization	Reviewed in Bowker 2007
biological soil crusts	native seed germination, adult plant establishment, and soil	of cyanobacteria produce crusts in lab but not in field tests;	Buttars et al. 1998
	nutrient availability. Various inoculation methods exist; most	introduction of cyanobacteria cultured on cloth resulted in	Kubecková et al. 2003
	successful approach requires	short-term growth at only one of	Lesica and Shelly 1992
	destruction of intact crusts for inoculum used to restore crusts at local scales	five sites	St. Clair et al. 1984
Addition of carbon	Can be very effective in	Can have no impact or increase	Alpert, this issue
(e.g., sawdust, sugar) to decrease soil	controlling some invaders (e.g., diffuse knapweed)	other invaders. Carbon additions do not always decrease	Blumenthal et al. 2003
available nitrogen through microbial immobilization		nitrogen (and can sometimes increase nitrogen). There may be site-specific threshold levels of carbon that must be added to decrease nitrogen	Blumenthal 2009
Activated carbon to	Has been effective with spotted	Can also increase invaders and/	Kulmatiski, in press
sequester allelochemicals	knapweed, diffuse knapweed, and cheatgrass	or decrease natives. Because binding is indiscriminate,	Kulmatiski and Beard 2006
		additions can decrease allelochemicals, change nitrogen	Lau et al. 2008
		availability, and alter microbial communities, making the mechanism of impact uncertain	Ridenour and Callaway 2001
References available	online at www.srmjournals.org.		

useful to minimize the effects of invaders currently at a site. To ameliorate potential longer-term legacies of allelochemicals deposited through plant litter,¹⁴ best practices should include removing all invasive plant material from a site. Activated carbon not only binds organic substrates, but can also change soil nitrogen availability, the ratio of carbon to nitrogen in soil, and soil microbial communities, so its effects on soils and plants may be for different reasons in different trials (Table 3).

Summary

Invasive plants in western US rangelands not only greatly decrease native diversity and cover, but also compromise many ecosystem services, resulting in millions of dollars lost each year due to diminished productivity, water quantity, water quality, erosion control, and other key services. These invader-induced changes to the ecosystem can also benefit the invasive species at the expense of natives, making invasive plant control even more intractable. In cases in which invasive species cause positive feedbacks, simply eradicating invaders will only lead to reinvasion. Thus, management needs to go beyond basic invader control by reversing the changes invaders make to ecosystem properties, with a particular emphasis on soils. There is considerable variation in effects of invasive species across sites and time and our understanding of feedbacks and their management is still developing. Yet there are some underexploited tools that show promise in disrupting plant-soil feedbacks and collaborations between managers and researchers can accelerate our understanding and control of these feedbacks.

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Ecosystem Impacts of Exotic Plants Can Feed Back to Increase Invasion in Western US Rangelands

ABSTRACT

Large areas of rangeland in the western United States are now dominated by invasive nonnative plant species. Not only do these invasions greatly decrease native plant diversity and cover, but many also decrease forage quantity and/or quality, leading to direct negative impacts on livestock production. Invasions by exotic species are also altering the functioning of ecosystems by changing water availability and flow, soil carbon storage, nutrient availability, erosion rates, fire frequency, soil microbial communities, and wildlife habitat. While these ecosystem changes are a concern in their own right, invasive species can also modify the habitat to their own benefit and often at the expense of native species. This is particularly important when the ecosystem effects of an invader persist after the invader has been removed by weed control measures. In such situations, long-term control of invasive species likely requires mitigation of not only the invasive plants, but also their ecosystem effects. In this paper, we review the ecosystem effects of common invasive plants in rangelands of the western US, how these ecosystem effects promote some invasive species through positive feedback loops, and potential management options for disrupting these feedbacks.

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