Process-Based Management Approaches for Salt Desert Shrublands Dominated by Downy Brome

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ABSTRACT

*Downy brome grass (*Bromus tectorum *L.) invasion has severely altered key ecological processes such as disturbance regimes, soil nutrient cycling, community assembly, and successional pathways in semi-arid Great Basin salt desert shrublands. Restoring the structure and function of these severely altered ecosystems is extremely challenging; however new strategies are emerging that target and attempt to repair ecological processes associated with vegetation change. In this paper, we review the essential processes required to reduce downy brome abundance and assist with creating suitable conditions for revegetation of Great Basin salt desert shrublands.*

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INTRODUCTION

Ecosystem processes of Great Basin shrublands have been altered by the persistent effects of past land-use and subsequent invasion of exotic annual plant species (West 1983a, b; Blaisdell and Holmgren 1984; Anderson and Inouye 2001; West et al. 2005). The invasive annual grass downy brome (*Bromus tectorum* L.) is the most notable invasive species in this region. Downy brome dominance is known to alter disturbance regimes, soil nutrient cycling, community assembly, and successional pathways (Belnap et al. 2003; Rimer and Evans 2006; Adair et al. 2008). As an ecosystem driver, downy brome poses serious obstacles to ecosystem resilience and the ability of land managers to repair ecosystem structure and function (Belnap and Phillips 2001; Booth et al. 2003; Chambers et al. 2007).

Restoring ecosystems to pre-disturbance conditions is not always feasible because biotic and abiotic thresholds may have been crossed (King and Hobbs 2006). A pragmatic alternative is to develop management goals to restore key ecosystem properties and processes, including ecosystem resilience (Whisenant 1999; Walker and Langridge 2002). The science of restoration ecology, and the application of ecological restoration to accelerate or initiate ecosystem recovery have emerged in the last few decades (Jordan et al. 1987), and the principles and tools to influence recovery are emerging for damaged Great Basin shrublands (Pickett et al. 1987; Sheley and Krueger-Mangold 2003; Krueger-Mangold et al. 2006; Sheley et al. 2009b). Collectively, these principles suggest that three critical elements are needed: 1) assess the underlying above and belowground processes responsible for invasive plant dominance (Eviner and Chapin III 2003; Eppstein and Molofsky 2007); 2) develop and apply effective management strategies that affect the causes of invasion and reduce invasive plant dominance (Krueger-Mangold et al. 2006; Sheley et al. 2010); and 3) re-establish native and introduced plant species with appropriate traits to perform well in a restoration setting (Call and Roundy 1991; Jones et al. 2010). This process-based approach requires more than just controlling invasive species, but also actions that influence above and belowground ecological processes (Ehrenfeld 2003, 2004), directly remedy colonization dynamics (Adair et al. 2008), mediate interactions between invasive and desirable species (Eiswerth et al. 2009), and recognize the existence of potential plant-soil feedbacks (Ehrenfeld et al. 2005). A primary challenge facing rangeland management today is to integrate these elements.

ASSESSING ECOLOGICAL PROCESSES

Site assessment seeks to identify a broad array of potentially important ecosystem processes and predict which are likely responsible for continued dominance by invasive plants. These fall into three primary categories: 1) processes that regulate colonization referred to as *site availability*, 2) processes that regulate the relative abundance of different species termed *species availability*, and 3) the final category consisting of processes regulating the interactions of plants with the above and belowground environment that are referred to as *species performance* (Pickett et al. 1987). Site assessment is a necessary exercise because it reveals how ecological processes are influenced by historical events and the current ecological conditions, and how they can be modified to attain desired ecosystem trajectories and targets (Sheley and Krueger-Mangold 2003; King and Hobbs 2006). Below, we briefly review these three primary categories in reference to salt desert shrublands in the Great Basin.

Site Availability

Historical disturbances are widely recognized as important drivers of invasive plant dominance in Great Basin shrublands. Since colonization by European immigrants in the 1840s, these ecosystems have been used for dryland farming and managed grazing systems, which broadly expanded in response to homesteading acts of 1862-1916 (Gates 1936). The dry farming boom was short-lived and unsustainable in the Great Basin because of the combined effects of low soil moisture and precipitation, changing climate conditions, and soil erosion (Stewart and Hull 1949). Consequently, this practice was largely abandoned; except where climatic conditions and soils matched the requirements of crop species, such as wheat and barley (Young and Evans 1989). Managing these shrublands as grazing systems was also unsustainable, as native grasses and forbs had not evolved with heavy grazing pressure by domesticated ungulates (Mack and Thompson 1982). In addition, native vegetation could not possibly recover from stocking rates and grazing practices that were developed within mesic regions where immigrants had originated. Although grazing intensity has substantially declined in the last 50 years (Piemeisel 1951), the legacy of overgrazing and abandoned farming practices remain today (Jones 2000; Morris and Monaco 2010).

Theoretically, ecosystems that experience novel disturbances are believed to have crossed irreversible thresholds, and will remain in an altered ecosystem state, bounded by current climatic and edaphic conditions (King and Hobbs 2006; Suding and Hobbs 2009). Understanding and characterizing how these disturbances have altered site conditions and key ecosystem processes has been a major research thrust in the last 20 years (Allen-Diaz and Bartolome 1998; Elmore et al. 2006; Chambers et al. 2007). This research indicates that novel disturbances and altered ecosystem processes within Great Basin shrublands have reduced biological soil crusts, diminished the abundance of native herbaceous species, accelerated soil loss and erosion, and enabled broad scale colonization, spread, and dominance by exotic annual species, foremost among them, downy brome (*Bromus tectorum* L.) (Brandt and Rickard 1994; Young and Longland 1996; Young and Allen 1997; Muscha and Hild 2006).

Exotic annual plant dominance primarily influences site availability by maintaining a disturbance regime that makes it nearly impossible for native species to persist. When abundant, senesced biomass produced by annual species creates a contiguous supply of fine fuel that increases the extent and intensity of fire (Young and Evans 1978; Young and Blank 1995; Brooks et al. 2004). Fire can kill certain shrub species with poorly protected meristems located above ground, including big sagebrush (*Artemisia tridentata* Nutt.) (Ziegenhagen and Miller 2009). In addition, perennial native grasses and forbs can be injured and experience reduced growth and seed production when fire return intervals are decreased (Wright and Klemmedson 1965; West 1994). On the contrary, annual grasses, which complete their life cycle prior to the hot and dry conditions when summer fires occur, are not directly hindered by fire, but their seeds can be diminished by fire, depending on fire dynamics (Sweet et al. 2008; Diamond et al. 2009). Consequently, the fires fueled by annual species favor their further dominance and the subsequent decline in desirable species abundance (D'Antonio and Vitousek 1992; Brooks et al. 2004). Fire frequency in Great Basin shrublands are believed to have increased since European colonization, but this trend has not been fully quantified, and is often implied from historical patterns and indicators (Baker et al. 2009; Mensing et al. 2006). However, in salt desert ecosystems, fire has indeed emerged as a novel disturbance to these low elevation shrublands in the last 30 years (West 1994; Jessop and Anderson 2007; Haubensek et al. 2008).

Mechanistically, disturbance regimes alter site availability through their influence on niches and safe sites for plants and seed (Eckert et al. 1986; Lamont et al. 1993). For example, disturbance directly modifies competitive interactions (Eliason and Allen 1997), micro environmental conditions (Melgoza et al. 1990; Bradford and Lauenroth 2006), litter dynamics (Sheley et al. 2009b), seed movement (Chambers 2000), and resource supply rates (James and Richards 2007). Characterizing how disturbance influences these processes is an important aspect of clarifying how site availability can be modified by managers to yield a more desired plant community.

Species Availability

Species availability and subsequent colonization depends on propagule dispersal and propagule pressure (Marlette and Anderson 1986; Rodríguezi-Gironés et al. 2003; Chytry et al. 2008). These mechanisms of colonization are critical components of succession because viable seeds must be present through dispersal, from seed banks, or be introduced artificially, as in a rangeland seeding (Call and Roundy 1991; Cox and Anderson 2004). Recent theoretical discussions suggest that colonization dynamics follow certain assembly rules (Ackerly 2003), where both biotic and abiotic filters regulate propagule dispersal and propagule pressure (D'Antonio et al. 2001; Mazzola et al. 2008). In altered shrublands of the Great Basin where disturbances are frequent, colonization is dominated by exotic annual species, which produce abundant seed that dominate seed banks (Humphrey and Schupp 2001). For example, individual plants of downy brome can produce up to 6,000 seeds, most of which will germinate the following fall and rapidly recolonize after disturbance (Smith et al. 2008). In contrast, native perennial grass and shrub species have much slower growth rates and have lower seed output (Young and Evans 1978). Thus, remnant native species experience a highly competitive environment, with reduced fecundity and productivity caused by exotic annual species dominance, which allows it to persist even after earnest control efforts (Borman et al. 1991; Morris et al. 2009).

Assembly rules following disturbance also suggest that priority effects may be responsible for exotic annual species dominance (Tilman 1994; Corbin and D'Antonio 2004; Ludlow 2006). Priority effects describe how exotic annual species achieve greater colonization following disturbance because they often have earlier phenological development, and are more represented in seed banks (Humphrey and Schupp 2001; Rice and Dyer 2001). For example, species that arrive and germinate first can gain dominance and control subsequent community pathways, i.e., successional trajectories (Mack and D'Antonio 1998; Corbin and D'Antonio 2004). Priority effects must be diminished before the performance of desirable perennial species can even be realized. These colonization and species availability obstacles suggest that management actions will need to systematically reduce propagule pressures of invasive species in unison with artificially seeding desirable species and fostering their future dispersal (Corbin and D'Antonio 2004). Furthermore, assessing site conditions will provide critical information about colonization dynamics and indicate potential ways to manipulate species availability when developing a management plan.

Species Performance

There is a robust scientific literature demonstrating functional differences between invasive species and the native species that are negatively impacted by their presence (Vitousek et al. 1997; Ehrenfeld 2003). However, because many factors and processes regulate species performance within an ecosystem, predicting why certain species become invasive, and identifying which ecosystems will be invaded has been challenging (Reichard and Hamilton 1997; Moles et al. 2008). A few of the widely recognized factors important to regulating species performance include resource availability, and the ability of plants to capture resources, ecophysiological traits, plant response to stresses, and tradeoffs in life history traits (James et al. 2010).

The influence of resource availability on plant performance has long been recognized. However, formal theories that seek to explain how resource dynamics regulate relative species competitive ability, species diversity, ecosystem functions, and exotic species invasion are relatively recent (Huenneke et al 1990; Burke and Grime 1996; Goldberg and Novoplansky 1997; Davis et al. 2000). In general, temporal and spatial aspects of resource capture have emerged as critical components explaining these processes. Annual exotic species perform better under elevated resources for many reasons, including the coincidence of their phenology and temporal resource availability in shrubland ecosystems (Blank 2008). Alternatively, native perennial species often initiate growth and resource capture after exotic species have pre-empted limiting resources (Melgoza et al. 1990; Chambers et al. 2007). Pre-emption is a consequence of exotic annual species having lower temperature thresholds for root growth (Bradford and Lauenroth 2006), higher nutrient and water uptake rates (Melgoza et al. 1990; Evans et al. 2001), and faster growth rates than native perennial grasses (Arredondo et al. 1998). Thus, without management intervention of ecological processes, invaded sites favor exotic annual species performing at their full biological potential, and their continued dominance.

High exotic annual species performance and dominance on Great Basin shrublands may also be perpetuated by plant-soil feedbacks wherein soil nutrient cycling processes have been altered in ways that primarily benefit annual species (Ehrenfeld and Scott 2001; Evans et al. 2001; Norton et al. 2004; Blank 2008). For example, evidence suggests that downy brome-dominated patches have higher nitrogen mineralization rates, higher total nitrogen availability, abundant low C: N ratio leaf litter, and higher litter decomposition rates than adjacent patches dominated by native species (Evans et al. 2001; Booth et al. 2003; Norton et al. 2004; Rimer and Evans 2006). Not only do these alterations favor downy brome, but they may promote soil organic matter decomposition and further impoverish sites, making them potentially more difficult to rehabilitate with native species (Norton et al. 2004).

Reducing the performance of exotic annual species requires carefully executed management efforts that effectively manipulate the processes responsible for their success while influencing processes that favor desirable species. For example, if site and species availability have been adequately remedied by reducing disturbance frequency and priority effects that favor annual species, the performance of desirable species can be enhanced to trigger different ecosystem assembly patterns where interference from exotic annual species is minimized. Achieving these conditions may be one of the most challenging aspects of land management in salt desert ecosystems dominated by downy brome.

PROCESS-BASED MANAGEMENT

Managing processes has not been the primary objective of land management in the past. For example rangeland managers in grazed semiarid shrubland systems historically adopted the notion that plant communities change linearly toward a climax endpoint dominated by certain late successional species (Clements 1936), and that managers could adjust livestock stocking rates to reverse successional trends (Dyksterhuis 1949). However, this interpretation could not predict non-linear dynamics, or indicate underlying mechanisms responsible for vegetation dynamics (Westoby et al. 1989). Thus, a successional model that incorporates the mechanisms and pathways of succession into a mechanistic framework for process-based management was developed for predicting vegetation change and developing desired changes (Connell and Slatyer 1977; Pickett et al. 1987; Sheley et al. 1996). This model has recently been shown to greatly increase restoration success over traditionally applied integrated weed management (Sheley et al. 2009a), and is gaining credence within rangeland and restoration ecology (Sheley and Denny 2006; Sheley et al. 2007; Sheley and Bates 2008; Sheley et al. 2008). This process-based approach to managing invasive plants advocates assessing site conditions, identifying the ecological processes in need of repair, applying appropriate tools, and re-assessing management outcomes (figure 1; Sheley et al. 2010).

A primary challenge to process-based management is developing the appropriate methods and tools to go beyond treating symptoms of invasive plant problem and begin influencing processes that yield desirable change (Sheley and Krueger-Mangold 2003; Krueger-Mangold et al. 2006). Although, many tools currently exist to remedy invasive annual grass infestations, there is a need for greater understanding of their ability to affect site availability, species availability, and species performance, and whether these tools effectively direct succession to a more desirable vegetative state. Assessing whether potential tools influence the intended ecological processes and yield the desired outcomes is thus necessary to develop predictive, process-based management strategies.

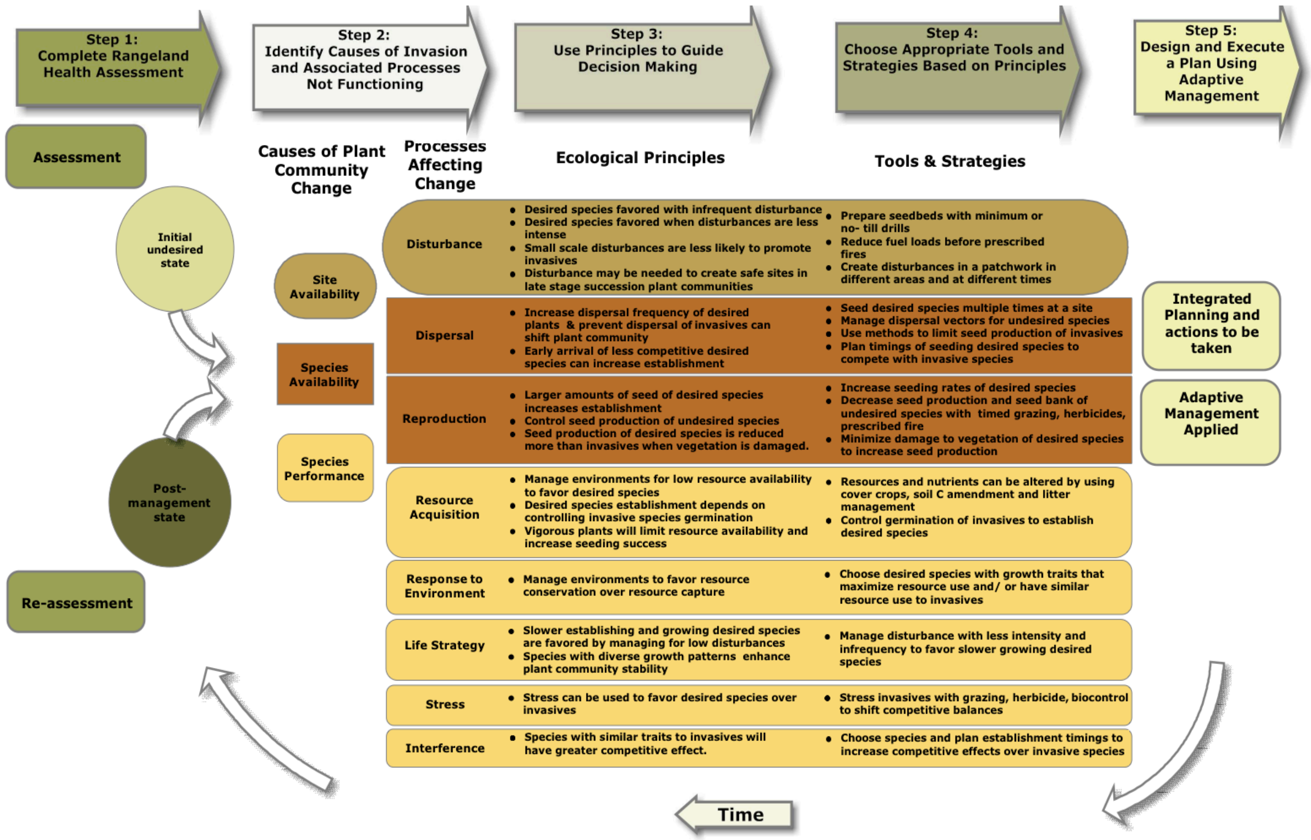

Figure 1. Ecologically based invasive plant management (EBIPM) model (Sheley et al. 2010).

SUMMARY

Process-based management is intended to manage invasive species through targeting the causes of community change. It is likely that no tool alone simultaneously impacts all causes of community change. Therefore, it may be more prudent to use tools in combinations in order to realize the maximum effects. For example, research that evaluates the combined influence of fire, mowing, and pre-emergence herbicides in the Great Basin is currently limited, especially for salt desert shrublands. Quantifying how these integrated tools impact the ecological processes that effect plant community change could help clarify ecological principles, and define improved strategies for annual grass invaded ecosystems in the Great Basin.

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