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Chapter 1

MANAGING INVASIVE PLANTS IN NATURAL AREAS: MOVING BEYOND WEED CONTROL

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ABSTRACT

Exotic invasive plants present one of the greatest challenges to natural resource management. These weeds can alter entire communities and ecosystems, substantially degrading important ecosystem services such as forage for wild and domestic herbivores, water and soil quality, recreational values, and wildlife habitat. Traditionally, weed management in natural areas has focused on removing the target weed under the assumption that its impacts would dissipate and the system would recover following control or suppression of the invader. This approach arose presumably because most weed management tools originated in agricultural systems where removal of the weed commonly translates to increased crop yields. However, accumulating studies in natural areas indicate that simply suppressing the target weed does not ensure mitigation of its impacts. This is due primarily to the complexity of natural systems and the limitations of available management tools. To improve weed management in natural systems, we need to better understand three important factors that greatly complicate natural areas weed management: invader impacts, management side effects, and secondary invasion. Weed invasion is complex. Weeds not only impact native plants, they affect higher trophic levels, alter community interactions, and sometimes disrupt ecological processes structuring the system. Therefore, mitigating weed impacts first requires determining what the impacts are and which ones may be amenable to mitigation given current tools. Additionally, weed management tools are imprecise. As a result, management tools inevitably incur side effects on native species and system processes due to their limited selectivity and the often complex response of system components to management action. Minimizing deleterious side effects requires understanding how and why they occur. Finally, even when weed control is successful, suppression of the target weed commonly results in secondary invasion by other exotic invasive plants, thereby undermining mitigation objectives. Thus, successful natural areas weed management requires that we understand much more than just weed suppression. First, a basic understanding of the system under consideration and the impacts of the target weed on system components and processes is required to determine to what extent mitigation may be feasible. Additionally, a working knowledge of how management tools interact with the target weed, nontarget species, and system processes is necessary to maximize intended outcomes and minimize side effects of management actions. Finally, further knowledge of the ecological conditions and processes underlying successive weed invasions is needed to develop strategies for reducing the risk of secondary invasion following target invader suppression. Here, we explore these issues by examining research and management of spotted knapweed (*Centaurea maculosa*) in Western North America.

INTRODUCTION

Exotic invasive plants (also referred to here as weeds) present a formidable threat to the economic productivity and ecological integrity of natural systems (Mack et al. 2000; Pimentel et al. 2005). As a result, weed management is now a primary objective for many federal, state, and private land stewards (e.g., Randall 1996; Hulme 2006). However, achieving successful weed management in natural areas has proven elusive and unpredictable (D'Antonio et al. 2004; Smith et al. 2006). One potential reason for this is an overly narrow focus on controlling the target weed. Historically, management strategies have focused on removing or suppressing the invader under the assumption that its negative impacts would dissipate in its absence or reduced vigor (Hobbs and Humphrey 1995). Presumably, this approach arose because most weed management practices originated in agricultural systems where controlling the target weed often results in a direct increase in the productivity of the desired crop plant (Smith et al. 2006). However, in natural areas, controlling the target weed commonly fails to result in system recovery (e.g., Story et al. 2006; Ortega and Pearson in review). Addressing this problem requires explicitly recognizing how differences between natural areas and crop systems may influence management outcomes so we can better adapt strategies for natural areas management.

The fundamental distinction between natural areas and crop systems is ecological complexity. Natural areas contain a great variety of species whose composition, productivity, and relative abundance are determined by an array of community interactions and system-level processes. As a result, weed management in natural areas involves management of entire communities, not just individual weeds. That is, natural areas weed management is in essence *directed community assembly* (Holt and Hochberg 2001; Pearson and Callaway 2005). As such, it requires that we understand community- and system-level processes and how invasion and management actions influence these processes in order to determine specifically which weed impacts may be mitigated and how.

Prior weed management assessments have evaluated standard practices, explored theoretical frameworks, and offered guidelines for integrated approaches that have advanced both our thinking and applications in this field (Hobbs and Humphries 1995; Randall 1996; Sheley et al. 1996, 1998, 2006; DiTomaso 2000; D'Antonio et al. 2004; Smith et al. 2006; Hulme 2006). Several such assessments have indicated the importance of setting forth clear weed management objectives that take into account larger land management objective before initiating weed management actions (e.g., Randall 1996; Sheley et al. 1998; Rew et al. 2007). However, before we can effectively identify the feasibility of weed management actions, we must determine the nature and extent of weed impacts on the system and understand how management actions can influence overall outcomes through their interactions with the weed and other system components and processes. Here, we focus on these issues in an effort to move natural areas weed management beyond simple weed control toward a more holistic discipline.

Although weed management in natural areas has become quite prevalent in recent years, a formal definition of natural areas for weed management purposes is lacking. This situation has hindered natural areas weed management by not clearly distinguishing issues in natural areas from those associated with agricultural systems. For our purposes, we define natural areas as non-crop systems with residual native vegetation where management objectives include retaining or augmenting native vegetation to generate ecosystem services. This definition encompasses a range of conditions from virtually pristine areas with few weeds to heavily invaded or otherwise degraded areas that still contain some semblance of the original natural vegetation. Thus, urban environments and cropland systems are excluded, but most timber production lands, recreational lands, and grazing lands are included where native vegetation is intended to generate some or all of the primary productivity or other ecosystem services such as soil stability, water conservation, wildlife populations, natural aesthetics, etc. With this definition in hand, we can begin to discuss the complexities of natural areas weed management as a distinct discipline.

In many regards, natural areas management is analogous to the practice of human medicine. In human medicine we use a variety of physical and chemical treatments in an effort to alleviate ailments within complex biological organisms. Due to the sheer complexity of the human body, and in many cases insufficient precision of the drugs and treatments used, virtually every medical treatment has a cadre of side effects, which may range in severity from minor to quite serious (e.g., Evans and McLeod 2003; Niggemann and Gruber 2003). Thus, successfully managing human health requires the weighing of potential treatment side effects against the intended treatment outcome for a given illness. The same is true in natural areas management. Within natural systems, all management actions have side effects due to the complexity of natural systems and the limited specificity of the tools employed. Management side effects can vary from innocuous to rather severe, and, as with human medicine, the severity of the illness determines the acceptable risk of side effects. Thus, effective resource management requires balancing management side effects against the intended outcome for a given management objective. Accomplishing this requires a thorough understanding of the potential range of side effects associated with different resource management tools.

As the history of medicine shows, advancing an applied science involves evolution by trial and error. In ancient Peru, France, and Egypt, a primitive form of brain surgery was developed called trepanation (Arnott et al. 2003). This practice involved physically opening the skull with primitive metal tools and was believed to be used for a variety of purposes ranging from treating head injuries from battle to curing epilepsy and relieving headaches. Modern forensic analysis indicates many patients survived and often received multiple treatments, suggesting the practice was successful. Today trepanation might seem to be an extreme treatment for headaches, with potentially excessive side effects, given contemporary medicine. Modern medicine has come a long way since the early practices of trepanation through the development of better understandings of the human body, the diseases that ail it, and refinement of the tools and techniques we use as treatments. In contrast, natural areas weed management is in many ways still in its infancy. To date, we have developed relatively few effective tools, they tend to exhibit limited selectivity, our understandings of particular "diseases" such as biological invasions are still quite primitive, and although we are beginning to gradually improve knowledge of natural systems, we are not particularly efficient at integrating this new knowledge into applied management approaches (D'Antonio et al. 2004; Smith et al. 2006). Thus, in many regards contemporary weed management may be likened to ancient trepanation – we commonly deploy tools that have rather severe side effects largely because we lack more precise tools and have insufficient knowledge of the complex systems we work in and the diseases or threats we wish to abate. This is not intended as a casual criticism, but rather as an objective assessment of the current state of this relatively young science.

At this stage in our evolution, we need to further refine the science in an effort to develop more surgical precision and improve the field as a whole. We acknowledge and accept that the state of any science will progress through trial and error. However, much as the Hippocratic Oath guides the ethic of human medicine, we feel that the guiding principal for invasives management should be "*to do no harm.*" That is to say, management actions should improve the system as a whole, as measured by the overall system response to management and not simply by the degree to which the target weed is suppressed. As we illustrate below, using tools without carefully considering the collective outcome can actually make conditions worse (e.g., Pearson and Callaway 2003; Lenhoff et al. in press; Ortega and Pearson in review). Expending limited funds and resources to make matters worse is not an acceptable outcome. To improve natural areas management we need to better understand the ecology of the systems we are working in, the nature of the threats we wish to mitigate, and the efficacy of the tools we employ. In this context, we examine three major factors that must be understood to improve natural areas weed management: invader impacts, management side effects, and secondary invasion.

Effective weed management in natural areas begins with understanding the nature and extent of weed impacts in the invaded system. When an exotic invades a natural area, it develops numerous interactions with system components. These interactions may be positive, negative, trophic, nontrophic, biotic, abiotic, direct and indirect. The overall result is that strong invaders (*sensu* Ortega and Pearson 2005) do not just reduce the abundances of individual native organisms, they may alter community interactions, abiotic resources and/or physical conditions in ways that restructure the community and sometimes alter fundamental ecological processes such as nutrient cycling, hydrologic conditions, and disturbance regimes (e.g., Vitousek 1990). Notably, the specific impacts that an invader has may differ across communities (Rew et al. 2007; Maxwell et al. 2008), requiring that we understand the mechanisms underlying observed changes. Thus, effectively mitigating invader impacts requires understanding how the invader alters not only abundances of individual species but also community interactions and the processes structuring the system.

A major obstacle to successful weed management in natural areas is the fact that management tools inevitably have side effects. This is due to the limited selectivity of management tools and the complexity of the organisms and processes they interact with. Because management tools can themselves be biotic or abiotic, pulsed or persistent, widespread or localized, and broad or narrow in their intended selectivity, they can exhibit a wide array of side effects in natural systems. These side effects can further vary as a function of local site conditions (Shea et al. 2005; Ortega and Pearson in review). Side effects of management actions include reducing vigor or abundance of native or desirable species, inhibiting overall productivity or diversity, shifting community structure and function, altering physical conditions, and more (Louda et al. 1997; D'Antonio et al. 2004; Smith et al. 2006; Hulme 2006; Ortega and Pearson in review). Therefore, effective weed management requires weighing the success of control measures (e.g., impacts on target weeds and recovery of native species) against the side effects of management actions. This necessitates a thorough understanding of how management tools interact with nontarget system components as well as the target weed (e.g., Pearson and Fletcher 2008).

Weed management in natural areas is further complicated by secondary invasion. Secondary invasion occurs when successful control or suppression of the target weed results in proliferation of another exotic invader. In many cases, the secondary invader may cause more problems and present a greater management challenge than the original target weed (Hulme 2006; Ortega and Pearson in review). Although we note that secondary invasion could be considered a management side effect, we treat it as a separate condition because it involves additional species extrinsic to the original native system. Thus, we treat management side effects as the unintended effects of the management action on native system components or processes, whereas we treat secondary invasion as a compensatory response of the exotic subset of the community to suppression of the target weed. We feel this distinction is helpful because secondary invasion is not so much a side effect of a specific management tool on nontarget species as it is a failure or incapacity to address the weed problem itself, i.e., the system-level processes such as propagule pressure or disturbance underlying and promoting invasions (e.g., Hobbs and Huenneke 1992; Davis et al. 2000; Seabloom et al. 2003; McDougal and Turkington 2005; Smith et al. 2006; Thomas and Reid 2007). Readers not fully comfortable with this distinction may choose to think of secondary invasion as a special case of management side effects, albeit one that is sufficiently important to warrant special attention.

We explore these challenges in natural areas weed management by examining spotted knapweed (*Centaurea maculosa*) invasion and management in the western United States and supplementing this case study with complementary research on other invaders. *Centaurea maculosa* has been identified as the single most studied terrestrial invasive plant (Pysek et al. 2008) and is prominent among a group of knapweeds identified as among the most serious plant invaders in the western United States (Sheley et al. 1998; LeJeune and Seastedt 2001). *C. maculosa* is a perennial, tap-rooted forb in the Asteraceae family that was first discovered in North America in the late 1800s (Strange et al. 1979) and is thought to have arrived from Europe as a contaminant of alfalfa seed (Groh 1944). It is an aggressive invader that rapidly spread across the United States and has become a particular problem in semi arid habitats of the western United States (Sheley et al. 1998).

Several studies have examined a broad range of *C. maculosa*'s impacts and interactions in natural systems (Tyser and Key 1988; Ridenour and Callaway 2001; Ortega and Pearson 2005; Ortega et al. 2006; Pearson 2009), while others have explored potential mechanisms to explain its successful invasion (Ridenour and Callaway 2001; Callaway and Ridenour 2004). Its infamy has made *C. maculosa* a primary target of weed management using biocontrol, herbicides, and grazing (Harris and Myers 1984; Rice et al. 1997a; Olson et al. 1997; Sheley et al. 1998). Importantly, *C. maculosa* management outcomes have been some of the most thoroughly studied for weed management of natural areas (Thompson 1996; Rice et al. 1997a; Rice and Toney 1998; Tyser et al. 1998; Pearson et al. 2000; Ortega et al. 2004; Olson et al. 1997; Story et al. 1995, 2006, 2008; Pearson and Fletcher 2008; Pearson and Callaway 2003, 2006, 2008; Ortega and Pearson in review). Thus, *C. maculosa* offers a comprehensive case study for examining invasive species management. Here, we examine *C. maculosa*'s impacts on and interactions with native system components, the efficacy and side effects of major management tools, and the extent and severity of secondary invasion to better understand the challenges of natural areas weed management.

C. MACULOSA IMPACTS AND INTERACTIONS IN THE INVADED SYSTEM

If simply controlling weed populations in natural areas resulted in full restoration of all system components, there would be no need to assess weed impacts. We could simply focus on suppressing weed populations, because this would fix the problem. However, as highlighted in later sections, weed management actions rarely mitigate all weed impacts, and they virtually always have side effects on nontarget species. Therefore, understanding weed impacts and interactions within the invaded system is prerequisite to assessing which impacts may be amenable to which mitigation efforts. Yet, despite numerous studies documenting the profound ecosystem-level effects strong invaders can have (e.g., Vitousek 1990; Levine et al. 2003), there are surprisingly few cases where a weed's impacts on and interactions with native species and community processes have been examined in detail. The case of *C. maculosa* invasion in the western United States offers one of the best such examples. Extensive research indicates that *C. maculosa* has a range of positive and negative direct and indirect interactions with native species that have altered community interactions at multiple trophic levels and have important implications for its management. We briefly discuss these results here.

At the lowest trophic levels, evidence suggests that *C. maculosa* substantially suppresses a range of native plant species (Tyser and Key 1988; Ridenour and Callaway 2001; Ortega and Pearson 2005, in review). However, not all species are equally at risk. A detailed analysis of the relationship between *C. maculosa* and native plant functional groups suggested that *C. maculosa* had the strongest negative effects on native perennial forbs, moderate negative effects on perennial grasses, and no detectable effect on annual forbs (Ortega and Pearson 2005). These results suggest that *C. maculosa* invasion initiates a trajectory within these systems that shifts the plant community by suppressing perennial forbs and grasses that typically dominant native biomass. Since forbs are the primary source of diversity, commonly making up ≥80% of species richness in these systems (Mueggler and Stewart 1980; Pokorny et al. 2005), *C. maculosa* invasion also takes a toll on native plant diversity (Ortega and Pearson 2005). This impact trajectory has important implications for management. Ideally, management actions would be directed at reversing the trajectory, but limitations in the selectivity of management tools may result in management efforts that actually exacerbate certain invader impacts. For example, broadleaf herbicides commonly suppress native forbs (Rice et al. 1997a; Crone et al. 2009; Ortega and Pearson in review), potentially exaggerating trajectories initiated by *C. maculosa* invasion even if the invader is successfully removed (see *Efficacy and side effects of management actions* below).

Most studies of exotic plant impacts do not extend beyond lateral plant-plant interactions to examine how plant invasions affect higher trophic levels, particularly at the level of predators. Most efforts to assess higher trophic level effects have been limited to extrapolating forage production to estimate impacts on domestic or wild ungulates (e.g., Trammell and Butler 1995). *C. maculosa* is believed to reduce forage for domestic and wild ungulates through its direct reductions in native plant biomass (Thompson 1996; Rice et al. 1997b). However, native ungulates do use *C. maculosa* as forage to some extent (e.g., Wright and Kelsey 1997), and no studies to our knowledge have examined the effects of *C. maculosa* or other invasive plants on population-level responses of large herbivores. This is undoubtedly due to the difficulty of conducting studies at the necessary scale to effectively accomplish this. Nonetheless, it is reasonable to assume that there is some threshold of *C. maculosa* abundance, and therefore reductions in native plant biomass, beyond which large wild herbivores such as deer (*Odocoileus* spp.), elk (*Cervus elaphus*), and sheep (*Ovis canadensis*) might experience population-level impacts, which may also affect higher trophic levels.

One study provides evidence that weed-induced reductions in native plant biomass and diversity impact not only herbivores, but also higher trophic levels by eroding food chains (Ortega et al. 2006). Pitfall sampling in *C. maculosa* invaded and comparable uninvaded sites suggests that *C. maculosa* invasion reduced biomass and richness of invertebrate groups such as grasshoppers (Orthoptera), which are important food resources for many small predators such as birds, small mammals, and spiders. In this scenario, *C. maculosa* invasion and resulting declines in invertebrates were associated with negative impacts on an insectivorous songbird, the chipping sparrow (*Spizella passerina*), as indicated by delayed nest initiation, lower site fidelity of breeding adults, reduced likelihood of double brooding, and, overall, projected lower fecundity for sparrows on *C. maculosa*-invaded sites (Ortega et al. 2006). Because chipping sparrow nests are located in trees, which are unaffected by *C. maculosa* invasion, and nest predation did not vary between invaded and uninvaded habitats, *C. maculosa* impacts on chipping sparrow fecundity appear to arise through reductions in food for parents and possibly also offspring. In addition to showing that *C. maculosa* can impact invertebrates and other wildlife, these results illustrate how invasion by exotic plants like *C. maculosa* may erode native food chains by reducing herbivore populations and impacting the predators they support. This suggests that removing the weed without restoring the native plant biomass and diversity, may fail to restore certain herbivores and predators due to residual impacts on food chains.

Exotic plant invasions may affect higher trophic levels and trophic interactions through less obvious means as well. Invasion of western North American grasslands by *C. maculosa* and other European forbs is shifting the vegetation architecture of these grasslands, with substantial implications for predator populations and predator-prey interactions (Pearson 2009). European forbs like *C. maculosa* that are invading these grasslands are generally larger, more rigid, and more structurally complex compared to the native grassland vegetation. This has lead to a dramatic increase in native web-building spiders by providing a superabundance of new substrates favorable for web construction. It has also affected the hunting behavior of these predatory spiders by allowing them to become more efficient. Webs of *Dictyna* spp. spiders constructed on *C. maculosa* plants were three to four times larger and captured two times more total prey and four times more large prey compared with webs on native substrates. The overall result was that *C. maculosa* increased predation rates on spider prey by ≥89 fold in invaded grassland due to the cumulative effects of *C. maculosa* architecture on spider density and hunting behavior. This research shows that exotic plant invasions can influence higher trophic levels not only through food chains as described above for chipping sparrows, but also through changes in vegetation architecture that directly affect predator densities by altering their habitat. Additionally, because plant architecture provides the arena for predator-prey interactions, such changes can have complex effects on predator-prey dynamics. It also shows that invasive plants can have substantial positive effects on populations of some native species, as noted elsewhere (Rodriguez 2006; White et al. 2006). However, due to indirect interactions, even very strong positive direct effects of invasion on some species may lead to very strong negative effects on other native species such as spider prey (Pearson 2009).

In addition to biotic effects, *C. maculosa* may affect abiotic components of native systems as well. For example, *C. maculosa* appears to increase soil erosion (Lacey et al. 1989), a condition that could result in long-term residual damage to a site even if *C. maculosa* is completely removed. *C. maculosa* also produces chemicals such as the root exudate, ±catechin (Bais et al. 2003), that can have phosphorus chelating effects within soils (Callaway and Ridenour 2004). Although catechin is not thought to be particularly persistent in the absence of *C. maculosa*, possible effects on nutrient availability could persist for unknown periods after the weed's removal. In general, exotic species that alter soil chemistry, soil structure, or hydrologic conditions may have residual community- and ecosystem-level effects that persist following control.

Collectively, these studies show that *C. maculosa* affects not only plant communities, but also soils, consumers, predators, and important community processes through positive, negative, direct, indirect, biotic and abiotic interactions. Because most *C. maculosa* impacts on the native system arise as a result of its effects on vegetation, controlling *C. maculosa* populations is only likely to restore preinvasion conditions to the extent that native vegetation recovers (one exception is *C. maculosa*'s direct effects on spiders and indirect effects on spider prey, which may be largely reversed by simply removing the weed). Recovery of the plant community may in turn depend on the ability to mitigate abiotic impacts of invasion, restore seed sources, and address similar factors that may interfere with native plant recovery (e.g., Seabloom et al. 2003; McDougal and Turkington 2005). Although full restoration may represent the Holy Grail of natural areas weed management, due to the extent and complexity of interactions that exotic plants may establish in natural systems and their own pervasiveness, full restoration following heavy invasion is rarely feasible. On more intensively managed natural areas such as grazing lands, it may not even be desirable, and it is often not the primary objective. Nonetheless, the more weed impacts can be mitigated, the more ecosystem services are likely to be restored to preinvasion conditions. This should be the gold standard for managing pubic lands.

EFFICACY AND SIDE EFFECTS OF MANAGEMENT ACTIONS – A BALANCING ACT

The intended effect of a management tool on the target weed is only one aspect of its influence on the treated system. As with human medicine all treatments have side effects, and successful management requires finding an appropriate balance between negative side effects of treatment and the intended treatment response. To accomplish this, we need to understand what kinds of side effects can arise from different management tools.

Limited selectivity of weed management tools is perhaps the greatest cause of side effects and therefore one of the greatest limitations to improving management in natural areas. However, side effects can also arise from highly selective control measures due to indirect interactions involving nontarget species (Pearson and Callaway 2003). Additionally, side effects can arise through physical factors such as when management tools such as grazing or fire create disturbances. Duration or persistence of a treatment can determine the strength and therefore the biological significance of its side effects. For example, the lack of selectivity of an herbicide may not result in biologically significant side effects on nontarget species if the effect is sufficiently short-lived. However, the same side effect may become biologically significant if it persists over time (Crone et al. 2009). Here we evaluate management tools and how they interact with natural systems to better understand how deleterious side effects of management actions can be avoided or minimized. We do so by focusing on *C. maculosa* management using some of the more prominent tools employed for weeds in natural areas: herbicide, classical biological control, and grazing. Because secondary invasion can be an important consequence of any weed management measure, we address issues of secondary invasion separately in the next section.

Herbicide

Herbicide applications are increasingly used in natural areas weed management, with an emphasis on broadleaf herbicides for controlling exotic forbs (DiTomaso 2000). Broadleaf herbicides are heavily used for *C. maculosa* control and extensive research has been conducted to evaluate the efficacy of this method and identify ways to minimize its side effects on native plants (Rice et al. 1997a; Rice and Toney 1998; Tyser et al. 1998). These studies show that *C. maculosa* is fairly sensitive to several broadleaf herbicides. As a result, herbicides can be used at low dosages in an effort to minimize side effects on nontarget plants while still achieving effective *C. maculosa* control (≥80% reductions of the target species for several years; Rice et al. 1997a; Sheley and Jacobs 1997; Rice and Toney 1998). Additionally, because *C. maculosa* is actively growing later than many native forbs, selectivity can be enhanced by applying herbicides after other forbs have senesced (Rice et al. 1997a). Yet, despite these refinements, broadleaf herbicide treatments for *C. maculosa* can still have serious side effects (Ortega and Pearson in review).

The use of broadleaf herbicides for *C. maculosa* control has been shown to shift the composition of native communities away from forbs toward grasses (Ortega and Pearson in review). This is of particular significance in intermountain grasslands where *C. maculosa* is most problematic because forbs generally comprise ≥80% of the species richness in these systems and can dominate biomass (Mueggler and Stewart 1980; Ortega and Pearson 2005; Pokorney et al. 2005). It is also of concern because, as discussed above, *C. maculosa* invasion itself shifts community composition away from dominance by perennial forbs (Ortega and Pearson 2005). Thus, if not carefully used in this system, broadleaf herbicides may exacerbate certain invader impacts even if they control the target weed.

Herbicide-driven declines in forbs can potentially be substantial due to demographic effects. In addition to suppressing cover of adult native forbs, broadleaf herbicides can kill young plants and suppress reproduction for several years following treatments (Crone et al. 2009; Ortega and Pearson in review). Such effects can create population bottlenecks for native forbs that can result in demographic declines over time. Long-term demographic analysis suggests that the degree to which such impacts may threaten persistence of a species in herbicide treatment areas will depend on the persistence of the herbicide and the reapplication rates required to maintain control of the target weed relative to the life history characteristics of the plant (Crone et al. 2009). These efficacy studies offer suggestions for further refining broadleaf herbicide applications to reduce side effects in natural areas. Emphasizing spot spraying of target weeds over broadcast spraying can reduce the spatial extent of side effects and encourage recovery of native species by providing vigorous seed sources in uninvaded patches that are protected from herbicides. Additionally, target weed recovery should be carefully monitored to ensure that re-treatment to maintain control of the target weed is not premature. This will reduce the risk of excessively reapplying herbicides at rates that can further depress native forb populations (Crone et al. 2009).

Most of the lessons learned from studies of *C. maculosa* herbicide management will also apply to management of other exotic forbs using broadleaf herbicides. However, many other exotic forbs are less sensitive to herbicides and require stronger dosages (Rice and Toney 1998; Tu et al. 2001), so the types of side effects described here will tend to be stronger and more difficult to mitigate. Although side effects such as loss of forbs may be acceptable for relatively restricted areas under specific management objectives such as intensive forage production for domestic and wild herbivores, large scale reductions of forb diversity in grassland systems should be a major concern for natural areas management. Forbs commonly represent the bulk of the species and functional diversity in natural grasslands (Seabloom et al. 2003; Pokorney et al. 2004). They support communities of pollinators, herbivores, and higher trophic levels (e.g., Potts et al. 2003; Ortega et al. 2006). They also may be an important factor in maintaining resistance of natural areas to future invasion (Dukes 2002; Zavaleta and Hulvey 2004; Maron and Marler 2007).

Grazing

Grazing for the purpose of controlling range weeds has gained interest and application over the past 10-15 years (Olson et al. 1997; Sheley et al. 1998; DiTomaso 2000). Grazing is generally less effective at controlling weeds than herbicides because it does not usually kill plants outright but rather reduces biomass, flowering, and seed production (Olson et al. 1997; Sheley et al. 1998). Like herbicide applications, grazing tends to target exotic forbs by using domestic herbivores such as sheep (*Ovis aries*) or goats (*Capra aegagrus hircus*) that either have a natural affinity for the target weed or can be trained to feed on the target weed (e.g., Walker et al. 1994; DiTomaso 2000). Within intermountain grasslands, the fact that many exotic forbs are green after most natives have begun to senesce is exploited to increase selectivity by timing grazing so animals will focus on the actively growing and hence more palatable target weed (Olson et al. 1997). To be most effective, grazing must be short in duration to minimize disturbance from trampling and reduce the tendency of animals to forage on nontarget species. The numbers of animals grazed must also be minimized for similar reasons. Thus, grazing to reduce weeds requires careful oversight to ensure it is effective. Depending on the target weed and the ability to control the timing and specificity of the foraging, grazing may be more or less selective than broadleaf herbicides. Use of forb eaters like sheep can result in reductions in forbs and increases in grasses similar to herbicides (R. Kott, Montana State University, Bozeman, MT, pers. comm.). In this regard, grazing can push a community away from grasses and exacerbate the trends begun by the weed itself. Excessive grazing is well known to facilitate weed invasion (e.g., Loeser et al. 2007), so if grazing for weed management is not *very* carefully conducted, it will almost certainly exacerbate the weed problem.

Biological Control

Classical biological control (referred to hereafter as biocontrol) involves the introduction of exotic organisms, usually invertebrates from the native range of the invader, to suppress pest populations through top-down control (Thomas and Reid 2007; Müller-Shärer and Schaffner 2008). When successful, biocontrol can be an extremely powerful and economical tool over large areas (Gurr and Wratten 2000). As a result, biocontrol is perhaps the most widely used weed management technique in natural areas (DiTomaso 2000; Coombs et al. 2004). The history of biocontrol illustrates not only the importance of selectivity of weed management tools, but also the limitations. Historically, biocontrol was practiced using generalist species including vertebrate predators and polyphagous insects that resulted in extensive side effects when they attacked nontarget species (Howarth 1991; Simberloff and Stiling 1996; Louda et al. 1997; Henneman and Memmott 2001). To address this problem, weed biocontrol has become progressively more stringent in selecting for highly specialized agents that attack only the target weed (McEvoy 1996). Today, weed biocontrol agents are highly host-specific (Pemberton 2000), and biocontrol of weeds is arguably the single most selective weed management tool currently in use aside from hand pulling. However, recent examination of *C. maculosa* biocontrol has established that even highly host-specific biocontrol agents can have rather significant nontarget effects, indicating a need to better understand these side effects to guard against them (Pearson and Callaway 2003, 2005).

Until recently, host-specificity was deemed the ultimate assurance that exotic organisms introduced for biological control would not harm nontarget species. However, studies now show that even if a biocontrol agent is completely host-specific, it can still exhibit nontarget effects through food-web interactions simply by being consumed by other organisms (Pearson et al. 2000; Pearson and Callaway 2003). Although, it is well documented that exotic invertebrates introduced for biological control are commonly consumed by a variety of native and nonnative species, such interactions had previously been studied only as potential sources of biocontrol interference (Goeden and Louda 1976). Community-level examination of *C. maculosa* biocontrol shows how such consumer interactions can bring about indirect nontarget effects.

The gallflies, *Urophora affinis* and *U. quadrifaciata*, introduced for *C. maculosa* biological control, are eaten by numerous native generalist species (Story et al. 1995; Pearson et al. 2000). Several studies suggest that gallfly consumption by native deer mice (*Peromyscus maniculatus*) results in food subsidies that elevate deer mouse populations by two to three fold (Ortega et al. 2004; Pearson and Callaway 2006; Pearson and Fletcher

2008). Moreover, gallfly–subsidies to deer mice have been correlated with higher incidence of Sin Nombre hantavirus in deer mouse populations (Pearson and Callaway 2006). Because Sin Nombre hantavirus is the etiological agent for the deadly hantavirus pulmonary syndrome in humans (Childs et al. 1994), elevating hantavirus over large regions of the landscape has potentially significant implications for the ecology and epidemiology of this disease. Biocontrol food subsidies to deer mice also appear to negatively impact some of the native plants they were introduced to benefit. As efficient seed predators, deer mice can reduce recruitment of juveniles and, ultimately, abundance of adults in native plant populations through seed predation (Maron and Kauffman 2006; Bricker et al. in press). A recent study in western Montana showed that deer mice reduced recruitment of the dominant native grass, *Pseudoroegneria spicata*, and forb, *Balsamorhiza sagittata*, through seed predation and this effect was significantly greater for *B. sagittata* where biocontrol food subsidies elevated mouse populations (Pearson and Fletcher 2008). These results suggest that gallflies that were introduced to reduce *C. maculosa*'s impacts on native plants may actually be increasing *C. maculosa*'s negative impacts on some native plants through food subsidies via second-order apparent competition. Ongoing work suggests that gallfly food subsidies to black-capped chickadees (*Poecile atricapillus*) may influence foraging behavior and competitive interactions among chickadee species and possibly other songbirds (L. Greenwood, unpublished data). In contrast, other work suggests that spiders that live on *C. maculosa* and consume adult *Urophora* are far more affected by structural attributes of *C. maculosa* than food resources provided by *Urophora* (Pearson 2009).

The study of *C. maculosa* biocontrol illustrates that host-specific agents can have significant impacts on nontarget species through food-web interactions. Understanding how such interactions take place is crucial to mitigating these side effects in the future. The strength of the indirect effects originating from *Urophora* biocontrol agents may be attributed to several factors: *Urophora* are highly palatable, they are readily available over extended periods of time, they are super-abundant, they are exploited by strongly interacting generalist consumers, and they have not controlled the target weed. If one or more of these criteria are not met or greatly diminished, indirect effects of a biocontrol agent arising through food-web interactions will likely be attenuated or weakened. Even if a biocontrol agent meets all of the criteria described above, as *Urophora* do, any indirect food-web effects may be rendered ephemeral and biologically unimportant if the control agent ultimately suppresses the target species (Pearson and Callaway 2003). This is because the host-specificity of the biocontrol agent will ensure that it too declines by eating itself out of house and home as it reduces its host populations.

Recent reports of local reductions in *C. maculosa* populations have been attributed to successful biocontrol of this weed (Story et al. 2006, 2008) and interpreted as an example of biocontrol success ultimately nullifying indirect nontarget effects arising from gallfly subsidies to deer mice (Van Driesche et al. 2008). Hopefully, these assertions will ultimately be born out, but they are currently premature. Long-term monitoring shows that the key agent postulated as controlling *C. maculosa*, the root weevil (*Cyphocleonus achates*), is absent at many locations where *C. maculosa* has recently declined (Sturdevant et al. 2006). Most other *C. maculosa* biocontrol agents are also absent from numerous sites where *C. maculosa* has declined (Sturdevant et al. 2006). Thus, biocontrol alone cannot explain these observations.

Reductions in spring precipitation offer the most parsimonious explanation for widespread *C. maculosa* declines. Spring precipitation is highly correlated with *C. maculosa* declines and is the only factor consistently present at all locations where declines have been reported (Pearson and Fletcher 2008; D. E. Pearson unpublished data). Notably, Sturdevant et al. (2006) did report trends toward more severe declines in *C. maculosa* vigor at sites where *C. achates* was present. Although these effects were not statistically significant, they could suggest an interaction whereby *C. achates* may impact *C. maculosa* populations when the plant is drought stressed. Carefully designed experiments are currently underway to evaluate this hypothesis by examining the independent and interacting effects of spring precipitation inputs and *C. achates* herbivory on *C. maculosa* populations (D. E. Pearson and Y. K Ortega, ongoing research). Although it is presently unclear whether current biocontrol agents actually offer sufficient control over *C. maculosa* to relieve indirect nontarget effects due to food-web interactions, the case study of *C. maculosa* biocontrol illustrates the importance of efficacy for safe and effective biocontrol. If biocontrol is successful, i.e., reduces populations of the target weed below its ecological threshold of impact, then indirect nontarget effects should dissipate to levels that are biologically insignificant (Pearson and Callaway 2003, 2005). As the *C. maculosa* saga continues to unfold, *C. maculosa* may ultimately provide an empirical case study showing how efficacy can guard against indirect nontarget effects, but such an outcome will depend on the degree to which biocontrol agents can actually be shown to reduce *C. maculosa* populations over large areas.

SECONDARY INVASION

As investigations into the efficacy of weed management have begun to expand beyond the target weed to incorporate general vegetation responses, an alarming trend is emerging. Successful control of the target species is far too often resulting in their replacement by secondary invaders (Table 1). This result does not appear to be limited to any one particular management strategy, target weed, or secondary invader. For example, secondary invaders flourish following *C. maculosa* control using herbicide, biocontrol, and grazing (Olson et al. 1997; Story et al. 2006; Ortega and Pearson in review, Rinella et al. in review). Control of crownvetch (*Coronilla varia*), St. Johnswort (*Hypericum perforatum*), artichoke thistle (*Cynara cardunculus*), and diffuse knapweed (*Centaurea diffusa*) have also given rise to secondary invaders (Huffaker and Kennett 1959; Symstad 2004; Bush et al. 2007; Seastedt et al. 2008). Secondary invasion following successful control of *H. perforatum* in the mid nineteen hundreds (Huffaker and Kennett 1959) indicates this is not merely a contemporary problem, but likely results any time additional species of strong invaders are present at a site where a dominant weed is controlled and the secondary invader proves relatively insensitive to the control method.

Although secondary invasion appears somewhat ubiquitous, a few general patterns do emerge. First and foremost, most prominent secondary invaders we could find documentation of were grasses. The principal grass was cheatgrass (*Bromus tectorum*), but Kentucky bluegrass (*Poa pratensis*) was another key secondary invader. Additionally, most target weeds were forbs. Thus, there is a general pattern suggesting that control of invasive forbs is shifting communities toward exotic grasses, though we also found one case where control of

Table 1. Secondary invasion following control of the target weed.

Target Weed	Secondary Invader	System	Control Method	Source
Artichoke thistle (*Cynara cardunculus*)	Exotic spp.	grassland	herbicide	Seastedt et al. (2008)
Diffuse knapweed (*Centaurea diffusa*)	Cheatgrass (*Bromus tectorum*)	grassland	biocontrol	Bush et al. (2007)
Leafy spurge (*Euphorbia esula*)	Canada thistle (*Circium arvense*)	meadow	herbicide	Smith et al. (2006)
Crownvetch (*Coronilla varia*)	Kentucky bluegrass (*Poa pratensis*)	prairie	herbicide	Symstad (2004)
Spotted knapweed (*Centaurea maculosa*)	Cheatgrass (*Bromus tectorum*)	grassland	herbicide	Ortega and Pearson in review
Spotted knapweed (*Centaurea maculosa*)	Cheatgrass (*Bromus tectorum*)	agricultural	biocontrol	Story et al. (2006)
Spotted knapweed (*Centaurea maculosa*)	Kentucky bluegrass (*Poa pratensis*) and other exotic grasses	grassland	herbicide	Tyser et al. (1998)
Spotted knapweed (*Centaurea maculosa*)	Kentucky bluegrass (*Poa pratensis*)	grassland	grazing	Olson et al. (1997)
Spotted knapweed (*Centaurea maculosa*) Sulfur cinquefoil (*Potentilla recta*)	Cheatgrass (*Bromus tectorum*) and other exotic grasses	grassland	herbicide	Sheley et al. (2006)
St. Johnswort (*Hypericum perforatum*)	Cheatgrass (*Bromus tectorum*) and other exotic grasses	grassland	biocontrol	Huffaker and Kennett (1959)

dominant exotic grasses allowed increases in exotic forbs (Cox and Allen 2008). To some extent, this pattern could be attributed to control methods such as herbicides and grazing that tend to generically suppress either forbs or grasses, thereby favoring weeds in unaffected functional groups. However, even controlling exotic weeds with highly selective methods such as biocontrol can give rise to secondary invaders like downy brome (a.k.a cheatgrass) (Huffaker and Kennett 1959; Story et al. 2006). This raises the question of whether, at least in some cases, weed control is simply accelerating general patterns of invader succession, or creating an “invasive species treadmill” (McEvoy and Coombs 2000). For example, seven years of monitoring of native grasslands, *C. maculosa*-dominated grasslands, and *C. maculosa*-dominated grasslands that had been treated with picloram showed that although cheatgrass invasion was greatly accelerated in herbicide treated areas, it also increased substantially in the native and untreated *C. maculosa*-invaded sites over time (Y. K. Ortega and D. E. Pearson, unpublished data). None of these sites were grazed by domestic herbivores over the study period, suggesting that disturbance was not increased over natural levels. Cheatgrass may simply be increasing in intermountain regions, and it may ultimately overtake *C. maculosa*-invaded habitats. In general, remarkably little is known about invader succession. However, knowledge of invader succession may prove extremely valuable for predicting and preventing secondary invasion following various weed management activities.

Recent ecological studies indicate that understanding the processes underlying invasion may be essential to understanding the problem of secondary invasion. If invaders are acting as passengers in a system and are merely responding to changes in disturbance regimes or other processes like climate change (Hobbs and Huenneke 1992; MacDougall and Turkington 2005), or if invasion persists as a residual effect of system-level changes such as loss of native seed inputs (Seabloom et al. 2003), then management must move beyond suppression of the dominant weed to management of system-level processes, where possible, to reverse the invasion trend. In contrast, if invaders are drivers, particularly as in the case of some grasses that usurp system-level processes such as fire to their advantage (D'Antonio and Vitousek 1992), the problem may be untenable and resources may be best deployed elsewhere. Additional ecological studies are needed that identify such system-level causes of invasion as well as studies that begin to apply these understandings to restoration problems (e.g., Orrock et al. 2008).

Unfortunately, any current discussions about secondary invasion are largely speculative, because there simply is not enough information presently available to effectively assess patterns and potential causes, at least not in a readily accessibly form. Our searches of databases for studies documenting secondary invasion proved largely fruitless, because there is no formally recognized term for this phenomenon and many studies only casually note increases in secondary exotic species following weed control. One reason for this may be that secondary invasion by grasses in many cases may not be recognized as a problem because exotic grasses, even cheatgrass, are commonly valued as forage species (Mosely 1996). Similarly, exotic grasses are rarely included on noxious weed lists (Rice 2008). We suggest that more attention should be paid to evaluating the response of exotic plants to weed control in natural areas, whether exotics are grasses or forbs. Formal use of terminology such as "secondary invasion" to describe this phenomenon and its inclusion in published key word lists could rapidly expand our knowledge of the extent of this problem through meta-analyses that may possibly suggest some solutions. Current information suggests that secondary invasion may pose a serious and widespread problem. In fact, it may well be the greatest challenge to successful weed management in natural areas, as natural areas are increasingly bombarded by hoards of aggressive invaders trying to gain dominance. There is currently a gaping hole in our understandings of the extent and causes of secondary invasion that represents a major impediment to weed management.

CONCLUSION

Natural areas are highly complex systems involving many individual species whose composition and relative abundance both influence and are influenced by a variety of community interactions and ecosystem-level processes. Exotic plant invasions affect not only the biomass and richness of native plants, but higher trophic levels and many of the processes that structure native communities and systems. Moreover, weed management tools themselves can interact with native species and system processes in complex ways, as they are rarely so selective that they affect only the target weed. Even when management tools are highly selective, directly affecting only the target weed, they can still have strong side effects on nontarget species due to complex community interactions. Thus, weed management in natural areas is in essence community management or directed community assembly. In order to effectively and predictably manage invaded communities, we need to understand how the weed affects species, community-level, and system-level processes. We also need to understand how prospective management tools interact with the weed and other system components and processes to determine the potential for management side effects. Only with this information can we effectively evaluate the potential for management actions to mitigate certain weed impacts and weigh these against potential management side effects to ensure that the ultimate management outcome is one that maximizes efficacy and minimizes deleterious side effects. Secondary invasion appears to be a large and increasing obstacle to successful weed management because it derails attempts to effectively reassemble a community even after successful control of the target weed. Better understandings of the processes underlying exotic plant invasions are needed to evaluate the causes of secondary invasions and the potential for addressing this serious problem. We urgently need more studies documenting community- and ecosystem-level outcomes of weed management measures in order evaluate the extent to which such actions mitigate invader impacts but also incur deleterious side effects and promote secondary weed invasions.

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