

## Harry Stobbs Memorial Lecture, 1993<sup>1</sup> Herbivore mediation of grass-woody plant interactions

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### Abstract

Historical increases in the density of unpalatable shrubs and trees have reduced the carrying capacity and threaten the sustainability of livestock production in arid and semi-arid grasslands and savannas around the world. Biodiversity, wildlife habitat and nutrient cycling (rates, magnitude, seasonality and spatial patterns) are also affected by these changes in vegetation. While historical increases in woody plant abundance have been widely noted, the rates, dynamics, spatial patterns and proximate causes have not been well documented. Here, I briefly review potential explanations for increased abundance of woody plants in dryland ecosystems and discuss how activities of domestic and native herbivores might influence the balance between grasses and woody plants. Conceptual models of woody plant seedling establishment in grazed ecosystems are presented and evaluated with case studies of an invasive North American arborescent, honey mesquite (*Prosopis glandulosa*). Reduction in grass interference, achieved experimentally or by grazing, may have a positive effect on woody plants but is not a prerequisite for successful seedling establishment in many systems. It is argued that thresholds of herbaceous utilisation required for woody plants to establish successfully may be readily exceeded, even at light levels of grazing. Thus, grazing management schemes must aggressively incorporate the use of fire as well as emphasise

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the degree of grass utilisation and maintenance of species composition, if dominance of woody plants is to be regulated successfully.

### Introduction

Harry Stobbs' career was dedicated to studying grassland production and sustainability (Minson 1978). These issues remain at the forefront of much of the research in grassland and savanna conservation and management. Definitions of the concepts embodied in the terms 'production' and 'sustainability' are elusive, as these words mean different things to different people (Kessler *et al.* 1992; Swank and Van Lear 1992; Levin 1993). In many arid and semi-arid systems, grazing by domestic herbivores is a primary land use for commercial enterprises, pastoral societies and subsistence cultures. Ecosystem sustainability for livestock production requires, among other things, management which maintains the soil resource and ensures a favourable balance between palatable and unpalatable vegetation. In many arid and semi-arid systems, this means: (a) regulating grazing to maintain cover and production of palatable, perennial grasses (which serve as the forage base for livestock or wildlife); and (b) limiting the invasion or encroachment by unpalatable woody vegetation (Walker 1993).

Historical accounts, photographic records and quantitative studies have demonstrated extensive invasion of grasslands by woody plants and increases in woody plant density in savannas over the past 200 years (see review by Archer 1994). Available data indicate that rates and patterns of these increases have been:

- rapid, with substantial changes occurring over 50- to 100-year time spans;
- non-linear and accentuated by episodic climatic events;
- locally influenced by topo-edaphic factors; and
- non-reversible over time frames relevant to management.

Increases in tree or shrub abundance on rangelands are often viewed negatively where management for grazing animals is a priority. Even so, their presence may provide numerous positive benefits which should be considered (McKell 1989; Archer and Smeins 1991). Depending on the species, growth form and density, woody plants may variously suppress production of grasses, increase the difficulty of livestock handling and adversely alter habitat for game and non-game wildlife. Woody plants that increase in systems grazed by livestock do so because they typically receive relatively little utilisation owing to their unpalatability or the presence of thorns or spines (Bergström 1992). Shifts in woody plant abundance or composition may be symptomatic of past management transgressions (such as improper grazing or fire suppression). In systems with a history of long-term, heavy grazing, woody vegetation may be all that is holding the ecosystem together with respect to vegetative cover, energy flow and nutrient cycling. Characteristics common to many woody species that increase in grazed environments include:

- high levels of seed production;
- persistent seed or seedling banks;
- effective seed dispersal;
- tolerance to water and nutrient stress, or deep, extensive root systems;
- chemical or physical deterrents to minimise browsing;
- ability to regenerate vegetatively after top removal; and
- extended longevity (decades to centuries).

Various combinations of these traits may enable woody plants to invade readily and establish in grassland or savanna ecosystems, and make them difficult to displace after establishment. Chemical and mechanical manipulation may not be ecologically sound, biologically effective or economically feasible at large scales. Given the effort and expense required to reduce woody plant cover or biomass, it would be desirable to manage grazing lands to minimise their establishment. Experience to date supports the adage 'an ounce of prevention is worth a pound of cure'. However, climatic variability, the unpredictable occurrence of extreme climatic events and oscillations between different climatic regimes on decadal time scales, may effect rapid shifts in plant recruitment and mortality. These may unexpectedly promote grass die-off

(O'Connor 1993) or enhance woody plant seed production and seedling establishment (McPherson and Wright 1990; Harrington 1991), leaving land users and managers little opportunity to adjust animal numbers/composition or implement a prescribed burn. Socio-economic externalities may interact further to impede or constrain deployment of desired management practices.

#### Proximate causes of woody plant encroachment into grasslands

Historical increases in woody plant stature and density in savannas and grasslands have been observed and acknowledged worldwide. Even so, there has been surprisingly little quantification of the rates, dynamics and proximate causes of these shifts in vegetation structure. Explanations for the proliferation of woody plants at the expense of grasses over the past century have typically centred around alterations in climatic, grazing and fire regimes (Hastings and Turner 1965; Smeins 1984). It has also been suggested that atmospheric CO<sub>2</sub> enrichment since the industrial revolution has favoured C<sub>3</sub> woody plants over C<sub>4</sub> grasses (Idso 1992; Johnson *et al.* 1993). Interactions among such factors may be responsible for the changes in vegetation observed to date, but it is difficult to rank their relative importance (see review by Archer 1994; Archer *et al.* 1995). However, a number of studies have associated the onset of woody plant encroachment with intensification of livestock grazing (Madany and West 1983; Schofield and Bucher 1986; Bucher 1987; Gardener *et al.* 1990; Archer *et al.* 1995).

#### Lessons from case studies

There is little quantitative evidence in south-western North America to support the contention that directional shifts in climate have produced changes from grass to woody plant domination over the past 100 years (Conley *et al.* 1992; Bahre and Shelton 1993). In addition, striking differences in the rate, pattern and extent of woody plant encroachment have occurred on nearby landscapes with similar topo-edaphic properties experiencing similar climates and atmospheric CO<sub>2</sub> concentrations (Table 1). These examples suggest that land management practices were the proximate cause of vegetation change,

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not changes in climate or atmospheric chemistry (Archer *et al.* 1995). Such studies indicate that, if changes in broad-scale factors such as climate or atmospheric chemistry, which potentially favour woody plants, have occurred, they were not, by themselves, sufficient to cause the observed vegetation change.

**Table 1.** Patterns of tree recruitment in a semi-arid savanna in Utah, USA (from Madany and West 1983). Sites were located within a few km of each other on similar soils and would have experienced similar climate and levels of atmospheric CO<sub>2</sub> enrichment. Livestock grazing was initiated in the 1860s.

Tree genera	Density (stems/ha)	
	Ungrazed	Grazed
Plants >100 yr old:		
<i>Acer</i>	0	0
<i>Juniperus</i>	6	5
<i>Pinus</i>	56	23
<i>Quercus</i>	0	0
Plants <100 yr old:		
<i>Acer</i>	0	14
<i>Juniperus</i>	6	76
<i>Pinus</i>	39	252
<i>Quercus</i>	6	256

At local scales, an understanding of land-use history often explains why rates, patterns and dynamics of vegetation change have varied substantially for similar habitats within climatic zones experiencing similar levels of post-industrial CO<sub>2</sub> enrichment. In the Mitchell Grasslands of Australia, prickly acacia (*Acacia nilotica*), a leguminous arborescent from Africa, was introduced along artesian bore drains on some properties in the 1940s to provide shade for livestock. Since that time, it has spread to form dense stands. Pastures have been maintained as grassland where prickly acacia was not introduced. The fact that the spread of the plant has, in many areas, been limited by fencelines suggests that livestock rather than native fauna are the principal agents of seed dispersal. Field observations indicate that seed production and seedling establishment of prickly acacia away from bore drains and watercourses is episodic, occurring only during periods of sufficient rainfall, which are infrequent and widely spaced (Burrows *et al.* 1990). Thus, while climatic variables are a key component in dictating the dynamics of prickly acacia stand development, they cannot account for differences in its distribution or density on adjacent properties.

Fire, grazing and soil properties interact within a variable climate to determine the balance between grasses and woody plants. Temporal patterns of fire and soil moisture are the primary factors influencing woody plant versus grass abundance in the semi-arid regions of south-eastern Australia. Episodic rainfall events trigger woody plant seedling establishment (Burrows *et al.* 1990; Harrington 1991). However, because such rainfall events also stimulate grass production, fire (either natural or prescribed) becomes a possibility for killing most juvenile and many adult woody plants (Harrington and Hodgkinson 1986) and maintaining a grassland or savanna physiognomy. Grazing by high concentrations of livestock or wildlife may reduce the capacity of grasses to competitively exclude shrub seedlings and reduce the level and continuity of fine fuels, thus diminishing or even eliminating the role of fire as a mortality factor. Climate-fire interactions that maintain grassland or savanna are thus decoupled and succession to woodland may occur quickly. In this scenario, prevailing climatic conditions may be conducive to a high ratio of grasses to woody plants, but management intervention of disturbance regimes (fire x grazing interactions) at local scales produces quite the opposite outcome.

Woody plant abundance has also increased in the savannas of southern Texas since settlement and the introduction of livestock (Ingles 1964). Historical aerial photographs (1941–1983) of the La Copita Research Area indicate changes in woody plant abundance have been punctuated and abrupt, not gradual or linear (Archer *et al.* 1988). This site has been heavily grazed by livestock since the late 1800s, and fire-free. The 1941–1960 period was characterised by severe drought, whereas the 1960–1983 period received normal to above-normal rainfall. Changes in woody plant cover during the 1941–1960 period were minimal; however, a 3- to 4-fold increase in shrub cover occurred in the subsequent 20-yr period. Drought may have pre-disposed the system for rapid rates of woody plant invasion in the post-drought period. Would a change of this magnitude have occurred if livestock had not been grazing the site and (a) accentuating drought stress on grass plants; (b) spreading seeds of the dominant woody species; and (c) preventing fine fuels from accumulating and fire from occurring? Conversely, would these activities of livestock have produced this change even if the drought

had not occurred? Livestock, the absence of fire and climate have probably interacted to produce the observed change, but it is difficult to rank their order of importance.

*How important is herbivory relative to other factors?*

How might the relative contributions of interactions between climate, CO<sub>2</sub>, fire and herbivory be determined? In an unique field study in Utah, Madany and West (1983) documented a case in which a savanna protected from cattle grazing was maintained, whereas nearby edaphically similar sites grazed by cattle changed from savanna to dense woodland soon after the introduction of livestock in the 1860s (Table 1). The ungrazed site had a low fire frequency (56–79-yr interval) indicating that frequent fire was not required to maintain the savanna configuration. Both sites should have experienced the same climate and atmospheric CO<sub>2</sub>, yet only one had changed dramatically over the past 100 years. Livestock grazing was the obvious proximate cause of vegetation change on this site, not changes in fire or climatic regimes. Neither potential changes in climatic factors nor increases in atmospheric CO<sub>2</sub> in recent history were sufficient to cause change on the ungrazed site, but both may have influenced the change on the grazed site.

Activities of herbivores, which cause vegetation to change, may be both direct and indirect. Direct effects are those related to the consumption of plant tissue and loss of CO<sub>2</sub>, water and nutrient uptake associated with reductions in leaf and root mass and area. Indirect effects result from changes in microclimate, soil properties, nutrient cycling, competitive interactions and fire regimes. These are a consequence of trampling, changes in seasonal ground cover, and the differential utilisation of plant species that vary in palatability and tolerance to defoliation. Indirect effects may actually be more important than direct effects in terms of shaping ecosystem dynamics and properties. Activities of native and domestic herbivores can interact to influence plant communities, and it may be difficult to distinguish their relative effects.

*Native herbivores and grass-woody plant dynamics*

Utilisation of woody plants by rodents (Crisp and Lange 1976; Yeaton 1988; Cantor and Whitham

1989), browsers (Hunter *et al.* 1980; Pellew 1983; Belsky 1984; Naiman 1988) and invertebrates (Berdowski 1987; McPherson 1993) can create or maintain a grassland or savanna in locations where the climate and soils might otherwise support forest or woodland. Conversely, the preferential utilisation of grasses by grazers may lead to increased woody plant density and abundance by directly or indirectly creating conditions suitable for tree and shrub seedling establishment and stand development. Shifts in the relative abundance of browsers and grazers over time can thus influence the ratio of grasses to woody plants across a landscape. Replacement of native browsers by domestic browsers such as goats can also influence the structure and composition of woody plant communities, but may accentuate shifts in dominance from palatable to unpalatable woody plants (e.g. Riggs and Urness 1989; Stuart-Hill 1992).

The complexities and intricacies of interactions between grasses, woody plants, grazers, browsers, climate and fire have been illustrated in the Serengeti of East Africa (Sinclair and Norton-Griffiths 1979). In one example, wildebeest numbers doubled over a 6-year period after control of the introduced Rinderpest virus (Figure 1). The expanding wildebeest populations grazed primarily during the dormant season and after flowering, so their effects on grass composition were minimal. However, trampling and consumption of fine fuels reduced fire frequency, intensity and continuity of spread during the dry season, thus enabling tree regeneration from seed and from established root stocks, whose growth had been previously suppressed by recurring fire. Lengthening of the fire-free interval enabled woody plants to attain seed-producing sizes that were minimally affected by subsequent fires. Browsers, such as giraffe, potentially benefit from the increase in small trees and shrubs and may regulate woody plant recruitment into larger size classes, while contributing to the decline of larger, older trees. Woody plant density may increase in the absence of sufficient browsing pressure, creating a positive feedback to further suppress grass production either directly (via interference) or indirectly, by concentrating grazing pressure on remaining grass patches. In either case, the probability of fire would decline, while probabilities of woody plant recruitment increase. Woodlands or thickets may be relatively stable and persistent components of the

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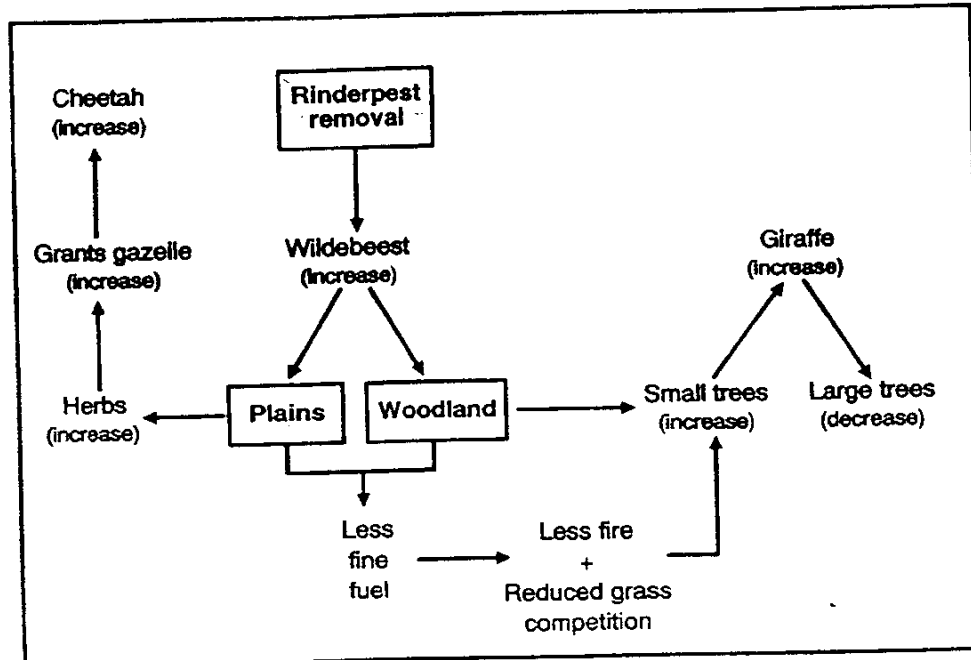


Figure 1. Interactions and linkages between grazers, browsers, grasses and woody plants in a Serengeti ecosystem (modified from Sinclair 1979).

landscape, unless elephants, for example, open up tree canopies, thus stimulating grass production and increasing the opportunity for fire (Guy 1989; Dublin *et al.* 1990).

The influence of small herbivores (e.g. grasshoppers, termites, rodents, lagomorphs, jack-rabbits) on vegetation can also be pronounced. For example, in the 12 years following removal of a nocturnal granivore, the kangaroo rat (*Dipodomys* spp.), from a Chihuahuan Desert site in the south-western USA, the cover of tall grasses increased, bare ground decreased, litter accumulated and snow cover persisted longer relative to plots where kangaroo rats remained (Brown and Heske 1990). Exclusion of cattle only during the same period produced no detectable change in vegetation. In addition, kangaroo rats are important agents of shrub seed dispersal in this system (Cox *et al.* 1993). Changes in herbaceous and woody vegetation ostensibly attributed to livestock or other large herbivores may thus reflect activities of less conspicuous native herbivores.

The North American prairie dog (*Cynomys* spp.) is an example of a once widespread native

herbivore whose activities are known to influence grassland patch structure, nutrient cycling and feeding-site selection by other herbivores (Whicker and Detling 1988). Their role in historically regulating the distribution and abundance of trees and shrubs in grasslands has not been widely considered. Available data suggest that, on landscapes otherwise suited for woody plants, recruitment of trees and shrubs would be minimal when prairie dogs are present (Weltzin 1990). Spatial/temporal variation in prairie dog distribution may help explain inconsistencies in historical accounts of woody plant distribution and abundance in arid and semi-arid regions of North America where this rodent occurred. Elimination of prairie dogs from landscapes by natural (drought, famine, disease) or anthropogenic (poisoning has been extensively practised since the early 1900s) causes would remove a primary and locally pervasive mortality factor and either release suppressed populations of woody plants or make new habitats available for their colonisation.

Human intervention has invariably altered the distribution and abundance of native herbivores.

Water developments for livestock have contributed to an increase in the abundance of kangaroos in Australia (Caughley *et al.* 1987) and antelope in Africa. The result has been an intensification of overall grazing pressure. In these situations, manipulation of livestock numbers to promote sustainability of grazing lands may be of little consequence, unless native wildlife densities can be managed simultaneously. This can be difficult to achieve, as actions taken to influence animal numbers on one property may have little effect (or even a negative effect), if management of adjoining properties is not similarly adjusted. In addition, regulation of wildlife numbers is an economic cost to the land manager and may invoke controversy with animal rights and conservation groups.

Most research has focused on the effects of above-ground grazers on vegetation even though below-ground herbivores (root-feeding nematodes, larvae and grubs) may consume more plant material and may have a proportionally greater impact on total primary production than would be predicted from their consumption rates (Coleman *et al.* 1976; Detling *et al.* 1980; Lura and Nyren 1992). Preferential utilisation of herbaceous vegetation by these organisms may create opportunities for establishment and growth of woody vegetation. Unfortunately, estimates of the distribution and abundance of subterranean herbivores and their importance in regulating plant productivity and composition are seldom available. It is therefore difficult to gauge their impact or to relate their activities to changes in plant composition and production.

#### *Domestic grazers and grass-woody plant dynamics*

Plants of many grasslands and savannas have evolved with herbivory (Milchunas *et al.* 1988). However, in contrast to native herbivores whose numbers or patterns of grazing may vary widely, concentrations of domestic livestock can be artificially maintained at consistently high levels by supplemental feeding, watering and protection from natural predation and disease. Fences prevent migration to new areas when the abundance of preferred forage decreases, resulting in higher frequencies and intensities of defoliation and maintenance of grazing pressure over a greater portion of the year and over a higher frequency of years than might otherwise occur. The impacts of

domestic herbivory on plants (Briske 1994) and ecosystem processes (Detling 1988; Archer and Smeins 1991; Skarpe 1991; Pieper 1994) and soils (Williams and Chartres 1991; Thurow 1991; Milchunas and Lauenroth 1993) have been reviewed recently. In this section, I will consider factors contributing to the replacement of grasses with woody plants.

The invasion of, or encroachment on, grasslands and savannas by woody plants is often associated with livestock grazing (e.g. Table 1). The preferential utilisation of grasses, variously tolerant of defoliation, alters plant competitive interactions in a community and changes patterns of resource distribution and availability. Grazing by livestock can potentially increase the probability of woody plant recruitment in numerous, self-reinforcing ways:

- Livestock may effectively disperse woody plant seeds, particularly those of some leguminous shrubs and arborescents (Janzen 1986; Brown and Archer 1987; Miller 1993).
- Decreases in grass leaf area result in increased light levels at the soil surface, which could increase chances for germination and early establishment of woody seedlings in mesic systems characterised by high levels of grass production and litter accumulation.
- Reductions in transpirational leaf area, root biomass and root activity associated with grazing of grasses can —
  - increase surface soil moisture (Archer and Detling 1986) to enhance woody seedling establishment and growth;
  - increase the amount of water percolating to deeper depths and benefit established woody species with deep root systems;
  - increase nutrient availability to woody plants (Caldwell *et al.* 1985; 1987); and
  - “release” suppressed populations of established tree or shrub seedlings (Harper 1977).
- Grazing decreases plant basal area, increases mortality rates and decreases seed production and seedling establishment of palatable grasses (e.g. O'Connor and Pickett 1992). Grazing may also increase susceptibility of grasses to other stresses such as drought (Paulsen and Ares 1962;

Herbel *et al.* 1972; Clarkson and Lee 1988). These factors would combine to increase the rate of above- and below-ground gap formation and available area for shrub seedling establishment (Owens and Norton 1989; Diemont and Linthorst Homan 1989), especially in post-drought periods.

- Shifts in herbaceous composition accompanying grazing may lead to assemblages less effective at sequestering resources and competitively excluding woody plants or limiting their growth and seed production.
- Reductions in fine fuel biomass and continuity reduce fire frequency and intensity (Madany and West 1983; Savage and Swetnam 1990).
- Invading woody species often possess structural deterrents (thorns, spines) or are unpalatable relative to grasses and forbs and are thus not browsed with sufficient regularity or severity to limit establishment or growth.
- Reductions in soil water-holding capacity and fertility, and alterations in physico-chemical properties often occur with loss of vegetative cover and erosion (Thurrow 1991; Williams and Chartres 1991; Chartres *et al.* 1992). Systems where soil resources are plant-controlled rather than terrain-controlled are particularly sensitive to alteration by grazing (Ludwig *et al.* 1994; Tongway and Ludwig 1994). Grazing on such sites would favour N<sub>2</sub>-fixing woody plants (e.g. *Prosopis*, *Acacia*) and evergreen growth forms tolerant of low nutrient conditions (Goldberg 1982; Bush and Van Auken 1989; Cohn *et al.* 1989; Van Auken and Bush 1989) and water stress.

Modification of microclimate, plant competitive interactions, soil fertility and fire frequency associated with the defoliation and preferential utilisation of grasses can increase the likelihood of successful tree or shrub seedling establishment and growth (Blackburn and Tueller 1970; Van Auken and Bush 1987, 1988, 1990; McPherson *et al.* 1988; Brown and Archer 1989; McPherson and Wright 1990; Skarpe 1990; Bush and Van Auken 1990, 1991), decrease time to reproductive maturity (McPherson and Wright 1987), increase the frequency and magnitude of seed production, and extend woody plant longevity (West *et al.* 1979).

### Conceptual models of woody plant establishment

The life-span of trees and shrubs in arid and semi-arid systems is typically of the order of decades to centuries (see Archer 1994 and references therein). For woody plants with potentially long life-spans and low post-establishment mortality rates, the seedling-recruitment phase is the most critical stage in the life history. Once established, woody plants may persist in a small, suppressed state. These inconspicuous 'seedling banks' may later be an important source of 'new' plants which grow rapidly after environmental conditions change, or when competition is relaxed (Harper 1977; Hara 1987).

Most research on woody plant germination and establishment has focused on abiotic and edaphic factors. Studies of shrub seedling establishment in competition with grasses are often short-term and involve potted plants with restricted rooting volumes. Such experiments conducted in controlled environments are often done under relatively low light intensities and artificially high CO<sub>2</sub> concentrations. Field investigations pertaining to biotic limitations are scarce. Controlled environment experiments and qualitative field observations suggest that lateral grasses would competitively exclude woody seedlings and that heavily grazed areas would be more prone to woody plant invasion than lightly grazed areas, other factors held equal. Yet there are few guidelines for relating changes in woody plant establishment probabilities to levels of grazing or grass utilisation. It is also well known that herbaceous retrogression accompanies intensive grazing. However, the extent to which sites with different grazing histories differ in their susceptibility to woody plant encroachment is largely unknown.

### Woody plant establishment and grazing pressure

Figure 2 depicts an idealised representation of the probability of establishment of unpalatable woody plants as a function of grazing pressure. The model proposes an interaction between above- and below-ground biomass and a shift from fire and competition as primary regulators of woody seedling establishment to climatic controls as grazing pressure increases. At low levels of grazing (Zone A), above- and below-ground biomass are relatively high, litter has

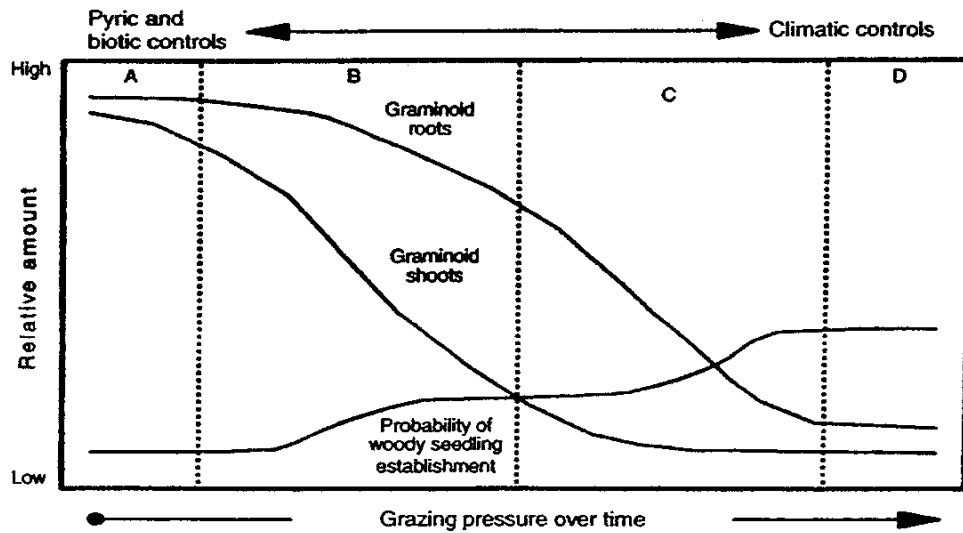


Figure 2. Hypothesised interaction between above- and below-ground competition, grazing intensity and woody plant seedling establishment. See text for elaboration.

accumulated, bare ground is relatively low and light levels at the soil surface are reduced by grass canopies and litter. Woody plant seedlings emerging under these conditions would potentially face high levels of competition for light, soil resources or both (Becker and Levy 1983; Facelli and Leon 1986; Eissenstat and Caldwell 1988; De Steven 1991a, 1991b; Facelli and Facelli 1993; Hughes and Vitousek 1993). Woody species with large seeds and greater stored reserves should produce more shoot and root growth under these resource-limiting conditions. Such species should have a greater chance of elongating shoots and roots into micro-environments where resources are relatively more abundant. In mesic grassland or savanna communities dominated by mid- or tall-statured grasses, light can be limiting (Schimel *et al.* 1991). Woody species with preferential above-ground allocation and shoot elongation (strong red/far-red response) may be favoured under these circumstances (Goerner 1993). Rapid shoot growth would ensure elevation of foliage into a favourable light environment and put the plant in a positive carbon balance earlier in its life cycle. In more xeric, short-grass systems, light may not be a limiting factor and competition for soil resources may predominate. In these situations, woody species with preferential allocation to

roots may be favoured. Establishment, in both cases, may occur primarily during years or periods of the year when resources are abundant and competitive effects are minimal. In either case, the persistence of seedlings is limited by fire, which has a relatively high probability of occurrence given the abundance and continuity of fuel in a lightly grazed system.

Above-ground leaf area, litter and biomass decline and light levels at the soil surface increase as grazing pressure increases (Zone B, Figure 2). Gaps formed by patch grazing represent opportunities for recruitment of woody seedlings. Below-ground competition may be somewhat relaxed, as soil water use by grasses decreases because of the loss of transpirational leaf area and reductions in allocation to root initiation, growth and physiological activity.

Grass root biomass, density and penetration depth begin to decline with continued grazing (Zone C), making grasses more susceptible to other environmental stresses. Reductions in plant canopy cover are now accompanied by reductions in basal area and density. As a result, gaps begin forming both above and below ground and resources are freed up for other plants. Microsites may become less suitable for establishment of mesophytic grasses, and are more likely to be colonised by seedlings of xerophytic woody



plants. As the size and abundance of gaps increase, probabilities for successful woody plant germination and establishment increase, the result of simultaneous reductions in herbaceous interference and fire frequency, intensity and continuity of spread.

Continued loss of herbaceous cover and continuity (Zone D) disrupts nutrient cycling by increasing erosion and decreasing quality and quantity of above- and below-ground litter inputs. Woody plants established prior to this time may now be of sufficient size and density to suppress grass basal area and density further and to serve as a seed source for additional recruitment. Herbaceous vegetation now has little influence on woody plant seedling establishment. Opportunities for fire, natural or prescribed, may be rare.

*Woody plant establishment and grazing history*

Structural changes in herbaceous vegetation associated with long-term, heavy grazing include shifts from tall- to short-statured species, and from strong perennials to weak perennials and annuals, reductions in plant density and basal area, and increases in bare ground. The latter may contribute to erosion and loss of nutrients. In addition, fire frequency typically declines, the result of active suppression, or the result of low and ephemeral ground cover characteristic of

sites with histories of heavy grazing. As grazing-induced retrogression occurs, bare ground often increases, creating opportunities for establishment of ephemeral and unpalatable herbaceous species. Weak perennials and annuals on retrogressed sites are potentially less effective at competitively excluding invading woody plants than the perennial grasses they have replaced. Safe sites for perennial grass recruitment decline and grazing is concentrated on the remaining preferred plants. Loss of perennial grass seed production accompanied by changes in soils, seed bank and vegetative regenerative potential may make it difficult for grasses to re-colonise the site even when grazing is relaxed. Shifts in composition to less palatable plants also occur with grazing. Such plants slow rates of nutrient cycling subsequent to their establishment (Pastor and Naiman 1992). Xerophytic, evergreen and N<sub>2</sub>-fixing woody plants, well adapted to water stress and nutrient-poor conditions, may therefore be favoured relative to perennial grasses on sites where long-term grazing has adversely affected soil physical properties and fertility (Schlesinger *et al.* 1990; Aerts and van der Peijl 1993). It is therefore hypothesised that, for a given level of grazing pressure, sites at an advanced stage of retrogression should be more susceptible to woody plant encroachment than sites where herbaceous retrogression has been minimal (Figure 3).

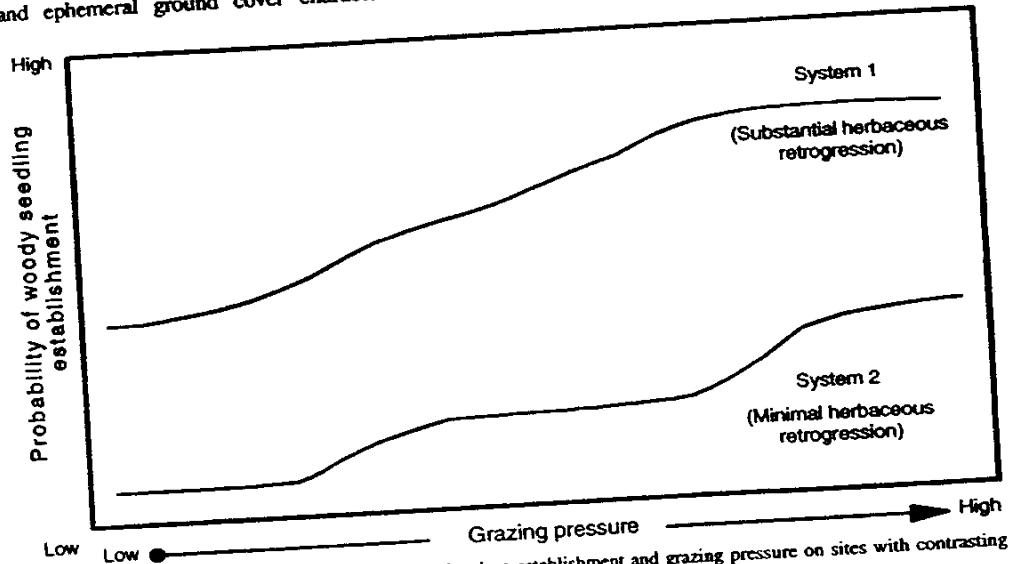


Figure 3. Hypothesised relationship between woody plant establishment and grazing pressure on sites with contrasting grazing histories.

Case studies of model validity

The conceptual models in Figures 2 and 3 have been tested for honey mesquite (*Prosopis glandulosa* var. *glandulosa*), an invasive arborescent legume of south-western North America. Experiments examining *P. glandulosa* seedling establishment were conducted on 4 sites (Table 2). The south Texas *Prosopis* Savanna site had a history of long-term, continuous grazing and had experienced substantial retrogression. The hypothesis was that further reductions in above-ground biomass achieved by clipping (to simulate grazing) and by reducing grass density (to simulate gap formation associated with plant mortality) would enhance *P. glandulosa* seedling establishment. Similar experiments in central Texas Post Oak (*Quercus stellata*) Savanna and San Antonio True Prairie sites were conducted on pastures with contrasting livestock grazing histories (long-term grazed vs. long-term ungrazed). These pastures differed substantially with respect to herbaceous composition and above-ground biomass. *Prosopis* — grazing history interactions on a fourth site in northern Texas were evaluated by comparing seedling establishment on areas intensively grazed by native rodents with that on areas grazed by livestock. It was hypothesised that, at any level of simulated grass utilisation, *P. glandulosa* seedling

establishment would be greatest on the most retrogressed sites. The ability of herbaceous vegetation to exclude woody seedlings was tested by planting scarified *P. glandulosa* seeds into grass-dominated plots on each site. Plots received one of 3 defoliation regimes (none, moderate [plants clipped to 20 cm stubble], and heavy [plants clipped to 5 cm]). Defoliations were imposed monthly over a 2-year period and *P. glandulosa* germination and seedling establishment were monitored.

*Prosopis glandulosa* seedling recruitment: *Prosopis savanna* site

This site had a long history of heavy continuous grazing by cattle. Tall-grass species with annual above-ground net primary production (ANPP) of 300–600 g/m<sup>2</sup> have given way to short-statured perennial grasses and forbs with ANPP of 100–300 g/m<sup>2</sup>. Woody plant cover has increased by a factor of 2–3 over the last 50 years (Archer 1995). To quantify the extent to which the herbaceous vegetation on this site is limiting *P. glandulosa* seedling establishment, grass density was reduced 50% in some plots by individual plant application of a foliar herbicide and was not altered in other plots. In addition, half of the plots received supplemental bi-monthly irrigation to simulate an above-average rainfall year (see

Table 2. Characteristics of 4 study sites used to examine relationships between grass defoliation, grazing history and *Prosopis glandulosa* seedling establishment. For additional site details, see Brown and Archer (1989; 1990) for the *Prosopis* Savanna site; Brown (1987) for the Post Oak site; Goerner (1993) for the True Prairie site; and Weltzin (1990) for the Rolling Plains site.

Parameter	<i>Prosopis</i> Savanna	Post Oak Savanna	True Prairie	Rolling Plains
Location	Southern Texas	Central Texas	Central Texas	Northern Texas
Lat/Long	27°40'N; 98°12'W	30°35'N; 96°21'W	30°35'N; 96°21'W	33°48'N; 99°29'W
Annual temp (°C)	24	21	21	17
Study dates	1984–85	1984–85	1986–87	1988–89
Annual PPT (mm) <sup>1</sup>	507/830	976/967	1053/995	489/564
Long-term mean PPT	720	996	996	682
Standing crop (g/m <sup>2</sup> ) <sup>2</sup>				
Grazed	280	380	486	100 <sup>4</sup>
Protected	—	407	602	339 <sup>5</sup>
Root biomass (g/m <sup>2</sup> ) <sup>3</sup>				
Grazed	466	560	580	—
Protected	—	1270	927	—
Bare ground (%)				
Grazed	51	8	21	—
Protected	—	4	7	—

<sup>1</sup>Precipitation (PPT) during each year of study.

<sup>2</sup>Peak above-ground.

<sup>3</sup>To depth of 30 cm.

<sup>4</sup>Prairie dog colony — heavily grazed.

<sup>5</sup>Off prairie dog colony.

Brown 1987 for additional details). It was hypothesised that *P. glandulosa* seedling establishment in this system might be episodic, occurring primarily during high rainfall years associated with tropical storms or hurricanes.

Results from this study (Table 3) showed: (1) *P. glandulosa* seedling emergence was high (38–48%) without supplemental watering, even though monthly rainfall during the experiment was slightly below the long-term average and temperatures were 'normal'; (2) Supplemental watering enhanced emergence only slightly (10–20%), and had even less effect on subsequent survival; and (3) Manipulating herbaceous biomass and density had no significant influence on *P. glandulosa* seedling emergence or survival. Such data suggest that the current herbaceous vegetation has little influence on rates or levels of *P. glandulosa* establishment. In addition, it appears that neither *P. glandulosa* emergence nor survival is contingent upon the occurrence of unusual climatic events. *P. glandulosa* appears well adapted to germinate and establish at relatively high rates in years with 'normal' rainfall and temperature. Continued invasion by this plant can be expected on this site, the rates and dynamics determined primarily by factors influencing dispersal of seed into grass patches.

*Prosopis glandulosa* seedling recruitment: Post Oak savanna site

The high rates of *P. glandulosa* emergence and establishment observed on the southern Texas site might indicate that retrogression had progressed to the point where the herbaceous species present

were ineffective in garnering patch resources and competitively excluding woody plant seedlings. If extensive retrogression has not occurred, or if succession following relaxation of grazing has resulted in the re-establishment of late-seral competitive dominants, *P. glandulosa* germination and establishment should be much lower. Results from the Post Oak savanna study do not support this generalisation. Despite substantial differences in herbaceous composition and above- and below-ground biomass on long-term grazed versus long-term protected pastures, rates of *P. glandulosa* emergence (30–40%) and establishment (80–90%) over 2 years were high, and were generally not significantly affected by the level of grass defoliation (Brown and Archer 1989). Contrary to expectations, recruitment over the longer term (8 years) has actually been higher on the long-term protected site (Figure 4). *P. glandulosa* shoot growth was, however, greatest on the long-term grazed site. Note that mean plant height was < 25 cm for the first 5 years and that differences in above-ground growth on the 2 sites were not apparent until ca. Year 5.

*Prosopis glandulosa* seedling recruitment: True Prairie site

An experiment like the one conducted at the Post Oak savanna was implemented on a True Prairie site in central Texas. The results were similar to those obtained in the Post Oak savanna study, in that *P. glandulosa* seedling emergence and survival within a pasture were not strongly influenced by level of grass defoliation (Table 4). In contrast to the Post Oak savanna study, grazing

Table 3. Emergence and survival of 2 *Prosopis glandulosa* seedling cohorts on a savanna site with a history of heavy, continuous grazing in southern Texas, USA (from Brown 1987). *P. glandulosa* seeds were sown into grass-dominated clearings where density and level of defoliation were manipulated (see text for details). Irrigation stimulated emergence and survival by 10–20% across most treatments (data not shown).

Grass density	Defoliation regime	Emergence (%)		Survival (%)		
		1984 cohort	1985 cohort	1st Year	1985 cohort	2nd Year
				1984 cohort		1984 cohort
Unaltered	Not defoliated	43	46	73	78	63
	Moderate	39	43	70	72	63
	Heavy	45	48	80	72	75
Reduced 50%	Not defoliated	42	44	75	80	67
	Moderate	42	42	78	78	66
	Heavy	38	43	78	88	62

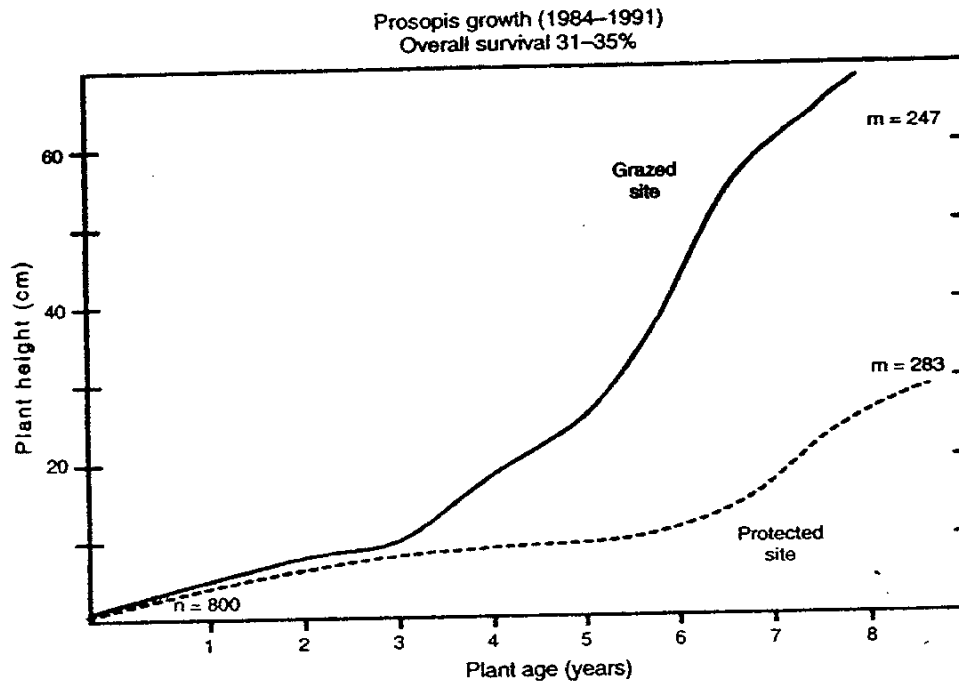


Figure 4. Height of *Prosopis glandulosa* planted from seed in 1984 on sites with contrasting grazing histories (S. Archer, D.M. Miller and J.R. Brown, unpublished data). Numbers of seeds planted ( $n$ ) and number of plants present in Year 8 ( $m$ ) shown. Level of grass defoliation (moderate vs. heavy) had no influence on *P. glandulosa* height on either site. See Brown and Archer (1989) for details on experimental design, emergence and survival during first 2 years. Below-normal rainfall in 1988 (Year 4; ca. 50% of normal) and 1989 (Year 5; ca. 75% of normal) had little effect on growth or mortality.

history did have a significant effect on mean seedling emergence (grazed = 25–27%; ungrazed = 6–9%). Even so, these effects were observed in only one year. When the trial was repeated in a second year, mean emergence was statistically comparable for the 2 sites (grazed = 14–20%; ungrazed = 11–13%). In addition, grazing history had little influence on survival of emerged seedlings. The one exception was a reduction in first-year survival among seedlings on the non-defoliated plots in the long-term protected pasture.

#### *Prosopis glandulosa* seedling recruitment: Rolling Plains savanna site

Prairie dogs are large (ca. 1 kg) burrowing rodents native to North America. Where they congregate and form extensive colonies, plant composition and production are significantly altered

(Whicker and Detling 1988). A prairie dog colony in northern Texas was utilised to examine the effects of herbaceous composition and production on *Prosopis* seedling establishment. In 1988 and 1989, seeds of *Prosopis* were sown on and off a prairie dog colony. Emerging seedlings were protected from vertebrate herbivores by wire mesh enclosures. Estimated peak above-ground biomass production on the colony (77 g/m<sup>2</sup>, 1988; 100 g/m<sup>2</sup>, 1989) was comprised primarily of short-statured grasses and forbs and was substantially lower than that off the colony (202 g/m<sup>2</sup>, 1988; 339 g/m<sup>2</sup>, 1989), where tall-statured grasses dominated. First-year survival of *Prosopis* seedlings on- and off-colony was uniformly high (ca. 75%) (Weltzin 1990), despite the fact that these experiments were conducted during years of significantly below-normal annual rainfall (Table 2), when abiotic stress or intensity of herbaceous interference should have been substantial.

**Table 4.** Mean ( $\pm$ SE) emergence and end-of-season survival of *Prosopis glandulosa* seedlings in True Prairie grasslands with a history of livestock grazing and protection from grazing (from Goerner 1993). Survival % is based on the number of seedlings emerging ( $n=250$  seeds/treatment). Grasses in plots on each of the contiguous pastures received one of 3 monthly defoliation regimes (none, moderate, heavy; see text for details). The 1987 seedlings were not observed in their second year. Means within a column followed by the same letter(s) were not significantly different ( $P < 0.05$ ).

Grazing history	Defoliation regime	Survival (%)				
		Emergence (%)		1st Year		2nd Year
		1986 cohort	1987 cohort	1986 cohort	1987 cohort	1986 cohort
Long-term grazed	Heavy	25 $\pm$ 8a	16 $\pm$ 4a	79 $\pm$ 4a	59 $\pm$ 6a	34 $\pm$ 4b
	Moderate <sup>1</sup>	—	14 $\pm$ 3a	—	46 $\pm$ 10ab	—
	None	27 $\pm$ 8a	20 $\pm$ 3a	74 $\pm$ 3a	21 $\pm$ 5b	23 $\pm$ 5a
Long-term protected	Heavy	8 $\pm$ 4b	11 $\pm$ 3a	70 $\pm$ 15a	44 $\pm$ 32ab	19 $\pm$ 8a
	Moderate	9 $\pm$ 2b	11 $\pm$ 3a	67 $\pm$ 30ab	43 $\pm$ 8ab	20 $\pm$ 4a
	None	6 $\pm$ 1b	13 $\pm$ 4a	24 $\pm$ 14b	34 $\pm$ 9ab	19 $\pm$ 5a

<sup>1</sup>Moderate defoliation treatment not implemented in grazed pasture until the second year.

**Lessons learned with *Prosopis glandulosa***

The conceptual models in Figures 2 and 3 can be applied at patch, community and landscape scales. They will require parameterisation for species or functional groups and the relationships may vary with edaphic and climatic factors. In the case of *P. glandulosa*, field experiments and diverse field observations indicate that herbaceous competition may have little influence on *P. glandulosa* establishment over a broad range of grazing levels or grazing histories (Brown and Archer 1989 and references therein; see Bush and Van Auken 1990 for alternative perspective). It seems that thresholds of herbaceous biomass production required to limit its establishment may be exceeded even at low levels of grazing. Grasses did not effectively exclude *P. glandulosa* on any of the 4 sites studied. However, after 4–5 years, site grazing history and herbaceous composition did begin to influence *P. glandulosa* growth rate and time to reproductive maturity (Figure 4). On the True Prairie site, recruitment was greater in pastures with a history of grazing. However, even in pastures protected from grazing and dominated by late-seral perennial grasses, emergence was still 6–13% and first- and second-year survival of emerging seedlings exceeded 24–34 % and 19 %, respectively (Table 4). It would thus appear that, in the absence of fire, grasses may slow, but not prevent, *P. glandulosa* stand development on this site. Four field experiments in 4 different systems indicate that apparent reductions in grass interference achieved experimentally or by varying

grazing history are not prerequisite for *P. glandulosa* establishment. This also appears to be the case for woody species in other systems (Smeins and Merrill 1988; Brown and Archer 1989 and references therein; San Jose and Farinas 1991; Hall *et al.* 1992; Schmidt and Stubbendieck 1993).

The ability of *P. glandulosa* seedlings to compete successfully with grasses appears related to their rapid root elongation. By the end of their first season of growth, their tap roots can extend more than 50 cm and may be exploiting soil moisture at depths below those effectively utilised by grasses (Brown and Archer 1990). This partitioning of resources becomes more pronounced as the plants age. In addition, shallow lateral roots also contribute significantly to *P. glandulosa* water balance (Ansley *et al.* 1990). *P. glandulosa* has numerous additional adaptations, which further contribute to its success in arid and semi-arid systems. These include: high seed production; extended seed longevity; effective seed dispersal by ungulates; N<sub>2</sub>-fixation capability; an ability to germinate and establish over a wide range of soil types, light and moisture regimes; tolerance to fire and defoliation which develop very early in its life cycle; and tolerance to extreme drought (see Archer *et al.* 1988 and references therein). For these reasons, the plant is highly persistent once established.

Given the potential ability of *P. glandulosa* to establish successfully in stands of highly productive, late-seral grasses, why has its abundance increased only recently in many areas of North

America? One hypothesis is that: prior to settlement and the introduction of livestock, *P. glandulosa* was absent from grass-dominated portions of the landscapes because of dispersal limitations (Brown and Archer 1987). Alternatively, *P. glandulosa* may have been widely present but suppressed, though not eliminated (Wright *et al.* 1976; Menaut *et al.* 1991; Hochberg *et al.* 1994), by frequent fire. Competition from grasses would have been relaxed and set-backs associated with periodic fire eliminated with the advent of livestock grazing. *Prosopis* plants would then have rapidly increased in stature and dominance. As more plants reached seed-bearing size, more propagules would be available for dissemination and encroachment would progress at an ever-accelerating rate.

**Summary**

It is generally assumed that late-seral grasses are better competitors than those of retrogressed sites and that light to moderate utilisation of herbage will effectively prevent or minimise encroachment of woody vegetation. However, data from case studies with *P. glandulosa* suggest that, for some aggressive woody invaders, grazing management based primarily on regulating utilisation and maintaining a species composition dominated by late-seral perennial grasses will not suffice to maintain a favourable grass-woody plant balance. While such management may slow the rate at which stands of woody plants develop (Figure 4) it will not prevent their occurrence if seeds are being actively dispersed into an area. The thresholds of herbaceous utilisation required by plants such as *P. glandulosa* to establish successfully appear to be exceeded easily, even at light levels of grazing. Grazing management strategies should therefore:

(1) Seek ways to curtail production and dispersal of seeds of invasive woody plants.

This may be achieved by: (a) maintaining certain levels of grass biomass in order to lengthen the time to woody plant reproductive maturity and reduce the frequency and magnitude of viable seed production; (b) favouring populations of woody plant seed predators. Care must be taken here, for there is a fine line between seed predation and seed dispersal (e.g. Brown and Heske 1990; Cox *et al.* 1993); and (c) limiting dissemination of seeds by livestock (e.g. many *Prosopis* and *Acacia* spp.).

This may be partially achieved by deferring grazing of pastures during periods of seed production; by fencing off areas within pastures where high densities of seed-producing trees occur (and grazing only when trees are not bearing fruit); and by detaining animals, which have had access to seeds, in holding areas before moving them to other pastures.

(2) Enable the use of periodic fire.

Fire will not necessarily eliminate woody plants (Menaut *et al.* 1991; Hochberg *et al.* 1994), but it can slow their rate of spread and prevent them from reaching large sizes such that they: (a) less effectively shade herbaceous vegetation; (b) do not develop large or extensive root systems; (c) do not initiate seed production; (d) are more accessible to small browsers (native or domestic); and (e) are more susceptible to drought, subsequent fires, mechanical/chemical treatments or other perturbations (e.g. Noble *et al.* 1992). Periodic fire may also limit or reduce the persistence of woody plants in the soil seed bank. For fire to be used as an effective management tool, grazing must periodically be relaxed so fine fuels can accumulate. The economic cost of such deferment must be weighed against the future costs (direct and indirect) associated with: (a) increased animal handling difficulty; (b) decreased forage production; (c) periodic application of mechanical or chemical treatments to reduce woody plant cover; and (d) land devaluation which often accompanies bush encroachment.

Relatively predictable primary production and continuity of standing crop are desirable, as planning for livestock deferment must often be done a year or more in advance. Predictability and continuity in primary production can be potentially achieved by managing livestock numbers and season of use (e.g. grazing which causes a shift from perennial grass to ephemeral plants often decreases fuel continuity and increases annual variability and unpredictability of primary production). Options for 'reclamation burns' during the hot, dry periods of the year also exist and may be more effective in regulating woody plants than cool season fires. Such prescriptions should be deployed with caution, as they can be difficult to control and have the potential to cause mortality of perennial grasses.

Woody plant encroachment is a subtle process

that operates at decadal time scales. The forces setting the process of invasion in motion may occur long before the results are readily apparent. By the time the results are manifested, cost-effective management options may have been eliminated. Communities and landscapes may have a gross, outward appearance of stability for many years, then change radically over a short period of time. In some systems, this reflects the importance of rare or infrequent events which trigger episodes of seed production, seed dispersal or seedling establishment. It can also reflect patterns of plant growth and development. In the case of *P. glandulosa*, seedlings may persist for years as small, short-statured plants which are inconspicuously distributed throughout the herbaceous vegetation. Such plants are actively photosynthesising, suggesting that their lack of shoot development is the result of preferential allocation of carbon for root growth (Brown and Archer 1990). After several years, there is a dramatic shift in allocation to shoot growth (Figure 4). Such plants may not be apparent to the casual observer until many years after their establishment, by which time they are highly persistent members of the plant community. Given these patterns of growth, it is important to monitor closely those rangelands for which bush encroachment is a potential problem and to have pro-active, integrated, whole-system management plans in place (e.g. Scifres *et al.* 1985; Noble *et al.* 1991; Dankwerts *et al.* 1993). In order to limit the abundance or dominance of aggressive woody invaders such as *Prosopis glandulosa*, grazing management schemes must actively incorporate fire in addition to emphasising grass utilisation and maintenance of species composition.

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