Woody-Herbaceous-Livestock Species Interaction

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ABSTRACT

Woody-herbaceous-livestock species interactions have attracted a great deal of research attention due to global land cover changes and increasing livestock production systems around the world. It has been well recognized that many local and regional factors, physical and biological, influence the interaction between woody and herbaceous species. While impacting the dynamics and tipping the balance, between woody and herbaceous species, livestock grazing effects also interact with these factors leading to various ecosystem states and woody/herbaceous ratios. The result is a complex set of multiple interacting factors that are difficult to experimentally control in long-term studies at large spatial scales. Ecological processes and empirical relationships observed in woody-herbaceous-livestock interactions, therefore, have largely been developed based on site-specific, local-scale studies emphasizing limited number of factors, processes, and relationships. Many of the proposed processes and empirical relationships have not been explicitly tested outside of the areas where they were developed. Future studies need to use such site-specific data in quantitative models and simulation-based approaches and test the validity of empirical models that are based on local data and relationships.

KEYWORDS: woody species, herbaceous species, livestock grazing, interaction

INTRODUCTION

Woody and herbaceous species interaction in disturbed and natural environments has attracted a great deal of research attention due to its implications for land cover change, land surface-atmosphere interaction, global carbon cycle (House et al., 2003), biodiversity, primary and secondary productivity, and the associated land use management (Archer, 1994). Ecosystems of mixed woody and herbaceous plants comprise 15-35% of the terrestrial surface area and are distributed from hot tropical to cold temperate climates across varying topography and soils (House et al., 2003). Mixed woody-herbaceous ecosystems are often heavily impacted by natural and anthropogenic factors such as fire and grazing (House et al., 2003).

Livestock grazing is known as one of the major factors that influence woody and herbaceous species interaction (Werner, 1990) throughout the world, as livestock grazing occupies 25% of the global land surface (Asner et al., 2004). Over the last 300 years, livestock grazing systems have increased 600% in extent and are projected to continue to increase with growing global human population and the associated increase in demand for meat and dairy products (Asner et al., 2004). A recent review of livestock grazing effects and ecosystem responses by Asner et al. (2004) identifies three major responses of ecosystems to livestock grazing observed at regional scales: desertification, woody species encroachment, and deforestation. In Asner et al.'s definition, desertification refers to grassland and steppe conversion to desert shrubland in arid regions of the world, while woody encroachment refers to grassland conversion to savanna and woodland in semiarid regions. In this review, both ecosystem responses are discussed and combined into a single term woody encroachment.

Livestock grazing interacts with multiple other physical and biological factors at various spatial and temporal scales while influencing woody-herbaceous species balance. The complex interaction of livestock grazing with other factors such as climate, topography, fire, and soils has often made it difficult to quantitatively assess livestock grazing effects on woody-herbaceous species interaction at decadal and centennial scales (Archer, 1994). To fully understand livestock grazing effects, all variables need to be controlled simultaneously in various environments and at a range of spatial and temporal scales. Due to the logistics involved in such a study and the lack of quantitative historical data, most ecological research is not able to do this. The current knowledge of woody-herbaceous-livestock species interaction is largely based on short-term studies and ecological investigations of only one or two variables with limited control on other potential factors.

When woody-herbaceous species balance is disturbed, one of the two life-forms is likely to dominate the other and a shift occurs in the density of woody and herbaceous plants and the location of woody-herbaceous boundaries, known as ecotones. Proximate causes of shifts in woody-herbaceous ecotones have been studied in many different parts of the world to understand the dynamics and balance between woody and herbaceous species. A few of these causes have been widely agreed upon to be the main driving factors. Most conceptual models of woody-herbaceous balance shifts acknowledge the interactive effects of multiple factors rather than a single driving force (Daly et al., 2000; House et al., 2003; Kupfer and Miller, 2005). Among them are climate change, increased CO_2, nitrogen pollution, drought, fire suppression, and grazing (Dando and Hansen, 1990; Archer, 1994; Bachelet et al., 2000; Bartolome et al., 2000; Asner et al., 2004). Topographic slope and aspect, snow accumulation, and soil texture and depth further influence changes in the balance and determine spatial patterns of the balance shift (Brown, 1994; Walsh and Butler, 1994; Kupfer and Cairns, 1996).

Woody-Herbaceous Species Interactions and Associated Models

Mixed woody-herbaceous communities are diverse in composition, structure, functional forms, and spatial patterns due to their wide-spread distribution across the world (House et al., 2003). The co-existence of woody and herbaceous species and the key driving factors that facilitate the co-existence have been well studied (Figure 1), although different conceptual models emphasize different driving factors (Belsky, 1990). Woody and herbaceous species can influence each other in many different ways and the effects can be expressed in various forms.

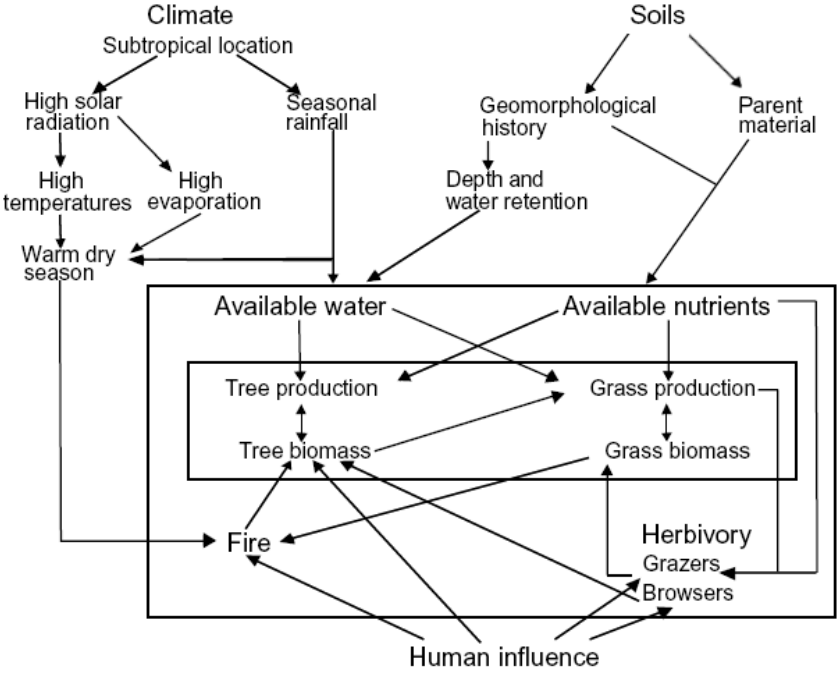


Figure 1. Key driving factors for mixed woody-herbaceous systems (from House et al., 2003). Water, nutrients, fire, and herbivory are defined as the determinants of structure and function in woody-herbaceous systems and they collectively affect the innermost level, the balance between tree and grass.

The effects of woody plants on herbaceous species can be positive, neutral, or negative depending upon the characteristics of the woody and herbaceous growth-forms, ecophysiological features, photosynthetic pathway (C_3 versus C_4) and habit (deciduous versus evergreen), and water and nutrient requirements (Scholes and Archer, 1997 and references therein). The effects of woody plants can also be expressed in varying forms. Firstly, woody plants can affect herbaceous species composition (Burrows et al., 1990). In mixed woody-herbaceous communities, herbaceous species composition under a tree canopy might be very different compared to that in the inter-tree space. C_3 grasses might be found mostly under the tree canopy, while C_4 grasses might dominate in-between trees in subtropical and temperate regions. Furthermore, herbaceous species composition can vary under the canopy from the tree trunk to the edge of the canopy (Scholes and Archer, 1997). Secondly, woody species can influence herbaceous species production, biomass allocation, and phenology. Trees can often reduce herbaceous species biomass production (Burrows et al., 1990). However, herbaceous biomass production under tree canopies can also increase (Burrows et al., 1990) due to improved nutrient supply, reduced evapotranspiration (Reid and Ellis, 1995), and increased water availability (Walker et al., 1981). Alteration of the geologic parent material and soil characteristics and the improvement of harsh environmental conditions are considered other facilitation effects of woody species for herbaceous plants. These facilitation effects might not be observed for many years after tree establishment, because the effects are dependent on tree size, age, and density and are not obvious until woody species reach a critical size and age (Scholes and Archer, 1997). In other cases, trees/shrubs can have facilitation effects for herbaceous plants only when they are young. As the trees/shrubs grow bigger, the facilitation effects might be outweighed by their competition effects on herbaceous plants. This competition often results in a strong, negative correlation between tree density or cover and grass cover or biomass (Stuart-Hill and Tainton, 1989). Herbaceous production and diversity, therefore, might be low at high tree/shrub density (Burrows et al., 1990). The negative correlation might be due to the tree/shrub litter accumulation (which might increase soil acidity), canopy shading, reduced rainfall under the canopy, and root competition.

The effects of herbaceous species on woody plants are most critical during woody seedling establishment stage, although the effect can be variable. Firstly, herbaceous species can impact woody seedling establishment and recruitment directly by effectively competing for light, water, and nutrients (Knoop and Walker, 1985). The competition can prevent woody seedling emergence, increase the mortality of newly established woody seedlings, and reduce woody seedling growth and recruitment. Even the growth of mature woody plants can be reduced by herbaceous species competition for water in wetter years, when herbaceous biomass is high (Knoop and Walker, 1985). Secondly, herbaceous species can influence woody seedling recruitment indirectly (Scholes and Archer, 1997 and references therein). Herbaceous species biomass can increase fine fuel loads, which increases fire frequency and intensity, leading to increased mortality of small woody seedlings that are especially vulnerable to fire (Dando and Hansen, 1990; Archer, 1994). However, the direct and indirect influences of herbaceous species on woody plants are often not enough to completely exclude woody plants and to prevent woody encroachment. Woody plants still might be able to expand into adjacent grassland with a wide range of herbaceous species composition and production (Scholes and Archer, 1997). Woody plants can establish during wet periods, when competition from herbaceous species are limited. Once woody seedlings establish and grow beyond the height of the herbaceous layer, they can establish vertical dominance and herbaceous species might have little or no influence on them. Scholes and Archer (1997) summarize that experimental studies in savanna environments largely found no significant effects on woody species, when herbaceous plants were cut and cleared. Only on fine textured soils with greater clay content herbaceous species appeared to limit water recharge from rainfall deeper in the soil profile where tree roots uptake water.

In mixed woody-herbaceous communities, the interaction between woody plants themselves has been considered important. Tree-tree interaction or shrub-shrub interaction can lead to competition for belowground resources such as water and nutrients as well as competition for light. This intraspecific competition is often assumed to lead to self-thinning and ultimately a regular spatial pattern of woody plants. Clumped and random spatial patterns are also possible in savanna tree distribution due to fire effects, topography, soils, and resource patchiness (Scholes and Archer, 1997 and references therein). Clumped and random spatial patterns can be associated with some level of facilitation effects such as increased seed dispersal and improved environmental conditions under canopies and nearby existing trees/shrubs.

Three different types of models describe woody-herbaceous species interaction and coexistence, particularly in savanna ecosystems: niche separation models, balanced competition models, and disequilibrium models (Scholes and Archer, 1997 and references therein). Niche separation models are based on the assumption that a variable, such as water, is a limiting factor and woody and herbaceous species, therefore, have to use resources at different times or places (House et al., 2003). For example, grasses and shrubs can have different root systems at different depths in the soil profile so that they can use water at different soil depths to coexist (Walker et al., 1981; Knoop and Walker, 1985).

Balanced competition models are based on the concept of intraspecific competition, which is assumed to be stronger than interspecific competition (House et al., 2003). In other words, competition between herbaceous species is assumed to be stronger than competition between woody and herbaceous species. Likewise, competition between woody species is assumed to be stronger than competition between woody and herbaceous species. The result would be woody species that outcompete herbaceous species and establish dominance or herbaceous species that outcompete newly establishing woody seedlings and prevent woody establishment and encroachment. Balanced competition models, therefore, predict two stable states: woodland and grassland. Similar to the balanced competition models, Walker and Noy-Meir's 1982 model predicts the two stable states after adding grazing as a factor to a niche separation model centered on soil water, which was initially proposed by Walter in 1971 (Jeltsch et al., 2001).

Following the simpler models that predict stable equilibrium of woody and herbaceous vegetation, newer concepts emerged modeling and predicting non-equilibrium dynamics in the woody-herbaceous interactions (Jeltsch et al., 2000). Equilibrium models might explain the co-existence of woody and herbaceous species at smaller scales, whereas disequilibrium models are more appropriate for describing landscape- and decadal-scale dynamics (Sharp and Whittaker, 2003). Disequilibrium models predict cycles and oscillations in the relative abundance of woody and herbaceous species at larger scales (Sharp and Whittaker, 2003). They suggest that mixtures of woody and herbaceous species only exist due to disturbances such as fire and grazing and, therefore, represent a transitional state between the possible stable states (Jeltsch et al., 2000). Further development of the disequilibrium models predicts multiple stable states with varying tree-grass ratio (House et al., 2003). Disequilibrium models have also been extended to include a spatial aspect and a concept of patches of disequilibrium which result from stochastic processes such as gap dynamics (Jeltsch et al., 2000).

Woodland and Grassland Stables States and Conceptual Models

Ecosystems respond in different ways when external conditions change over time. Some ecosystems might respond gradually in a smooth, continuous manner, while others respond abruptly, especially after a certain threshold is passed in external conditions (Figure 2). Many different ecosystem studies have demonstrated the existence of alternative stable states and multiple stable states in different environments (Werner, 1990; Scheffer et al., 2001 and references therein). Studies of woody-herbaceous interactions have been common among such research demonstrating two possible alternative states: woodland and grassland. Scheffer et al. (2001) term the changes between the two alternative stable states "catastrophic shift", because shifts occur very rapidly and there is often no "early warning signals". Moreover, it is extremely difficult to recover an ecosystem after such shifts and many ecosystems remain in the new alternative state (Walker et al., 1981; Sharp and Whittaker, 2003), even if previous environmental conditions are restored.

Numerous studies documented a shift from a grassland stable state to a woodland stable state (Figure 3) in Africa, south-western USA, drier parts of India, and in Australia (Walker et al., 1981), while shifts from a woodland state to a grassland state have also been observed (Burrows et al., 1990). African grasslands, for example, were kept open by herbivory and fire until herbivore numbers drastically declined allowing successful establishment of woody plants. Once successfully established and recruited, the woody species were no longer kept in balance by herbivores and their canopy shade reduced herbaceous biomass accumulation, which then reduced fire frequency. Reduced fire frequency further increased successful woody establishment and encroachment (Scheffer et al., 2001). Returning this ecosystem to the grassland stable state would require drastic measures taken at substantial spatial and temporal scales. In contrast, conditions in dry environments can enable a shift from a woodland stable state to a grassland stable state (Scheffer et al., 2001 and references therein). In dry environments, if well-established tree populations are heavily disturbed and killed due to fire and other factors, conditions might be too harsh to allow woody seedlings to establish in the absence of nurse trees and herbaceous species might dominate. Restoring the woodland stable state might require a rare combination of adequate precipitation and reduced grazing effects.

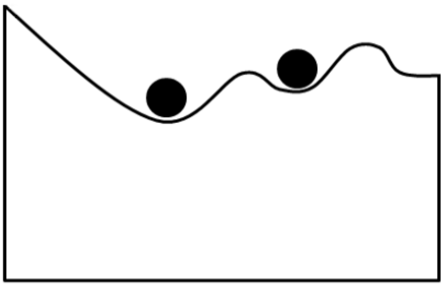


Figure 2. Alternative stable states and their basins of attraction (modified from Scheffer et al., 2001). Stable equilibria correspond to the valleys or attraction basins, while unstable transitional periods correspond to the hill between the valleys. If the size of the attraction basin is small, ecosystem resilience is small and even small changes in the external conditions might move the system into an alternative stable state.

The dynamics and shifts between woodland and grassland are dependent upon processes and mechanisms that influence the resistance, resilience, and persistence of the associated woodland and grassland ecosystems. Both ecosystems create positive feedbacks to persist. Such positive feedback mechanisms in woodlands include tree suppression of grass through shading (Menaut et al., 1990), increased seed input within areas around tree patches (Archer, 1990), and reduced fire frequency (Archer, 1990; Menaut et al., 1990). Woody-herbaceous ecotones exist as a result of a balance in such feedback mechanisms. Equally strong persistence and feedback mechanisms of the two ecosystems create a stable ecotone that does not change rapidly in space over time. In contrast, imbalance in the feedback systems might result in unstable conditions over time (Werner, 1990) and constant fluctuations in ecotones.

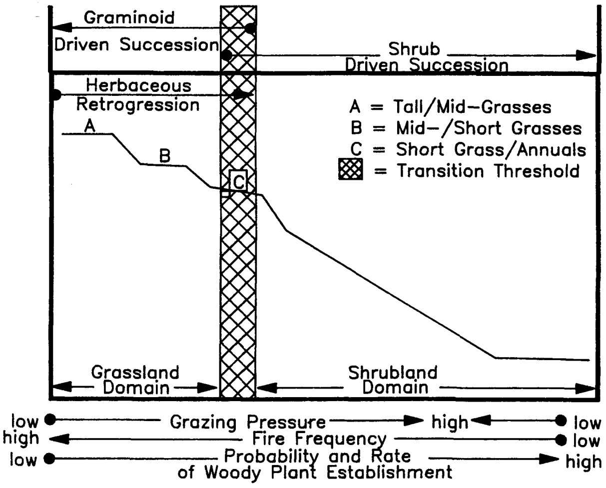


Figure 3. A conceptual model of shrubland and grassland stable states and a transition between the two states (from Archer, 1994). This model demonstrates the conversion from a grassland stable state to a shrubland stable state and the existence of a threshold in livestock grazing pressure.

Woody-Herbaceous Ecotones

Ecotones play a vital role in understanding the interaction between woody and herbaceous species. Clements defined ecotone in 1905 as "the junction zone between two communities, where the processes of exchange or competition between neighboring formations might be readily observed" (Holland and Risser, 1991). The current definition of ecotone is a "zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales, and by the strength of the interactions between adjacent ecological systems" (Holland and Risser, 1991). The ecological importance of ecotones and their roles in understanding global environmental changes have long been recognized (Holland and Risser, 1991). Ecotone characteristics, including their location, size, shape, and composition are more sensitive to global environmental changes than those of homogenous landscape units (Turner et al., 1991). Ecotones thus provide good early indicators of such changes (Gosz, 1991).

Biophysical characteristics of forest-grassland ecotones are defined by a complex interaction of biotic and abiotic factors, including plant interactions, disturbance regime, physiography, topography, geologic parent materials, soil properties, and climate variables (Alverson et al., 1988; Tilghman, 1989; Smit and Olff, 1998; Carmel and Kadmon, 1999; Mast and Veblen, 1999; Zald, 2002). Changes in these factors can have a substantial impact on woody-herbaceous ecotones and cause a shift in their location (Camarero et al., 2000, Taylor, 1995). Shifts in forest-grassland ecotones impact carbon sequestration and land surface-atmosphere interactions and have important implications for biodiversity, primary and secondary productivity, soil development, and populations and carrying capacity of both domestic and wild animals (Archer, 1994).

Rates and Patterns of Woody-Herbaceous Ecotone Shift

Previous studies of forest-grassland ecotones have demonstrated varying rates and patterns of forest encroachment into the adjacent grassland. Sankey et al. (2006) documented rates and patterns of forest encroachment using dendrochronological data with individual tree maps along a lower ecotone in southwestern Montana of western USA. The aspen (*Populus tremuloides*) and Douglas-fir trees (*Pseudotsuga menziesii*) along this ecotone appeared to encroach into the adjacent grassland at different rates and patterns (Sankey, 2007). A similar study was conducted in northwestern Mongolia (Sankey et al., 2006) and the results indicated that the dominant tree species along the northern Mongolian forest-grassland ecotones, Siberian larch (*Larix sibirica*), shifted into the adjacent grassland at different rates and patterns compared to aspen and Douglas-fir observed in the previous study. Neither of these studies documented a shift into the forest or a retreat in the forest boundary location during the 20th Century. The results of these studies indicate that three general patterns of tree encroachment into the adjacent grassland are evident (Figure 4).

Type I change is a shift in the forest-grassland boundary location into the adjacent grassland. This type of ecotone change results from a mechanism where new trees establish in the adjacent grassland advancing the ecotone location towards the grassland (Sankey et al., 2006). Type I ecotone change might mostly occur in systems where the dominant tree species regenerates through seed dispersal, although it can be observed in systems with vegetatively-reproducing species. For example, Douglas-fir is a seed-dispersed species. Its seeds are dispersed through wind, animals, and birds (Hermann and Lavender, 1965). Seeds usually fall within 100 meters from a seed tree or a stand edge, but they can fall 1-2 km away from the seed sources (Hermann and Lavender, 1965).

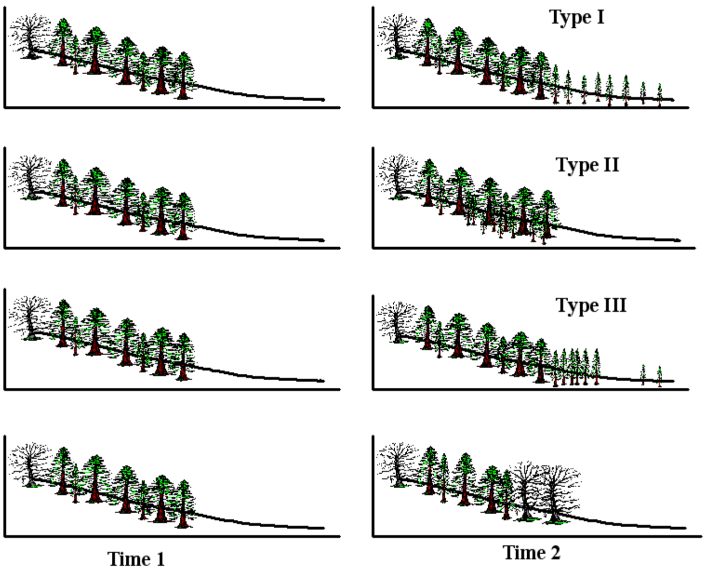


Figure 4. Patterns of tree encroachment into the adjacent grassland observed in grazed areas. Trees might encroach into the adjacent grassland in three different patterns. These patterns are not mutually exclusive and can occur simultaneously. Type I pattern is a shift in the forest-grassland ecotone location over time into the adjacent grassland. Type II pattern is tree density increase within the same forest-grassland boundary location. Type III pattern is fairy ring establishment that advances the forest-grassland boundary into the adjacent grassland. Forest-grassland ecotones might also retreat and herbaceous species might expand into the adjacent forest over time (bottom panel).

Type II change is an increase in tree density at the forest-grassland boundary (Arno and Gruell, 1986). During this change, new trees establish within the same boundary location and do not advance the boundary towards the adjacent grassland. Type II ecotone change occurs in systems where tree establishment sites are available under the forest canopy, but no establishment occurs outside of the forest boundary due to unfavorable site conditions and disturbance. Type II ecotone change can occur with Type I ecotone change at the same time, if conditions outside of the forest boundary change allowing Type I ecotone change. Type II change can be observed in systems with both tree species that regenerate vegetatively and through seeds. For example, Douglas-fir, aspen, and Siberian larch all can result in Type II ecotone change.

Type III change is an establishment of a fairy ring in the grassland along the edge of the forest (Sankey, 2007). This change occurs when new trees establish as a fringe in the grassland, adjacent to the forest boundary. Fairy rings consist of new stands of densely distributed new stems of similar age. Fairy ring establishment is often associated with wave regeneration mechanisms. During this mechanism, new regenerations occur as pulses advancing the forest boundary into the adjacent grassland. Both seed-dispersed and vegetatively-reproducing species can regenerate in pulses. For example, aspen regenerates in pulses after a fire disturbance event (DeByle and Winokur, 1985), whereas Siberian larch can regenerate in pulses following reductions in grazing disturbance forming a fringe (Didier, 2001).

Woody-Herbaceous-Livestock Species Dynamics

Most ecological processes in woody-herbaceous species dynamics can be impacted by herbivory, an important local control over vegetation. Vertebrate and invertebrate herbivores can regulate plant cover types, their composition, structure, and productivity (Alverson et al., 1988; Tilghman, 1989; Mast et al., 1997; Carmel and Kadmon, 1999; Mast and Veblen, 1999; Bachelet et al., 2000; Bartolome et al., 2000; Scheffer et al., 2001; Wahungu et al., 2002). Herbaceous and woody plant species react to herbivory differently due to their differences in tolerance to grazing and palatability (Archer, 1994). This makes their interaction in grazed environments more complex than in undisturbed environments. This complexity has generated abundant interest in the interaction between herbaceous and woody plant species and, in particular, the changes from herbaceous vegetation cover to woody species cover due to grazing. Some studies show that the processes of woody species seedling emergence, growth, and survival are facilitated by grazing (Walker et al., 1981; Dando and Hansen, 1990; Reid and Ellis, 1995; Archer, 1994; Sharp and Whittaker, 2003), while others suggest the seemingly conflicting result that these processes are inhibited by grazing (Reid and Ellis, 1995; Carmel and Kadmon, 1999; Bartolome et al, 2000). In most cases, the assumption is that co-existing herbaceous species and woody species within an ecosystem show the opposite trends under livestock grazing effects. If woody species increase with increasing grazing effects, herbaceous species are assumed to decrease and vice versa.

Woody species encroachment due to grazing has been demonstrated throughout the world, including southern Asia, Australia, Africa, South America, and North America (Walker et al., 1981; Archer, 1989). Ecological processes described in studies that proposed woody species encroachment due to grazing are: (1) Grazing decreases seed production, seedling establishment, biomass, and basal area of palatable herbaceous species and increases their mortality; (2) Reduced herbaceous species ground cover increases sunlight levels on the ground, which increases seed germination and early establishment of woody species seedlings; (3) Reduced herbaceous species biomass decreases fine fuel accumulation and reduces fire frequency, which increases woody species invasion; (4) Invading woody species are less palatable than herbaceous species and are not browsed enough to be eliminated; (5) Grazing makes herbaceous species less able to compete for resources and unable to limit woody species growth and their seedling establishment; and (6) Livestock disperse woody species seeds across the landscape, which facilitates woody species expansion (Archer, 1994).

The opposite effects of grazing on woody species establishment have also been demonstrated (Carmel and Kadmon, 1999; Bartolome et al., 2000). Studies of these effects suggest that grazing can inhibit tree seedling establishment, survival, and growth. Grazing, therefore, might be expected to control woody species encroachment into grasslands. Ecological processes described in studies of negative effects of grazing on woody species include: (1) Slow growth rate of most woody species allows repeated grazing in their seedling stage when they are most vulnerable to grazing (Alverson et al., 1988; Tilghman, 1989); (2) Intense grazing causes shoot loss, tissue damage, and biomass loss for woody species (Hjalten et al., 1993), which decreases their seedling growth (Alverson et al., 1988; Tilghman, 1989) and increases seedling mortality (Hjalten et al., 1993); (3) Increased seedling mortality reduces recruitment into the tree population (McInnes et al., 1992; Rooney et al., 2002); and (4) Trampling and rubbing against the bark by grazing animals damage woody species and their seedlings (Kay and Bartos, 2000).

The current literature indicates two seemingly conflicting linear relationships between grazing effects and woody species (i.e., increasing woody species with increasing grazing effects and thus decreasing herbaceous species or vice versa). The vast majority of grazing impact studies in the current literature, however, has compared only two or three levels of grazing intensity. Such comparisons of limited number of grazing levels might provide only a simple linear relationship between woody species establishment and grazing effects. The potential variability in woody establishment due to varying levels of grazing intensity needs to be investigated across a wider gradient of multiple levels of grazing intensity.

Sankey et al. (2006) examined aspen and Douglas-fir tree encroachment into the adjacent grassland in Montana, USA under ten different levels of livestock grazing intensity using non-experimental observational data of 60 years (Table 1). The objective of this study was to determine if tree establishment-livestock grazing relationship always had a simple linear trend as suggested by previous studies or if patterns were different at decadal time scales. When aspen tree establishment was analyzed with a gradient of all ten grazing levels, increasing in intensity from 1 to 10, grazing levels 2, 8, and 10 had significantly greater aspen establishment than all other grazing levels (p-value <0.001) (Figure 5 (a)). Grazing level 3 had significantly greater aspen establishment than grazing levels 4, 5-7, and 9 (p-value <0.001). There were no other significant differences in aspen establishment along this gradient. A similar test indicated that grazing level 1 had significantly greater Douglas-fir establishment compared to grazing levels 4 and 7 (p-value of 0.002) (Figure 5 (b)). There were no other significant differences in Douglas-fir establishment. There was no apparent trend of linear increase or decrease in aspen and Douglas-fir establishment with increasing grazing intensity along this gradient. A regression model of all 10 grazing levels (AUM ha^{-1}) and aspen establishment was built with a significant squared term (Figure 5 (c)). The statistically significant squared term might suggest a possibility of a curvilinear relationship between aspen establishment and grazing levels (Sankey et al., 2006). The regression model of all ten grazing levels and Douglas-fir establishment did not have a statistically significant squared term, but indicated a linear relationship between Douglas-fir and grazing levels with a trend of decrease (Figure 5 (d)). However, the regression model produced a low correlation coefficient and did not suggest a strong relationship.

Table 1. Long-term averages of grazing pressure estimated in AUM ha^{-1} in the Sankey et al. (2006) study in Montana, USA

Grazing levels	AUM ha^{-1}
Grazing level 1	0.00
Grazing level 2	0.11
Grazing level 3	0.12
Grazing level 4	0.17
Grazing level 5	0.28
Grazing level 6	0.41
Grazing level 7	0.50
Grazing level 8	0.79
Grazing level 9	1.00
Grazing level 10	2.00

The collective results of this study indicated varying relationships between tree establishment and livestock grazing intensity. The relationships were not always simple linear increase or decrease in tree establishment with increasing livestock grazing intensity, although linear relationships were observed in some cases. At decadal time scales, simple linear trends of inhibition and facilitation effects as suggested by previous studies did not appear to hold across varying gradients of grazing levels and two different tree species (Sankey et al., 2006). Indeed, complex curvilinear trends might be possible at decadal time scales across wider gradients of grazing intensity (Sankey et al., 2006). This is consistent with other studies that suggest that mixed woody-herbaceous systems can have non-linear trends in woody plant abundance and rates of change in tree abundance (McPherson, 1992; Archer et al., 1988; Miller and Wigand, 1994).

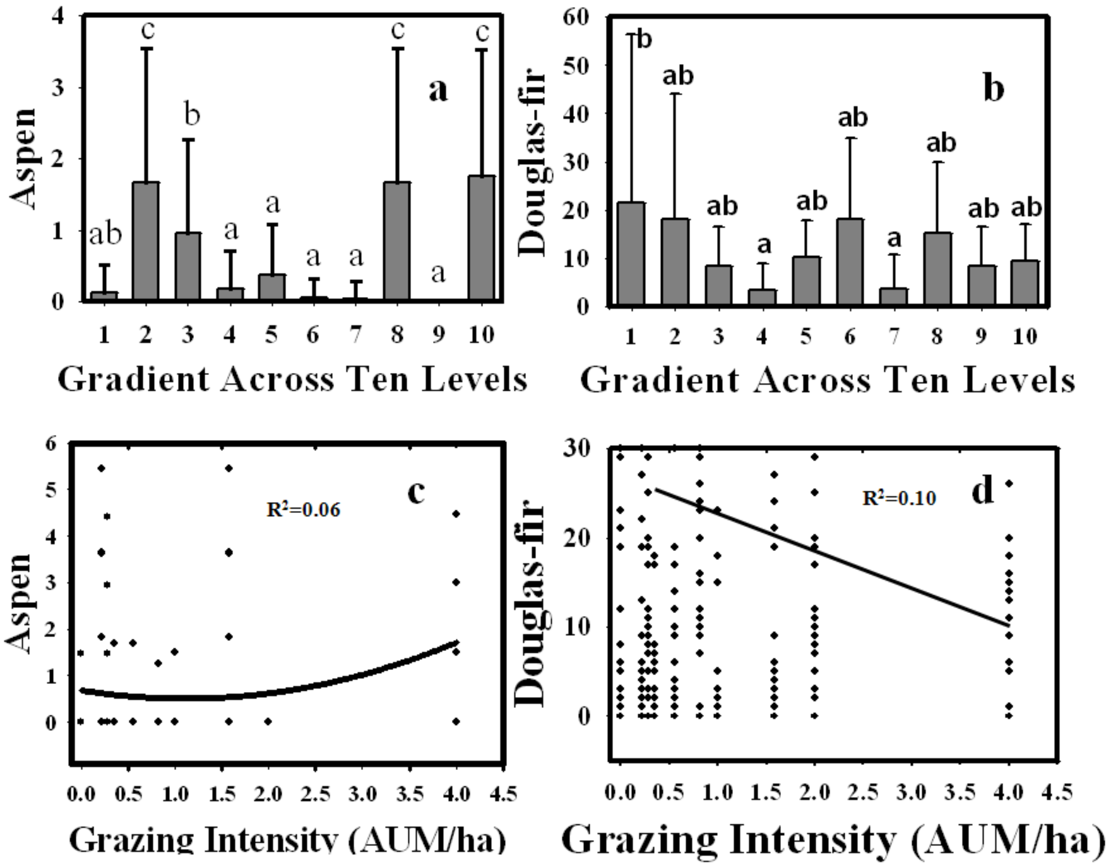


Figure 5. Aspen (*Populus tremuloides*) and Douglas-fir (*Pseudotsuga menziesii*) tree establishment with varying grazing pressure in Sankey et al. (2006) study in Montana, USA. Number of new tree stems established (expressed in percent) under each grazing level is on the Y-axis. The ten grazing levels on the X-axis in figures a and b correspond with categorical classes of grazing pressure, while the grazing levels in figure c and d are livestock grazing pressure estimated in Animal Unit Months per hectare (AUM ha^{-1}).

Previous studies collectively indicate that multiple trajectories might be observed in livestock grazing effects on woody species. Most of these trajectories might be difficult to discern in long-term studies with limited control on grazing treatments and other potential factors that influence woody-herbaceous species interaction. Better controlled experimental designs and process-based studies might allow conclusive tests of the possible trajectories that have been hypothesized in the current literature. Currently proposed, but not exclusively tested, trajectories in the relationship between woody establishment and livestock grazing effects include four possible trends: 1) facilitation effect or a simple linear increase in woody species with increasing grazing intensity (Figure 6 (a) (Archer, 1994), 2) inhibition effect or a simple linear decrease in woody species with increasing grazing intensity (Figure 6 (b)) (Carmel and Kadmon, 1999; Bartolome et al, 2000), 3) a curvilinear relationship in which inhibition effects dominate at low and high grazing intensities, but facilitation effects dominate at medium grazing intensities (Figure 6 (c)) (Cairns and Moen, 2004), and 4) a curvilinear relationship in which facilitation effects dominate at low and high grazing intensities, but inhibition effects dominate at medium grazing intensities (Figure 6 (d)) (Sankey et al., 2006).

The first two trajectories can be explained by the ecological processes described in the positive and negative effects of livestock grazing discussed earlier in this section. The first trajectory, facilitation effects, predicts decreasing herbaceous species and increasing woody species with increasing grazing intensity. This trend might be observed in systems where herbaceous species are palatable and are preferred by the livestock species over the woody species. The second trajectory, inhibition effects, predicts increasing herbaceous species and decreasing woody species with increasing grazing intensity. This trend might be observed in systems where woody species are palatable and are commonly grazed or browsed by livestock. In this case, woody establishment can be greatest under low grazing intensity. In the third trajectory, woody and herbaceous species are balanced at medium grazing intensity, but woody species are expected to decrease at low and high grazing intensities. This trend is expected to occur where grazing effects largely include woody species trampling, seed dispersal, and seed predation, but woody species foliage consumption is relatively low (Cairns and Moen, 2004). It is also expected to occur in systems where multiple grazing animal species are present (Cairns and Moen, 2004).

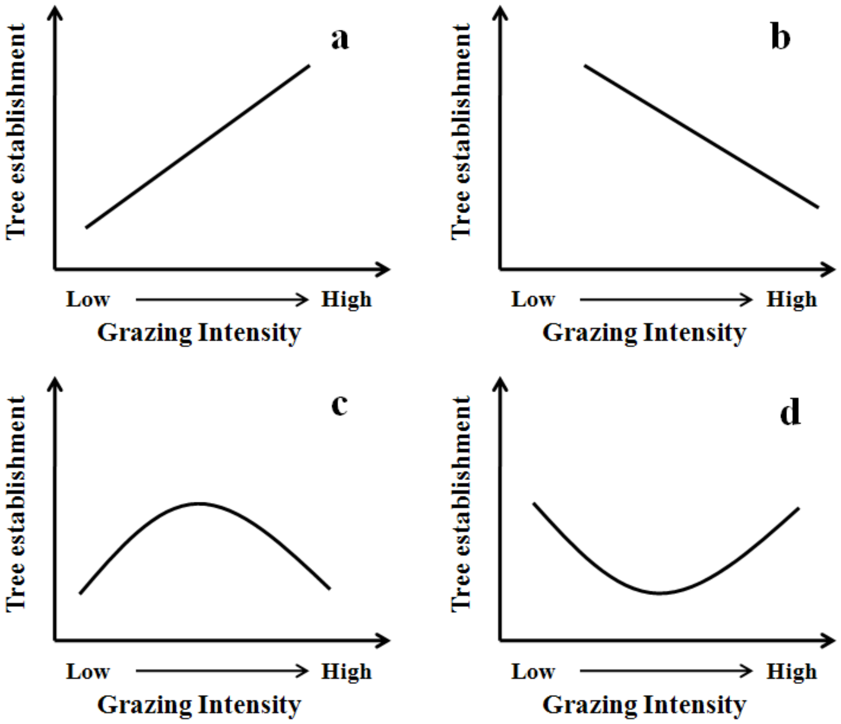


Figure 6. Currently proposed trajectories in the relationship between tree establishment and livestock grazing effects. Herbaceous species compete for similar resources and are assumed to show the opposite trend compared to trees. Livestock grazing can have facilitation or inhibition effects on tree establishment resulting in simple linear trends. Facilitation and inhibition effects can also dominate at varying levels of grazing pressure resulting in complex curvilinear trends.

In the fourth trajectory, woody and herbaceous species are hypothesized to be balanced at medium grazing intensity, but woody species are expected to increase at low and high grazing intensities. This trajectory might be explained by the grazing optimization hypothesis. The grazing optimization hypothesis, developed for herbaceous species, states that herbaceous species productivity increases with increasing grazing intensity at low grazing levels due to overcompensation (McNaughton, 1979). This trend continues up to a point called “the level of optimal grazing” and then declines with increasing grazing intensity at high grazing levels. Since co-existing herbaceous and woody species compete for largely similar resources, woody species might be expected to show the opposite trend. Therefore, at lower levels of grazing intensity, we might expect tree establishment to be relatively high. Even if woody species are grazed/browsed at this intensity, they can show increasing competitiveness due to stimulatory effects of grazing (Stuart-Hill and Tainton, 1989). Tree establishment might then decrease with increasing grazing intensity as herbaceous species productivity increases due to overcompensation. At medium levels of grazing intensity, tree establishment might reach its minimum because herbaceous species productivity is highest at these levels and, thus, tree competition with herbaceous species is greatest. At higher levels of grazing intensity, however, we expect tree establishment to increase because herbaceous species at these levels show a trend of decrease.

Walker et al. (1981) proposed conceptual models of woody-herbaceous-livestock interaction that the four trajectories in Figure 6 don't fully describe. Walker et al.'s conceptual models describe the stability of woody-herbaceous species balance under livestock grazing effects in semi-arid savanna ecosystems. In their definition, semi-arid savanna includes regions in which scattered to numerous trees/shrubs are distributed across continuous grass cover. They first describe the effects of livestock grazing on grass recruitment curve (Figure 7 (a)) based on McNaughton's (1979) grazing optimization hypothesis and suggest that grazing has the greatest stimulating effect at intermediate values of grass. They also describe the effects of woody vegetation on grass recruitment curve (Figure 7 (b)), because woody and herbaceous species compete for the same water resource in the top-soil in semi-arid regions (Walker et al., 1981). Their conceptual model suggests that small and medium amounts of woody species (W) have greater effects on high amounts of grass (G) than small amounts of grass. Walker et al. (1981) then describe the effects of grass on woody vegetation (Figure 7 (c)) and suggest that high values of grass (G) do not have strong effects on the woody vegetation recruitment curve, because woody species have exclusive access to subsoil water. Lastly, Walker et al. (1981) describe the zero-isocline or zero recruitment of grass as related to grass, woody species, and the effects of grazing (H) (Figure 7 (d)). The zero grass recruitment curve indicates the equilibrium between woody plants and grass under grazing effects. Similar to some of the previously discussed trajectories, this model suggests a curvilinear relationship in the woody-herbaceous-livestock species interaction. However, this model suggests varying curves with increasing grazing pressure. The equilibrium always indicates a similarly-shaped curve at varying grazing pressure, but the curve falls at varying amounts of total vegetation and varying woody-grass ratios. Unlike the other models, which largely assume unvarying total vegetation amount, this model assumes decreasing amounts of total vegetation with increasing grazing pressure. The assumption might depend on the relative palatability and tolerance of the plant species involved to grazing as well as the forage preferences of the grazing animal species. Total vegetation amount might decrease with increasing grazing pressure in some systems, while in other systems only the palatable species might decrease and unpalatable species might remain constant or increase with increasing grazing pressure.

Sankey et al. (2006) examined the relationship between Siberian larch forest-grassland ecotone shift and a gradient of five different livestock grazing regimes dominated by different livestock species (Table 2) in northern Mongolia (Sankey et al., 2006). The five grazing regimes varied in overall grazing intensity from 3.3 AUM ha^{-1} to 5.9 AUM ha^{-1}. They varied in species composition such that each site represented either sheep-dominance, sheep-goat mix, sheep-goat-cattle mix, or cattle-dominance (Table 3). Forage preferences between these animal species are known to be substantially different (Vallentine, 2001). Cattle are grazers and consume mostly graminoids. Sheep are intermediate feeders and consume grasses, forbs, and woody species. Goats are browsers and prefer leaves and tender twigs of new growth on trees and shrubs. The results indicated that Siberian larch forest-grassland ecotone response to grazing varied among different grazing regimes and tree establishment varied statistically significantly. The number of new trees established varied significantly between Site 2 (goat-sheep-dominated and low overall grazing intensity) and Site 4 (cattle-dominated and medium overall grazing intensity) and between Site 2 (goat-sheep-dominated and low overall grazing intensity) and Site 5 (sheep-dominated and high overall grazing intensity) (Figure 8). The number of new stems established also varied between Site 3 (cattle-sheep-goat mix and medium overall grazing intensity) and Site 4 (cattle-dominated and medium overall grazing intensity). There was no statistical difference between sheep-dominance at low and high overall grazing intensities. This might indicate that sheep, in general, do not have substantial negative effects on tree establishment regardless of sheep grazing intensity, which might be explained by their lower consumption of woody species compared to herbaceous species. The sites with high numbers of goats had lower tree establishment than all other sites with lower numbers of goats, regardless of overall grazing intensity. The implications of this study are important for future studies of woody-herbaceous-livestock species interaction and future land resource management. It is not only the overall grazing intensity that researchers and land managers should be concerned with, but also the types of grazing animal species and the different combinations of varying grazing intensities and livestock species (Sankey et al., 2006).

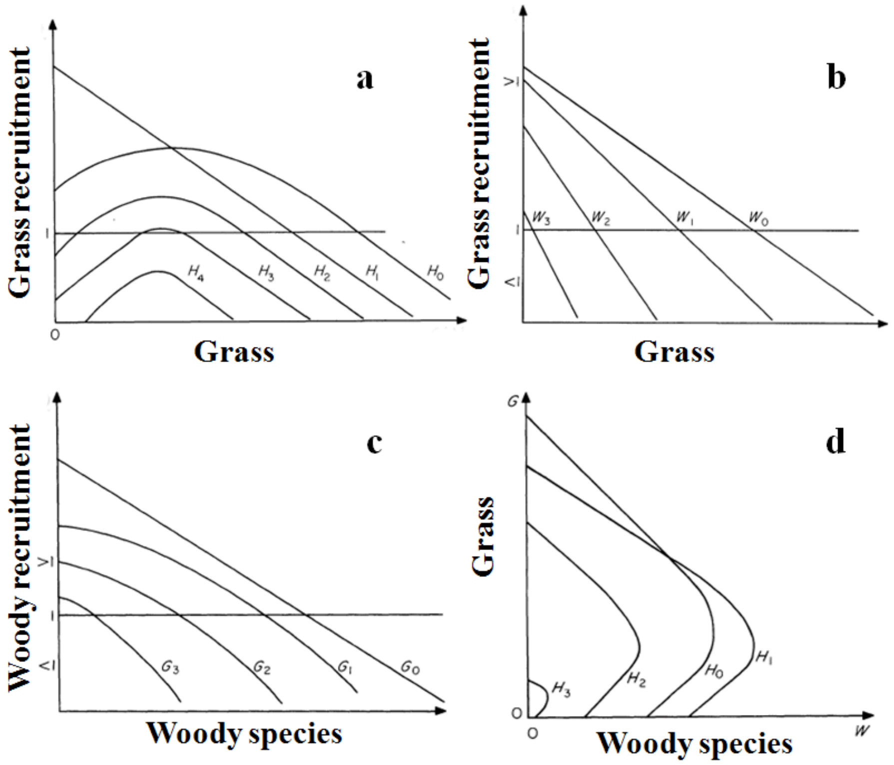


Figure 7. Livestock grazing effects, grass and woody species recruitment, and their interactions (from Walker et al., 1981). Figure a shows the hypothesized effects of increasing grazing pressure (H_0=none, H_4=heavy) on grass recruitment. Figure b shows the hypothesized effects of woody species (W_0= no woody plants, W_3=dense woody plants) on grass recruitment, while figure c demonstrates the potential effects of grass (G_0= no grass, G_4=dense grass) on woody species recruitment. Figure d shows the zero grass recruitment in relation to increasing grazing pressure, grass, and woody species simultaneously.

Sankey et al. (2006) also suggested that many new trees established during the decades when livestock were distributed in numerous small herds in northern Mongolia. Prior to these decades (1930-1950), livestock were distributed in a few large herds owned by a few religious leaders. After a revolution, many socio-economic changes occurred and consequently the large herds were re-distributed into small herds. A pulse of tree regeneration appears to have established following the herd re-distribution (Sankey et al., 2006). This indicates that herd distribution at the landscape scale and the driving socio-economic changes and policy changes are important variables to consider when studying woody-herbaceous-livestock interaction. Human legacies can have lasting effects on this interaction at varying spatial and temporal scales.

Table 2. Long-term averages of grazing intensity observed in the Sankey et al. (2006) study in northern Mongolia.

Sites	Overall Grazing Intensity	Overall Grazing Intensity (AUM ha^{-1})	Dominant livestock species	Number of households at the site
Site 1	Very low	3.3	Sheep	20
Site 2	Low	4.2	Goat-sheep	32
Site 3	Medium	4.8	Cattle-sheep-goat	56
Site 4	Medium	4.9	Cattle	36
Site 5	High	5.9	Sheep	43

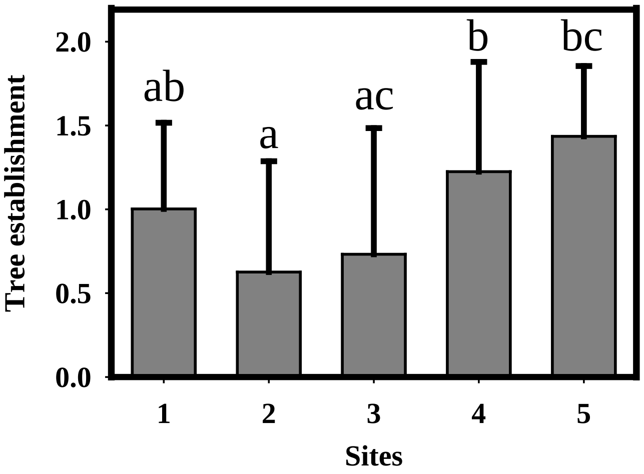


Figure 8. Siberian larch (*Larix sibirica*) tree establishment with different grazing regimes in Sankey et al. (2006) study in northern Mongolia. Site 2 had significantly lower tree establishment than Site 5. Sites 2 and 3 also had significantly lower tree establishment than Site 4.

Previous studies indicate that several variables are important to consider in livestock grazing effects on woody-herbaceous dynamics. They include overall grazing intensity, grazing animal species and their forage preferences (herbaceous vs. woody species), spatial distribution of grazing pressure (few large herds vs. many small herds), and temporal distribution of grazing pressure (winter grazing vs. summer grazing), tree and herbaceous species composition, their palatability, and tolerance to grazing (Figure 9). Accurate understanding of these variables has important implications for modeling and managing woody-herbaceous-livestock species interaction. Different combinations of varying grazing intensities and livestock species composition, for example, can be used to either facilitate or inhibit directional changes in the woody-herbaceous species balance. Forest-grassland ecotone shift can be influenced by both overall grazing intensity and different grazing animals, if a shift is occurring. Different gradients of overall grazing intensity and grazing animals might correspond with different trajectories of change in woody-herbaceous balance. Grazers, for example, might facilitate tree encroachment, while browsers might inhibit tree encroachment and facilitate increased herbaceous species distribution. Furthermore, different levels of grazing effects might be observed in different tree species due to their differences in palatability and their response to grazing. Douglas-fir, for example, is unpalatable to most livestock species, while aspen is highly palatable to livestock species. Siberian larch can also be highly palatable to livestock species. Changes in woody-herbaceous species balance, therefore, might be facilitated or inhibited to different levels depending upon the dominant tree species.

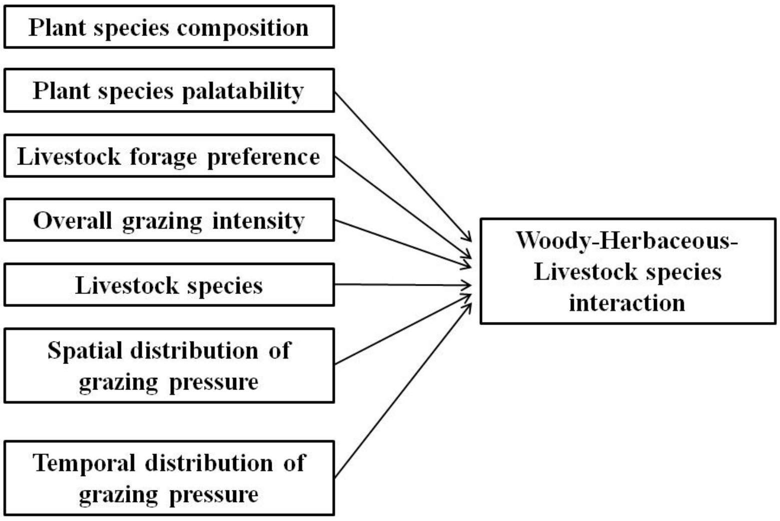


Figure 9. Potential factors influencing grazing effects on woody-herbaceous dynamics.

Other Potential Factors Influencing Woody-Herbaceous Species Dynamics

In addition to livestock grazing, several other variables have been proposed as potential factors that tip the balance in woody-herbaceous dynamics and cause a shift in the ecotone (Figure 10). In savanna environments, four factors have been acknowledged as the main determinants that create and maintain the co-existence. These four determinants are water, nutrients, herbivory, and fire (Werner, 1990). In other mixed woody-herbaceous systems, atmospheric CO_2 increase has been suggested as one of the potential factors that can cause woody-herbaceous shift. Carbon dioxide affects plant photosynthetic rates, stomatal conductance, water-use efficiency, resource allocation, growth, and architecture (Bazzaz, 1996). An increase in CO_2 from 270 ppm to 370 ppm in the last 200 years has been proposed as a possible cause of woody species expansion (Archer, 1994 and references therein). Increased CO_2 is expected to change competitive abilities of different plant species, altering the interaction among species and, consequently, species composition in the community (Bazzaz, 1996). Archer (1994) summarizes that increased atmospheric CO_2 is hypothesized to favor woody plants over herbaceous species due to the following specific reasons: 1) woody plants have C_3 photosynthetic pathway, while many grass species have C_4 photosynthetic pathway, 2) C_3 species have greater advantage for growth and competition with increased CO_2, 3) C_4 grasses evolved at lower CO_2 concentrations (~200ppm) and woody encroachment into C_4 grasslands occurred during a 30% increase in atmospheric CO_2 over the last 200 years. However, Archer (1994) argues that C_3 grasses would also be expected to invade C_4 grasses, if atmospheric CO_2 increase was a probable cause of C_3 woody species encroachment. C_3 grasses, however, have not invaded C_4 grasses. Furthermore, Archer (1994) suggests that C_3 cold desert and temperate grasses have also been invaded by woody species.

Changes in climate variables such as mean annual temperature, rainfall, and evapotranspiration are expected to influence the balance between herbaceous and woody species, because the distribution of many grasslands and savannas throughout the world are closely related to these variables (Archer, 1994 and references therein). Potential changes that might lead to woody encroachment at the expense of herbaceous species include increased or decreased rainfall, shifts in the seasonality of rainfall, shifts in the distribution of precipitation events, increased temperature, and drought (Archer, 1994 and references therein). Increased rainfall might facilitate increased woody species establishment in mixed herbaceous-woody communities. Under normal precipitation conditions, herbaceous and woody species would utilize soil moisture at different depths and herbaceous species would not competitively eliminate woody species. However, when precipitation increases, woody species have the advantage to utilize deeper and more abundant soil moisture. This might increase successful establishment of more woody plants, after which woody and herbaceous species would continue to exploit soil moisture from different depths and herbaceous species would not eliminate newly established woody species. When precipitation decreases, herbaceous species mortality might increase leading to gaps that can be colonized by woody species that are more drought tolerant (Archer, 1994).

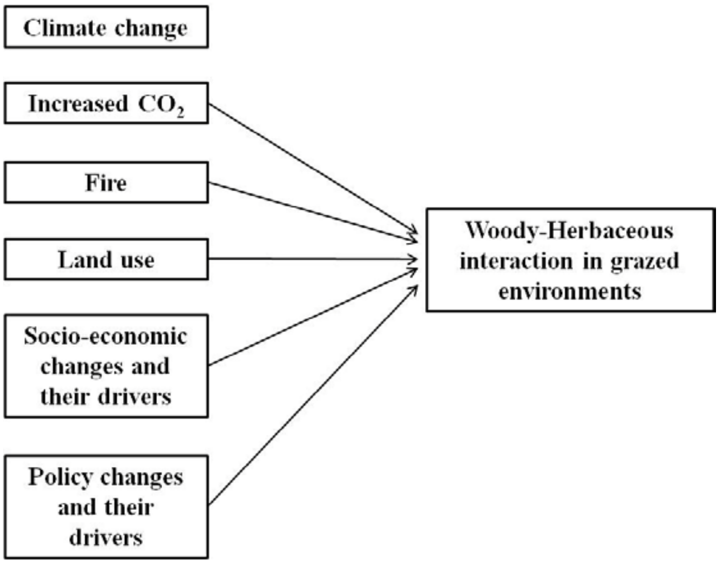


Figure 10. Multiple interacting factors that are commonly proposed as causes of shifts in the woody-herbaceous species balance. In grazed woody-herbaceous systems, the effects of these factors might reduce or increase the effects of livestock grazing.

Archer (1994) summarizes that shifts in seasonality of rainfall in the last century might have contributed to shrubland expansion in southwestern USA and future shifts from summer to winter precipitation associated with increased atmospheric CO_2 might make the current grasslands vulnerable to woody encroachment. In arid and semi-arid environments, cool season moisture favors woody plants, while warm season precipitation favors grasses. When precipitation falls during the cool season, soil moisture percolates down the soil horizons and accumulates at deeper depths. Woody species with deeper root systems are able to utilize such soil moisture. Grasses, however, are unable to exploit such soil moisture and can be especially vulnerable during summer drought. Small frequent precipitation events would favor herbaceous species with shallow root systems, while larger precipitation events would benefit woody species with deeper roots. Therefore, a shift in precipitation distribution would have important implications for herbaceous-woody species balance. In arid environments, changes in extreme climatic events might have more profound effects on vegetation than the gradual change in mean conditions.

Increased atmospheric CO_2-increased temperature models predict that woodland distribution would increase in extent in tropical, subtropical, and cool temperate regions of the world under increasing temperature conditions, potentially because woody species are more stress tolerant than herbaceous species (Archer, 1994 and references therein). Similarly, during drought periods woody species are better able to persist, while herbaceous species decline. The resulting gaps can be occupied by woody species. Periodic droughts, therefore, might be associated with episodic woody plant establishment.

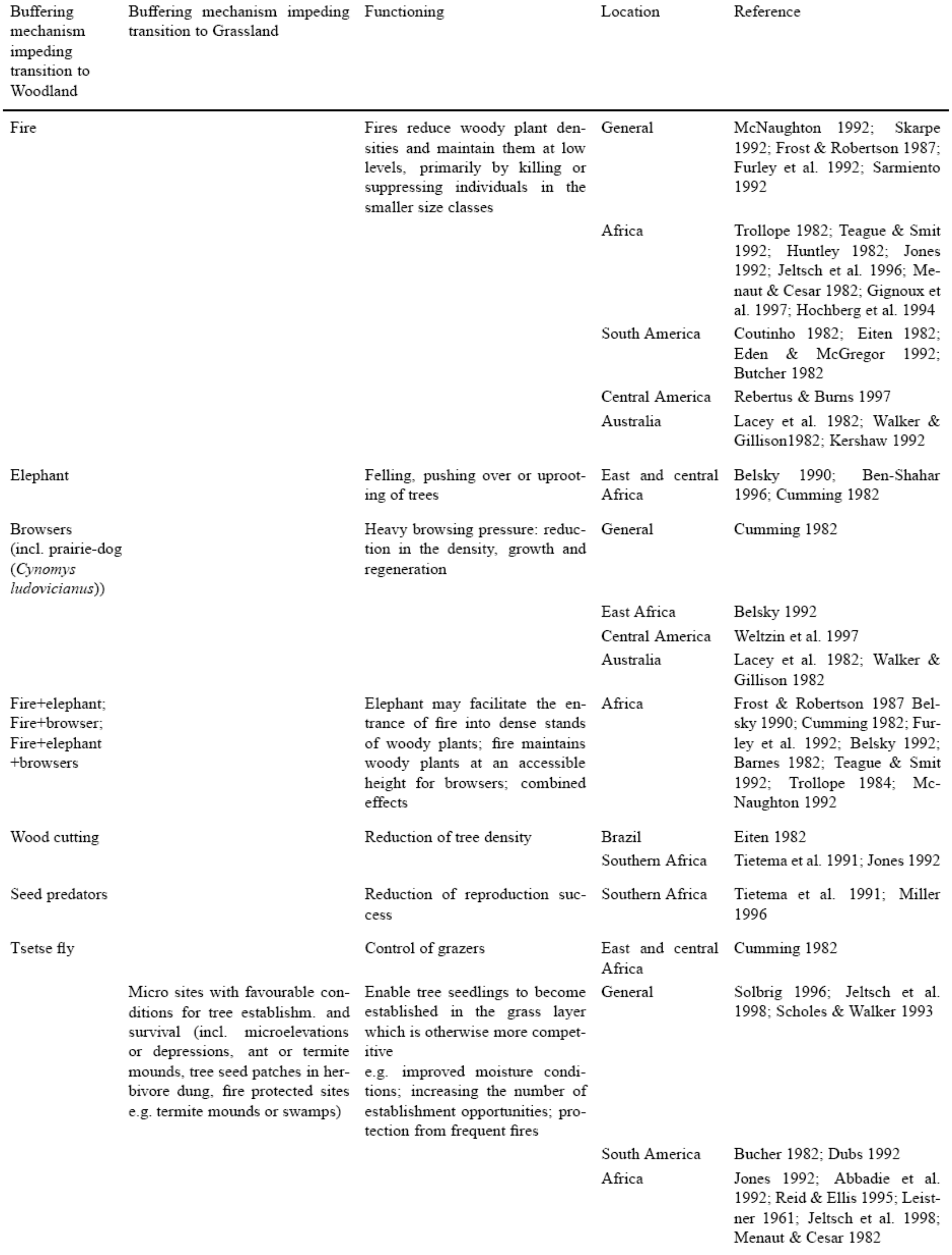
Fire suppression is another explanation that has been proposed for increased woody species distribution. Fire has been shown to be a primary factor that creates and maintains grasslands (DeByle, 1981; Arno and Gruell, 1986; Dando and Hansen, 1990; Covington and Moore, 1994; Mast et al., 1997). When fire is suppressed, woody species encroach into grasslands (DeByle, 1981; Arno and Gruell, 1986; Dando and Hansen, 1990; Covington and Moore, 1994) through increased woody seedling establishment (Mast et al, 1997; Archer, 1994) and survival (Dando and Hansen, 1990; Archer, 1994). Once seedlings reach a sufficient size and age, they are able to tolerate fires and dominate grasslands (Archer, 1994). When fire was suppressed, many different grasslands of varying composition were encroached by woody species of *Juniperus, Artemisia*, and *Prosopis* in western and southwestern USA (Burkhardt and Disdale 1969; Blackburn and Tueller, 1970; Young and Evans, 1981; Johnson 1987, Brown and Archer, 1989; Miller and Wigand, 1994; Miller and Rose, 1995; Miller and Rose, 1999; Baker and Shinneman, 2004), and by *Pseudotsuga* and *Pinus* in other parts of the USA (Arno and Gruell, 1986; Dando and Hansen, 1990; Mast et al, 1997; Mast and Veblen, 1999).

Mixed woody-herbaceous ecosystems are sensitive to land use changes (Werner, 1990). However, land use in many savanna environments are intensifying around the world (Werner and Stott, 1990) and the extent of area modified by human use is continually increasing (House et al., 2003). The above described factors, especially changing climate and increasing carbon dioxide accelerate the effects of land use and changes in land use on woody-herbaceous-livestock species interaction (House et al., 2003). Land use policies and socio-economic interests of the pastoral livestock industry, the most common land use in mixed tree-herbaceous ecosystems, are increasingly focused on improved pasture production through additions of fertilizers and supplements, improved breeds and types of livestock, and manipulations of the plant species composition through introducing new species (e.g. legumes) and removing trees (Werner, 1990). Lastly, many different local factors have been proposed, in addition to the proximate factors discussed above, as important variables influencing the woody-herbaceous interaction and leading to a transition into grassland or a transition to woodland. Jeltsch et al. (2000) reviewed these local factors from studies around the world (Table 3) to propose ecological buffering mechanisms as their unifying theory that explains long-term tree-grass co-existence.

Current and Future Research on Woody-Herbaceous-Livestock Species Interaction

Current studies provide detailed, field-based observations of woody-herbaceous-livestock species interactions (Sankey et al., 2006, Sankey et al., 2006). Tree/shrub age and distribution are often characterized with livestock grazing information and the data are used to make inferences regarding woody-herbaceous-livestock species interaction and to build empirical models (Burrows et al., 1990). However, models of interactions have not been explicitly tested outside of the regions and sites for which they were developed (House et al., 2003). Further studies need to use such data in quantitative models and simulation-based approaches (McKeon et al., 1990) and test the validity of empirical models that are based on site-specific data and relationships. Future research can also include process-based studies with carefully designed experiments. Such studies, although they are likely to be short-term, would provide important details on ecological processes involved in the woody-herbaceous-livestock interaction. Using the detailed understanding of the processes involved, accurate empirical relationships and simulation models could be built to observe potential patterns and changes at longer time-scales (Daly et al., 2000). This would further enhance our understanding of woody-herbaceous-livestock species dynamics and their changes at different spatial and temporal scales. Process-based studies should also have more controlled experiments, where effects of different grazing intensities and the effects of varying grazing animals can be statistically separated. This can further improve our understanding of the effects of overall grazing intensities and different grazing animals and allow an understanding of the importance of overall grazing intensity versus grazing animal species.

Table 3. Local factors that impede the transition savanna to woodland or to grassland in different regions of the world (from Jeltsch et al., 2000)



Buffering mechanism impeding transition to Woodland	Buffering mechanism impeding transition to Grassland	Functioning	Location	Reference
Fire		Fires reduce woody plant densities and maintain them at low levels, primarily by killing or suppressing individuals in the smaller size classes	General	McNaughton 1992; Skarpe 1992; Frost & Robertson 1987; Furley et al. 1992; Sarmiento 1992
			Africa	Trollope 1982; Teague & Smit 1992; Huntley 1982; Jones 1992; Jeltsch et al. 1996; Menaut & Cesar 1982; Gignoux et al. 1997; Hochberg et al. 1994
			South America	Coutinho 1982; Eiten 1982; Eden & McGregor 1992; Butcher 1982
			Central America	Rebertus & Burns 1997
			Australia	Lacey et al. 1982; Walker & Gillison1982; Kershaw 1992
Elephant		Felling, pushing over or uprooting of trees	East and central Africa	Belsky 1990; Ben-Shahar 1996; Cumming 1982
Browsers (incl. prairie-dog (*Cynomys ludovicianus*))		Heavy browsing pressure: reduction in the density, growth and regeneration	General	Cumming 1982
			East Africa	Belsky 1992
			Central America	Weltzin et al. 1997
			Australia	Lacey et al. 1982; Walker & Gillison 1982
Fire+elephant; Fire+browser; Fire+elephant +browsers		Elephant may facilitate the entrance of fire into dense stands of woody plants; fire maintains woody plants at an accessible height for browsers; combined effects	Africa	Frost & Robertson 1987 Belsky 1990; Cumming 1982; Furley et al. 1992; Belsky 1992; Barnes 1982; Teague & Smit 1992; Trollope 1984; McNaughton 1992
Wood cutting		Reduction of tree density	Brazil	Eiten 1982
			Southern Africa	Tietema et al. 1991; Jones 1992
Seed predators		Reduction of reproduction success	Southern Africa	Tietema et al. 1991; Miller 1996
Tsetse fly		Control of grazers	East and central Africa	Cumming 1982
	Micro sites with favourable conditions for tree establishm. and survival (incl. microelevations or depressions, ant or termite mounds, tree seed patches in herbivore dung, fire protected sites e.g. termite mounds or swamps)	Enable tree seedlings to become established in the grass layer which is otherwise more competitive e.g. improved moisture conditions; increasing the number of establishment opportunities; protection from frequent fires	General	Solbrig 1996; Jeltsch et al. 1998; Scholes & Walker 1993
			South America	Bucher 1982; Dubs 1992
			Africa	Jones 1992; Abbadie et al. 1992; Reid & Ellis 1995; Leistner 1961; Jeltsch et al. 1998; Menaut & Cesar 1982

Another trend in current studies of woody-herbaceous species dynamics with or without livestock grazing effects is the use of digitally available data such as satellite imagery and digital aerial photography to map and monitor changes in woody-herbaceous plants. In northwestern USA, for example, several studies have used digital imagery to detect the commonly field-observed expansion of juniper and pinyon-juniper woodlands into adjacent shrublands and grasslands (Strand et al., 2006; Weisberg et al., 2007). Field-based approaches for detecting woody cover increase provide highly accurate and valuable results, but they can be labor-intensive, time-consuming, and limited in the spatial extent they can cover. In comparison, the application of remote sensing methods can be more cost-effective and timely due to the large areal extent they cover. Digital satellite imagery also provides opportunities for more robust and comprehensive analysis of change, as the imagery can be easily integrated with other sources of digital data, such as digital maps of grazing lands and topography. Moreover, data from satellite platforms, such as Landsat, can be acquired in retrospect to examine past changes or past vegetation distribution and to compare with current distribution in order to quantify the extent and rates of change. Such analysis of remote sensing data along with detailed field data could provide information on indicators of global environmental changes and enhance our understanding of processes, signals, extent, and rates of woody-herbaceous vegetation changes under herbivory effects. The information would also be useful in grazing management and land use decision making regarding desired vegetation patterns across the landscape.

Quantitative models woody-herbaceous-livestock species interaction could also include data of other important factors that contribute to changes in woody-herbaceous species such as climate change, CO_2 increase, and fire suppression. This would enhance our ability to quantitatively describe the combined effects of multiple interactive factors on ecotone shift. This would also improve our predictive ability and forecasting skills regarding when, where, and under what conditions changes occur leading to a regional environmental change. Finally, currently proposed hypotheses and empirical models should be quantitatively tested in varying regions with different plant and livestock species.

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