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Ecological considerations for woody plant management

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onversion of grasslands to woodlands is a worldwide problem. In the United States, woody plants have increased over the past 100-150 years (Fig.1). These changes have been variable with weather patterns, influenced by soil and topography, and are often non-reversible over management time-frames (Archer 1994). Increases in woody plants result in decreased livestock carrying capacities, altered wildlife habitat and changes in nutrient and water cycling on rangelands. Focus is often on negative influences, but in some cases woody plants can improve livestock production, wildlife habitat and soil stability. Over the past 50-100 years, control of increasing woody species with the intent to maximize livestock production has been the focus of much discussion. Unfortunately, some management decisions are based upon public perception and not always supported by quantitative research. Too often, management efforts have not considered the general biology and ecology of these woody plants. As a result, many species continue to increase and, in some cases, are more abundant today than ever before.

Plant Adaptations

A combination of plant traits enable woody species to invade into a relatively open environment and limit the success of management practices. By identifying these adaptations and understanding some basic ecological generalizations a land manager can more efficiently evaluate the need for management and accurately focus on critical phases of vegetation change.

Seed Dispersal

Seed dispersal refers to the spreading of plants by wind, water, humans and animals. Effective dispersal agents transport many seeds and deposit them in sites where they can establish and survive. Most woody plants that are increasing on rangelands are at least partially dependent upon animal dispersal of seeds. An important distinction, in terms of woody plant management, is the relative importance of livestock compared to other seed dispersal agents. Dispersal of woody plants by free-roaming wildlife is difficult to control suggesting that management of woody plants dependent upon wildlife, should focus on stages other than dispersal. Some species are more effectively dispersed by livestock than wildlife largely because they are less likely to be destroyed by mastication (Brown and Archer 1987). For species that are dependent upon livestock for dispersal, management that minimizes dispersal into an area may be one of the more efficient approaches to limit woody plant expansion.

Seed Production and Seed Bank

Seed production of woody plants on rangelands is highly variable. Periodic high seed production can enhance the probability of survival by increasing the likelihood that a seed will reach a safe site. It may also provide food (Schupp 1993) which attracts birds and mammals which disperse the seeds. Some woody species have persistent seed banks, i.e. seeds remain viable in the soil or on the surface for several years. Long-term viability and high production of seeds allow woody plants to exist in environments where conditions appropriate for germination and establishment are infrequent. In good years, where sufficient moisture is available for germination, many seeds are either produced or available in the seed bank to capitalize on resources that are normally limited. Also, numerous viable seeds allow rapid response following disturbance of mature canopies which enhances a species ability to recover following events of high mortality.

Seedling Establishment and Growth

Favorable conditions for seedling establishment are highly variable on most rangelands and may require fairly specific conditions. When conditions are appropriate for germination, seedlings may not survive dry seasons (O'Connor 1995). In addition, woody plant establishment may be greatest on specific sites for some rangelands. Following germination and establishment, woody plants continue to develop to a mature age which can take 5-70 years. Growth of individual trees is initially slow, but becomes more rapid as the plant increases in size. Initial growth of individuals may alter nutrient/water availability, increase seed dispersal, reduce herbaceous fuel, and eventually increase seed availability resulting in an increased rate of shrubland/woodland development. A critical point or threshold is reached once plants become well established, increase their growth rate and reach seed producing maturity (Fuhlendorf et al. 1996). Beyond this threshold, changes are rapid and difficult to reverse and an area that was once an open grassland or savanna can eventually be converted to a closed canopy shrubland or woodland.

A primary objective of vegetation management should be the recognition of these thresholds because frequently management efforts may be necessary before the changes become obvious. Efficient long-term management of rangelands prone to woody plant increases may require that efforts to avoid these thresholds be given priority over traditional considerations of maximizing short-term livestock production. Typically, seedlings and saplings are much more susceptible to disturbance than larger, more developed plants, suggesting that successful management may be more difficult through time.

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Plant Community Influences

Woody plants can have positive, negative or neutral influences on composition, productivity and spatial distribution of associated grassland species. Negative influences of woody plants on other species may result from rainfall interception, litter accumulation, shading, and/or root competition (Fuhlendorf et al. 1997). Importance of each factor is dependent on ecological traits of the associated species, availability of resources, extent of grazing or browsing, and fire frequency and intensity (Scholes and Archer 1997). Positive influences can occur through the reduction of environmental extremes at the soil surface, altered soil structure, increased resource availability, or exclusion of grazing which are also dependent upon the factors described above.

Management of woody plants is usually directed toward increasing forage production for domestic livestock. As woody plant cover increases, there is often a decline in production of grasses resulting in a decrease in livestock production. In addition to improving livestock production, management of invasive woody plants can enhance wildlife habitat, biological diversity and maintain ecosystem function under some situations. Alternatively, some management strategies can cause irreversible damage to rangelands by permanently altering ecosystem processes, reducing diversity, and contributing to soil erosion. The response of rangelands to management varies with the size and density of woody plants, method of control, condition and composition of other vegetation, weather patterns, and grazing or browsing intensity following management (Scholes and Archer 1997). An understanding of these ecological relationships may suggest selective control of individual plants instead of broad level prescription on an entire landscape.

Stress Tolerance

Many of the woody plants on rangelands are capable of surviving in stressful environments (water- and nutrient-limited). Plant traits that promote stress tolerance include evergreeness, nitrogen fixation, leaf size and shape, photosynthetic pathway, and extensive root systems. Many management practices on rangelands can lead to a reduction in resource availability resulting in a more stressful environment. Degraded sites or sites with low productivity may be more susceptible to increases in woody plants because of their tolerances to stress. In addition, woody plant management on low productive sites for increased livestock production may not result in sufficient increases in forage to suggest treatment. In fact, some management practices may actually lead to further degradation. Management approaches should consider variability in production within a landscape and consider the influence of different management strategies on site productivity and ecological processes.

Resistance to Disturbance

Many species that have increased in abundance on rangelands possess traits that contribute to their persistence in communities with specific types of disturbance. These resistance traits can be divided into either avoidance or tolerance mechanisms. Avoidance mechanisms, such as thorns or secondary chemicals that reduce preference by

grazers, minimize the probability and severity of disturbance. Tolerance mechanisms, such as the ability of some plants to resprout following top-kill, facilitate growth following disturbance (i.e. control efforts). This will allow plants to re-establish following severe disturbances without following the progression of dispersal, establishment and development and can limit the success of many management practices. Management of these species should consider focusing on developmental stages prior to the initiation of these mechanisms, or utilize alternative methods that limit the success of resistance traits.

Environmental Changes Contributing to Woody Plant Dominance

Plant adaptations are useful in explaining the dominance of woody plant on rangelands today, but many of these areas were historically (past 100–200 years) more open grasslands or savannas. This suggests that environmental conditions have likely changed, resulting in a more suitable environment for establishment and growth of woody plants. A review of the literature indicates that several factors can be attributed to these changes including 1) altered fire regimes, 2) introduction of livestock, 3) increases in atmospheric trace gases, and 4) shifts in climate (Archer 1994, Polley et al. 1997).

Altered Fire Regimes

Prior to European settlement, periodic fires burned across grasslands limiting woody plants to discrete portions of the landscape where fire impacts were minimal. At the time of settlement, fire was used to clear the land of woody vegetation and provide more open areas for grazing and crops (Smeins et al 1997). Not long after settlement, however, natural occurring and man-induced fires were reduced (Fig. 1) because most settlers feared fires and control of wildfires was given high priority. Also, heavy stocking of rangelands with livestock reduced fuel available for natural occurring fires (Fuhlendorf and Smeins 1997). Studies have demon-

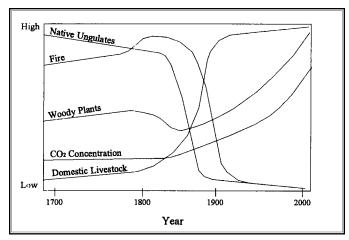


Fig. 1. Hypothetical pattern of woody plant dominance, fire frequency and intensity, native grazer populations, CO₂ concentrations, and domestic livestock densities on North American rangelands over the past 300 years.

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strated that fairly infrequent fires can maintain an open grassland and when fire is removed many grasslands will eventually become closed canopy woodlands. Mortality to woody plants following fire provides an advantage to grasses. Even if mortality of grass does occur, their shorter life cycle allows them to respond more rapidly than woody plants.

Reintroduction of fires to control woody plants is limited by landowner inexperience, fear of fire, removal of fuel by livestock, air pollution regulations, and sub-division of many rangelands. In many cases, reintroduction of fire and proper grazing management can restore and maintain sustainability of livestock enterprises. However, many rangelands are already past fire thresholds where woody plant increases reduce the production of fine fuels restricting the movement of manageable fires (Fuhlendorf et al. 1996). It is evident that fires were historically important and could be useful in maintenance and restoration of many grasslands provided they are accompanied with proper grazing management and focused toward the appropriate plant developmental stages. However, many of these species are capable of resprouting indicating that management efforts with fire may be short-lived and inefficient or require a frequent return interval.

Introduction of Domestic Livestock

Over the past 20,000 years, animal influences on rangelands have gone from a high diversity of now extinct large herbivores (mammoths, sloths, giant bison, camels, etc.) to vast herds of smaller herbivores (primarily bison) at the time of settlement (Burkhardt 1996). Many of our rangelands evolved under fairly heavy grazing while others were only grazed periodically or by small resident herds. It is difficult to determine the importance of grazing on current rangelands of North America but it is likely that the introduction of livestock 100-150 years ago has caused many changes that are described today. Livestock mortality rates were reported as high as 85% in the southwest before the turn of the century suggesting that the resource had been severely impacted soon after settlement (Smeins et al. 1997). This historic over-utilization probably resulted in high rates of erosion and alterations of vegetation structure that may still be reflected on today's rangelands. These historic influences should be considered when evaluating vegetation change, particularly when many of our discussions are based on descriptions of pre-settlement rangelands.

Due to their simultaneous occurrence (Fig. 1), the prevalent assumption has been that the increase in woody plants was largely caused by the introduction of livestock through the creation of gaps in the grassland which allowed the establishment of woody plants (Walker et al. 1981). However, several studies have suggested that the presence of dense grassland vegetation, as in ungrazed conditions, may actually improve conditions for seedling survival and development (Schultz et al. 1955, O'Connor 1995). These studies suggest that grazing can result in harsher conditions for seedling establishment and greater mortality of seedlings through their continued defoliation.

Regardless of the variable importance of direct influences through seedling consumption and altered competitive relationships, grazing has contributed to the increase of woody plants through the removal of fuel required to initiate and carry a fire (Fuhlendorf and Smeins 1997). Without proper grazing management, it is not likely that prescribed fires could be used to maintain grassland production and the success of other techniques may be reduced. Alteration of historic fire regimes and increased seed dispersal may be the most important influences of grazing on the increase in woody plant species.

Increase in Atmospheric Trace Gases

Recently, it has been suggested that increases in atmospheric trace gases, such as CO₂ (Fig. 1), can facilitate the establishment of woody plants on rangelands. The ultimate relationship between increases in CO₂ and increases in woody plants has yet to be determined (Archer et al. 1995). Woody plant growth and establishment was improved directly by increases in CO₂ and indirectly by reducing soil water depletion by grasses (Polley et al. 1997). However, grasses also responded positively to increases in CO₂ which would suggest that woody plants may not gain an advantage (Owensby et al. 1993). Comprehensive analyses of all available information would not suggest that CO₂ is the primary cause of woody plant increases (Archer et al. 1995). However, this does suggest that focusing management toward restoring 'pristine' conditions by recreating historic fire and grazing regimes may not accomplish management objectives.

Climatic Influences

Woody plants have increased and decreased with fluctuations in climate over the past 20,000 years (Smeins et al. 1997). From about 600 to 150 years ago, the earth experienced a cooling period known as the Little Ice Age when temperatures were cooler and moister than they were both before and after this period. It has been suggested that these conditions favored grassland vegetation and the warming since has been a factor in recent changes in vegetation structure (Nielson 1986). Grasslands described by many settlers may have been established under very different climatic conditions than those that exist today and the increase in woody plants could potentially have been initiated before settlement. Alteration of grazing and fire regimes could have acted as the catalyst that initiated woody plant responses to climate. This is another indication that our management should be cautious when focusing on 'pristine' historical descriptions.

Ecological considerations for woody plant management

Man-induced and 'natural' environmental changes on rangelands have contributed to increases in woody plants by creating conditions that are better suited for their adaptations. Introduced grazing, reduction in naturally occurring fires, periodic droughts, and increases in atmospheric trace gases have all occurred simultaneously on rangelands (Fig. 1) making it difficult to isolate the importance of any single factor. Additionally, climatic fluctuations over the past several thousand years may have played an important role in the recent vegetation changes. These multiple factors inter-

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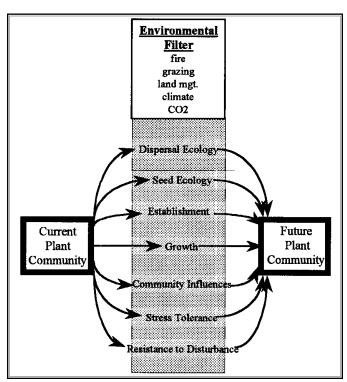


Fig. 2. Current, and future environment on rangelands acts as a filter that permits the dominance of species with certain plant adaptations while limiting others. This environmental filter should be the framework to evaluate and plan management of woody plant increases.

act to create a complex environment that changes continuously and inhibits efficient resource management.

When combined with land-use objectives/practices, historical changes can be viewed as an environmental filter that encourages the dominance of species with certain plant adaptations, while limiting other species (Fig. 2). The species that increase are those that possess certain traits allowing them to pass through the environmental filter. As the environment on rangelands change, the filter allows species with different traits to eventually become dominant, depending upon the persistence of current vegetation. By incorporating different management strategies the environmental filter can be altered promoting species with certain plant adaptation that meet the land management objectives.

Historically, woody plants on rangeland have often been considered a nuisance because our primary focus has been maximizing livestock production. Managers, at times, have aggressively attempted to reduce woody plants without scientific evidence supporting their approach. Even with the most rigorous efforts to control these species they continue to dominate many rangelands. Efficient land management requires that we understand the basic biology and ecology of these species so management efforts can focus on life history traits that are most sensitive, as well as identify potential thresholds that can limit future alternatives. As natural resource managers, our focus has recently shifted to include factors other than livestock, such as wildlife, water quality and yield, and biodiversity resulting in a better appreciation of woody plants. It is difficult to place general

value on the occurrence of these species on rangelands because they have many beneficial and detrimental impacts. However, by understanding their biology and ecology, a landscape level approach can be developed to minimize negative impacts and maximize the positive aspects of each species.

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