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ABSTRACT

Invasive species have become an increasingly large concern, particularly in already degraded ecosystems, such as sagebrush (Artemisia tridentata*)-steppe of the Intermountain West. Much of this ecosystem is already infested with large cheatgrass (*Bromus tectorum*) stands and is potentially at risk for future invasions depending on biotic and abiotic conditions. In these ecosystems, the existing vegetation, whether native or non-native, may not effectively utilize the soil moisture resources in the upper portion of the soil, termed the growth pool. If the existing vegetation does not effectively utilize moisture in the growth pool, an open resource is left for the establishment of other plants, including invasives. Through a combination of soil moisture modeling and observational studies, we identified three potential invasion pathways, particularly by annual plants, into a cheatgrass-dominated system, all consistent with the fluctuating resource hypothesis, and all resulting from an available water resource in the growth pool. Results suggest these arid and semi-arid systems are likely to be protected from novel invasive species by complete utilization of growth pool soil water resources by any existing vegetation, whether native or non-native. Our results also suggest the same features which make the site more prone to novel annual invaders may also be useful in guiding establishment of desired vegetation during restoration efforts.*

INTRODUCTION

The ecohydrology of arid and semi-arid regions can often be characterized by water resources supplied in two forms: a growth pool containing nutrients utilized earlier in the season, typically located in the upper portion (e.g., 0-30 cm depth) of the soil profile, and a maintenance pool to support the transpiration demands of plants growing through the later, and typically hotter, period of the growing season (Ryel and others 2008; Leffler and Ryel 2012). In water-limited ecosystems, effective depletion of soil moisture by established native or non-native vegetation may be the controlling factor in protecting against invasion (Prevéy and others 2010). Failure to utilize the soil moisture resources leaves the system vulnerable to establishment by other plants, either native or exotic.

Several hypotheses to explain plant invasion have been proposed, and some are consistent with the resource pool framework. The empty niche hypothesis considers invasions to be more likely if species are able to access open resource pools (Mitchell and others 2006). The fluctuating resource hypothesis states invasion is probable when a community either is experiencing a time of unusually high resources, where existing vegetation cannot completely utilize them, or damaged existing vegetation is unable to effectively use normal to high resource levels (Davis and others 2000), provided propagule pressure exists (Davis and others 2000; Chambers and others 2007). The resource-release hypothesis combines the assumptions of resource opportunities in the new environment with release from pathogens or herbivores associated with native habitats (Mitchell and others 2006). The invasion windows may be species-specific or more general (Johnstone 1986). The windows that are species-specific arise through alterations to the biotic or abiotic conditions at a site, as do more general windows (Johnstone 1986). Species-specific windows may also be created through entrance to a community as a seed and establishing once the existing vegetation senesces or is removed through some form of disturbance (Johnstone 1986). In both

frameworks, there is the possibility for invasion failure if invasive propagules are unable to germinate at the time corresponding to open resource pools.

Biotic impoverishment due to land-use practices and invasive plants, particularly annuals, have altered ecosystems in arid and semi-arid areas (Billings, 1990). In the Intermountain West of the US the widespread Artemisia sp. (sagebrush)-steppe community has been affected by reduction in the perennial herbaceous community, and dense stands of woody vegetation and novel herbaceous invaders are now present on the landscape (West 1988; Young and Allen 1997). Of particular interest is the invasive annual grass, *Bromus tectorum* L. (cheatgrass) that has altered the soil moisture dynamics of the sagebrush-steppe where it has come to dominate (Kremer and Running 1996; Ryel and others 2010). Cheatgrass is a winter annual, a vegetation type not previously found in the Great Basin (Bradford and Lauenroth 2006). These vegetation changes are linked to altered resource value and ecosystem function.

The stability of these systems prior to anthropogenic alterations may be linked to reduced inter-annual variation in soil water use in the growth pool than is currently found for graminoid and herbaceous rangeland communities in the sagebrush-steppe zone (Ryel and others 2008; Prevey and others 2010). The benefits of system stability as a result of increased species or plant functional type diversity and increased probability of completely utilizing soil moisture resources, arise from biotic interactions among plants (Davis and others 2000; Shea and Chesson 2002) and perhaps the coevolution of species (Thompson 2009) within the original woody-herbaceous communities.

Dense stands of sagebrush effectively deplete both the growth and maintenance pools in most water years (Ryel and others 2010). Given this, sagebrush co-occurring with a cheatgrass understory should provide some degree of protection against novel invaders, even in years when cheatgrass fails to become established. However, cheatgrass monocultures subject to periodic establishment failures may be at high invasion risk, since they essentially revert to bare ground in these years.

We conducted an observational and modeling study to assess whether more complete utilization of the upper soil moisture contained in the growth pool in a degraded sagebrush-steppe acted to reduce the potential for novel annual invaders. A goal of the study was to identify possible pathways for establishment of an exotic species, all consistent with the availability of sufficient resource pools. An invasion was considered likely if there was an unusually large open resource pool present in the system, with or without damage to the existing vegetation. Since both warm and cool season plants occurred near the study site, we were able to assess the importance of the timing of the open resource pool.

METHODS

Site Description

The field site was located in Rush Valley in west-central Utah (112°28′W, 40°17′N, and elevation 1,600 m). Vegetation types include large patches of near monocultures of cheatgrass (*Bromus tectorum*), big sagebrush (*Artemisia tridentata*) and crested wheatgrass (*Agropyron desertorum*); some big sagebrush stands are growing in association with or bordering cheatgrass, crested wheatgrass or other native perennial tussock grasses. The study area is grazed by cattle each spring.

Soils at the site are silt-loam to over 3.0 m depth. The climate is temperate with cold winters and hot summers. Mean annual precipitation at nearby Vernon, Utah is 240 mm and mean annual temperature is 8.3° C (Ryel and others 2002). The period of temperatures sufficient for plant growth ranges from late March through late October. Soil moisture is recharged mainly by accumulating snowmelt in early spring (Ryel and others 2010); the few summer rains are typically not sufficient to recharge moisture via infiltration to depths greater than 0.1 m (Ryel and others 2003, 2004).

Field Measurements

Measurements were conducted within three patches of vegetation. These included two patches of cheatgrass (~0.5-1.8 ha) and a field of crested wheatgrass (~80 ha). Cheatgrass established at the site following fire in 1992 (Hooker and Stark 2008). The cheatgrass plots are bordered in places by largely monotypic stands of big sagebrush (~5-60 ha). Crested wheatgrass was planted in 1992 and has

remained largely a monoculture since. The portion of the field used in this study has not been grazed since 1999. In spring 2002, an herbicide (Roundup, Scotts Company LLC, Marysville, Ohio) was applied to kill all vegetation within two 10x10m plots. These plots were compared with the undisturbed crested wheatgrass within 30 m of the plot edges.

Soil moisture was measured using two methods. Individually calibrated screen–cage thermocouple psychrometers (J.R.D. Merrill Specialty Equipment, Logan, Utah and Wescor, Logan, Utah) were installed at nine depths through the profile from 30 cm to 300 cm in March, 1999 in cheatgrass, sagebrush and crested wheatgrass monocultures; measurements were collected nearly continuously from spring 1999 to 2003 and converted to volumetric soil water content as in Ryel and others (2002). For 2007-2009, soil moisture data in cheatgrass monocultures were collected with a capacitance probe (model Diviner 2000, Sentek Technologies, Stepney SA, Australia) with soil cores taken periodically for comparison; cores were used to determine volumetric water content from measured gravimetric water content as described in Ivans and others (2003).

Community composition data were collected using 50-m line transects through relatively homogeneous stands or vegetation patches. Species were identified every 0.5 m along four transects and species cover was estimated as the portion of points that contained each species.

In spring 2008, an area dominated annually by cheatgrass with scattered sagebrush experienced a failure in the cheatgrass crop. That spring, sagebrush seedlings established in the bare spaces between mature sagebrush, which had in prior years been dominated by cheatgrass. Sagebrush seedlings were counted and tagged in a 10 m x 15 m plot after this event and monitored for survival in fall 2009 and summer 2010.

Simulation Modeling

Soil moisture, root growth and uptake, and soil hydraulic conductivity were simulated for spring through fall 2000-2002 and 2007-2009 using HYDRUS 1-D (Šimůnek and others 2008). Inputs to the model include soil hydraulic properties (table 1) determined for our study area (Ryel and others, 2002), root distribution, and root water uptake rates. Temperature, precipitation, and potential evapotranspiration data were obtained from the Cooperative Observer Program (COOP) monitoring station in Tooele, Utah. Based on depth of water extraction (Ryel and others 2010; Ryel, unpublished data), roots of cheatgrass and halogeton were assumed to be limited to the top 45 cm of the soil, while Russian thistle and pepperweed roots were assumed to tap moisture stored deeper in the profile, at 90-120 cm. Root growth and uptake for each vegetation type were initiated at the start of the appropriate growing season for each species. Root growth was specified as daily values to allow for rapid cheatgrass root growth to 45 cm once the upper portions of the growth pool are depleted. The root water uptake parameters (table 2) were estimated from psychrometer mesaurements for cheatgrass and pepperweed (Ryel and others 2010; Ryel unpublished) and Diviner 2000 and soil core data for Russian thistle and halogeton.

Table 1. Soil hydraulic parameters used in Hydrus 1-D to simulate soil water dynamics and root water uptake. The hydraulic parameters are from the soil catalog (Carsel and Parrish 1988) loaded in Hydrus 1-D for silt-loam.

Soil depth	300 cm
θ_r	0.067
θ_s	0.45
α	0.02
n	1.41 cm^{-1}
K_s	10.8 cm/day

The model was run for March 15-November 10 and was initiated with the soil at 25 percent volumetric water content (field capacity). In 2001 and 2008 the site experienced extensive establishments of novel exotic annuals and minimal cheatgrass cover. In 2009 an eruption of halogeton occurred, following a normal cheatgrass life cycle. All other years in the period 2000-2010 experienced normal cheatgrass establishment and are treated as near monocultures.

The model was also run for 2008 for what would have been a mixed sagebrush and cheatgrass stand had cheatgrass not experienced germination failure. Sagebrush roots were limited to the top 160 cm of the soil (Ryel and others, 2002). Root water uptake between March 15 and November 10 was modeled for only the shrub component. Sagebrush establishment was represented in the model by adding to the root distribution in the upper soil layers.

Table 2. Root water uptake parameters for use in Hydrus-1D estimated for the vegetation types at our site in pressure head (cm). Root water uptake occurs between P0 and P3, with a maximum at P0pt, where it is assumed that root water uptake ceases at soil pressure heads below P3. P2H and P2L are the pressure heads where the roots begin to be limited in their water uptake assuming a transpiration rate of r2H and r2L (cm/day).

Model Parameter	Cheatgrass	Pepperweed	Russian thistle	Halogeton
P0	-15 cm	-15 cm	-15 cm	-15 cm
P0pt	-546 cm	-546 cm	-546 cm	-546 cm
P2H	-920 cm	-1500 cm	-1500 cm	-1500 cm
P2L	-3783 cm	-1800 cm	-4500 cm	-4500 cm
P3	-9102 cm	-9102 cm	-9102 cm	-9102 cm
r2H	0.7 cm/day	0.5 cm/day	0.7 cm/day	0.7 cm/day
r2L	0.1 cm/day	0.1 cm/day	0.1 cm/day	0.1 cm/day

RESULTS

Crested Wheatgrass

The two crested wheatgrass plots subject to herbicide application in early spring 2002 were invaded by halogeton (*Halogeton glomeratus*) during the 2002 growing season. In September 2002, 53 halogeton individuals had established in one plot and 17 in the other (figure 1). No halogeton plants were found outside the two removal plots in the surrounding undisturbed crested wheatgrass stand (> 10 ha), indicating the invasions were limited by existing, undisturbed crested wheatgrass plants. As a summer annual, the halogeton in the plots became established after the crested wheatgrass had been removed and were still green and succulent in September (figure 1).

Sagebrush Establishment

Following the cheatgrass crop failure in fall 2001, 214 sagebrush seedlings established in spring 2008 within a 10 m x 15 m plot where none had established in the previous 10 years. When the plot was re-surveyed in fall 2009 only one of the seedlings had died. Vegetation in the plot in summer 2010 was mature big sagebrush, the new, establishing big sagebrush, and cheatgrass in the spaces between the mature and newly established sagebrush plants.

Vegetation Composition

Although the species composition, especially of the minor members, has changed over the course of our study period, the cheatgrass dynamics are the most important (table 3). The early germination and failure of cheatgrass predisposed the system to novel annual, spring-germinating invasive plants in 2001 and 2008 (table 3). Cheatgrass re-established as a near-monoculture in spring 2002 and 2009.

Figure 1. The extent of the invasion in two crested wheatgrass plots treated with herbicide in early spring 2002. The pictures were taken on September 26, 2002. The plots had 17 (upper) and 53 (lower) halogeton plants.
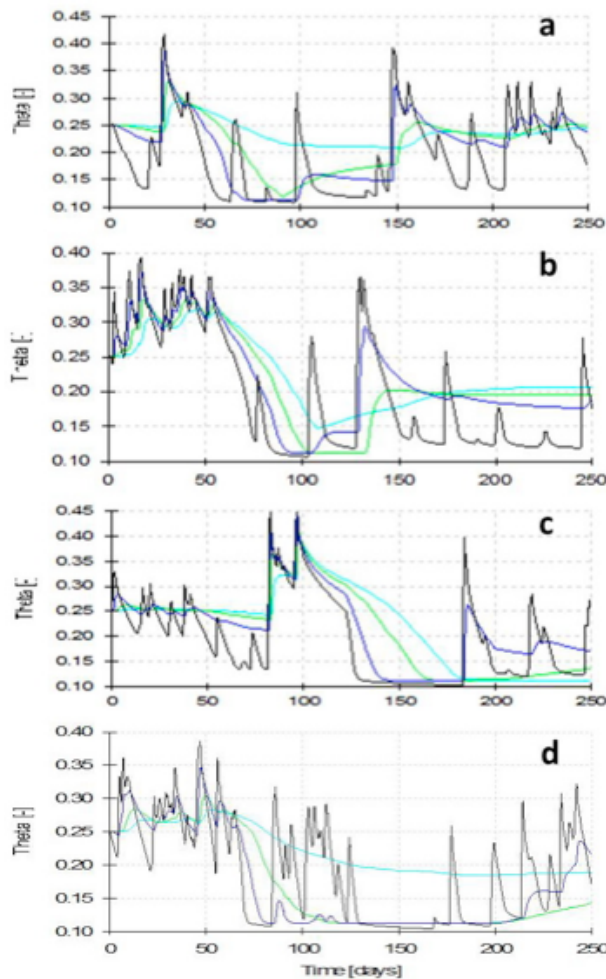
Figure 2. Modeled volumetric soil moisture (theta) trends over the simulated period March 1 (day 1)-November 6 (day 250). Soil moisture in the 3 cm (black), 15 cm (blue), 30 cm (green), and 45 cm (light blue) layers are shown. a. 2007, a normal cheatgrass year. b. 2001, a year of pepperweed eruption in the spring. c. 2008, a year with a July Russian thistle eruption; the large spike on the graph at day 100 corresponds to the start of Russian thistle establishment. d. 2009, a year with halogeton establishment in June following cheatgrass senescence in late May.

Community Invasion Pathways

Soil moisture dynamics in the growth pool were modeled in the cheatgrass community for four years of interest. The model was run for the period March to early November (figure 2). In a typical growing season when cheatgrass was dominant (figure 2a), volumetric water content was 11 percent at the time of senescence at day 90. Although the growth pool was

recharged to 30 cm depth in early August, no further vegetation established at the site during the summer.

A different dynamic was seen in 2001 and 2008 following the fall failure of cheatgrass establishment. In 2001, an eruption of a cool-season novel invader, pepperweed (*Lepidium perfoliatum*) occurred. The pattern of recharge of the growth pool from snowmelt and spring rains and subsequent soil moisture depletion in the growth pool by the pepperweed plants was similar to the water dynamics seen for a typical year dominated by cheatgrass (figure 2a, 2b). No further community changes were found at the site in that year despite a sizable recharge event in mid-July (figure 2b). Some recharge of soil moisture occurred from this event after the cool-season plants senesced as the only water losses from the soil was through evaporation, in the uppermost portion of the soil column.

The growth pool water dynamics in 2008 over the growing season of March-November were much different when the site experienced an eruption of the invasive exotic forb Russian thistle (*Salsola kali*) (figure 2c). As in 2001, the site was nearly bare ground in spring with very minimal cheatgrass cover in early spring, but this continued until mid-summer. The uppermost portion of the soil experienced evaporative losses, but the rest of the profile below 5 cm remained close to field capacity (25 percent water content) until Russian thistle was observed at the site in July following two summer storms. The already large growth pool was added to after the recharge events (figure 2c).

An anomalous June soil moisture recharge event occurred in 2009 (figure 2d), precipitating a substantial halogeton invasion during the rest of the summer. However, by the following spring 2010, the site reverted to a cheatgrass-dominated community. Unlike the situation in 2008, which had water remaining from overwinter recharge (figure 2c), limited water was available below 15 cm and the infiltration from the large event was only sufficient to recharge the uppermost layers of the growth pool (figure 2d).

As an example of the invasibility of bare ground at the site, a simulation was run for bare ground subject to 2007 environmental conditions (figure 3). This year was chosen because it was one of the driest years during our study period. While the top layer of the

growth pool was subject to evaporative losses and recharge, the moisture content in all layers of the growth pool remained higher in the absence any plants drawing down the water content (figure 3). This higher moisture content over the growing season demonstrates the increase in invasion potential.
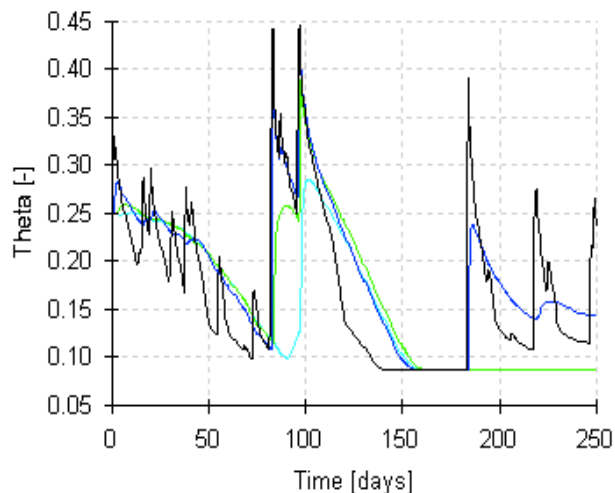
Figure 3. Modeled volumetric water content over the simulation period March 1 (day 1)-November 6 (day 250) for 2007 for bare ground. Soil moisture in the 3 cm (black), 15 cm (blue), 30 cm (green), and 45 cm (light blue) layers are shown.

DISCUSSION

Our results show the importance of the utilization of the growth pool to reduce invisibility, and are consistent with findings in Chambers and others (2007) where cheatgrass invisibility in sagebrush-steppe systems was found to occur when soil moisture was available. In 2008, an unusually large open resource led to invasion by Russian thistle in mid to late July (figure 2c). Community composition surveys in 2001 suggest pepperweed erupted in the system in late spring, during a period of naturally high resource availability. June 2009 was an unusually wet month and this created a resource for establishment of a novel invader during the warm season, a time when this system would be expected to have a reduced risk of invasion. Vegetation dynamics in the cheatgrass stands have experienced rapid community assembly and disassembly during our study period (table 3).

We have identified four pathways into these systems for a novel invader, all consistent with the fluctuating resource hypothesis of Davis and others (2000). Of the other possible hypotheses for invasions, we find limited support for only the empty niche hypothesis

and the invasion windows hypothesis (Mitchell and others, 2006; Johnstone, 1986), but neither of these frameworks can explain all invasion types we observed. The first invasion in the cheatgrass community during our study period in 2001 (figure 2b) was an example of the natural vulnerability of these arid and semi-arid sites where soil moisture recharge to depth is driven by large precipitation events constrained to a single season. Spring, following snowmelt, is a time of higher risk of invasion, given adequate propagule pressure. In the spring water in the growth pool, the most limiting resource, is available, even if the species involved have overlapping root water uptake strategies (Funk and others, 2008). The pepperweed eruption occurred in the spring, after snowmelt, a time of naturally high resources in this ecosystem (figure 2b). The second type of invasion tended to follow soil moisture availability enhanced by cheatgrass crop failure and a sizable early summer precipitation event (figure 2c). This type of invasion combines the two parts of the fluctuating resource hypothesis: disturbance to the existing vegetation and resource addition to the system. The difference between 2001 and 2008 may have been the dryer upper layers in spring and early summer in 2008 that did not favor germination of cool season species such as pepperweed.

The third type of invasion (figure 2d) emerged in 2009, where a normal cheatgrass lifecycle occurred, full germination with senescence in May; halogeton erupted following the recharge event to the shallow portions of the growth pool. In both 2008 and 2009, germination occurred subsequent to precipitation events that resulted in soil moisture that exceeded field capacity near the surface. The crested wheatgrass roundup plots also demonstrate this pathway (figure 1) with unused resources exploited by a summer annual. With disturbance to the existing vegetation, the soil resource created by the winter recharge only experienced evaporative losses, mostly from the uppermost portions of the growth pool. This is the part of the growth pool most likely to be recharged by sizable summer rains at our site. In all of these cases, an open soil moisture resource in the growth pool corresponded to the establishment of novel invaders. Regardless of the community composition, in all years except 2008, the existing vegetation has the ability to draw down the water in the upper layers of the growth pool to nearly the same level, around 11 percent volumetric water content (figure 2a-d).

Table 3. Annual plant community assembly and disassembly has been rapid as seen through yearly changes in species presence. When known, species names are given; otherwise community members are referred to by functional group or family. Plants are listed if one individual has been seen at the site. The community dominant is noted as (d) indicating >90 % of the vegetation cover. Other species had <10% of the vegetation cover.

2000	2001	2002	2007	2008	2009
Cheatgrass (*Bromus tectorum*) (d)	Pepperweed (*Lepidium perfoliatum*) (d)	Cheatgrass (*Bromus tectorum*) (d)	Cheatgrass (*Bromus tectorum*) (d)	Russian thistle (*Salsola kali*) (d)	Cheatgrass (*Bromus tectorum*) (d)
Forbs	Cheatgrass (*Bromus tectorum*)	Pepperweed (*Lepidium perfoliatum*)	Bur buttercup (*Ceratocephala testiculata*)	Cheatgrass (*Bromus tectorum*)	Scarlet globemallow (*Sphaeralcea coccinea*)
Cryptobiotic crust	Grass	Grass			Annual wheatgrass (*Eremopyrum triticeum*)
	Dandelion (*Taraxacum* spp.)	Dandelion (*Taraxacum* spp.)			Dyer's woad (*Isatis tinctoria*)
	Pink geranium (Geranium spp.)	Pink geranium (Geranium spp.)			Halogeton (*Halogeton glomeratus*) (d, after cheatgrass senescence)
	Bur buttercup (*Ceratocephala testiculata*)	Bur buttercup (*Ceratocephala testiculata*)			Bur buttercup (*Ceratocephala testiculata*)

'Ecological filtering' by existing vegetation can be done on many different environmental factors. George and Bazzaz (1999) found the fern understory to alter the light climate and soil litter depth across various sites in mesic hardwood forests, thus affecting seedling recruitment of some light-sensitive tree species. They found the tree species most likely to establish were those tolerant to reduced light conditions early in their seedling phases. Cheatgrass may act as an 'ecological filter', both in the cheatgrass monocultures and in areas where it occurs as the understory in association with sagebrush. In the monocultures, our results show the effect of removal of cheatgrass, coupled with open resources, on rapid community assembly and disassembly from year to year (table 3; figure 2). In areas where it grows in association with sagebrush, the filtering effect acts to prevent any of the yearly sagebrush seed rain from establishing until disturbance to the cheatgrass eliminates the filtering effect. Cheatgrass, like other plants, modifies its environment, in part through altering the soil moisture dynamics, drawing down the growth pool early in the growing season to levels where nutrient diffusion becomes limited (Ryel and others 2010). This may severely limit germination, growth and establishment of other species that germinate in spring or summer.

Convincingly explaining the mechanisms of past invasions is a significant but important challenge (Davis and Pelsor 2001). With the help of longer-term data sets, knowledge of the limiting conditions at our site, and a vegetationally simple site, we have reconstructed possible mechanisms linked to observed events. These mechanisms linked to invasion dynamics and rapid community assembly were related to ecohydrological dynamics, although, the evolutionary history of the invading species was likely also important. Given that the invaders were biome-shifting Eurasian species (Crisp and others 2009), additional Eurasian invaders, particularly annuals, with the evolutionary history required to effectively utilize water resources in arid or semi-arid regions would be expected to be possible future invaders.

Our work suggests the same features which make the site more prone to novel annual invaders may also be useful in guiding establishment of desired vegetation during restoration efforts. This includes the potential for developing new management strategies for dealing with these, and potentially other, invasive species based around the managing of resource pools (Leffler and Ryel 2012). In particular, arid and semi-arid systems are likely to be protected in large

part from novel invasives by complete or near full utilization of growth pool soil water resources by existing vegetation, whether native or non-native. Management should be directed toward minimizing the opportunities for invasion by minimizing the availability of the growth pools to undesirable species.

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