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Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts

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ABSTRACT

Across the globe, native savannas and woodlands are undergoing conversion to exotic grasslands. Here we summarize the current state of knowledge concerning the ecohydrological consequences of this conversion for the cold deserts (Great Basin, Colorado Plateau) and the warm deserts (Mojave, Sonoran, Chihuahuan) of North America. Our analysis is based on a synthesis of relevant literature, complemented by simulation modelling with a one-dimensional, soil water redistribution model (HYDRUS-1D) and a hillslope runoff and erosion model (MAHLERAN). When shrublands are invaded by grasses, many changes take place: rooting depths, canopy cover, species heterogeneity, water use, and fire regimes are radically altered. These changes then have the potential to alter key ecohydrological processes. With respect to the processes of runoff and erosion, we find that grass invasion influences cold and warm deserts in different ways. In cold deserts, runoff and erosion will increase following invasion; in particular, erosion on steep slopes (>15%) will be greatly accelerated following burning. In addition, evapotranspiration (ET) will be lower and soil water recharge will be higher—which after several decades could affect groundwater levels. For warm deserts, grass invasion may actually reduce runoff and erosion (except for periods immediately following fire), and is likely to have little effect on either ET fluxes or soil water. Significant gaps in our knowledge do remain, primarily because there have been no comprehensive studies measuring all components of the water and energy budgets at multiple scales. How these changes may affect regional energy budgets, and thus weather patterns, is not yet well understood. Copyright © 2011 John Wiley & Sons, Ltd.

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INTRODUCTION

The spread of exotic grasses has radically altered native habitats throughout the world. These grasses, among the most pernicious of biological invaders (D'Antonio and Vitousek, 1992; Mack and D'Antonio, 1998), are being found in habitats of many types and differing climates. Their impact has been especially profound in semiarid grasslands, savannas, and woodlands. In some cases, the conversion process is already complete (e.g. around 45 000 km^2 of formerly perennial grasslands in the California Central Valley are now populated entirely by exotic annuals) (Heady, 1977; Klinger *et al.*, 2008), whereas in other cases invasion is still under way.

The loss of native shrublands and woodlands is of particular concern. The best documented example—and probably the most extensive shrubland area lost to exotic grasses—is the sagebrush steppe of the United States, which has become dominated by cheatgrass (*Bromus tectorum*) (Knapp, 1996). By some estimates, cheatgrass already dominates some 7% of the Great Basin (Bradley and Mustard, 2005). Others suggest that the coverage is even higher (Smith *et al.*, 1997).

Similar conversions are occurring in many other locations. Shrublands and dry forests under siege by exotic grasses include the Sonoran and Mojave deserts in North America (Anable *et al.*, 1992; Brooks and Matchett, 2006; Franklin *et al.*, 2006; Rice *et al.*, 2008), coastal sage scrublands in southern California (Talluto and Suding, 2008), Catalan shrublands in Spain (Grigulis *et al.*, 2005), the Karoo in South Africa (Rahlao *et al.*, 2009), grassland savannas in Australia (Sharp and Whittaker, 2003, Clarke *et al.*, 2005, Rossiter-Rachor *et al.*, 2009), and tropical dry forests in Bolivia (Veldman *et al.*, 2009).

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Common to all the shrublands and dry forests in these regions under exotic grass invasion is a radically accelerated fire regime (more frequent and more intense fires)—one to which many native plants are not well adapted. Because the invading exotic grasses tend to form a more homogenous canopy than native or resident plants and are also highly flammable when dry, their presence increases fuel loads and fuel connectivity. However, they also tend to be more fire tolerant than the native species, which creates a positive feedback loop between the invasive grasses and the frequency, size, spatial pattern, and intensity of fires. All these factors favour the persistence and expansion of the exotic grasses and lead to ecosystem transformation (Brooks *et al.*, 2004).

The conversion of desert shrublands to exotic grasslands has such profound implications at the ecological, ecosystem, and even socioeconomic levels that it can appropriately be described as 'transformative change' (Wilcox, 2010, 2011). Some of these implications are reasonably well understood and documented at the local scale (Mack and Pyke, 1983; Kulmatiski *et al.*, 2006; Sperry *et al.*, 2006), but much less is known regarding larger scales. Some issues, such as carbon storage, have been investigated at the regional scale (Bradley *et al.*, 2006; Wolkovich *et al.*, 2010) but we know relatively little about other large-scale phenomena such as flooding, sedimentation, groundwater recharge, and changing weather patterns.

OBJECTIVES, SCOPE, AND APPROACH

In this article, we summarize the current state of knowledge concerning the ecohydrological consequences of the conversion of native shrublands to grasslands. Our objectives are to understand ecohydrological changes at the local scale, such as soil water content or hillslope erosion, and whether these small-scale changes have consequences for larger-scale phenomena such as flooding, sedimentation in rivers, groundwater recharge, energy budgets, and weather patterns. We contrast cold and hot deserts, as we expect that their ecohydrological responses to grass invasion will differ because of the higher evaporative demand in hot deserts.

Our analysis is based on a synthesis of relevant literature complemented by simulation modelling. The modelling portion of the analysis provides a framework for generalizing results from the literature synthesis, enabling us to fill data gaps where appropriate as well as to 'scale-up' the experimental results from these studies. We used a model for assessing hillslope and landscape erosion, runoff, and nutrients (MAHLERAN) to simulate surface fluxes (runoff and erosion) and we used HYDRUS-1D to simulate the vertical fluxes of evapotranspiration (ET) and groundwater recharge. MAHLERAN is a spatially explicit soil erosion model that is relatively new but has undergone extensive testing and some field application (Wainwright *et al.*, 2008a,b,c). HYDRUS-1D is a physically based vadose zone hydrology model that numerically solves Richards' equation for variably saturated porous media in one dimension (Simunek *et al.*, 2008). HYDRUS-1D has been extensively tested and broadly applied.

For our analysis, we examined the ecohydrological consequences of exotic grass invasion in a range of cold and warm deserts, which make up a large fraction of the land mass of North America (Figure 1). These deserts are arrayed along a gradient of increasing temperature, aridity, bimodality (summer and winter), and unpredictability of precipitation from north to south. The deserts include the Great Basin and Colorado Plateau (cold), the Mojave (transitional), and the Sonoran and Chihuahuan (warm).

Invasive grasses of concern in these deserts are cheatgrass in the Great Basin (Figure 1) and to a lesser extent in the Colorado Plateau, red brome (*Bromus rubens*) in the Mojave, buffelgrass (*Cenchrus ciliaris*) in the Sonoran, and Lehmann lovegrass (*Eragrostis lehmanniana)* in the Chihuahuan Desert.

HORIZONTAL FLUXES: RUNOFF AND EROSION

Cold deserts

In cold desert regions, conversion of native shrublands to invasive grasslands is commonly believed to disrupt watershed functioning (e.g., by increasing flooding and water erosion from steep slopes). Documentation of such effects at the watershed and hillslope scales is largely anecdotal (Stewart and Hull, 1949; Klemmedson and Smith, 1964; Pierson *et al.*, In press); however, for small- and large-plot scales, strong supporting evidence exists (Table I). Craddock and Pearce (1938) conducted large-plot ($4{\cdot}5 \times 15$ m) rainfall simulation experiments and compared runoff and erosion from steep slopes (96 locations in all)—some dominated by native bunchgrass, some by cheatgrass, and some degraded and infested with annual weeds. Their results showed that runoff and erosion are higher from cheatgrass-covered areas than from those covered by native bunchgrass, but lower than from degraded, annual weed slopes. Similarly, Boxell and Drohan (2009) demonstrated that soil infiltration capacity in areas dominated by cheatgrass was less than half that of sagebrush-covered slopes. Pierson *et al.* (2007) found that for very flat slopes (1%–2%), runoff and erosion from cheatgrass-covered areas are actually quite low.

On steep slopes, burning may increase runoff sixfold, and erosion up to 120 times, depending on the severity of the fire (Pierson *et al.*, 2001, 2002, 2008a,b, 2009). For 2–3 years following a fire, the burned areas displayed higher rates of erosion (generally returning to preburn levels after two growing seasons).

Although most of these studies were at the plot scale, anecdotal reports describe large-scale erosion on steep slopes following fires (Stewart and Hull, 1949; Klemmedson and Smith, 1964)—for example, the Boise Front Range, near Boise, Idaho, has experienced several large-scale erosion and mass-wasting events related to fire. Extensive areas of rangeland and forest along the Boise Front were burned in 1959 (3640 ha) and 1996

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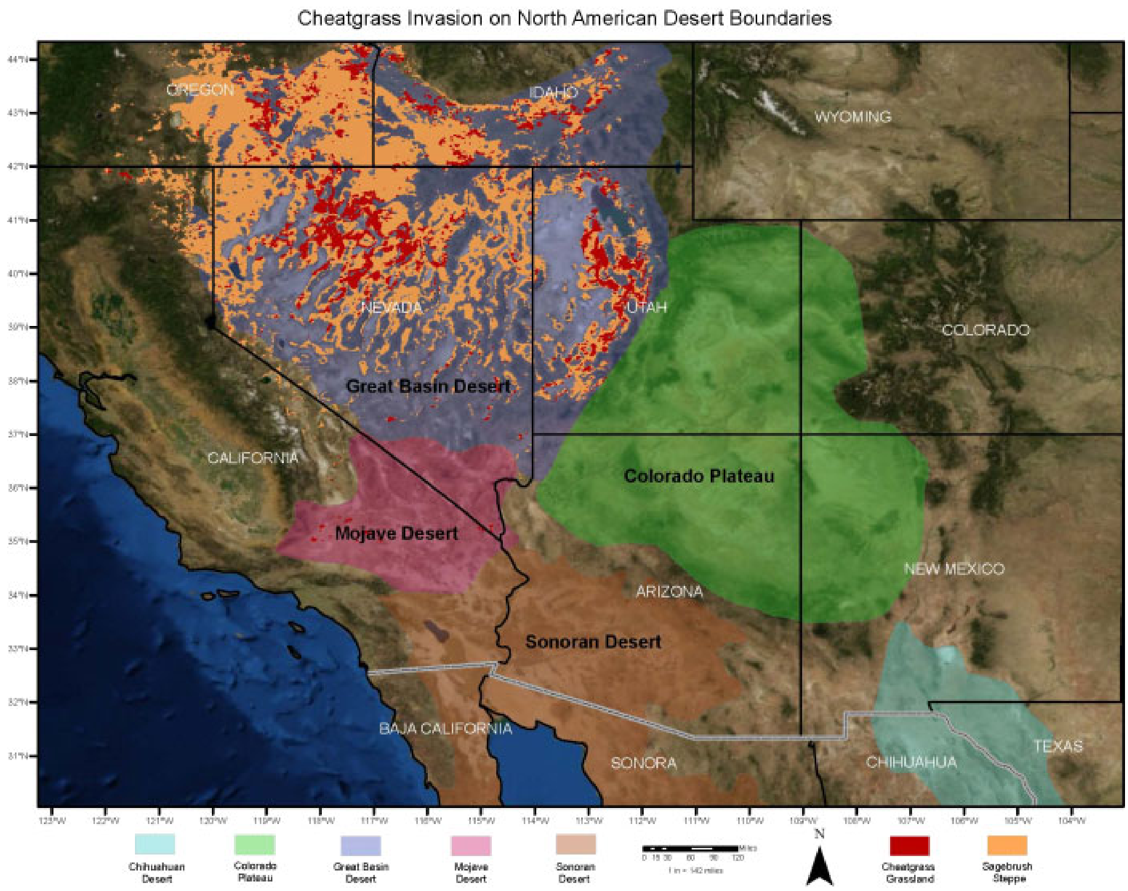

Figure 1. Major desert regions in the western United States. For the Great Basin, areal coverage of cheatgrass (as estimated by Bradley and Mustard, 2008) is shown in red, and the area consisting of sagebrush steppe in orange. Coverage of invasive grasses for the other desert regions is not available.

(6000 ha) in large fires fuelled by invasive annual grasses (*B. tectorum*). Two weeks after the 1959 fire, an intense, convective rainstorm produced widespread flooding and mudflows that caused some \$500 000 in damage to property and infrastructure. Then, 1 year after the 1996 fire, another intense rainstorm (70 mm h^{-1} intensity, 9-min duration) again flooded portions of Boise and inundated the flooded areas with sediment (Pierson *et al.*, 2002).

Transitional and warm deserts

For the warm deserts, most of what we know about the effects of shrubland-to-grassland conversion comes from comparisons of native grasslands with shrublands in the Chihuahuan Desert (Wainwright *et al.*, 2000; Nearing *et al.*, 2005; Mueller *et al.*, 2008; Michaelides *et al.*, 2009). This work has shown that runoff and erosion are lower from desert grasslands than from shrublands, primarily because the grasslands have more vegetation cover and smaller, less-interconnected bare patches. This finding is consistent with that of many other studies in semiarid environments, showing that surface runoff and erosion are negatively correlated with vegetation cover (Archer *et al.*, 2010). On this basis, we can infer that (in the absence of fire) the invasion of warm deserts by exotic grasses will probably reduce surface runoff and erosion—because generally, invasive grasses mainly fill in the bare interspaces. One might expect that erosion would increase following fire; however, this has not been experimentally verified. Several studies have examined the influence of fire on runoff and erosion in warm deserts of North America. One study (Emmerich and Cox, 1992) found that fire had little effect on runoff or erosion from native grasslands and from stands of introduced Lehmann lovegrass, probably because slopes were very low and soils quite permeable. For a native desert grassland, O'Dea and Guertin (2003) found that erosion (on slopes of only 1%–3%) was slightly elevated for 1–2 years following burning.

Modelling horizontal fluxes

As noted above, there are some gaps in our knowledge concerning how invasive grasses may modify the surface hydrology of desert shrublands. These gaps are especially acute for the Mojave and Sonoran deserts. In the case of the cold deserts, we know that erosion will dramatically increase on steep cheatgrass-covered slopes immediately following a fire, whereas erosion will increase very little on flat slopes, regardless of cover condition (it is not known at what slope gradient erosion begins to accelerate). For the Mojave, Sonoran, and Chihuahuan deserts, we have surmised—on the basis of work comparing native grasses with native shrubs—that invasive grasses

Table I. Site characteristics, runoff coefficients, and erosion data for unburned (unb) vs burned conditions of high (high), moderate (mod), and low (low) severity in both cold and warm deserts.

Study	Location	Plant Community	Treatment	Plot Size (m^2)	Slope (%)	Time Post-Fire (mths)	Rainfall Rate ($mm\ h^{-1}$)	Type of Rainfall	Bare Soil (%)	Canopy Cover (%)	Ground Cover (%)	Runoff Coef. (%)[a]	Sed. Yield ($g\ m^{-2}$)
Pierson et al., 2002[b]	Cold Desert Shrub-steppe (Snake River Plain, Idaho)	Shrub Coppice	Unb	0·5	35-60	12	67	Artificial	7	88	93	11	2
			Mod	0·5	35-60	12	67	Artificial	97	11	3	34	30
			High	0·5	35-60	12	67	Artificial	98	13	2	37	22
		Interspace	Unb	0·5	35-60	12	67	Artificial	89	18	12	24	4
			Mod	0·5	35-60	12	67	Artificial	95	16	5	26	12
			High	0·5	35-60	12	67	Artificial	99	5	1	49	148
Pierson et al., 2001a, 2008a	Cold Desert Shrub-steppe (Great Basin, Nevada)	Shrub Coppice	Unb	0·5	30-40	1	85	Artificial	1	100	99	30	12
			High	0·5	30-40	1	85	Artificial	99	1	1	37	41
		Interspace	Unb	0·5	30-40	1	85	Artificial	6	74	94	49	24
			High	0·5	30-40	1	85	Artificial	99	4	1	30	21
Pierson et al., 2009	Cold Desert Shrub-steppe (Snake River Plain, Idaho)	Shrub Coppice	Unb	0·5	35-50	1	85	Artificial	2	84	98	39	17
			Mod-High	0·5	35-50	1	85	Artificial	42	10	58	76	183
		Interspace	Unb	0·5	35-50	1	85	Artificial	25	31	75	63	195
			Mod-High	0·5	35-50	1	85	Artificial	84	0	16	55	705
		Shrub-Interspace Zone	Unb	32·5	35-50	1	85	Artificial	23	58	77	4	8
			Mod-High	32·5	35-50	1	85	Artificial	76	0	24	27	988
Craddock and Pearse, 1938	Cold Desert Shrub-steppe (Snake River Plain, Idaho)	Bunchgrass Community	Unb.	20·2	30	—	46	Artificial	—	—	~35	1	1
			Unb.	20·2	30	—	92[c]	Artificial	—	—	~35	1	1
			Unb.	20·2	40	—	46	Artificial	—	—	~35	<1	1
			Unb.	20·2	40	—	92[c]	Artificial	—	—	~35	<1	1
Craddock and Pearse, 1938	Cold Desert Shrub-steppe (Snake River Plain, Idaho)	*Bromus tectorum* Grassland	Unb.	20·2	30	—	46	Artificial	—	—	~20	10	31
			Unb.	20·2	30	—	92[c]	Artificial	—	—	~20	5	11
			Unb.	20·2	40	—	46	Artificial	—	—	~20	26	49
			Unb.	20·2	40	—	92[c]	Artificial	—	—	~20	53	331

Table I. (*Continued*).

Study	Location	Plant Community	Treatment/ Burn Severity	Plot Size (m^2)	Slope (%)	Time Post-Fire (mths)	Rainfall Rate ($mm\ h^{-1}$)	Type of Rainfall	Bare Soil (%)	Canopy Cover (%)	Ground Cover (%)	Runoff Coef. (%)	Sed. Yield ($g\ m^{-2}$)
Craddock and Pearse, 1938	Cold Desert (Snake River Plain, Idaho)	*Lupinus* spp./*Stipa lettermanii* Community	Unb.	20·2	30	—	46	Artificial	—	—	~25	44	274
			Unb.	20·2	30	—	92[c]	Artificial	—	—	~25	57	511
			Unb.	20·2	40	—	46	Artificial	—	—	~25	44	253
			Unb.	20·2	40	—	92[c]	Artificial	—	—	~25	55	468
Pierson et al., 2007[d]	Cold Desert (Snake River Plain, Idaho)	*Bromus tectorum* Grassland	Unb.	32·5	2	—	64	Artificial	34	54	66	2	1
			Unb.	32·5	2	—	64[e]	Artificial	34	54	66	8	2
O'Dea and Guertin, 2003	Hot Desert (Sonoran Desert, Arizona)	Grassland	Unb	30	1-3	—[f]	Variable	Natural	—	21	—	10	1700[f]
			Mod	30	1-3	—[f]	Variable	Natural	—	11	—	11	2800[f]
		Grassland	Unb	30	1-3	—[g]	Variable	Natural	—	37	—	14	1800[g]
			Mod	30	1-3	—[g]	Variable	Natural	—	29	—	14	2200[g]

[a] Runoff coefficient is equal to cumulative runoff divided by cumulative rainfall applied. Value is multiplied by 100 to obtain percent.
[b] Data presented from south-facing slopes solely.
[c] Rainfall applied for 30 min.
[d] This is a multiple-year study; means shown for soil, cover, runoff, and sediment yield are average of three simulation years.
[e] Rainfall applied for 30 min under wet conditions (24 h after application of 64 mm of rainfall).
[f] Cumulative runoff and erosion from natural rainfall events (57 mm) for the period 1 July 1998–1 October 1998. Most recent fire was in May 1998.
[g] Cumulative runoff and erosion from natural rainfall events (106 mm) for the period 1 July 1999–1 October 1999. Most recent fire was in May 1998.

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Table II. Model parameters for MAHLERAN, for warm and cold desert shrublands and for pre- and post-fire grasslands.

Vegetation	Vegetation cover (%)[a]	Initial soil moisture content (%)	Ksat (mm s^{-1})[a]	Particle size distribution[b,d,e]					
				$\varphi1$	$\varphi2$	$\varphi3$	$\varphi4$	$\varphi5$	$\varphi6$
Cold desert									
Shrubland	46[c]	8·8	0·0151[d]	0·458[d]	0·514[d]	0·015[d]	0·013[d]	0	0
Pre-fire grassland[f]	50		0·0140						
	66	8·8	0·0144	0·463	0·471	0·022	0·044	0	0
	80		0·0149[d]						
Post-fire grassland (moderate burn)	33	8·8	0·012	0·463	0·471	0·022	0·044	0	0
Post-fire grassland (severe burn)	0	8·8	0·01	0·463	0·471	0·022	0·044	0	0
Warm desert									
Shrubland	22	5	0·0065	0·223	0·328	0·022	0·088	0·202	0·137
Pre-fire grassland	50	5	0·011	0·214	0·427	0·025	0·056	0·161	0·117
	66	5	0·012	0·214	0·427	0·025	0·056	0·161	0·117
	80		0·013	0·214	0·427	0·025	0·056	0·161	0·117
Post-fire grassland (moderate burn)	33	5	0·009	0·214	0·427	0·025	0·056	0·161	0·117
Post-fire grassland (severe burn)	0	5	0·008	0·214	0·427	0·025	0·056	0·161	0·117

[a] Plot average value.
[b] $\varphi1$ = <63 μm, $\varphi2$ = 63 μm to 0·25 mm, $\varphi3$ = 0·25–0·5 mm, $\varphi4$ = 0·5–2 mm, $\varphi5$ = 2–12 mm, and $\varphi6$ = >12 mm.
[c] 40% with 100% shrub cover and 80% with 20% grass cover.
[d] Boxell and Drohan (2009).
[e] Turnbull *et al.* (2010).
[f] Pierson *et al.* (2007).

are likely to reduce erosion under normal (no fire) conditions; but we do not know to what extent erosion may be reduced. These and other data gaps may be partially addressed by simulation modelling (at least to the extent that the hypotheses may be formalized for guiding future research).

The MAHLERAN model was used to simulate runoff and erosion for functional groups (shrub, grass, burned grass) in both cold and warm deserts, over a range of slopes (1–40%). With limited parameterization data available, our simulations are not meant to be comprehensive, but rather are designed to provide insight into a number of issues—including the extent to which runoff and erosion may change with (1) slope gradient, (2) vegetation cover, and (3) moderate and severe burning. For the functional group comparison, we selected representative values for key variables, such as hydraulic conductivity and surface cover, for each functional group (Table II). For the warm desert shrubland simulation, we assumed that the interspaces are bare and interconnected, while for the cold desert shrubland we assumed that the interspaces have a 20% grass cover. Simulations were carried out across the range of slopes with grass cover of 50%, 66%, and 80% to evaluate the combined effects of slope and vegetation cover on runoff and erosion. All simulations assumed a rainfall duration of 30 min at a constant intensity of 60 mm h^{-1}, from a contributing area defined as a 30 × 100 m planar hillslope. To parameterize friction factor (ff), the simple depth feedback parameterization of Scoging *et al.* (1992) was used:

$$\mathrm{ff} = 14 - 0{\cdot}8\,h \qquad (1)$$

where h is the depth of runoff (mm). The key model parameter values are described in Table II.

For cold desert conditions, MAHLERAN model simulations indicate that runoff from all slopes is lower in shrublands than in grasslands (Figure 2), because of the higher hydraulic conductivity of shrubland soils (Boxell and Drohan, 2009). Following a moderate burn, runoff from all slopes is twice as high; and following a severe burn, runoff is approximately four times greater than preburn. It increases sharply as the slopes increase from 0–10%, then increases more gradually with gradient thereafter. These modelled results are generally consistent with experimental observations.

Even though runoff from the cold desert shrub functional group is lower, erosion (Figure 2) is slightly higher than from slopes in the grassland group (80% cover). The most likely reason is the higher proportion of readily entrained fine sediment in shrubland soils, which can be transported over longer distances than the coarser grassland sediment. After both moderate and severe burns, erosion greatly increases. Erosion from a 40% slope is nearly four times greater following a severe burn than when covered with grass (66% cover). The increase in erosion on post-fire grasslands becomes most pronounced at a slope of 10% for a moderate burn and 7·5% for a severe burn. This modelling analysis indicates that the slope threshold above which erosion accelerates is 10–12%. At a slope of 40%, erosion from severely burned grassland is nearly five times greater than from unburned grassland. This increase is much less than that estimated by Pierson *et al.* (2001, 2002, 2008a, 2009), but is a reasonable prediction given the effects of increasing scale on runoff and erosion processes from the plot to the hillslope scale (Parsons *et al.*, 2006).

For warm deserts, predicted runoff is much higher for shrubland than for unburned grassland (Figure 3). The extent and density of grass cover has a pronounced effect

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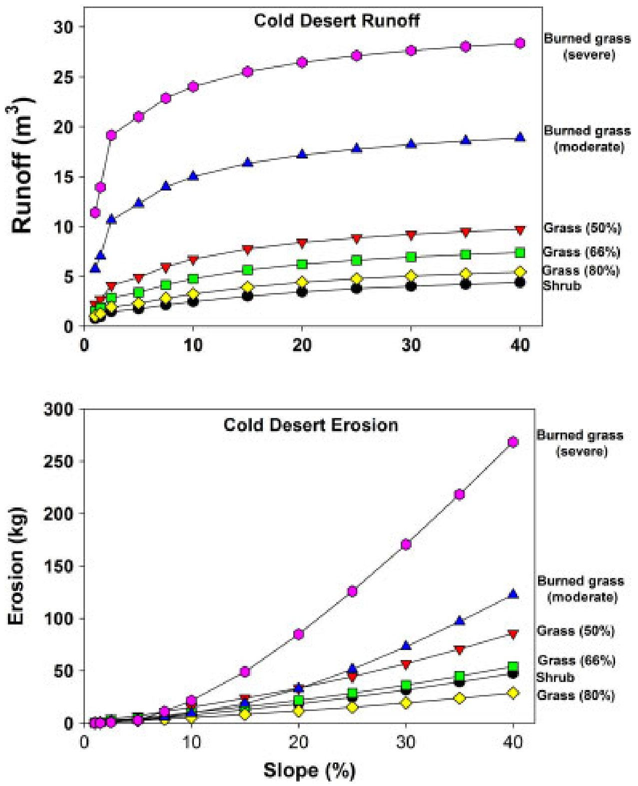

Figure 2. Cold deserts: changes in runoff (upper graphic) and erosion (lower graphic) for different surface cover types with changes in slope. Results are shown for slopes ranging from 1 to 40%, and for shrub, grass (50%, 66%, and 80% cover), moderately burned grass, and severely burned grass surface covers.

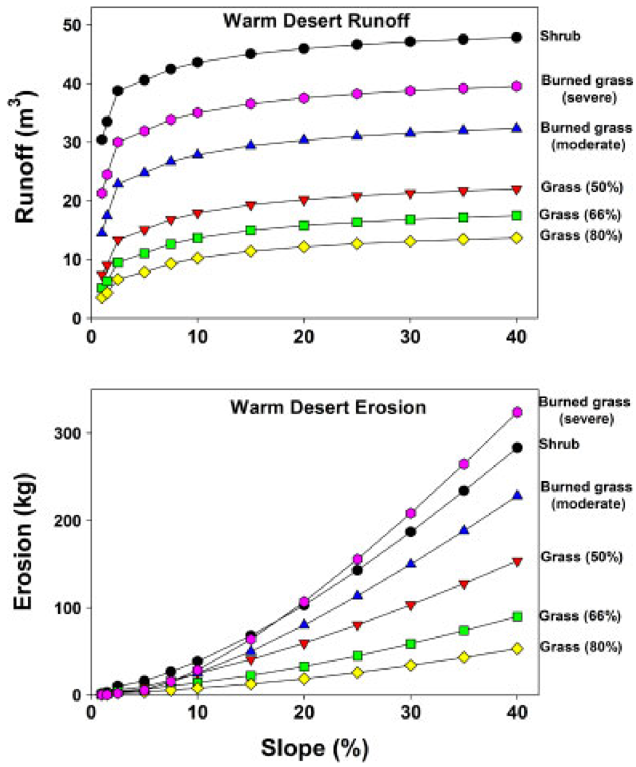

Figure 3. Warm deserts: changes in runoff (upper graphic) and erosion (lower graphic) for different surface cover types with changes in slope. Results are shown for slopes ranging from 1 to 40%, and for shrub, grass (50%, 66%, and 80% cover), moderately burned grass, and severely burned grass surface covers.

on runoff at the hillslope scale—a hillslope having 50% grass cover is predicted to generate almost double the runoff of a slope having 80% grass cover. Moderate or severe burning will greatly increase runoff from grassland slopes, but the amount is still less than from shrubland slopes. As with runoff simulations for cold desert regions, runoff increases greatly for all functional groups as slopes increase up to about 10°, after which the increase with gradient is more gradual.

Erosion, on the other hand, increases exponentially once the slope gradients exceed 10–15% (Figure 3). Erosion is relatively low for high grass cover (80%). Of all the functional groups, grasslands see the highest erosion on slopes greater than 15% following a severe burn that results in complete vegetation removal. Because burned grassland has a higher proportion of fine sediment and lacks a canopy to intercept rainfall, there is greater potential for sediment detachment by rainfall as well as a greater supply of fine sediment to be transported.

Collectively, these model predictions suggest that grass invasions will have different effects on runoff and erosion in warm deserts than in cold ones. In cold deserts, grass invasion will lead to higher erosion, particularly from slopes exceeding 15%. In contrast, in warm deserts grass invasion reduces surface runoff and erosion overall; and even following fire, erosion increases only marginally over that of unburned native shrublands.

VERTICAL FLUXES: SOIL WATER, ET, AND RECHARGE

Fundamental differences exist between the native shrubland communities and invasive grasslands that will influence the timing and rate of soil water use. Shrubs, in general, have deeper roots than grasses (Jackson *et al.*, 1996), particularly annual grasses (Abbott *et al.*, 1991), and therefore can extract water from greater soil depths. In addition, the leaf area index (LAI), which is correlated with transpiration (Kurc and Small, 2004), is generally higher for shrublands (Knapp *et al.*, 2008). Some studies have shown that exotic grasses use shallow water early in the season, while native shrubs use deep water later in the season (Frasier and Cox, 1994; Kulmatiski *et al.*, 2006).

On the basis of these differences, we would expect grasslands to use less soil water than shrublands; therefore, soils would generally have higher water content and more groundwater recharge. On the other hand, we know that invasive grasses—particularly annual grasses—green up earlier in the year than native vegetation, which would contribute to more rapid drying of the soil, at least in the early part of the year. These water use variables are further complicated by differences in the amount and distribution of precipitation. For example, if the wetting front rarely extends below the rooting zone of grasses, then rooting depth differences should have little influence. Finally, how much water enters the soil is also directly dependent on the type of vegetation cover,

Table III. A summary of soil water studies conducted on sagebrush steppe rangelands in the cold deserts of North America.

Source	Region	Technique	Period	Treatment	Treatment effect	Change in soil water	Depth instrumented (cm)
Gee *et al*. (1992)	Hanford Site, WA	Weighing lysimeter	—	Cheatgrass	Increase	62 mm year^{-1}	300
Gee *et al*. (1994)	Hanford Site, WA	Neutron probe	1988–1991	Cheatgrass	Increase	30–80 mm year^{-1}	180
Kremer and Running (1996)	Hanford Site, WA	Neutron probe	1992	Cheatgrass	Increase	46% greater	275
Link *et al*. (1990)	Hanford Site, WA	Neutron probe	1985–1989	Burned shrubs	Increase	14 mm year^{-1}	275
Seyfried and Wilcox (2006)	Snake River Plain, ID	TDR, Neutron probe	2003	Burned shrubs	Increase	60 mm year^{-1}	195
Sturges (1983)	Wyoming	Neutron probe	1969–1981	Herbicide	Increase	4–31% greater	180
Inouye (2006)	Southeast Idaho	Neutron probe	1999–2004	Native grasses	Increase	—	220
Cline *et al*. (1977)	Hanford Site, WA	Gravametric	1974	Cheatgrass	Increase	70 mm year^{-1}	180
Obrist *et al*. (2004)	Northern Nevada	TDR	2001–2002	Burned shrubs	Decrease	—	75
Forman and Anderson (2005)	Idaho National Lab, ID	Neutron probe	1995–2000	Crested wheatgrass	Increase	1·7–5·9% greater	240
Prevey *et al*. (2010a,b)	Cold Desert Shrub, SE Idaho	Neutron probe	2006–2009	Shrubs removed, cheatgrass invaded	Increase	21–35 mm year^{-1}	200

Treatment effect and change in soil water refer to the amount of soil water in treated compared to control plots that remained in their native sagebrush-steppe condition.

which modifies such factors as the distribution of snow drifts and the infiltration capacity of the soil.

Cold deserts

A number of studies have explicitly evaluated how the presence or absence of shrubs may affect soil water on sagebrush rangelands within the Great Basin and Colorado Plateau (Table III). These studies employed a number of different manipulative treatments and explored several variables, including cheatgrass versus sagebrush (Cline *et al*., 1977; Gee *et al*., 1992; Gee *et al*., 1994; Kremer and Running, 1996), unburned versus burned sagebrush (Link *et al*., 1990; Obrist *et al*., 2004; Seyfried and Wilcox, 2006), and sites where sagebrush had been removed versus sagebrush-covered plots (Sturges, 1980; Inouye, 2006; Prevey *et al*., 2010). Most of the research was conducted on undisturbed soils, but two studies used soil lysimeters filled with repacked soil (Gee *et al*., 1992, 1994).

All of this work (with the exception of Obrist *et al*., 2004, in which snow capture was enhanced under shrubs and soil water measured only to a depth of 75 cm) has found that soil water extraction is higher under native shrub communities than where shrubs are absent (burned and/or grass covered)—with the greatest differences at the deeper (>1 m) levels of the soil profile. Annual differences in soil storage ranged from 10 to 60 mm. In contrast, Obrist *et al*. (2004) found that soil water was about the same for burned and unburned sagebrush sites, except following periods of heavy snowfall, when soil water was higher under the unburned sagebrush. Presumably this is because the burned area, lacking canopy structure, had captured less wind-blown snow. Because Obrist *et al*. (2004) measured soil water only to a depth of 75 cm, their data may not reflect soil water differences related to differences in rooting depth.

Only a few studies have explicitly examined differences in ET between grasses and shrubs in cold desert regions. Two of these studies used gas exchange chambers (Obrist *et al*., 2003; Prater *et al*., 2006) and one used the Bowen ratio method (Prater and DeLucia, 2006b). In contrast to the soil water studies, summarized in Table III, these studies showed little difference in annual ET between the grass-covered and the shrub-covered sites. The greatest differences occurred in the spring, when ET was higher from the grass-covered sites—reflecting the earlier water use by cheatgrass. This finding is consistent with other soil water studies.

Transitional and warm desert regions

Surprisingly few studies have explored how invasive grasses alter soil water in the Mojave and Sonoran desert regions of North America. Some work has been done in the neighbouring Chihuahuan Desert to the southeast (Figure 1). The cumulative evidence from the Chihuahuan suggests that in deserts where snowfall is sparse and atmospheric evaporation demand is high year-round, any changes in vegetation cover will not significantly

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alter the soil water regime. We know that in these landscapes, most of the precipitation is lost to ET and little remains for recharge or runoff (Seyfried *et al*., 2005). It is unlikely that a shift from shrubland to grassland would change this. For example, in a study of the soil water dynamics at two sites in the Chihuahuan Desert of southeastern Arizona—a shrubland and a grassland—Scott *et al*. (2000) found that deeper infiltration (>30–50 cm) occurred only during wet winters when the vegetation was dormant. Moreover, even under wet conditions, moisture penetrated only to about 1 m, which was not below the root zone of either community. In another study, Kurc and Small (2004) found little difference in soil water or ET between native grasslands and shrublands in the Chihuahuan Desert in New Mexico. Similarly, Moran *et al*. (2008) found that total ET in a native Chihuahuan Desert grassland in Arizona was little affected following the invasion of Lehmann lovegrass (although soil evaporation made up a larger component of total ET than before the invasion). Examining this same invasion, Polyakov *et al*. (2010) found a temporary increase in the runoff ratio (R/P) during the transition year, at the small watershed (4 ha) scale; but once the invasion was complete, the ratio quickly returned to the same levels as found for the native grassland.

Modelling vertical fluxes

Our review of the literature suggests that grass invasion may lead to greater flux in cold deserts, but not in warm deserts—primarily because cold desert environments facilitate the movement of water below the root zone. The question that remains is what are the implications of higher soil water for deep recharge and groundwater response time? We used HYDRUS-1D (Simunek *et al*., 2008) to gain some insight into this question.

Model simulations were conducted for a single-layer soil profile to a depth of 10 m, under unit gradient conditions, for sand, loamy sand, loam, and silt loam soil textures (Schaap *et al*., 1998) (Table IV). The model was initialized with 24 years of meteorological data from a site on the Reynolds Creek Experimental Watershed in Southern Idaho (Station 076X59, available at ftp://ftp.nwrc.ars.usda.gov) during water years 1985–2008. The climate at this location (elevation 1207 m) is representative of much of the Great Basin that has undergone cheatgrass invasion. An additional 100 years of synthetic climate data having the same statistical characteristics as the 24 years of measured data was used as input to the model. Precipitation events were generated stochastically as a Poisson process, consisting of monthly storm arrival times and an exponential distribution of rainfall amount (D'Odorico *et al*., 2000). Maximum and minimum daily temperatures and vapour pressures were generated through a multivariate copulas random function, and solar radiation and wind speed were generated from normal distributions. Synthetic data were then used as input to the modified Penman equation (Allen *et al*., 1998), which generated the daily potential ET (PET).

PET was partitioned into potential evaporation (E) and potential transpiration (T) according to LAI and percent vegetative cover (Kemp *et al*., 1997) for grassland and shrubland, assuming 66% and 40% coverage, respectively (Table V) (Young *et al*., 2006), as a percentage of potential transpiration. Maximum rooting depths were 50 and 300 cm for grassland and shrubland canopies, respectively. Annual rainfall varied from 15 to 38 cm and averaged about 25 cm. Actual ET was obtained numerically, on the basis of PET components, root uptake, and soil hydraulic properties.

The simulation results, as illustrated by the loamy sand case, are summarized in Figure 4. As expected, the model predicted higher overall ET from the shrubland than from the grassland (mean values 25·4 vs 20·0 cm year^{-1}), primarily because predicted transpiration was higher in the shrubland (9·8 vs 3·4 cm year^{-1}). The higher shrubland ET led to a smaller amount of net soil recharge or storage than in grasslands (0·10 vs 5·22 cm year^{-1}).

Figure 5 plots the time (in years) for the wetting front to arrive at the specified depth for each vegetation and soil type. This information enables us to assess the time scales at which soil water, if altered in content or amount, may affect either the quality or quantity of groundwater. For the grassland, recharge was predicted for all four soil textures. As expected, travel times for sand and loamy sand soils (~3–6 years) were much faster than those for loam and silt loam soils (39 and 44 years, respectively)—the latter types being more

Table IV. Soil hydraulic properties for numerical simulations.

Soil type	θ_r - cm^3 cm^{-3}-	θ_s - cm^3 cm^{-3}-	α - cm^{-1}-	n —	K_s - cm d^{-1}-	l —
Sand	0·07	0·40	0·145	2·68	700	0·5
Loamy sand	0·07	0·40	0·124	2·28	350	0·5
Loam	0·07	0·40	0·036	1·56	25·0	0·5
Silt loam	0·07	0·40	0·020	1·41	10·0	0·5

θ_r - residual water content.
θ_s - saturated water content.
α—approximately the inverse of the air entry value.
n - empirical shape factor.
K_s- saturated hydraulic conductivity.
l—pore size distribution parameter.

Table V. Percentage of potential transpiration attributed to specific growth forms for above (and below) average winter precipitation water years for both the grassland and shrubland guilds.

	LAI	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
						% PT							
***Grassland* (66% Cover)**													
Grass and forb[a]	0·9	0·0 (0)	0·0 (0)	0·0 (0)	0·0 (0)	0·0 (0)	1·00 (1·00)	1·00 (1·00)	1·00 (1·00)	0·0 (0)	0·0 (0)	0·0 (0)	0·0 (0)
***Shrubland* (40% Cover)**													
Big Sage[1]	1·0	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)	0·65 (0·65)
Drought Deciduous Shrub[b]	0·84	0·0 (0)	0·0 (0)	0·0 (0)	0·0 (0)	0·0 (0)	0·0 (0)	0·13 (0·13)	0·13 (0·13)	0·32 (0·32)	0·32 (0·32)	0·32 (0·32)	0·32 (0·32)
Grass and forb[a]	0·9	0·0 (0)	0·0 (0)	0·0 (0)	0·0 (0)	0·0 (0)	0·17 (0)	0·17 (0)	0·17 (0)	0·0 (0)	0·0 (0)	0·0 (0)	0·0 (0)

LAI, leaf area index ($m^2\ m^{-2}$).

[a] Hibbard *et al.* (2005).
[b] Calculated from Steinwand *et al.* (2001).

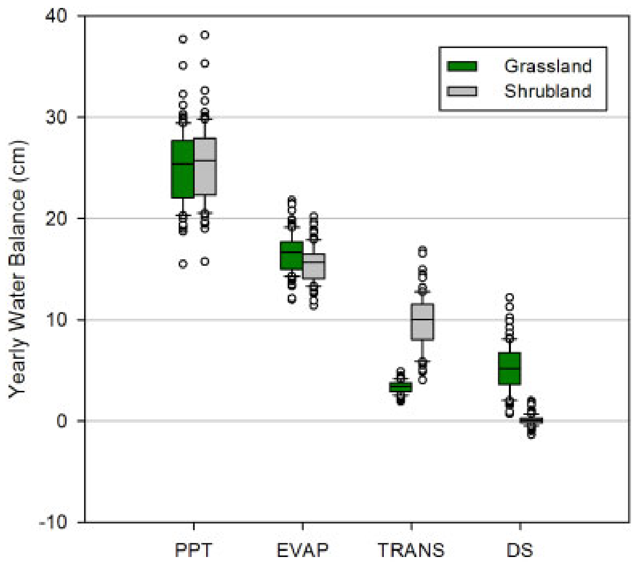

Figure 4. Box-and-whisker plots showing water budget components (PPT, precipitation; EVAP, evaporation, TRANS, transpiration, and DS, change in soil storage) for each water year for the loamy sand soil (100 years total). Boxes are 25% and 75% percentiles, whiskers are 5 and 95% percentiles, and symbols lie outside of 5 and 95% percentiles.

representative of soils in the Great Basin. Our modelling results suggest then that a soil water recharge rate of 5 cm year^{-1}, brought about by grass invasion, could lead to deeper (10-m depth) groundwater recharge after only 40–50 years, highlighting the close coupling between vegetation functional type and groundwater resources. Obviously, groundwater recharge times in grasslands would be longer if depth to groundwater was greater than 10 m and shorter if that depth was less than 10 m. For the shrubland site (Figure 5B), recharge to the 10-m depth occurs only in the sand soil type. For the loam and silt loam soils, no recharge was predicted to reach deep layers within the time frame assessed, although for the loamy sand soil type, the wetting front did reach a depth of 6 m after 73 years and recharge was predicted for years with above-average precipitation.

ENERGY BUDGETS: ALBEDO AND WEATHER

At the regional scale, changes in vegetation have the potential to alter energy budgets and therefore can influence the weather (Pielke *et al*., 2002; Bonan, 2008; Jackson *et al*., 2008). Establishing a link between land cover and climate is complicated, generally requiring some sort of comparative analysis using regional- or global-scale atmospheric circulation models. This approach has been used extensively to gain a better understanding of how changes in land cover, such as desertification and deforestation, affect climate (Dickinson and Kennedy, 1992; Hendersonsellers *et al*., 1993; Xue and Shukla, 1993; Asner and Heidebrecht, 2005; Beltran-Przekurat *et al*., 2008). These studies have shown that deforestation, desertification, and the conversion of savannas to grasslands have the potential to both lower rainfall and raise temperatures because of changes to albedo and ET.

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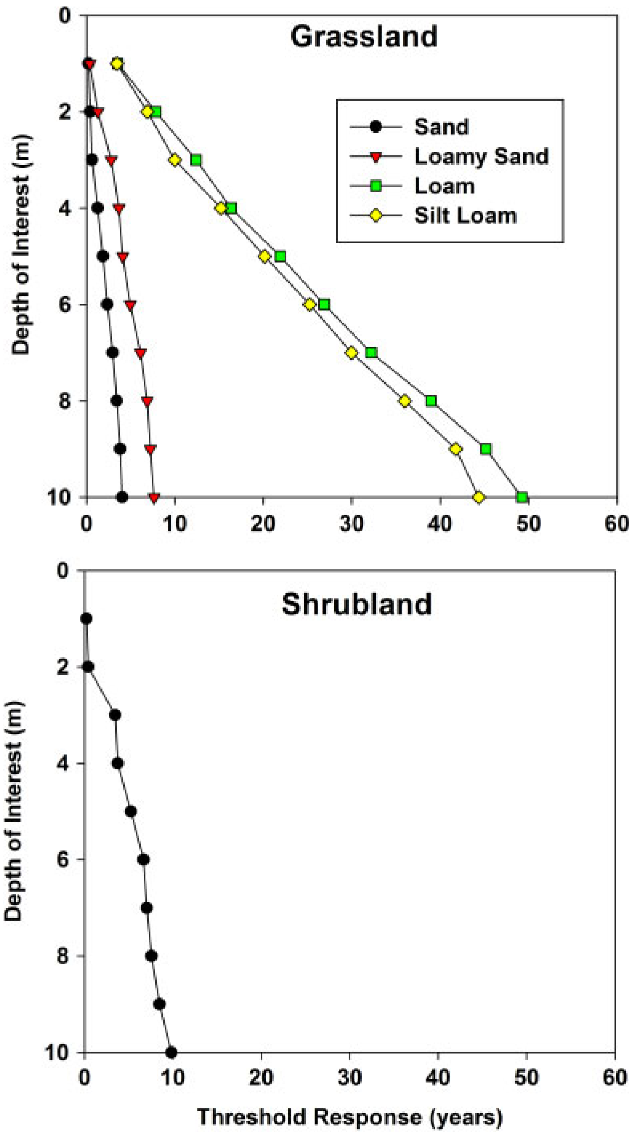

Figure 5. Response time for wetting front arrival at particular depths for (upper graphic) grassland and (lower graphic) shrubland. For the shrubland simulation, recharge only occurred where textures were sandy. Values were calculated on the basis of a 25% increase in maximum observed water content, signalling wetting front arrival.

Some have speculated that the conversion of shrublands to grasslands may have a similar effect (Chambers *et al.*, 2007); however, no such linkage has yet been verified.

In addition to changes in ET, vegetation conversion may affect albedo and aerodynamic exchange properties. Comparative studies are rare for either cold or warm deserts, but grasslands generally have higher shortwave albedo than shrublands (Baldocchi *et al.*, 2004; Asner and Heidebrecht, 2005; Beringer *et al.*, 2005). Albedo differences are amplified in the summer after invasive grasses have senesced and for months have a pale, straw-like appearance. Available energy (the difference between net radiation and heat flux/storage to the ground and vegetation canopy elements) is lower in the higher albedo grassland communities than in the shrublands (Prater and DeLucia, 2006a).

Taken together, these studies indicate that we do not currently have the capability to predict how large-scale conversion of arid shrublands to annual grasslands will influence the relative partitioning of available energy into latent and sensible heat. As demonstrated elsewhere, both the albedo and the Bowen ratio of vegetated surfaces potentially influence regional climate (Hoffmann and Jackson, 2000; Pielke, 2001; Beringer *et al.*, 2005; Chapin *et al.*, 2005; Gibbard *et al.*, 2005; Diffenbaugh, 2009), and it is reasonable to assume that they have similar effects in the cold and warm deserts of western North America. More work will be required to confirm whether this assumption is correct.

SUMMARY AND CONCLUSIONS

Horizontal fluxes

On the basis of our analysis, we conclude that the influence of grass invasion on surface runoff and erosion is different in cold desert regions than in warm ones. In cold deserts, runoff and erosion will increase with exotic grass invasion, whereas in warm deserts they are likely to decrease. However, this conclusion is tempered by the fact that much more information relative to horizontal fluxes is available for the cold desert regions, especially the Great Basin. Data for warm and transitional deserts are limited, highlighting a major research need.

For the Great Basin, the extent to which invasion by exotic grasses will lead to changes in runoff and erosion will depend on burning frequency, slope gradient, and the condition of the shrubland replaced by the exotic grassland. Following burning, erosion will be greatly accelerated on steep slopes (>15%), and runoff is likely to be somewhat higher as well. For unburned slopes, runoff and erosion are likely to be higher for exotic grasslands than for healthy shrublands that have a good mix of perennial grasses in the interspaces. If the intercanopy is mostly bare, however, conversion of a shrubland to an exotic grassland may cause little change in runoff and erosion and may even lower erosion rates. Where slopes are relatively flat (<5%), runoff and erosion are already very low and probably will not be greatly affected by vegetation change.

At the watershed scale in cold deserts, the weight of evidence suggests that the conversion of native shrublands to invasive grasslands does increase the risk of flooding and sedimentation—largely because of the decrease in overall cover as well as the increasing extent and frequency of fires. The more steeply sloping the terrain, the higher the vulnerability. At regional scales, we do not expect that changes in vegetation cover will affect water or sediment budgets. Separating the effects of exotic grass invasion on runoff and erosion from the disturbances that typically precede invasion remains an important research need.

For the warm and transitional deserts, grass invasion of native shrublands is likely to lead to lower runoff and erosion because of the net increase in cover. For periods immediately following burning, erosion may be higher than when the region was native shrubland, but probably not significantly higher considering the greater extent of bare ground in shrublands.

Vertical fluxes

The influence of grass invasions on vertical fluxes of water (evapotranspiration, soil water, groundwater recharge) also differs between cold and warm desert regions. In cold deserts, the weight of evidence suggests that grass invasion can in many (but not all) cases lead to higher soil water and groundwater recharge (Seyfried and Wilcox, 2006). This evidence comes largely from studies that have evaluated differences in soil water. The few studies that measured ET found no difference between cold and warm deserts; however, longer-term studies are needed to confirm these results. Under certain conditions, conversion to grassland may lead to less snow accumulation or drifting, in which case soil water storage may be lower. On the basis of our modelling analysis, we conclude that increased soil water recharge may affect groundwater, but there may be a lag of two to four decades (depending on depth to groundwater) before an effect is seen. Of course, for locations where depth to groundwater (or bedrock) is relatively shallow (less than 3 m), the effects could be much more rapid.

For the warm deserts, again relatively little work has been done directly comparing vertical fluxes in areas of native shrubland versus those invaded by exotic grasses. From the information that is available, we conclude that grass invasion will have little effect on vertical fluxes—primarily because no matter what the vegetation cover, most if not all the available water will be transpired or evaporated.

With respect to whether and how changes in surface characteristics might have regional-scale effects, such as changes in climate, we are unable to draw a definitive conclusion. It is possible that grass invasion may influence regional climate—especially in the Great Basin where the spatial extent of the conversion is greater—but much more detailed studies, both modelling and climate comparisons, need to be done before a definitive assessment can be made.

Research needs

Our review has highlighted a number of gaps in the available data that could shed light on the ecohydrological implications of the invasion of shrublands by exotic grasses. The need for research to fill these gaps is especially apparent for the warm deserts, for which we have identified two major research topics: (1) a systematic and comprehensive assessment of the extent of grass invasion, similar to that done for the Great Basin by Bradley and Mustard (2008); and (2) field-based comparisons of horizontal and vertical fluxes in areas covered by invasive grasses and in native shrublands. For both regions, studies that provide comprehensive measurements of all the water energy-budget components at multiple scales could be particularly insightful.

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