Ecological Syndromes of Invasion in Semiarid Rangelands and their Implications for Land Management and Restoration

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Abstract

An understanding of why infestations occur helps land managers target causes and not just symptoms of invasions. Syndromes, which are recurring sets of symptoms that are characteristic of a particular disorder or disease, help link basic and generalizable science with the specific treatment needs of individuals in clinical practice, or sites in land management. We hypothesized that management-related disturbances increase site resources in ways that selectively favor ecophysiological traits of invasive compared to established flora. In rangelands of Montana and Idaho, we measured 1) the effects of prescribed fire and shrub removal on plant community composition and soil water availability, and 2) differences in photosynthesis and water relations in *Centaurea maculosa* (spotted knapweed; CEMA) and established flora (mainly grasses). Soil water increased substantially below about 0.4 m depth in disturbed compared to control plots. Carbon uptake was about 50% greater in CEMA than the grasses, due apparently to greater water uptake from deep soils and correspondingly greater water status in CEMA. These results point to a possible ecological syndrome that may be applicable in some form to vast areas of sagebrush-steppe that 1) are disturbed in ways that 2) cause unusually low abundances of native, deep-rooted perennials, and 3) as a consequence, have unusually abundant deep soil water, and 4) are therefore more easily invaded by CEMA and similar exotic perennial forbs. If correct, this syndrome suggests that managing semiarid communities for complete utilization of soil water may be an important way that rangeland managers can avoid infestations by exotic perennial forbs.

Key words: invasive plants, fire, semiarid rangelands, sagebrush steppe, ecophysiology, soil water

Introduction

Exotic plant invasion is probably the greatest ecological problem in the management of semiarid rangelands of the American Intermountain west. Exotic plant infestations in semiarid rangelands have generally been persistent and difficult or impossible to eradicate, and have led to considerable ecological and economic damage. Much research has focused on eradication of invasive plants, while basic factors underlying the invasiveness of certain plants or the susceptibility of sites to invasion have received less attention. A better understanding of why invasions occur should lead to more effective, pro-active management and restoration strategies that prevent invasions from occurring.

Unfortunately, basic research is difficult to conduct on the short-time scales that are most relevant to land management decisions, and also tends to be too expensive to limit in scope to specific sites that concern land managers. Invasive plant management may benefit from adopting means by which clinical practice is linked with basic research in medical disciplines. Clinicians use sets of symptoms to identify disorders in their subjects, then prescribe remedial actions that are based in some way on basic, scientific knowledge of how the disorder functions. This system links the efforts of scientists who seek to provide basic information that can be broadly applied, and clinicians who are concerned with specific subjects.

In contrast to medical systems, restoration of infested rangelands and other habitats has typically focused entirely and usually unsuccessfully on application of unnatural chemicals or biological agents to reduce the abundance of invasive plants. Exotic plant infestations of rangelands may be symptoms of other, currently unknown 'disorders' in ecosystem structure and function that are likely to arise from natural and anthropogenic disturbance. If so, failed efforts to restore infested lands may be due to an emphasis on treating symptoms and not identifying and treating causes of infestations. Prescriptions of fire for agricultural or ecological restoration purposes, grazing, mechanical removal of shrubs, and other management practices are examples

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of practices which have been associated with invasions and perhaps are causative agents of infestations (eg. Fig. 1).

Figure 1. A 2004 photo of a near monocultural infestation of leafy spurge (*Euphorbia esula*) in a 1999 prescribed burn at the USSES, with unburned and uninfested sagebrush steppe in the background. Only 0.5 of >200 ha were infested in this area of the otherwise pristine USSES, and it is a small example of much larger problems in nearby rangelands.

Infestations result from dispersal of exotic seed into a site, followed by successful emergence, establishment, persistence, and proliferation of exotic plants within the site. Control of dispersal is a known and practiced aspect of exotic plant management, but infestations still occur and persist in semiarid lands of Idaho and Montana. The objective of our ongoing research is to determine factors that contribute to the persistence of non-indigenous, invasive, perennial forbs of semiarid rangelands. Previous research (eg. Mack 1985) demonstrated the widespread syndrome of infestations of semiarid lands by annual 'cheatgrass' (*Bromus* sp.) and fire-related mechanisms that contribute to its persistence. However, many exotic, invasive plants in semiarid rangelands of western North America are perennial forbs that can have deep taproots.

This paper describes preliminary findings from our research on basic mechanisms contributing to the success of spotted knapweed (*Centaurea maculosa*) and other, exotic perennial forbs (eg. leafy spurge, *Euphorbia esula*) in sagebrush steppe rangelands. Disturbance is a frequently cited cause of infestations, but few studies provide a comprehensive understanding of how site conditions change in ways that selectively favor invasive compared to native or established plants. Fire and eradication of sagebrush are two common disturbances that are associated with infestation by exotic perennial forbs in the sagebrush steppe. We hypothesized that fire or removal of shrubs cause increases in site resources that selectively favor the maintenance of populations of *Centaurea* compared to native or established plants. Water availability is the most limiting soil resource of semiarid lands, and was therefore our focus. We measured how fire and removal of shrubs affect patterns of soil water availability, and how the productivity and water relations of invasive and native plants respond to changes in availability of soil water.

Methods

Data presented here synthesize in abbreviated form the major findings from several other papers that are either in review or in preparation for submission elsewhere. Photosynthesis and water relations were measured for *Centaurea maculosa* L. near Bozeman and Helena, Montana and the US Sheep Experimental Station (USSES) near Dubois, Idaho. Native or established vegetation at the Montana sites consisted of sagebrush (*Artemesia tridentata* ssp. *wyomingensis*), brome grass (*Bromus inermis*), and wheatgrasses (*Psuedoregneria spicata, Agropyron smitthi*), and the USSES site consisted of *Artemesia tridentata* ssp. *vaseyana*, grasses such as *Psuedoregneria spicata, Fescue idahoensis*, and *Poa sp.*,., and forbs such as *Crepis*, *Erigeron*, *Balsamorhiza, and Lupinus* sp.. Elevation and mean annual precipitation for each site was 1650 m and 297 mm/yr for the USSES, 1500 m and 440 mm/yr for the Bozeman site, and 1200 m and 295 mm/yr for the Helena Site, respectively (Western Regional Climate Center, Desert Research Institute, Reno, NV).

Fire and shrub removal effects

In September of 2002, 12 replicate areas of the USSES ranging from 0.1 to >100 ha were burned (Fig. 2). In the same month, all sagebrush were mechanically removed using chainsaws in three, 25 x 25 m areas. Subsequently, soil water contents were measured using a neutron probe (CPN, Martinez, CA). Corresponding changes in vegetative cover were determined on the ground using visual estimates of cover in 100 1-m^2 frames that were deployed in a grid-like, stratified sampling scheme (see 'multiplots' in Fig. 2). We calculated the normalized difference vegetation index, which correlates with the vertical abundance or leaf-area index of vegetation, for areas around each soil water sampling location, using Quickbird satellite imagery. The Quickbird imagery had 3 x 3 m pixels, with reflectance measured in four visible wavebands.

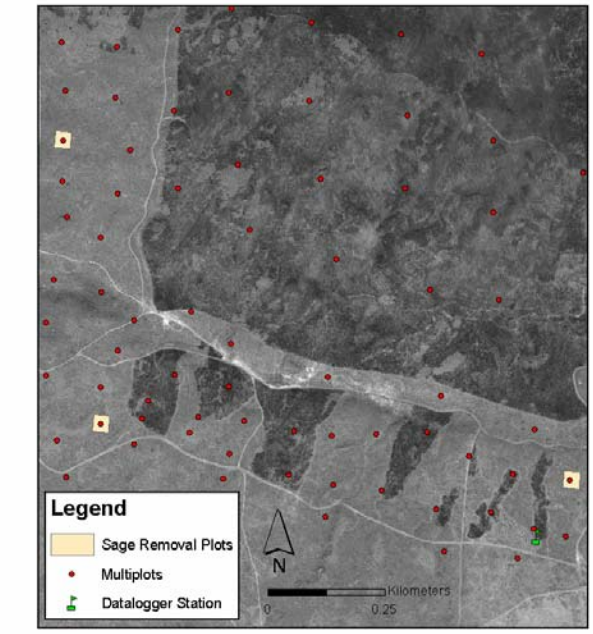

Fig. 2. Quickbird image of study site at the USSES.

Interspecific differences in use of soil water

In 2002 and 2003, we measured photosynthesis and water relations of *Centaurea maculosa* and co-occurring grasses in a greenhouse study and at the Bozeman and Helena sites. Photosynthesis was measured in situ using a portable photosynthesis instrument (model 6400, LiCOR Inc, Lincoln, NE) and plant water potential was measured using a pressure chamber (PMS, Corvallis, OR)

Results

Fire and Shrub Removal Effects

Over the whole summer of 2003, sites burned in 2002 had 20% greater soil water content than sites that had sagebrush removed or were undisturbed (Fig. 3). In midsummer, burned plots had about 40% less herbaceous cover and 10% lower NDVI than control plots. 'Cut' plots where sagebrush was removed had similar herbaceous cover and 10% lower NDVI than control plots (not shown). In shallow soils (< 30 cm) at early season, water contents became more than 50% greater in burned compared to control plots (Fig. 3). By mid summer, soil water contents had become 15-40% greater in burned compared to control sites, at all soil depths (Fig. 3). Subsequently, evaporative losses from shallow soils diminished any treatment differences except in soils deeper than about 40 cm. By July and especially September, water contents of deeper soils were about 50% greater in burned and shrub removal plots compared to control plots where sagebrush were apparently taking up deep soil water. From July to the end of the growth season, the only soil water contents that appeared to correspond to levels within nominal ranges for plant uptake were in soils deeper than about 50 cm in undisturbed or sagebrush-removed plots.

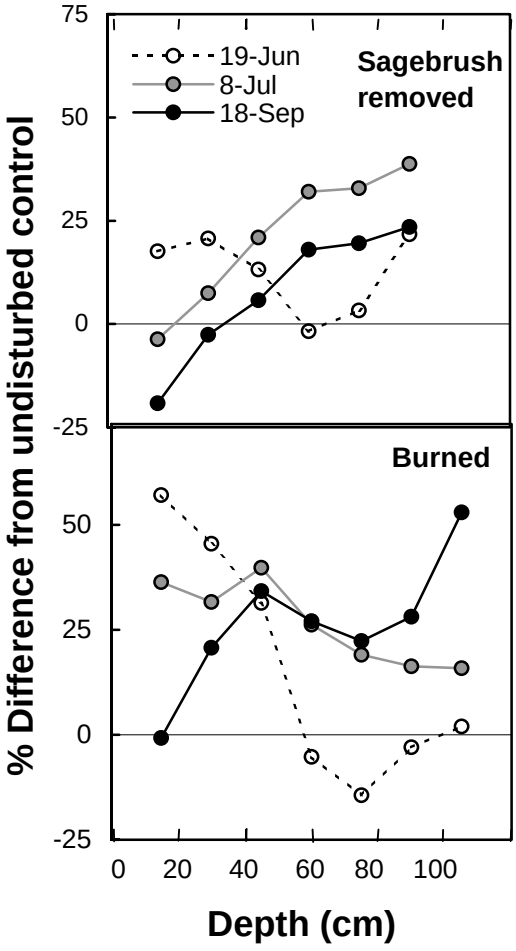

Fig. 3. Mean percent difference in soil water content at different depths in sites that were burned or had sagebrush mechanically removed, compared to unburned controls. Data were collected in 2003 and treatments were applied in 2002. N = 3.

Interspecific differences in use of soil water

No differences in photosynthesis or photosynthetic water use efficiency (mol CO_2/H_2O) were detected between *C. maculosa* or rangeland grasses in a greenhouse study following growth for 2 months at three water potentials. However, photosynthesis was several fold greater in *Centaurea maculosa* compared to co-occurring rangeland grasses over all sites and sampling dates in the field, and also was more persistent during the driest periods of summer, when other plants senesced (Fig. 4). Photosynthesis was

measured in *C. maculosa* when water contents of shallow soils were below nominal values for the permanent wilting point, in August of 2002 (Swan & Wraith, unpublished). When water contents of deep soils became less than levels corresponding to the permanent wilting point during unusually dry conditions of 2003, photosynthesis was no longer detectable in *C. maculosa* (Fig. 4). Photosynthetic water use efficiency appeared similar between *C. maculosa* and established flora under all conditions except the driest of sampling conditions in 2003, when water use efficiency became greater in *C. maculosa* (not shown).

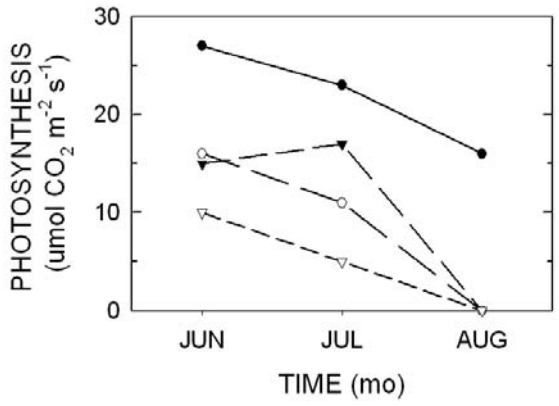

Fig. 4. Mean photosynthesis of *C. maculosa* (round symbols), and grasses (triangular, *Bromus inermis Pseudoregneria spicata*) in 2002 (solid) and 2003 (open). N = 2 means, one from each site, and each consisting of 15 replicates.

Plant water potentials decreased 30% less from predawn to midday in *C. maculosa* compared to co-occurring rangeland species, even though *C. maculosa* had much greater evapotranspiration (not shown). Plant water potential in *C. maculosa* decreased only 34 ± 9% from predawn to midday compared with 51 ± 1% and 78 ± 4% decreases in *P. spicata* and *B. inermis*. Accordingly, *C. maculosa* had midday water potentials that were 183% and 110% greater than *P. spicata* and *B. inermis*, respectively

Discussion

Fire and removal of shrubs, two widespread disturbances of sagebrush steppe rangelands, led to considerable increases in water contents of deep compared to shallow soils and for a substantial period of the growth season (Fig. 3). Photosynthetic carbon uptake appeared much greater in *C. maculosa* compared to other rangeland species, due apparently to greater maintenance of water status during solar periods. Greater maintenance of high water potentials during solar periods with high evapotranspiration in *C. maculosa* compared to grasses could only result from greater uptake of water in CEMA. Measurements of photosynthesis in *C. maculosa* when water contents of shallow but not deep soils were below levels that are within the range of availability to plants, combined with cessation of photosynthesis when deep soil water became depleted below plant-available levels indicates that the extra water taken up by *C. maculosa* compared to grasses is probably from deep soils. These ecophysiological data are evidence that the persistence of *C. maculosa* following initial invasion is enhanced by the availability of deep soil water.

Soil water contents were previously reported to be lower underneath stands of *C. maculosa* as well as *C. solstitialis* compared to similar sites that did not have these species (Sperber 2001, Gerlach 2003). Our findings indicate that differences in how invasive and established plants use soil water can contribute to invasions of semiarid rangelands, in addition to differences in nutrient use and potential allelopathic interactions (eg. Blicker et al. 2002, 2003; Rideneour & Calloway 2001). Increases in soil water that result from fire and shrub removal are likely to selectively favor *C. maculosa*, and probably similar tap-rooted invasive forbs of rangelands.

Our findings agree with those of Anderson et al. (1987) who demonstrated that intact sagebrush steppe communities nearly completely utilize all available soil water. The manner in which fire or shrub removal affected soil water contents appeared consistent with how these disturbances modified vegetation (Fig. 3). Both disturbances eliminated shrubs, which are the primary native users of deep soil water in these communities, and increases in deep soil water were the most consistent changes observed following these disturbances. Increased water content of shallow soils in early summer following fire likely results from reductions in herbaceous cover.

Our results indicate a potential syndrome of invasion in semiarid rangelands, whereby persistent infestations by herbaceous perennial forbs occur on sites that are disturbed in ways that select against native, deep rooted species and have elevated water contents in deep soils. Two factors indicate the potential generality of this syndrome to those sagebrush-steppe rangelands of western North America that receive most precipitation during winter and therefore have significant deep soil water: 1) the majority of invasive exotic species in these habitats (Pyke 1999) are forbs that are tap rooted like *C. maculosa*, and 2) much sagebrush steppe is disturbed by fire, shrub removal, and other disturbances that happen to select against deep rooted species. A significant portion of sagebrush steppe in slightly

drier areas than our study sites is currently dominated by cheatgrass, a shallow-rooted, spring annual, and local land managers and scientist have recognized the susceptibility of these lands to so- called 'secondary invaders', which consist primarily of invasive exotic forbs, such as those describe here.

Recurrent, expensive, and potentially hazardous efforts to eradicate *C. maculosa* and similar exotic forbs like leafy spurge (*Euphorbia*), skeletonweed (*Chondrilla*), thistles, and other *Centaurea* species may be treating the symptom instead of causes of their persistence. More effective restoration of infested rangelands might involve identifying and maintaining or increasing the abundance of those species which can best compete for soil water and resources that exotic species need to thrive.

Acknowledgements

Funding for this research was provided by the United States Department of Agriculture NRI program, and NASA. Thanks also to M. Pokorny and J. Jacobs for inviting this paper for the symposium entitled "Restoration of invasive plants infestations: On the edge between science and management". The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the United States Department of Agriculture or the Agricultural Research Service of any product of service to the exclusion of others that may be suitable.

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