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SPECIAL FEATURE

GRASS–WOODLAND TRANSITIONS

Shifts in plant functional types have time-dependent and regionally variable impacts on dryland ecosystem water balance

John B. Bradford[1]*, Daniel R. Schlaepfer[2], William K. Lauenroth[2] and Ingrid C. Burke[2]

[1]*U.S. Geological Survey, Southwest Biological Science Center, 2255 N. Gemini Dr., Flagstaff, AZ 86001, USA; and* [2]*Department of Botany, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA*

Summary

1. Terrestrial vegetation influences hydrologic cycling. In water-limited, dryland ecosystems, altered ecohydrology as a consequence of vegetation change can impact vegetation structure, ecological functioning and ecosystem services. Shrub steppe ecosystems dominated by big sagebrush (*Artemisia tridentata*) are widespread across western North America, and provide a range of ecosystem services. While sagebrush abundance in these ecosystems has been altered over the past century, and changes are likely to continue, the ecohydrological consequences of sagebrush removal and reestablishment remain unclear.

2. To characterize the immediate and medium-term patterns of water cycling and availability following sagebrush plant community alteration, we applied the SOILWAT ecosystem water balance model to 898 sites across the distribution of sagebrush ecosystems, representing the three primary sagebrush ecosystem types: sagebrush shrublands, sagebrush steppe and montane sagebrush. At each site, we examined three vegetation conditions representing intact sagebrush, recently disturbed sagebrush and recovered but grass-dominated vegetation.

3. Transition from shrub to grass dominance decreased precipitation interception and transpiration and increased soil evaporation and deep drainage. Relative to intact sagebrush vegetation, simulated soils in the herbaceous vegetation phases typically had drier surface layers and wetter deep layers.

4. Our simulations suggested that alterations in ecosystem water balance may be most pronounced in vegetation representing recently disturbed conditions (herbaceous vegetation with low biomass) and only modest in conditions representing recovered, but still grass-dominated vegetation. Furthermore, the ecohydrological impact of simulated sagebrush removal depended on climate; while short-term changes in water balance were greatest in wet areas represented by the montane sagebrush ecosystem type, medium-term impacts were greatest in dry areas of sagebrush shrublands and sagebrush steppe.

5. *Synthesis*. This study provides a novel, regional-scale assessment of how plant functional type transitions may impact ecosystem water balance in sagebrush-dominated ecosystems of North America. Results illustrate that the ecohydrological consequences of changing vegetation depend strongly on climate and suggest that decreasing woody plant abundance may have only limited impact on evapotranspiration and water yield.

Key-words: *Artemisia tridentata*, deep drainage, ecosystem water balance, evapotranspiration, plant–soil (below-ground) interactions, water yield

Introduction

The structure and abundance of terrestrial vegetation substantially influences patterns of water cycling and overall ecosystem water balance (Rodriguez-Iturbe *et al.* 1999). In dryland areas, where many ecological processes, including vegetation structure and function, are strongly limited by access to water, ecohydrological changes as a result of vegetation transition can impact ecological functioning and ecosystem services (Turnbull *et al.* 2012). Shifts in plant functional type can impact soil water availability and alter evaporation, transpiration and water yield (Sala *et al.* 1997; Prevéy *et al.* 2010).

*Correspondence author. E-mail: jbradford@usgs.gov

Although transitions in plant functional types over large areas are increasingly common and well recognized in dryland regions (D'Antonio & Vitousek 1992; Clarke, Latz & Albrecht 2005), the consequences of these changes for water cycling, especially over large areas, have received less attention (although see Wilcox *et al.* 2012; Huxman *et al.* 2005).

Several early paired-watershed studies in semi-arid areas reported that woody plant eradication decreased evapotranspiration and increased water yield (Folliott & Thorud 1977; Hibbert, Davis & Knipe 1982; Baker 1984; Davis 1984). These results, combined with studies demonstrating lower evapotranspiration when trees were removed in mesic climates (Zhang, Dawes & Walker 2001), promoted widespread acceptance of woody plant influences on water balance. However, recent experiments and syntheses have suggested that reduced evapotranspiration and enhanced water yield as a result of woody plant removal may only be significant in the semi-arid, subtropical, winter precipitation-dominated climates represented by the initial studies (Hibbert 1983; Huxman *et al.* 2005; Wilcox *et al.* 2005) and that cold dryland regions and/or dryland regions that do not receive precipitation primarily in the winter may respond differently (Wilcox *et al.* 2012).

The potential ecohydrological impacts of a shrub to grassland transition are particularly relevant for areas historically dominated by big sagebrush (*Artemisia tridentata*) because these ecosystems are widespread (covering approximately 500 000 km^2 in western North America) and rapidly changing (Knick *et al.* 2011; Schlaepfer, Lauenroth & Bradford 2012b). Vegetation in sagebrush ecosystems has been heavily altered over the past half-century by agriculture (Knick *et al.* 2011), shrub removal treatments designed to promote grass production (Beck, Connelly & Wambolt 2012), wildfire (Bukowski & Baker 2012) and exotic annual grasses invasion (Knapp 1996). Most of the drivers of change are not anticipated to decline in the coming decades (Schroeder *et al.* 2004), especially considering the anticipated rapid velocity of climate change in the sagebrush region (Loarie *et al.* 2009). Additionally, sagebrush recovers slowly following disturbance (Anderson & Inouye 2001) and active sagebrush restoration strategies are minimally successful (Davies *et al.* 2011).

Disturbances, natural or anthropogenic, that dramatically reduce the abundance of woody plants in sagebrush ecosystems have predictable impacts on vegetation structure, although the impacts vary with time since disturbance. In the first few years following disturbance, the biomass of perennial grasses is often not elevated above undisturbed conditions (Link *et al.* 1990; Davies, Bates & Miller 2007; Boyd & Svejcar 2011; Davies, Bates & Nafus 2011), although abundance of invasive annual grasses can be elevated in situations where they were present prior to disturbance (Prevéy *et al.* 2010). In approximately 2–7 years, grass biomass typically increases to levels significantly higher than in the original mixed community (Beck, Connelly & Reese 2009; Boyd & Svejcar 2011; Davies, Bates & Nafus 2012). This altered state often persists for decades (Wambolt & Payne 1986; McDaniel, Allen Torell & Ochoa 2005; Beck, Connelly & Reese 2009) with recovery of shrub biomass and canopy structure occurring at roughly 30–40 years post-disturbance (Watts & Wambolt 1996; McDaniel, Allen Torell & Ochoa 2005; Lesica, Cooper & Kudray 2007; Avirmed *et al.* 2014). Thus, the dynamics of sagebrush vegetation can be characterized by examining three vegetation conditions: intact sagebrush vegetation, low biomass grass vegetation (representing a recent disturbance), and grass-dominated but recovered vegetation (representing conditions between several years and decades after disturbance).

Previous studies of water balance response to sagebrush removal often examined a small number of easily measured components at one or a few sites, typically for only a few years. Results have suggested that, following sagebrush removal, there is no consistent impact on water content of shallow soils (top 20–50 cm), while water content of deeper soils can increase but often only for the first several years (Hedrick *et al.* 1966; Link *et al.* 1990; Inouye 2006; Seyfried & Wilcox 2006). Studies of long-term ecohydrological impacts are few and site specific, but there is evidence that water depletion increases in shallow soils and decreases in deep soils following sagebrush removal and that this effect can persist for 20 years (Sturges 1993). While direct measurements of deep drainage (water moving through the soil profile to groundwater) are rare, observations of higher water content and lower water depletion in deep layers when sagebrush is removed may indicate increased drainage (Sturges 1993; Seyfried *et al.* 2005).

Focusing on sagebrush ecosystems, we examined two fundamental unanswered questions about the ecohydrological consequences of plant functional type transitions in dry lands. First, how do short-term water balance changes following sagebrush removal differ from medium-term changes reflecting recovered, but still grass-dominated vegetation? Secondly, how do climate or soil conditions across a wide geographic area influence the ecohydrological consequences of sagebrush removal? We modelled ecosystem water balance at 898 sites spanning the geographical distribution of sagebrush ecosystems. Our objective was to characterize the ecohydrological consequences of a transition in plant functional types in sagebrush ecosystems. Specifically, we assessed patterns of water balance in vegetation comprising a) shrub and grass mixture of intact sagebrush vegetation, b) grass only with reduced biomass and c) grass only with recovered biomass (Fig. 1).

Materials and methods

STUDY SITES

We assessed ecosystem water balance in 898 sites that span the distributional range of big sagebrush (Fig. S1.1 in Supporting Information). Sites were randomly selected from the distribution of three sagebrush ecosystem types (as defined by the US GAP analysis program: http://gapanalysis.nbii.gov) and described previously (Schlaepfer, Lauenroth & Bradford 2012b). Average mean annual temperature across all sites is 6.7 °C (minimum of −1.7 °C and maximum of 16) and average annual precipitation is 352 mm (159–829) (Fig. 2). These 898 sites include 357 in sagebrush shrubland (average mean annual temperature and precipitation 7.6 °C and 301 mm), 348 in sagebrush steppe (average 7.2 °C and 330 mm,) and 193 in the montane sagebrush ecosystem type (average 4.0 °C and 488 mm). Additional geographic,

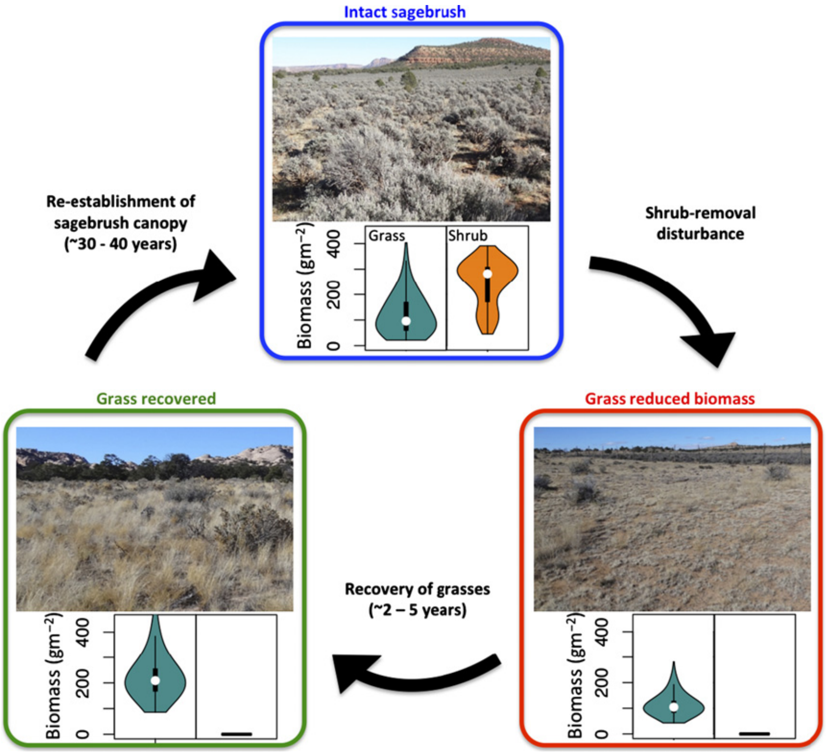

Fig. 1. Conceptual illustration of three vegetation conditions for sagebrush ecosystems including undisturbed (intact sagebrush), recently disturbed (reduced biomass grass) and after several years of herbaceous recovery (grass recovered). Violin plots illustrate the distribution of aboveground biomass for grasses and shrubs provided to SOILWAT, as detailed in the text.

climatic and edaphic information about the sites within each of the three sagebrush ecosystem types is available in Table 1 of Schlaepfer, Lauenroth & Bradford (2012b).

SIMULATION FRAMEWORK

We utilized SOILWAT, a daily time step, multiple soil layer, process-based, simulation model of ecosystem water balance (Parton 1978; Bradford & Lauenroth 2006; Lauenroth & Bradford 2006). SOILWAT has been applied and validated in dryland ecosystems, including grasslands (Parton 1978), sagebrush ecosystems (Schlaepfer, Lauenroth & Bradford 2012b) and low-elevation forests (Bradford, Schlaepfer & Lauenroth 2014). Inputs to SOILWAT include weather conditions (mean daily temperature and precipitation, mean monthly relative humidity, wind speed and cloud cover, latitude), vegetation (monthly live and dead biomass and litter as well as vegetation's active root depth profile) and soil properties (texture of each soil layer) to simulate the daily ecosystem water balance. SOILWAT estimates interception by vegetation and litter, evaporation of intercepted water, snow melt and loss (sublimation and wind redistribution), infiltration into the soil profile, percolation and hydraulic redistribution for each soil layer, bare soil evaporation, transpiration from each soil layer and deep drainage (Lauenroth & Bradford 2006; Schlaepfer, Lauenroth & Bradford 2012b). Potential evapotranspiration in SOILWAT is calculated using the Sellers' (1964) formulation of Penman (1948) which incorporates day length effects. A validation of SOILWAT for grasslands is available in Lauenroth *et al.* (1994) and for shrublands in Schlaepfer, Lauenroth & Bradford (2012b) and Bradford, Schlaepfer & Lauenroth (2014).

SOILWAT's estimation of canopy interception was modified for these runs. Precipitation interception is calculated as a linear function of daily precipitation: Intercepted precipitation = S*PPT + I, where the slope (S) and intercept (I) are determined by vegetation conditions. For shrubs, leaf area index (LAI, calculated from total biomass divided by biomass per unit leaf area: 372 g/LAI unit) is converted into % cover using the LAI conversion parameter (2.22 for shrubs; Schlaepfer, Lauenroth & Bradford 2012b). % cover is multiplied by height to estimate vegetation abundance (here called vegcov), which is used to estimate the S and I. Hull (1972) measured throughfall in plots with varying density of sagebrush plants. Assuming that average radius and height of sagebrush plants in Hull (1972) were 35 and 65 cm, respectively (consistent with Belmonte Serrato & Romero Diaz 1998; Flerchinger & Pierson 1991), we estimated vegcov for those treatments. Assuming that the difference between total precipitation and throughfall measured in Hull was a 50–50% mix of interception and stemflow, a proportion consistent with other studies in semi-arid shrublands (Belmonte Serrato & Romero Diaz 1998; Carlyle-Moses 2004), we used the proportion of rainfall lost to interception reported in Hull as an estimate S and quantified how S depended on vegetation cover, assuming that $S = 0$ when vegetation cover is 0. I was estimated using values reported in (Belmonte Serrato & Romero Diaz 1998), assuming that $I = 0$ when vegetation cover is 0. The resulting relationship between PPT and interception is consistent with previous studies (Hull 1972; West & Gifford 1976; Belmonte Serrato & Romero Diaz 1998; Domingo *et al.* 1998; Carlyle-Moses 2004). Other modifications to SOILWAT include the addition of hydraulic redistribution (Schlaepfer, Lauenroth & Bradford 2012b). Because empirical evidence indicates that hydraulic redistribution occurs in grasses as well as woody plants (Yoder & Nowak 1999; Espeleta, West & Donovan 2004), these simulations include hydraulic redistribution for woody and herbaceous roots.

PARAMETERS AND INPUT DATA

The primary categories of information required by SOILWAT include weather, soils and vegetation. For each site, we extracted interpolated weather data from 1/8-degree gridded, daily weather data from 1980 to 2010 (Maurer *et al.* 2002), and the first year of the simulation period was discarded for analysis to avoid impacts of assumptions about initial soil water content. We obtained estimates of mean monthly relative humidity, cloud cover and wind speed data from the 'Climate

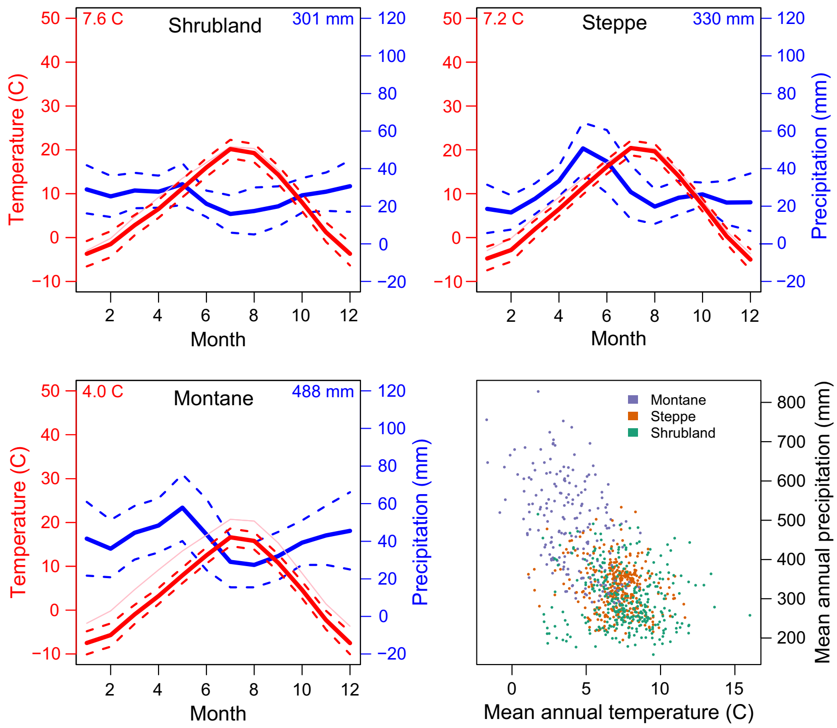

Fig. 2. Mean monthly climate conditions of sites within the three sagebrush ecosystem types and scatterplot of mean annual precipitation vs. mean annual temperature for all sites. Solid lines are means among sites within an ecosystem type and dotted lines are standard deviations.

Table 1. Median (and lower and upper quantiles defining 95% of sites) for water balance components, partitioned into three sagebrush ecosystem types, under three vegetation treatments. Rain and snow do not differ among vegetation treatments

		Native vegetation			Reduced biomass grass-only vegetation			Grass-only vegetation		
Water balance component	Ecosystem type	Median	0.025	0.975	Median	0.025	0.975	Median	0.025	0.975
Rain	Shrubland	–	–	–	212	143	348	–	–	–
	Steppe	–	–	–	269	176	349	–	–	–
	Montane	–	–	–	283	179	418	–	–	–
Snow	Shrubland	67	28	163	67	28	163	67	28	163
	Steppe	59	30	161	59	30	161	59	30	161
	Montane	188	73	411	188	73	411	188	73	411
Sublimation	Shrubland	39	15	86	38	15	85	38	15	85
	Steppe	37	18	82	37	18	81	37	18	81
	Montane	82	40	134	82	39	132	82	39	132
Interception	Shrubland	50	32	79	25	15	41	32	21	64
	Steppe	55	41	78	32	20	42	41	25	61
	Montane	62	36	111	32	19	50	53	24	108
Soil Evaporation	Shrubland	76	51	105	111	75	160	94	64	128
	Steppe	94	59	127	139	91	180	113	74	138
	Montane	70	37	103	116	73	159	81	42	114
Transpiration	Shrubland	79	32	184	65	21	158	78	28	185
	Steppe	106	55	173	81	36	144	105	49	173
	Montane	151	66	244	126	50	212	151	67	239
Drainage	Shrubland	26	7	131	32	10	141	28	9	135
	Steppe	17	6	108	22	8	117	18	7	110
	Montane	100	10	279	116	14	303	101	11	280

Maps of the United States' (http://cdo.ncdc.noaa.gov/cgi- bin/climaps/climaps.pl). Elevation estimates (RMSE = 2.44 m) were obtained from the 30 × 30 m^2 National Elevation Dataset (http://ned.usgs.gov). We utilized site-specific estimates of soil texture and depth. Soil texture (sand, silt and clay proportions for each layer) and depth at each site were derived from a version of the NRCS STATSGO data set gridded to 1 km^2 (Miller & White 1998). Soil textures at these sites span a wide range of conditions (Fig. S1.4, S1.5) and are not strongly related to climate conditions (correlation coefficients between per cent sand or clay and mean annual temperature or precipitation are all < 0.07). For this analysis, we simulated 9 soil layers (bottom depths of 5, 10, 20, 30, 40, 60, 80, 100 and 150 cm, unless soils were more shallow). Vegetation in SOILWAT is represented by monthly total above-ground biomass, live above-ground biomass, litter biomass and rooting distribution, expressed as transpiration coefficients for each soil layer (details of calculations provided in Appendix S2). Briefly, plant functional type composition (proportions of shrubs, C_3 grasses and C_4 grasses) is calculated at each site from climate (Paruelo & Lauenroth 1996). For each functional group, monthly aboveground total, live and litter biomass are calculated using precipitation to influence biomass abundance and temperature to influence growing season length. Root depth distributions (Schenk & Jackson 2003) are scaled to total soil depth and used to estimate transpiration coefficients for each functional type. Site-specific plant functional group composition and aggregate values for each sagebrush ecosystem type are available in Fig. S1.6. Site-specific monthly biomass and transpiration coefficients are calculated as a weighted average of the three functional types based on composition (Fig. S2.6, S2.7).

SCENARIOS

We examined three scenarios representing alternative vegetation conditions (Fig. 1) and ran SOILWAT three times for each site, implementing each vegetation condition. First, representing unaltered sagebrush ecosystems, we simulated native vegetation with the proportion of shrubs and grasses determined by climatic conditions as described above. Secondly, we simulated grass biomass at only 50% of its potential based on climate (as above). This represents where woody plants were recently removed and grasses have not yet recovered, a condition described in several studies examining the ecohydrological consequences of sagebrush removal (Link *et al.* 1990; Davies, Bates & Miller 2007; Boyd & Svejcar 2011; Davies, Bates & Nafus 2011). Thirdly, we simulated grass-only with grass biomass based on precipitation and temperature (see Appendix S2). This represents where woody plants have been removed and grasses have recovered from the disturbance and expanded to replace the woody plants (Sturges 1993; Boyd & Svejcar 2011; Davies, Bates & Nafus 2012).

We characterized water balance responses for 898 sites and averaged the resulting water balance components across the entire 30-year simulation period for each site. To examine the influence of climatic and soil conditions, we conducted linear regressions of individual water balance responses as a function of mean annual precipitation, mean annual temperature, average soil sand and clay content. All dependent and independent variables were examined for reasonable conformance to normality and transformed as necessary using natural logarithm or square root to achieve both skew and kurtosis between −1 and 1. Relationships were back-transformed for presentation. All analyses were conducted in R (R Core Team 2013).

Results

SOILWAT simulation of rain and snowfall is not influenced by vegetation conditions, so these processes did not differ among vegetation treatments (Table 1). However, rain and snowfall do vary among the sites that represent the three sagebrush ecosystem types among ecosystem types. Rainfall was lowest for the sites in shrubland ecosystem type, intermediate at the steppe ecosystem sites and highest at the montane sites. In contrast, snowfall and sublimation were lowest at the steppe sites, slightly higher at the shrubland sites and substantially higher at the montane sites. Potential evapotranspiration and sublimation varied only very modestly among vegetation treatments.

Simulated interception losses from the plant canopy and litter were lowest in reduced biomass grass vegetation, intermediate in the grass-only vegetation and highest in native, mixed vegetation (Fig. 3a,e,i). Interception was highest in the montane sagebrush sites, although differences between ecosystem types were modest in the reduced biomass grass vegetation. Interception differences between the vegetation treatments were driven primarily by canopy interception; while median litter interception varied only 2–3 mm year^{-1} among treatments, canopy interception was 23–32 mm year^{-1} (depending on ecosystem type) higher in intact sagebrush than reduced biomass grass vegetation. Higher interception in the intact sagebrush vegetation and lower interception in the reduced-biomass grass vegetation, compared with the grass-only vegetation, was consistent throughout the year (Fig. 3a,e,i). Compared with intact sagebrush vegetation, interception was lower for both grass vegetation treatments at almost all sites, especially for the reduced biomass grass, but the magnitude of the decrease depended on precipitation. For the reduced biomass grass vegetation, the magnitude of decrease was greatest at the higher precipitation montane ecosystem sites. By contrast, for the grass-only vegetation, the magnitude of decrease was greatest at the lower precipitation shrubland and steppe sites (Fig. 4a,b).

Estimated evaporation from soil was highest in the reduced biomass vegetation, intermediate in the grass vegetation and lowest in the intact sagebrush vegetation. Bare soil evaporation was consistently higher at sagebrush steppe sites and lower in montane and shrubland sites. Higher soil evaporation following shrub removal, especially in the reduced-biomass grass vegetation, was consistent throughout the warm season and most pronounced during the summer in all ecosystem types (Fig. 3b,f,j). Bare soil evaporation was only weakly related to mean annual precipitation in any vegetation type. Although all ecosystem types displayed highest soil evaporation with reduced biomass grass and lowest evaporation with mixed vegetation, the magnitude of those differences varied with precipitation (Fig. 4c,d). While total evaporative losses (sum of sublimation, interception and bare soil evaporation) were consistently higher in the reduced biomass grass vegetation than in intact sagebrush vegetation (median 9 mm year^{-1} higher at shrubland and montane sites, 20 mm year^{-1} higher at steppe sites), annual evaporation in grass vegetation was similar to intact sagebrush vegetation (median differences < 2 mm year^{-1}).

Simulated transpiration was similar between the intact sagebrush vegetation and the grass vegetation and lower in the reduced biomass grass vegetation. Peak seasonal transpiration rates were substantially higher at montane sites, and transpiration in the reduced biomass vegetation was consistently lower during the early and peak growing season periods, but similar to the other vegetation types during the fall and winter. Relative to the intact sagebrush vegetation, transpiration from grass vegetation was slightly higher in the spring and lower at the seasonal peak, especially at shrubland and steppe sites (Fig. 3c,g,k). Total transpiration was positively related to precipitation in all vegetation types. Transpiration in the reduced biomass grass vegetation was consistently lower than the other vegetation types, and the difference increased with precipitation (Fig. 4e,f). Lower transpiration in the reduced biomass grass vegetation was most pronounced in shallow

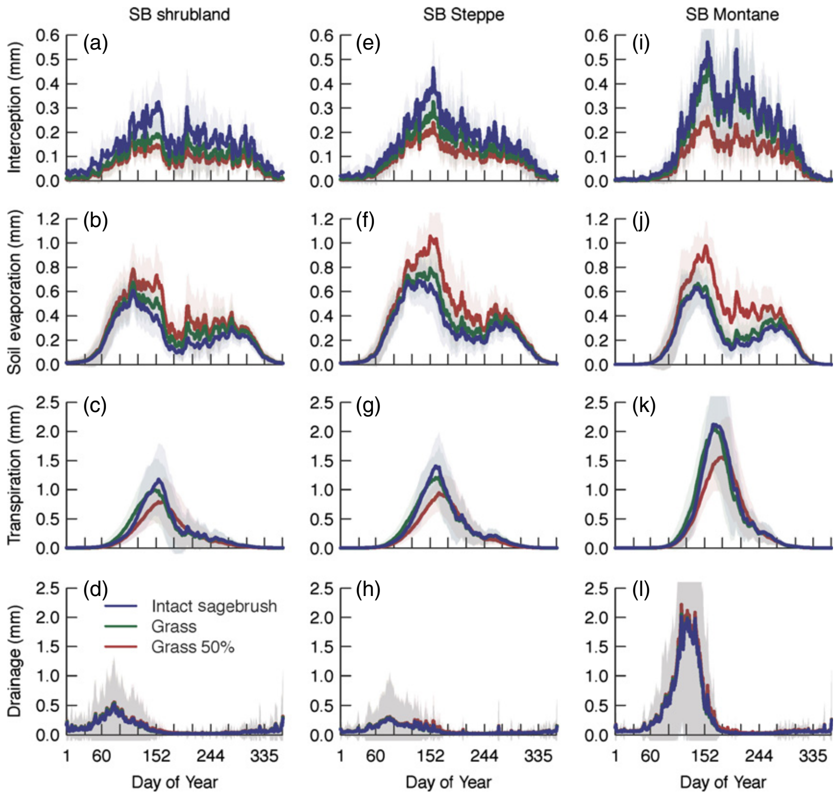

Fig. 3. Seasonal patterns of interception, soil evaporation, transpiration and drainage for intact sagebrush vegetation (blue), grasses only (green) and grass vegetation at 50% of potential biomass (red) in three sagebrush ecosystem types (columns). Lines are daily means of all sites within each sagebrush ecosystems type and shaded areas are ±1 standard deviation among sites.

soil layers; transpiration from the top 20 cm was lower (median 12–20 mm year^{-1} difference) in the reduced biomass grass vegetation compared with either the intact sagebrush or grass vegetation. By contrast, transpiration from deeper soil layers was similar between vegetation treatments (median differences < 7 mm year^{-1}).

Drainage was highest in the reduced biomass grass vegetation and lower in both the grass vegetation and the intact sagebrush vegetation. While modelled drainage increased in the reduced biomass grass vegetation treatments compared with the intact sagebrush vegetation, the magnitude of increase varied among ecosystems from 4 mm (20%) increase at steppe sites to 5 mm (16%) increase at shrubland sites and to 10 mm (9%) increase at montane sites. Seasonal peak drainage rates were higher at montane sites, and drainage occurred primarily during winter and spring with near-zero average values during the warm season (Fig. 3d,h,l). Total drainage was positively related to mean annual precipitation (Fig. 4g). Although the difference in drainage between the grass vegetation and intact sagebrush vegetation was only weakly related to mean annual precipitation, the difference in drainage between reduced biomass grasses and intact sagebrush vegetation was consistently positive, higher in wet areas and highest at montane sites (Fig. 4h). The average difference in drainage between reduced biomass grass and intact sagebrush vegetation was approximately 25% at the wettest montane sites.

Compared with the intact sagebrush vegetation, soils in the grass-only vegetation were slightly wetter in deeper layers during summer and fall and similar during the winter and spring (Fig. 5). Surface soil moisture was similar between vegetation conditions during fall and winter, but surface soils in reduced biomass grass were slightly wetter in spring compared with mixed vegetation. Surface soil moisture responses to vegetation during summer varied among ecosystems; reduced biomass vegetation surface soils were slightly drier in shrubland sites and slightly wetter at montane sites. The length of the dry season and the severity of summer dry conditions increased consistently from montane to steppe to shrubland sites.

Our simulations suggested that allocation of precipitation among sublimation, interception, transpiration, evaporation and drainage varied with mean annual precipitation and was subtly influenced by vegetation (Fig. 6). For all vegetation types, the proportion of precipitation lost via sublimation, transpiration and deep drainage increased with precipitation, while the proportion of precipitation lost via soil evaporation decreased with precipitation. Proportional interception losses decreased with precipitation for the intact sagebrush vegetation and the reduced biomass vegetation, while interception with the grass-only vegetation increased very slightly with precipitation. Relative to the intact sagebrush and grass-only vegetation, the reduced-biomass vegetation allocated less precipitation to interception and transpiration and more to evaporation and drainage.

Discussion

Changing vegetation structure, and in particular, shifting plant functional type abundance, is a common impact of global change in dryland ecosystems, and these changes are expected to increase in the future (Wilcox 2010). Several potential shifts in ecosystem water balance may be expected with a transition from woody plant dominance to grass dominance or *vice*

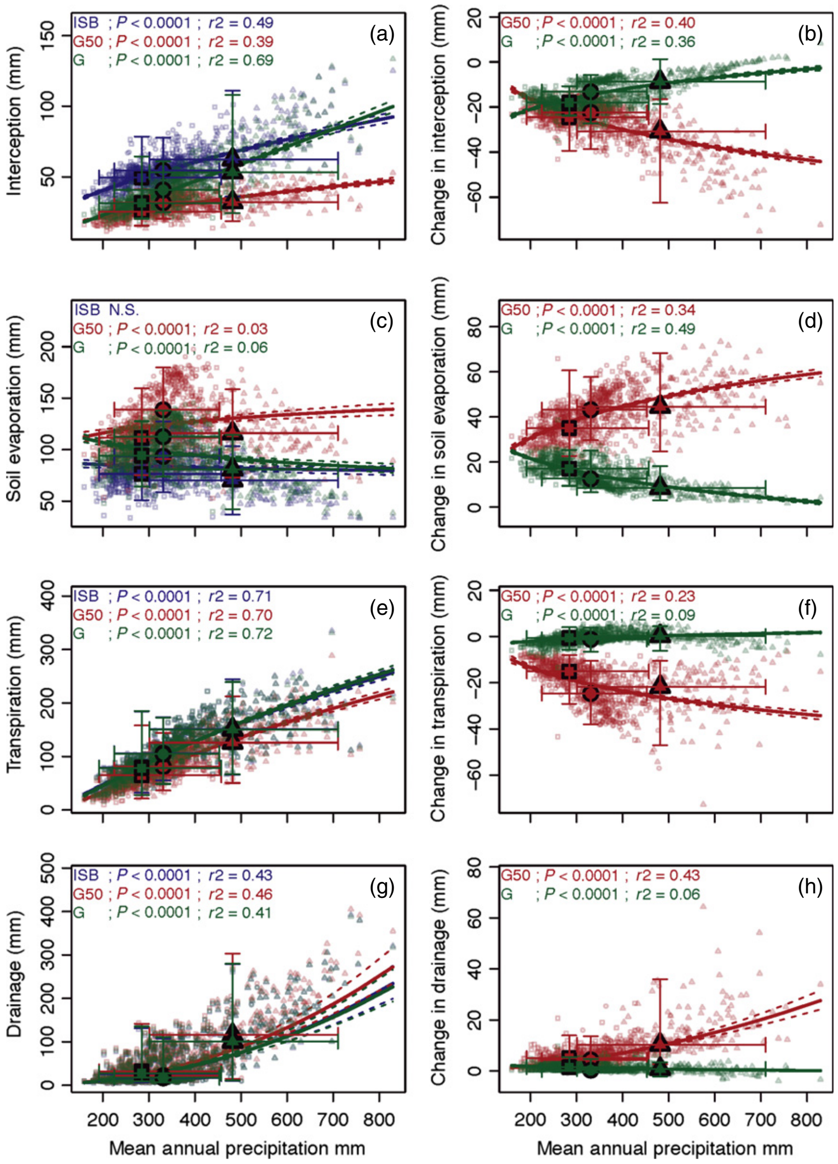

Fig. 4. Primary water balance components and differences in water balance components between intact sagebrush vegetation (blue, 'ISB'), reduced biomass grass vegetation (red, 'G50') and grass-only vegetation (green, 'G') as a function of mean annual precipitation. Symbols indicate sagebrush ecosystem types (square = shrubland, circle = steppe, triangle = montane); black-lined symbols are medians; bars are 95% CIs.

versa. Our simulations of highest evaporative losses (interception plus soil evaporation) in the reduced biomass vegetation are a consequence of higher soil temperatures and lower above-ground biomass and suggest that evaporation may be elevated following sagebrush removal, especially immediately after disturbance. We simulated higher surface soil temperatures (Fig. S4.1), decreased interception and increased bare soil evaporation in grass compared with intact sagebrush vegetation, consistent with Prater & DeLucia (2006), who reported that burning sagebrush caused increased infiltration, higher soil temperatures and higher ET when soils were wet, and by Beck, Connelly & Reese (2009), who observed higher bare soil evaporation even 14 years after sagebrush removal.

REGIONALLY VARIABLE PATTERNS DRIVEN BY CLIMATE

Our results imply that the ecohydrological consequences of a woody plant to grass transition in the sagebrush region may depend on climatic conditions (consistent with Huxman *et al.* 2005) and underscore important functional differences between sagebrush ecosystem types. While the estimated direction of change as a result of sagebrush removal was consistent across the region, the magnitude of change for many water balance components varied significantly with mean annual precipitation. This implies that climatic conditions influence the magnitude of short- and long-term water balance consequences of sagebrush removal. For example, differences in interception, bare soil evaporation, transpiration and drainage between intact sagebrush vegetation and reduced biomass grass were consistently greatest at high precipitation and at the montane sagebrush sites. Within SOILWAT, this is driven by inability of the reduced biomass grass vegetation to utilize all available water at relatively wet locations, a limitation suggested previously (Hibbert 1983). By contrast, differences in water balance between the intact sagebrush vegetation and high biomass grass-only vegetation were typically greatest at low precipitation (where water balance of grass-only

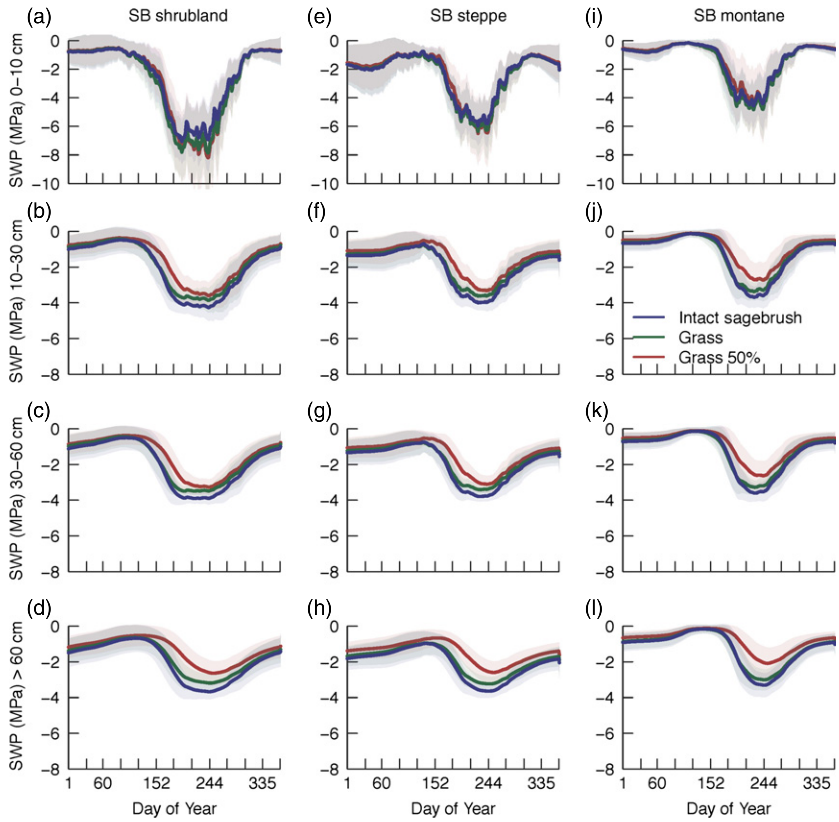

Fig. 5. Seasonal patterns of soil water potential in 4 soil layers for intact sagebrush vegetation (blue), grasses only (green) and grass vegetation at 50% of potential biomass (red) in 3 sagebrush ecosystem types (a-d, sagebrush shrubland; e-h sagebrush steppe; i-l, montane sagebrush). Lines are daily means of all sites within each sagebrush ecosystems type and shaded areas are ±1 standard deviation among sites.

vegetation was similar to reduced biomass grass). This may reflect the general unsuitability of extremely dry conditions to support grasses when precipitation is not concentrated during the growing season (Sala *et al.* 1997).

Differences between sagebrush ecosystem types and vegetation treatments imply several potentially important influences of climate, in particular precipitation amount and seasonality, on the ecohydrological impact of sagebrush removal. While the shrubland and steppe sites displayed similar simulated interception and deep drainage, they differed in partitioning of soil water between evaporation and transpiration. Shrubland sites, which receive much of their precipitation during the cool season (Fig. 2), had lower evaporation and higher transpiration than the steppe sites, which receive more precipitation during the warm season. Variations between shrubland and steppe sites were consistent for the grass-only vegetation and magnified in the reduced biomass vegetation, implying that evaporative loss of summer precipitation may be even greater when plant biomass is reduced following disturbance. Our simulations suggest that short-term ecohydrological consequences of sagebrush removal (represented by the reduced-biomass grass treatment) may be greatest at montane sites and particularly the wettest of the montane sites, where we estimated decreased interception and transpiration combined with increased evaporation and deep drainage.

Deep drainage provides important groundwater recharge and in our simulations is analogous to overall water yield. Our modelled results suggest that the potential for increased drainage following sagebrush removal is positively related to annual precipitation (Hibbert 1983; Huxman *et al.* 2005). Relative to the drier steppe and shrubland sites, the high precipitation montane areas had larger increases in drainage with sagebrush removal, reflecting an increased likelihood of water infiltration in spring overwhelming the soil water storage capacity and increasing drainage. Although measurements of deep drainage in sagebrush ecosystems are rare, impacts of vegetation change on drainage can be inferred from changes in other water balance components, and there is evidence that removing sagebrush does not increase annual ET (Obrist, DeLucia & Arnone 2003). Even with reduced biomass, the grasses in our simulations utilized most of the water that entered the soil profile at most sites (consistent with Anderson *et al.* 1987). Estimated increases in drainage accompanying a conversion to reduced biomass grass vegetation were modest where precipitation is lower than ~400 mm (increases < 10 mm year^{-1}) and higher when precipitation is > 600 mm (increases ≥ 20 mm year^{-1}).

TIME-DEPENDENT PATTERNS DRIVEN BY VEGETATION

The differences we observed between the grass-only vegetation and the reduced biomass grass vegetation indicate that many of the ecohydrological consequences of sagebrush removal anticipated by previous work and observed in some Mediterranean ecosystems (Hibbert 1983; Davis 1984) may be short-lived in sagebrush ecosystems, declining as grass biomass increases post-removal. Increases in evaporative losses, decreased transpiration and higher drainage are all

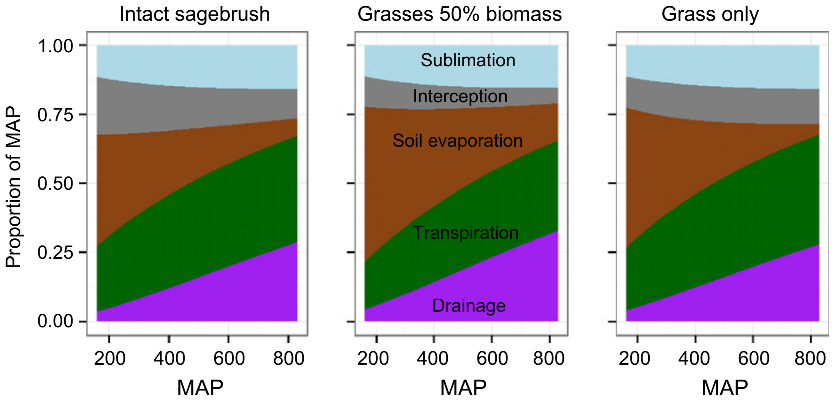

Fig. 6. Proportion of precipitation represented by the five primary water balance components for as a function of mean annual precipitation for intact sagebrush vegetation, grasses with reduced biomass and grasses only. Regressions estimating these proportions are presented in Appendix S3.

consequences of sagebrush removal that are very pronounced initially and are moderated in the high biomass grass vegetation. While both grass vegetation scenarios displayed decreased transpiration and increased deep drainage relative to the intact sagebrush vegetation, the magnitude of differences between the grass-only vegetation and the intact sagebrush vegetation was small. As expected with reduced overall biomass, we simulated lower transpiration in the reduced biomass grass-only vegetation compared with intact sagebrush or the grass-only vegetation. As observed by other studies (Anderson *et al.* 1987; Prater & DeLucia 2006), these simulations estimated higher spring transpiration rates in grasses followed by higher early summer peak transpiration rates in intact sagebrush vegetation.

Our simulations indicated that replacing woody plants with grasses will impact the seasonal and depth dynamic of soil moisture that typify sagebrush ecosystems (Schlaepfer, Lauenroth & Bradford 2012b). We estimated slightly drier surface soils accompanied by increases in soil moisture in deep soil, especially during the growing season and in the reduced biomass grass vegetation, consistent with observations of recently disturbed sites (Hedrick *et al.* 1966; Link *et al.* 1990; Inouye 2006; Seyfried & Wilcox 2006). Although previous studies have suggested that removing sagebrush can decrease plant water utilization of deep soil moisture (Cline, Uresk & Rickard 1977; Sturges 1993), our results indicated that the proportion of transpiration derived from soils > 30 cm deep did not differ consistently between intact sagebrush vegetation and grass-only vegetation because the increased amount of infiltrated water is already utilized in shallow layers by grass roots (results not shown).

IMPLICATIONS FOR SAGEBRUSH ECOSYSTEMS

The proportion of precipitation utilized by plants for transpiration (T/PPT) is a measure of ecosystem water use efficiency and has implications for overall ecosystem productivity and carbon balance (Huxman *et al.* 2005). In our results, the proportion of precipitation represented by each water balance component, and the relationships between these proportions and mean annual precipitation, was similar between intact sagebrush vegetation and grass-only vegetation. The proportion of precipitation lost to interception or bare soil evaporation was consistently highest in areas with less overall precipitation, making less water available for transpiration in these dry sites and resulting in a positive relationship between mean annual precipitation and T/PPT (Fig. 6 and Fig. S3.3 panels m-p). In shallow soils, water losses for most of the year reflect competition between evaporation and transpiration, which are impacted in SOILWAT by above-ground plant biomass (negatively and positively, respectively). Biomass was estimated from MAP using meta-analysis results that reflect steeper relationships for grasses than shrubs (see Appendix S2). Consequently, the slope of the relationship between T/PPT and MAP was steeper in grass-only vegetation than intact sagebrush vegetation (Fig. 6 and Fig. S3.3 m), resulting in higher ecosystem water use efficiency (T/PPT) in our intact sagebrush vegetation treatment when MAP is less than approximately 375 mm, but higher T/PPT in grasses when precipitation is higher.

Soil texture and depth influences on modelled changes in water balance were relatively weak compared with climate (Figs S3.1, S3.2, S3.3, S3.4), likely a consequence of examining sites that span a large range of climatic conditions. In addition, although snow dynamics represent a substantial component of water cycling in sagebrush ecosystems (Schlaepfer, Lauenroth & Bradford 2012a), our simulations did not include the potential effects of altered snow redistribution that might result from sagebrush removal, which may decrease snowpack and subsequent infiltration in areas without shrubs (Obrist, Yakir & Arnone 2004).

Previous work has suggested that the distribution of sagebrush ecosystems is tightly linked to ecohydrological conditions (Schlaepfer, Lauenroth & Bradford 2012b) and that ecohydrologically suitable areas for sagebrush will shift north, east and upslope over the next several decades (Schlaepfer, Lauenroth & Bradford 2012c). However, if disturbances increase in size and severity, successful regeneration will be increasingly important for both the maintenance and potential migration of plant species distributions in the context of a changing climate (Walck *et al.* 2011). In dryland areas, and sagebrush ecosystems in particular, regeneration is largely determined by seed availability and soil water availability: success requires avoiding dry surface soil conditions until the plant can develop a deep root system (Grubb 1977; Schlaepfer, Lauenroth & Bradford 2014a,b). The wetter soils we simulated in the reduced biomass grass vegetation (especially at depths > 10 cm) suggest that establishment of sagebrush, and/or other plant species including potential invaders, may be more likely immediately following sagebrush removal. While this implies that sagebrush has the potential to regenerate following removal, complete recovery of sagebrush vegetation structure clearly requires at least a 3–4 decade time frame (Sturges 1993; McDaniel, Allen Torell & Ochoa 2005; Lesica, Cooper & Kudray 2007; Avirmed *et al.* 2014). In addition, enhanced regeneration possibilities following disturbance also underscore the opportunity provided by sagebrush removal for invasive plant species (Anderson & Inouye 2001), notably exotic annual grasses (Knapp 1996).

Conclusions

Our results identify two general hypotheses about how global change processes that alter plant functional type abundance may impact water balance and availability in sagebrush ecosystems. First, the ecohydrological consequences of decreasing sagebrush abundance may depend on climate; this climatic influence creates differences between sagebrush ecosystem types. Short-term changes (increases in evaporation, drainage and soil water content and decreases in interception and transpiration) were most pronounced in wetter areas typical of montane sagebrush. Secondly, many of the changes in water balance anticipated with loss of sagebrush may be only temporary, especially the most dramatic changes in wet locations. Elevated soil water content and higher drainage in our reduced biomass grass simulations may only persist until grasses recover from the shrub-removing disturbance. Nevertheless, even these relatively short-term ecohydrological changes may have important consequences for plant community dynamics. In particular, higher water content of shallow soils following sagebrush removal may facilitate regeneration of native and exotic species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Climate and soil conditions at each site.

Appendix S2. Representation of vegetation in SOILWAT.

Appendix S3. Relationship between climate or soil conditions on water balance, the proportion of precipitation represented by each water balance component and the changes in water balance between intact sagebrush and grass.

Appendix S4. Seasonal soil temperature results by soil layer, sagebrush ecosystem type and vegetation condition.