SOME ASPECTS OF TREE-GRASS DYNAMICS IN QUEENSLAND'S GRAZING LANDS

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Abstract

This review examines the interactions between grasses and trees that are relevant to Queensland's grazing lands. Soils and climate determine the potential amount of woody vegetation within an area and clearing, fire and grazing management can modify that potential. In general, the presence of non-leguminous trees reduces the potential grass production beneath their canopy and within woodland patches. Some non-native leguminous trees (e.g. Indian siris, *Albizia lebbeck*) enhance production of grasses beneath their canopies, whereas the widespread native leguminous trees, mulga (*Acacia aneura*) and brigalow (*A. harpophylla*) have not been reported to enhance grass production in the same way. At the patch scale, pasture production beneath woodlands with moderate to high tree basal areas is generally less than in open patches under the same soil and climatic conditions. At a landscape level, tree density, rainfall amount and distribution, and soil type modify pasture production within forest/woodland/shrubland systems. Grasses can reduce tree seedling survival but have little impact on mature woody plants, apart from providing fuel to carry a fire.

Modelling studies have been used to examine some aspects of tree-grass production. Firstly, the relationship between grass production and an increasing amount of trees can vary from linear decrease, to exponential decrease to initial stimulation followed by a decrease, depending solely on the relative strengths of stimulatory and competitive effects of trees on grasses. Secondly, simulated pasture production within woodlands shows that the pasture production may be up to 50% higher in paddocks that have high variability in the distribution of those trees compared with areas where trees are uniformly distributed. This is due to the non-linear (negative exponential) relationship between pasture production and tree density that is commonly observed within Queensland. Lastly, simulation studies show that total aboveground production (trees and pasture) of mulga woodland increases as the number of trees per hectare increases.

The pasture production response to tree clearing or tree planting depends on tree species, rainfall, soil type, climatic history and post-clearing management including fire and grazing, and will change with time since clearing. The greatest relative increase in pasture production following the removal of woody vegetation occurs when the initial tree basal area is highest; where rainfall is evenly distributed though the year and on fertile soils with a low water holding capacity.

Key words: Tree-grass interactions; productivity; soil effects; rainfall effects; tree clearing; grazing; modelling

Introduction

There is a long history of theory and study that concerns the way in which trees and grass[1] co-exist in savanna systems (e.g. Scholes and Archer 1997). Although the details of these theories are not known by many land managers in Queensland, most have a very practical understanding of tree-grass interactions and their importance to their business. Tree clearing/killing has been undertaken from the early settlement period in Australia (see Bonyhady 2000 for early references) and was the topic of many agricultural journal articles until recently (e.g. Anderson and Dowling 1987). This practice has continued and resulted in extensive land clearing in Queensland, as land managers know that the removal of trees often increases grass production for domestic livestock.

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[1] Throughout this paper, *tree* is used in the general sense and includes shrubs, and *grass* is used as a general term, which includes other herbage. *Pasture* is also used as a general term with very similar meaning to grass.

The issue of tree-grass interactions needs to be considered at several scales. Failure to do so would result in an incomplete coverage of all the issues as well as the possibility of apparently inconsistent or conflicting observations and conclusions. Different scales of interest are an example of hierarchical structure. Several authors have discussed the applicability of hierarchy theory to community (Allen and Starr 1982) and ecosystem (O'Neill *et al.* 1986) ecology. The relevant aspect of hierarchy theory here is that behaviour at one level of the hierarchy (e.g. the individual tree level) will affect the dynamics at the next level (the 'patch' scale) but is unlikely to be a major influence on the behaviour of the next higher level (the 'landscape' level). Thus a detailed understanding of what happens around individual trees cannot be used to predict what will happen at the landscape level, without the inclusion of many other factors at the intermediate, patch scale.

This paper examines several aspects of tree-grass dynamics in Queensland. I start by reviewing the existing theoretical framework for tree-grass coexistence in savanna environments and discussing some environmental and management influences on tree-grass balance. I describe the direct effects of trees on grass production at the individual tree, the patch and the landscape scales and provide evidence of the consequences of tree removal on grass production. Finally, I use simulation modelling to generalise some of the responses reported in the literature. The longer-term issues of how trees might be involved in sustaining productivity in ecosystems are more adequately covered elsewhere (Schmidt and Lamble 2002 [this volume]).

Theory of tree-grass interactions

The major terrestrial biomes of the world are determined by temperature and rainfall (Whittaker 1975). Savannas occur within a zone of low to moderate rainfall and high mean annual temperatures (see Fig. 1 in Belsky 1991 for examples). Several theories have developed to explain the coexistence of trees and grasses. Many early explanations involved the two-layer soil hypothesis proposed by Walter (1971). In broad terms, this suggested that grasses were superior competitors for soil moisture in the upper soil layer, whereas only trees could access soil moisture in the lower soil layers. Based on these assumptions, Walker and Noy-Meir (1982) developed a model with a single, stable equilibrium of grass and trees. After further refinement to this model, Walker *et al.* (1981) suggested that an additional stable point existed, consisting of a woody thicket with little or no grass. The model has been developed and further refined (Schwinning and Parsons 1999).

Tree-grass mixtures have been described as inherently unstable, and in the absence of fire, savannas increase in woodiness until tree growth is limited by competition by other trees (Scholes and Walker 1993). In addition, savanna dynamics may be driven by factors outside the tree-grass system e.g. climate and fire frequency (Scholes and Archer 1997). Spatial aspects of seed dispersal and competition may be crucial for coexistence of trees and grasses in the long-term (Jeltsch *et al.* 1996). Thus, the coexistence of grasses and trees is the result of many stresses and disturbances that interact across space and time.

To overcome the shortcomings of previous hypotheses concerning grass-tree coexistence, Jeltsch *et al.* (2000) proposed the concept of ecological buffering. They examined those factors that prevent the transition from savanna to grassland and from savanna to forest, and discuss fire, browsing and the existence of microsites favouring tree establishment as being of major importance. Thus "savannas do not exist for positive reasons, but for negative reasons: they exist because buffering mechanisms prevent their non-existence" (Jeltsch *et al.* 2000 p. 167).

Below-ground processes have received little attention, especially experimentally. Studies of these processes are necessary to gain a better understanding of tree-grass competition (Wilson 1998).

Environmental influences on tree-grass balance

The ecosystems of Queensland range from dense rainforest to treeless grassland. Well-developed rainforest occurs within the limited area of coastal Queensland where rainfall is regular and abundant. Treeless environments such as the mitchell (*Astrebla* spp.) grasslands of the arid western parts of the State are at the other end of the spectrum. Although these areas are relatively free of trees at present, there is some dynamism where mitchell grassland adjoins gidgee (*Acacia cambagei*) shrubland (Blake 1938). Also, large areas of mitchell grasslands are being converted to shrubland following the expansion of the exotic weed prickly acacia (*Acacia nilotica*) (Mackey 1998). Most of semi-arid Queensland is neither dense scrub nor grassland and is dominated by woodlands and open-forests of two overwhelmingly important plant genera, *Eucalyptus* and *Acacia*.

Within the major bioregions of Queensland, grass production is influenced by rainfall, soil fertility and tree basal area. All three aspects should be considered when determining the grass production in 'undisturbed' forests/woodlands/shrublands. For example, tree basal areas are similar in the Mulga bioregion and Cape York, yet in the Mulga bioregion soil fertility and rainfall are low, and grass production is therefore low. By contrast, Cape York has high rainfall and low fertility, giving rise to moderate to high grass production in intact woodlands (Table 1). Any response to removal of woody vegetation will depend on soil fertility and rainfall as well as the tree basal area present.

The tree basal area of eucalypt communities varies with latitude and rainfall. In general, the higher the rainfall, the greater is the potential tree basal area or biomass (Walker and Noy-Meir 1982). However, rainfall distribution within and between years is also important. In south-west Queensland, droughts can be very severe with adverse impacts on woody vegetation. In the Charters Towers area, tree basal area declined by 26% because of an intense drought in north Queensland during the early 1990s (Fensham and Holman 1999). This drought was unprecedented in the available rainfall record suggesting that its occurrence may be expected only once every century or two. A major portion of the dynamism observed for the semi-arid savannas in Queensland may be related to these rare events suggesting long-term cycles of thickening and dieback. In areas with more even rainfall distribution throughout the year and fewer droughts, woody vegetation is more favoured, for example, rainforest areas. In areas with a monsoonal climate (e.g. inland parts of Cape York), the long dry period from May to October appears to limit the number of mature trees that can survive this annual dry period and tree basal area is low. This contrasts with moderate to high tree basal area in southern Queensland where rainfall is more evenly distributed through the year but has a similar total annual rainfall.

Prolonged wet period can also alter tree dynamics as well. Mass establishment of cypress pine (*Callitris glaucophylla*) seedlings can occur during periods of good rainfall (Wells 1974). A similar response has been observed within silverleaf ironbark (*Eucalyptus melanophloia*) woodlands in eastern parts of Desert Uplands, probably during the extended wet period during the 1950s (W.H. Burrows, pers. comm., author's observations).

Soil type/texture also influences tree-grass balance (Walker and Noy-Meir 1982) with perhaps the best example in Queensland being the mulga (*Acacia aneura*) woodlands and mitchell grasslands (more or less treeless) in the south-west of the State. The mitchell grasslands occur on deep cracking clay soils while, in the same locality, mulga woodlands occur on deep red earth soils. Tree basal area is low on cracking clay soils, regardless of rainfall (Williams *et al.* 1996). The tendency for more woody vegetation to occur on sandy soils is due to a higher proportion of rainfall moving to deeper soil layers where only the woody vegetation has access (Walker 1993). This was demonstrated in South Africa where a site with a higher proportion of soil moisture held below 30 cm (akin to the mulga site) had a greater woody biomass than a site with a more even distribution of water holding capacity down the profile (Knoop and Walker 1985).

Table 1. The landscape-level effect of trees at natural tree densities on herbaceous production (compared with areas without trees) within major bioregions of Queensland.

Bioregion	Key genera	Tree basal area[1] (m²/ha)	Soil fertility[2]	Rainfall	Grass production in 'intact' forests and woodlands[3]
Cape York	*Eucalyptus*	4-6	low	high	moderate to high
Einasleigh Uplands	*Eucalyptus*	4-6	low to moderate	moderate	moderate
North west Highlands	*Eucalyptus*	1-3	low to moderate	low	low
Gulf Plains	*Melaleuca*	4-8	low	moderate to high	low to moderate
	various	<1	moderate		high
Wet tropics	mixed	>30	moderate to high	high	low
Central Queensland coast	*Eucalyptus*	10-20	moderate	moderate to high	moderate
Brigalow	*Eucalyptus*	7-15	moderate	moderate	moderate
	Acacia	20-30	high	moderate	low
Desert Uplands	*Eucalyptus*	5-10	low to moderate	low-moderate	low to moderate
Mulga	*Acacia*	4-12	low	low	low
Mitchell	Various	<1	high	low	moderate
Channel country	Various	<1	moderate	low	low
South East Queensland	*Eucalyptus*/various	12-30	moderate	moderate to high	low to moderate
New England Tableland[4]	*Eucalyptus*	10-25	moderate	moderate	low to moderate

[1] Collated from: individual trials in Table 3, unpublished data from State Forests, a map produced by J.O. Carter from NOAA imagery and from personal observations of the author.
[2] Fertility refers to nutrient availability. Collated from various Land Resource surveys carried out by CSIRO and Queensland Department of Primary Industries.
[3] Collated from: Johnson (1964); Mott *et al.* (1985); Burrows *et al.* (1988); trials reported in Table 3; and author's personal observations and unpublished data.
[4] A small area of this bioregion occurs in southern Queensland

Grass composition is influenced by climate and soils (see Table 2 in Johnson and Tothill 1985). Aristideae and Eragrostideae dominate on sandy soils in lower rainfall areas (<750 mm annual rainfall); as rainfall and soil texture increase, there is a zone where Andropogoneae are codominant with Aristideae, Eragrostideae and Chlorideae; above 700 mm annual rainfall, Andropogoneae dominate on all soil types; and Oryzeae are the dominant grasses on clay soils receiving high rainfall (>1100 mm annual rainfall).

Climate influences tree-grass balance and, in turn, the degree of woody vegetation cover within a region can influence climate. The amount of woody vegetation may influence local rainfall in the short- and long-term through increased albedo and increased temperatures (e.g. Balling 1988 in Mexico, Hogg and Price 2000 in Canada). Some modelling studies have suggested that rainfall may decline by 10% due to the conversion of savanna to grassland in Africa, South America and Australia (Hoffman and Jackson 2000). The total amount of clearing and the location of clearing influence the magnitude of the effect on rainfall. For example, modelling by Clark *et al.* (2001) suggested that clearing reduced rainfall by 2 to 33% depending on location and extent of that simulated clearing in West Africa. Studies in Western Australia have shown that rainfall is higher in areas of natural forest cover than in areas with bare soils (Li and Komiyama 2000).

Management influences on tree-grass balance

Fire

It is widely believed that fire plays an important role in determining the structure of *Eucalyptus* and *Acacia* woodlands (Hodgkinson *et al.* 1984; Anderson *et al.* 1988). Simulations studies show that frequent fires (at least once in 6 years) resulted in a tree basal area of less than 1 m^2/ha whereas unburnt areas had a tree basal area in excess of 4 m^2/ha (Moore *et al.* 1997, Howden *et al.* 1999). This supports the contention of many graziers in the mulga lands that current tree densities are much higher than they were when the area was originally settled for grazing, and that the primary cause of this was the elimination of fire from these areas. Similar work and conclusions apply to eucalypt savannas of northern Australia (Ludwig *et al.* 1999). It has been widely assumed that thickening in eucalypt woodlands has also resulted from an absence of fire (Ryan *et al.* 1995, Burrows *et al.* 1998) although this is complicated by the historical changes in grazing regimes. There is some experimental evidence of this connection from long-term fire exclusion experiments in the monsoon tropics. Although some data on individual size classes have been published (Bowman *et al.* 1988, Fensham 1990, Lonsdale and Braithwaite 1991, Bowman and Panton 1995), the only study that has utilised the data from the time of the commencement of fire exclusion is in the process of being published (J. Russell-Smith, pers. comm.).

Other examples of where the absence of fire appears to be associated with increased woody vegetation include the expansion of gidgee into adjacent mitchell grass downs (Blake 1938, Jones *et al.* 1992, Reynolds and Carter 1993) and the increase of rainforest into areas of wet sclerophyll forest (Stanton 1991).

Grazing

In Queensland, the role of fire is nearly always complicated by the impact of grazing. Heavily grazed areas are infrequently burnt due to lack of adequate fuel and can become dominated by woody vegetation. This woody cover then prevents accumulation of sufficient fuel to carry a fire (Dyer and Mott 1999) even in the absence of heavy grazing. It is only in periods of exceptionally high rainfall that sufficient grass growth would occur for a fire to carry within such areas (Harrington *et al.* 1984).

Grazing alone can alter the tree-grass balance. For example, Scanlan *et al.* (1996a) demonstrated that eucalypt seedling densities could be reduced under heavy grazing in north Queensland. In the past, rabbits have been significant grazers (Scanlan and Berman 1999) and are suspected of influencing woody vegetation dynamics by grazing shrub seedlings. The large reduction in rabbit numbers as a result of myxomatosis during the 1950s was suspected of enhancing shrub establishment (Williams *et al.* 1995) and similar observations were made after the release of rabbit haemorrhagic disease (Sandell and Start 1999).

Clearing

Clearing has a direct and immediate impact on woody plant cover. However, there are also indirect effects of clearing on woody vegetation. Tree dieback in southern Queensland and northern New South Wales in remnant areas is associated with excessive clearing in adjacent areas (Landsberg and Wylie 1988, Voller and Eddie 1995). This problem is pronounced where a large proportion of the original woody vegetation has been cleared.

Regrowth occurs to some degree after all tree clearing operations. The amount of regrowth depends on the method of clearing, the conditions at the time of clearing and management after clearing. When chaining is used to clear woody vegetation composed of species which resprout (e.g. most eucalypts, brigalow) extensive regrowth occurs (Scanlan 1988). Chaining vegetation when soil moisture is high often results in greater reduction in woody plant density as a higher proportion of trees/shrubs are removed from the soil rather than broken-off as occurs under dry soil conditions. The use of a soil applied herbicide like tebuthiuron gives a substantial reduction in tree density in eucalypt communities (Burrows *et al.* 1999).

Post-clearing management has a major effect on the density of remaining woody biomass and its regrowth. Ploughing with blade ploughs results in little regrowth (Scanlan and Anderson 1981) while less severe mechanical treatment (e.g. stickraking) is not as effective in limiting regrowth (Scanlan 1988). Where burning is used, such treatment requires removal of stock and the control of unwanted fire to allow a build-up of heavy fuel loads (Anderson *et al.* 1988). Even in these circumstances, burning tends to reduce biomass of woody plants rather than reducing their number. Landholders need to factor into the economics of their clearing operation the probability of an ongoing cycle of clearing highly competitive regrowth.

Production benefits are generally greatest when all trees are removed (Burrows *et al.* 1988). Where some clearing is appropriate, it is generally better to remove all trees from some areas and retain all trees in discrete retention areas. While landscapes that have been cleared to an open savanna (i.e. scattered, isolated trees) are aesthetically pleasing, their value for grass production is less than for a pattern where the same number of trees were left in an undisturbed area and the remainder cleared (Table 6.3 in Burrows *et al.* 1988). In addition, the remaining trees produce seed and subsequent regrowth, and the cost of maintaining the savannas appearance is much higher than the maintenance of large areas essentially free of woody plants.

Herbaceous effects on woody plants

Within woodlands, the growth of mature trees is not greatly influenced by perennial grasses but grasses do have an indirect effect by providing fuel to carry a fire (Hodgkinson *et al.* 1984). Undisturbed grass can reduce the survival of shrub seedlings in semi-arid woodlands (Harrington *et al.* 1984) especially in dry years. Some overseas studies do suggest grasses may reduce growth (Knoop and Walker 1985) seed production (McPherson and Wright 1987) and seedling establishment (Van Auken 2000). However, this is not a universal pattern as the presence of perennial grasses did not effect survival of mesquite (*Prosopis glandulosa*) in Texas rangeland, nor did the lower than normal rainfall conditions (Brown and Archer 1999). Pot studies of introduced woody weeds in Queensland have also shown that competition from perennial grasses had no effect on emergence and survival (Brown *et al.* 1998).

Tree-canopy scale effects on grass

Individual trees can have a variety of impacts on grass growth beneath their canopy and beyond (Belsky *et al.* 1989, Belsky *et al.* 1993). An individual tree may enhance the growth of understorey species due to ameliorated microclimate (Dupont 1998), improved soil physical and chemical properties (Ebersohn and Lucas 1965, Tiedemann and Klemmedson 1973a, Dowling *et al.* 1986, Jackson and Ash 2001), and higher infiltration rates of the soil (Dunkerley 2000). However, the tree also competes with the understorey for light, rainfall, soil water and nutrients. What is observed around an individual tree is the net result of these counteracting effects. The available data for Queensland are shown in Table 2.

Trees generate islands of increased fertility beneath their canopy (Tiedemann and Klemmedson 1973b, Scholes and Archer 1997, Jackson and Ash 2001) with the degree of soil change related to the period that trees have occupied the site (Archer *et al.* 2001). There are various mechanisms proposed for the creation of fertile islands beneath tree canopies, especially in arid areas (Garner and Steinberger 1989) and these can be divided into physical or biological mechanisms. In drier areas, biological mechanisms predominate.

Tree species that are known to, or suspected of, fixing nitrogen (*Acacia, Prosopis, Ziziphus*) are commonly reported as increasing grass growth beneath their canopies (e.g. Scifres *et al.* 1982, Lowry 1989, Belsky *et al.* 1993) whereas non-leguminous trees and shrubs normally decrease grass production within their projected tree canopies and beyond (House and Hall 2001). Where soil fertility is high, individual trees will have much less effect on soil nutrient levels than where soil fertility is low. Trees with low, dense canopies produce much more shade than ones with high or sparse canopies (e.g. Belsky *et al.* 1993) and, in some cases, shade tends to increase grass growth (Wilson *et al.* 1990). Trees with shallow root systems, or trees in shallow soils will compete with grass for water and nutrients more intensively than ones with a deeper root system (Knoop and Walker 1985 for a field study; Scanlan and McKeon 1993 for a simulation study).

Where trees are planted into cleared areas, there is often no effect of these trees or even a slight improvement in grass biomass (Cameron *et al.* 1989). At least part of this is associated with soil disturbance and/or fertilisation of the young trees. When these trees increase in size (i.e. are no longer seedlings) the competition they exert on grass increases (Cameron 1990).

Trees influence the nutrient content and digestibility of understorey plants. Reductions in soil and air temperature through shading increased growth and nitrogen uptake of rundown green panic pasture on brigalow clay soils (Wilson *et al.* 1986). Digestibility increases when temperature decreases (Minson 1990) as occurs in shaded areas (Dupont 1998). Shade also increases nitrogen content of grass in some situations (Wilson and Wild 1991). Both of these factors will tend to improve livestock production per head.

Grass species that require higher fertility are also more common beneath canopies than in adjacent areas. In central Queensland, green panic (*Panicum maximum*) is often seen growing beneath canopies of chinee apple (*Ziziphus mauritiana*) and less often beneath poplar box (*Eucalyptus populnea*) but not in adjacent areas (author's observations). In central western Queensland, Christie (1975) reported buffel grass (*Cenchrus ciliaris*) growing beneath poplar box canopies. He noted that the canopies of poplar box covered only 6% of an area, but that this area produced about one quarter of the total pasture growth. Thus, sub-canopy patches may be very important in terms of livestock carrying capacity.

In an attempt to synthesise the evidence on tree-grass interactions around isolated trees, Mordelat and Menaut (1995) proposed that the stimulation of grass beneath tree canopies was greatest in arid and semi-arid areas (see Fig. 1). This would seem to be supported by the work of Garner and Steinberger (1989). When the limited data from Queensland are plotted on the same

Table 2. Data and observations on tree-grass interactions at the individual tree scale in Queensland.

Bioregion	Tree Species	Relationship between grass production and trees	Experimental units	Native or exotic herbaceous species	Source
Brigalow	Ziziphus mauritiana (exotic)	Increase under canopy	Individual trees	exotic	JC Scanlan personal observations
	Eucalyptus crebra	Decrease under canopy	Individual trees in woodland	native	Scanlan (1992)
Einasleigh uplands	Albizia lebbeck (exotic)	Increase under canopy	Individual trees	exotic	Lowry (1989) Lowry et al. (1988)
	Eucalyptus spp.	Reduction under individual trees	Natural areas	native	Jackson and Ash (1998) Jackson and Ash (2001)
South East Queensland	Eucalyptus grandis	Increase under canopy	Planted trees with fertiliser	exotic	Wilson et al. (1990) Wilson et al. (1986)
	Eucalyptus grandis	Increase under canopy	Planted trees	exotic	Wild et al. (1993)
New England	Eucalyptus spp.	Change in composition under canopy	Natural areas	native	Chilcott et al. (1997) Chilcott (2000)
Mulga lands	Acacia aneura	Increase under canopy if ungrazed	Individual trees	native	Page et al. (2000)
Desert uplands	Eucalyptus populnea	Increase under canopy	Individual trees	exotic	Christie (1975)
Mt Isa Highlands	Eucalyptus spp.	Increase under canopy	Individual trees	exotic	T.J. Hall unpublished data

graph, there is an even greater spread of data, with the only area of the graph not occupied being high percentage increases at high rainfall. Given the wide variety of factors that can influence grass and tree growth separately, it is unlikely that one factor alone (mean annual rainfall in this case) will account for a large percentage of the observed variation in tree-grass productivity interactions.
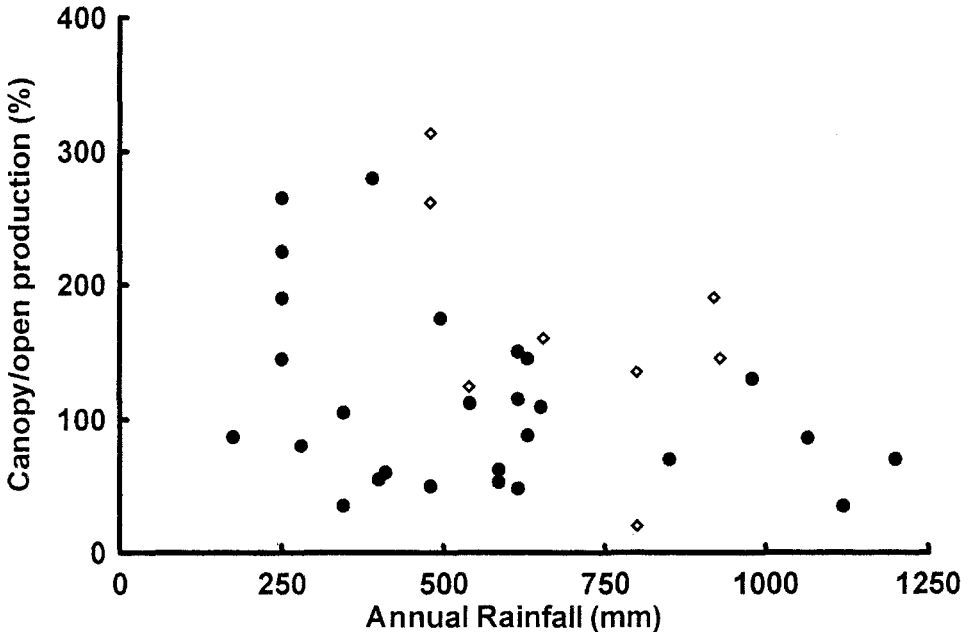
Fig. 1. Relationship between above-ground grass production (expressed as a percentage of the production in open areas) and annual rainfall. (● data reported in Mordelat and Menaut 1995; ◊ data from Queensland presented in Table 2).

Patch-scale effect of trees on grass

Studies have been conducted examining the effects of woody vegetation on grass production in six bioregions within Queensland (Tables 3 and 4). These studies included native and exotic species, and thinned versus natural tree stands. These studies generally reported results over a 5-10 year period and pasture standing crop or pasture production was the main aspect measured. In some studies, soil water partitioning (run-off, evaporation, transpiration by grasses, transpiration by trees, deep drainage) was also studied. Detailed field experiments have been conducted in the Charleville area (Beale 1973), Dirranbandi (Walker *et al.* 1972), Mundubbera (Tothill 1983), Kingaroy (Walker *et al.* 1986), Dingo (Burrows *et al.* 1999), Duaringa (Scanlan and Burrows 1990) and Charters Towers districts (McIvor and Gardener 1995). The majority of experimental studies involved little if any soil disturbance and only one had burning to remove pulled timber as one of its treatments.

The common feature from those studies that examined grass production in a range of tree basal areas is that grass production decreased as tree basal area increased, with an exponential decrease being reported in the majority of studies (Table 3). An analysis of studies available in 1990 showed that the reduction in grass production was influenced by potential productivity at the site as well as the actual tree density (Scanlan and Burrows 1990). Trees had less impact on grass production in sites with high potential productivity than in sites with low potential productivity. Thus, the tree basal area that results in 50% less grass production (compared with adjacent open areas) increases as site productivity increases. For example, if grass production in

Table 3. Influence of increasing tree density/basal area on grass production at the patch-scale in Queensland.

Bioregion	Tree Species	Relationship between grass production and trees[1]	Sampling units	Native or exotic herbaceous species	Source
Brigalow	Eucalyptus populnea	Exponential decrease	Thinned plots	native	Walker et al. (1972)
	Callitris glaucophylla	Exponential decrease	Thinned plots	native	Wells (1974)
	Eucalyptus populnea	Exponential decrease	Thinned plots	native	Harrington and Johns (1990)
	Acacia harpophylla	Exponential decrease	Observed densities	exotic	Scanlan (1991)
	Eucalyptus melanophloia	Exponential decrease	Observed densities	native	Scanlan and Burrows (1990)
	Eremophila mitchellii	Exponential decrease	Thinned plots	exotic	Scanlan (1991)
	Eucalyptus crebra	Linear decrease	Thinned plots	native	Walker et al. (1986)
	Eucalyptus crebra	Exponential decrease	Observed densities	native	Scanlan and Burrows (1990)
	Eucalyptus crebra	Exponential decrease	Thinned plots	native	Scanlan (1984); Scanlan (1992)
	Eucalyptus populnea	Exponential decrease	Observed densities	native	Scanlan and Burrows (1990)
Mulga lands	Acacia aneura	Exponential decrease	Thinned plots	native	Beale (1973)
	Acacia aneura	Exponential decrease	Thinned plots	native	Pressland (1975)
	Eremophila gilesii	Exponential decrease	Observed plots	native	Burrows et al. (1990)
	Dodonaea viscosa	Exponential decrease	Thinned plots	native	Noble (1997)
	Cassia nemophila	Exponential decrease	Thinned plots	native	Noble (1997)
Mitchell grasslands	Acacia nilotica (exotic)	Exponential decrease	thinned plots	native	Burrows et al. (1990)
	Acacia cambagei	Exponential decrease	Natural stands	native	Jones et al. (1992)
	Acacia cambagei	Exponential decrease	Regrowth after clearing	exotic	Jones et al. (1992)
South East Queensland	Eucalyptus grandis	No effect or slight increase at low densities; decrease at moderate to high densities	Planted plots fertilised	exotic	Cameron et al. (1989)

[1] Exponential decrease – when grass production is plotted against tree basal area, the relationship is a concave downward curve – see bottom line in Fig. 2.

open areas is 1000 kg/ha, then grass production in an adjacent woodland area with a tree basal area of 2.3 m^2/ha would be half of that; if grass production in open areas was 3000 kg/ha, then grass production would reach 50% of that in an area with a tree basal area of 13 m^2/ha (calculated from Fig. 4 in Scanlan and Burrows 1990).

For those studies that examined the grass production in cleared and uncleared plots (Table 4), grass production in open areas was 2 to 4 times than of the production within intact woodlands.

From the studies in Tables 2, 3 and 4, from some simulation studies (Scanlan and McKeon 1993, Howden et al. 1999, Ludwig et al. 1999) and from some theoretical considerations, a number of principles can be derived. Table 5 shows how rainfall, soil characteristics, fire and livestock grazing influence the impact of trees on grass production. These factors can vary between patches in the same general locality and may give quite different responses. *The greatest increase in grass production following the removal of woody vegetation occurs: where the initial tree basal area is highest; where rainfall is well distributed throughout the year; on fertile soils with a low water holding capacity.*

An important question concerning clearing is the longevity of the pasture responses following clearing. Anecdotal evidence and observations of cleared/remnant boundaries suggest that grass production in cleared areas remains higher than within the original woodlands for many decades, provided the cleared areas remain free of woody vegetation. However, little is known about the magnitude of the pasture response and how that may change over time and how this may differ between regional ecosystems.

Initial productivity from sown pastures is high, but typically declines with time (Robbins et al. 1987, Burrows et al. 1994). A study of long-term changes in pasture productivity following clearing in brigalow lands (Graham et al. 1981) showed that the main factor responsible for pasture deterioration was reduced nitrogen availability under perennial grass pastures. There was no overall effect of clearing on soil nitrogen content and no trend between soil nitrogen changes and time since clearing. Immediately after clearing and burning, the level of available nutrients in cleared brigalow lands is very high (Lawrence et al. 1993). As these nutrients are immobilised in grass root systems and are lost from the area, productivity will decline to a new 'stable state' with nutrient availability that is similar to open areas (Frost and Edinger 1991). Even though the net mineralisation of soil nitrogen under pasture may be only two-thirds of that under brigalow woodlands (Myers and Robbins 1991) pasture production in the 'stable state' is still much higher than in the original brigalow forest. This stable state should be regarded as the standard against which to compare productivity, rather than the initial, transitory state of very high production.

There are no comprehensive studies on changes in pasture production with time since clearing in eucalypt communities. Many studies span 1 to 2 years (Walker et al. 1972, Tunstall et al. 1981, Scanlan 1984, Watson and Reid 2001 in northern New South Wales), some are longer-term (Walker et al. 1986, author's unpublished data) and few published data exist for studies greater than 10 years (McIvor 2001 is an important exception). Over these timeframes, clearing woody vegetation increased grass productivity.

Trees can influence understorey composition within Queensland savannas and woodlands (Johnson and Tothill 1985) with Panicoid grasses dominating the sparse understorey in rainforest and brigalow forests. In brigalow open-woodlands, Andropogonoid grasses are dominant. In central Queensland eucalypt communities, Scanlan and Burrows (1990) found that as tree basal area increased, Panicoid grasses and non-grasses made up a greater proportion of the understorey biomass and Andropogonoid and Eragrostoid grasses made up a lower proportion.

Table 4. Grass production following tree clearing at the patch-scale for bioregions present in Queensland.

Bioregion	Tree Species	Changes in grass production	Sampling units	Native or exotic herbaceous species	Source
Brigalow	Acacia harpophylla	3-5 fold increase	Cleared plots	Exotic	Fossett and Venamore (1993); Murphy et al. (1993)
	Eucalyptus crebra	2-3 fold increase	Cleared plots	Native	Murphy et al. (1993)
	Eucalyptus populnea	Increase	Cleared plots	Native	Burrows (1992)
	Eucalyptus populnea	2 fold increase	Cleared plots	Native	Bishop et al. (1993)
	Eucalyptus melanophloia	No change	Cleared plots	Native	R.G. Silcock pers. comm.
	Eucalyptus populnea	Increase (~2 fold)	Cleared plots	Native	R.G. Silcock pers. comm.
Einasleigh uplands	Eucalyptus drepanophylla	Increase	Cleared plots	native and exotic	McIvor and Gardener (1995)
	Eucalyptus erythrophloia	Increase	Cleared plots	native and exotic	McIvor and Gardener (1995)
	Eucalyptus crebra	~2 fold increase	Cleared plots	native and exotic	Gillard (1979)
Mulga lands	Acacia aneura	Increase – more on dunefields than on sandplain	Cleared plots	native	Page et al. (2000)
Mitchell grasslands	Acacia nilotica (exotic)	~10 fold increase	Cleared plots	native	Murphy et al. (1993)
South-east Queensland	Eucalyptus spp.	Increase	Cleared and fertilised plots	exotic	Cook and Grimes (1977)
	Eucalyptus maculata Casuarina cunninghamiana Albizia lebbeck (exotic)	No change/increase	Planted and fertilised plots	exotic	Dunn et al. (1994)
	Eucalyptus crebra	Increase	Cleared and fertilised plots	native and exotic	Cook and Ratliff (1992)
New England Tableland[1]	Eucalyptus spp.	Increase	Cleared plots	native	Chilcott et al. (1997); Chilcott (2000)

[1] Data are from NSW, but are included here as results are relevant to Queensland section of this bioregion.

Table 5. How various influences affect the herbaceous production (production in woodland/production in open areas) under a constant tree density/cover/basal area.

Influence of increased:	Effect on herbaceous production under a fixed tree density/cover/basal area (production in woodland/production in open areas)
Annual rainfall	Increase: The greater the total rainfall, the shorter will be the period when tree-grass competition for soil moisture occurs
Soil depth	Increase: Deeper soils have a higher soil water holding capacity, so more water is potentially available to both trees and grasses
Soil fertility	Variable: Interacts strongly with rainfall. If rainfall is low, trees will have major effect, irrespective of fertility; if rainfall is moderate, then increasing fertility leads to decreased relative effect of trees; if rainfall and nutrients are high, trees will be dominant and increased fertility will have little effect; if rainfall is high and nutrients are low, trees have little effect. The response of areas located beneath tree canopies before clearing may differ from the response of interspaces.
Soil texture	Increase: Soils with a heavier texture potentially store more water for a given depth; this effect is similar to increasing soil depth and/or annual rainfall.
Fire	Regular fires decrease woody regrowth, which gives higher grass production for pastures in good condition. Very frequent fires may result in increased overall stocking pressure that can tend to reduce grass production. Fire can accentuate patch-grazing effects if burns are 'incomplete'.
Grazing	More stock gives less cover gives more runoff gives less grass production. Grazing can lead to a shallower grass root system, which can lead to lower grass production (and greater water availability to trees).

Landscape-scale effects of trees on pastures

Landscapes[2] are mosaics of different soils and vegetation, often with a superimposed pattern of clearing. The potential pasture production within these patches may vary widely due to differences in soil fertility, soil water availability, temperature (e.g. frost) and tree density or basal area. Some overall impacts of these factors at a regional level are shown in Table 1.

Landscape structure (the spatial relationship among distinctive landscape units or elements) can influence pasture production within patches through run-on/run-off processes. These processes can operate at scales from a few square metres to thousands of hectares (Ludwig *et al.* 1997). Some redistribution of water and nutrients between landscape units is natural and has partly shaped current soil and vegetation patterns. However, tree clearing modifies these patterns of redistribution and therefore the productivity of these landscape elements may depend in part on landscape structure.

As well as considering productivity of landscape units, it is necessary to consider use of the landscape by native and introduced animals, as landscape structure will influence patterns of use. *Landscape complementation* describes the efficient and safe use of forage and shelter resources when complementary patches are close (Dunning *et al.* 1992). An example of complementation occurs with feral goats. Feral goats may be influenced by topography and woody cover (Freudenberger and Barber 1999) with patches of high pasture production adjacent to residual outcrops being favoured (Thompson *et al.* 2002). The increase in eastern grey kangaroos is western Queensland would be another example of complementation (McAlpine *et al.* 1999). *Landscape supplementation* allows increases in animal populations if additional resources become available within some landscape elements. The provision of permanent stock watering points in area with little or no natural surface water would be an example.

Domestic livestock are also influenced by landscape structure. Cattle require shade for survival (Daly 1984) and sheep require shade to reduce lamb losses before and after birth (Roberts 1984). Within areas having little shade, overgrazing occurs close to shade patches, while other parts of the landscape are underutilised. This variation in grazing patterns will impact on vegetation dynamics and some soil processes, for example, high grazing pressure can kill perennial grasses, thereby reducing surface cover which increases run-off and soil loss (Silburn *et al.* 1992, McIvor *et al.* 1995, Scanlan *et al.* 1996b).

Landscape structure and the way in which land management (especially clearing) has modified these patterns has been the subject of a great deal of study by wildlife researchers (see Section 6.1.5 in Boulter *et al.* 2000). Suggestions have been made about the highest proportion of properties that should be cleared (70%) or used intensively (30%) (McIntyre *et al.* 2000) in an effort to ensure landscape function is maintained.

Exotic weeds are a major factor influencing vegetation dynamics within Queensland (Scanlan and McIvor 2002). They can substantially influence the functioning of landscapes and are regarded as a threatening process for the environment (Woinarski *et al.* 2000). A prime example is prickly acacia which is changing one of the major grassland areas of the world into a thorn shrubland (Mackey 1998) in a similar way that mesquite altered many western areas in United States of America (Archer 1994). An indication of the 'success' of exotic leguminous shrubs is that they make up 5 of the 20 Weeds of National Significance in Australia *(see www.weeds.org.au).*

Introduced woody weeds could be seen as 'just another tree' and therefore not relevant as a special case in relation to tree-grass dynamics in Queensland. However, their impact does differ

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[2] I use *landscape* to refer to the scale between the patch (which may represent 10-1000 ha) and the bioregion (with 13 bioregions to cover the 173 million ha within Queensland).

from native species. The major difference is that native species rarely spread outside their original range whereas introduced weeds can occupy large areas. In both cases, grass production is severely affected by high woody plant density, reducing the grazing capacity of both native and introduced herbivores. However, introduced weed species support a different suite of insects, which could in turn influence vegetation dynamics (e.g. through alteration of pollination and related processes) and other fauna (e.g. insectivorous birds) (McFadyen 2002).

Exotic weeds often exhibit differential invasion of landscape elements. For example, rubber vine (*Cryptostegia grandiflora*) becomes most abundant along watercourses, excluding herbaceous vegetation and even causing the death of large trees (Tomley 1998). These landscape elements are generally the most productive for vegetation, wildlife and domestic stock, and the invasion by weeds has a greater impact on landscape productivity than would be expected from a consideration of the proportion of the landscape affected.

Modelling of pasture production in tree-grass systems

The search for simple rules to describe tree-grass interactions seems doomed for failure because of the range of factors influencing pasture growth and the complex interactions between these factors. A more rewarding approach is to seek an understanding of the principles behind tree-grass interactions and to apply those principles to each different situation. The use of models can help account for many interacting factors and their use in studying tree-grass interactions should increase. One example has been the workshops conducted at National Centre for Ecological Analysis and Synthesis, University of California, Santa Barbara (Parton *et al.* 1999). Participants at these workshops used a variety of models to examine the effect of trees on grass production and the total productivity within tree-grass systems. The following section describes the use of models to explain the shape of the relationship between grass production and the amount of trees, the total aboveground production in mulga woodland and the impact of spatial distribution of trees on grass production.

Relating herbaceous production to tree quantity within patches

When considering the relationship between tree basal area and grass productivity, there is considerable discussion of the shape of the relationship between a measure of the quantity of trees and understorey production (e.g. McPherson 1992). Reported relationships between tree basal area and herbaceous productivity are shown in Fig. 2 and vary from:
- linear decline in pasture production from a maximum at zero tree basal area; to
- concave decrease in pasture production from a maximum at zero tree basal area; to
- initial stimulation of pasture production at low tree basal area, followed by a decrease (relative to production in open areas).

There are several measures of the quantity of trees. Basal area, canopy cover and density (numbers per hectare) have all been used as measures. Tree basal area is a good integrator of numbers and size in water-limited systems as there is a reasonably close relationship between tree basal area and leaf biomass and therefore potential tree transpiration and competitive potential for water (e.g. Kline *et al.* 1976, Calder *et al.* 1992). However, it does not work well when comparing very different plant sizes. For a given tree basal area, a large number of small trees (e.g. regrowth) will have a greater leaf biomass than for a smaller number of larger trees with the same tree basal area. Thus the competitive effect of the smaller trees or regrowth will be greater due to the greater potential for tree transpiration (a brief discussion of some of these matters is given in Scanlan 1991).

For the following discussion, tree density is used as a measure of increasing tree 'amount' for simplicity. In most cases, tree basal area could also be used, but this makes the explanation more cumbersome.

Linear

If individual trees can be regarded as discrete entities that do not interact, and have a constant effect on understorey vegetation, then the canopied areas can be treated as one zone and the open areas as another zone. Thus, as more and more trees are added to an area, the effect of each tree on herbaceous vegetation will be constant, irrespective of tree density - a linear relationship (Fig. 2). This would approximate the situation in landscapes where tree densities are comparatively low, where tree root systems do not extend beyond the canopy zone and where the effect of trees on understorey vegetation is marked. The first limit of this relationship would be that density at which trees started to interact with each other. The relationship will continue to be linear as tree basal area increases only if the herbaceous production in areas of overlap is reduced/increased by the same absolute amount. This relationship has been reported in narrowleaf ironbark (*Eucalyptus crebra*) in central Queensland (Walker *et al.* 1986).
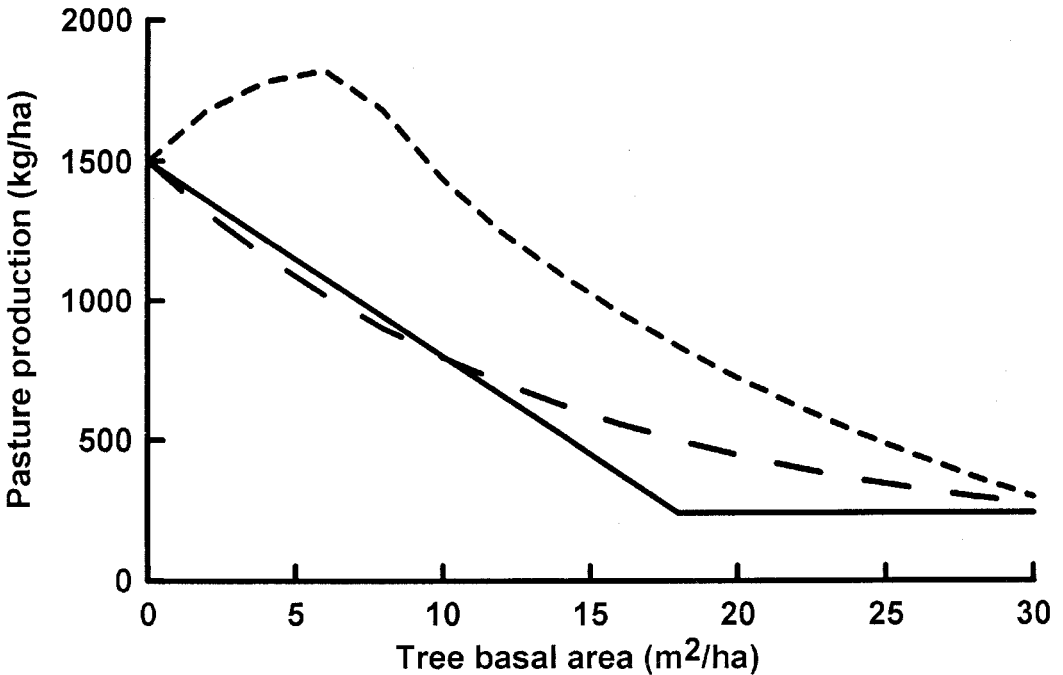
Fig. 2. The herbaceous production (relative to that in open areas) in simulated tree communities with initial stimulatory effect (- - - -), exponential decrease effect (− − −), and a linear decrease effect (———). Note that at high tree basal areas, herbaceous production is reduced even where individual isolated trees stimulate production under and near its canopy - top line).

If tree aggregation is very high, then trees are present as clumps. As more and more trees are added to a landscape, either the size of clumps increases, or more clumps are present (assuming a constant tree density within clumps). Provided these clumps do not substantially influence the herbaceous vegetation outside their combined canopy zone, then the effect of adding more trees will be a more-or-less linear change in herbaceous production. This clumping of trees is commonly observed in undisturbed savanna lands (e.g. North America - Archer *et al.* 1988; South America - Fuentes *et al.* 1984; Philippines - Tupas and Sajise 1977) and in 'derived savannas' in Queensland (Ludwig *et al.* 2000).

Exponential decrease

The most commonly reported relationship between grass production and tree density in Queensland is an exponential decrease (also referred to as concave downward). Where trees

interact, their influence at a particular location in a landscape can be considered as a multiplicative effect (Wu *et al.* 1985). As tree density increases past the range where trees are essentially independent elements in the landscape, the effect will depart from linearity. This concept is referred to as ecological field theory and was applied to eucalypt woodlands by Walker *et al.* (1989).

These relationships are considered in Scanlan (1992) where the impact of trees on understorey is separated into stimulatory and competitive effects. A basic assumption of that model is that at any point in the landscape, there are stimulatory and competitive influences from more than one tree. At a point that is within the zone of influence of n trees, the net effect at that point is $\text{effect}_{tree\ 1} * \text{effect}_{tree\ 2} * .. * \text{effect}_{tree\ n}$. When the net effect of stimulatory and competitive effects is to decrease grass productivity under an individual tree canopy, the patch-level response of grass production with increasing tree density is an exponential decrease (Fig. 2).

The absolute difference between the linear and the exponential decrease lines in Fig. 2 is small for most tree basal areas. Given the variability in field data, it may well be impossible to differentiate between which of these relationships best represents what is observed in the field. The narrower the range of tree densities considered, the smaller the absolute differences between the two lines. Most observations and experiments from Queensland display this relationship between grass production and tree density (Table 3).

Initial stimulation

If the overall effect of an individual tree is to increase grass production under its canopy, then the landscape-level response to increasing tree density will be increased production at low densities. At some intermediate density, the stimulation of grass production due to trees will reach some environmental limitation, for example, all available water is used at maximum efficiency. However, each additional tree uses at least some of the resources (water, light or nutrients) that would otherwise be available to the herbaceous layer. Thus, there is a net competitive effect due to the additional tree. As this continues, the landscape-level herbaceous production decreases at moderate to high tree densities (top line, Fig. 2), even though individual, isolated trees have a net stimulatory effect on production (e.g. Scifres *et al.* 1982).

Individual trees may have no net effect on herbaceous production under their canopies. This occurs when stimulatory and competitive effects are of equal strength. As the density of these trees increase initially, total production is not altered. At some low to moderate tree density, trees begin to interact and the total production will tend to decrease. The shape of the decrease is dependent on the distance from the tree that the effects are expressed and the strength of those effects. If the stimulatory and competitive effects are small and operate for a short distance from the tree, then the landscape effect will be negligible up to relatively high tree densities. Where the effects are small, but operate over a larger distance, then a sigmoid shape is observed. Where the effects are large and operate a large distance from each tree, then the landscape level response is the commonly observed exponential decrease. Scanlan (1992) provided field validation of these responses.

Total productivity of tree-grass system

In the previous section, I described the grass productivity in relation to the quantity of trees present. Also of interest from an ecological perspective are the productivity of the total tree-grass system and the relative contributions of trees and grasses.

The total system productivity of a mulga community was estimated using the model developed by Moore *et al.* (1997) and the field data provided by Beale (1973) as part of the workshops described in Parton *et al.* (1999). The field trial was a tree-thinning trial where an original density of approximately 3000 stems/ha was thinned to 40, 160 and 640 trees/ha. Grass standing

crop, tree size and tree litterfall were measured for a period of seven years after thinning, with data from the last four years used in this study. Aboveground production of grasses was estimated from the model using the field observations of standing dry matter for validation. Tree productivity was calculated from growth increments in tree size (using equations from Pressland 1975) and from foliage and litterfall figures from the trial described in Beale (1973). The total aboveground productivity was then obtained by adding the grass and tree productivity for the three tree densities averaged over the last four years of the field trial (Fig. 3).

The results show tree production increases with increasing tree density, as would be expected. The productivity of grasses decreased as tree density increased, again consistent with the field observations in many woodland systems. The total above ground production also increased as tree density increased. This suggests that trees are more efficient than grasses at converting resources into biomass. Few calculations of this type have been made for a tree-grass system in Queensland. This analysis of productivity has particular relevance to the greenhouse/climate change debate and has been examined in this context by Howden *et al.* (1999).
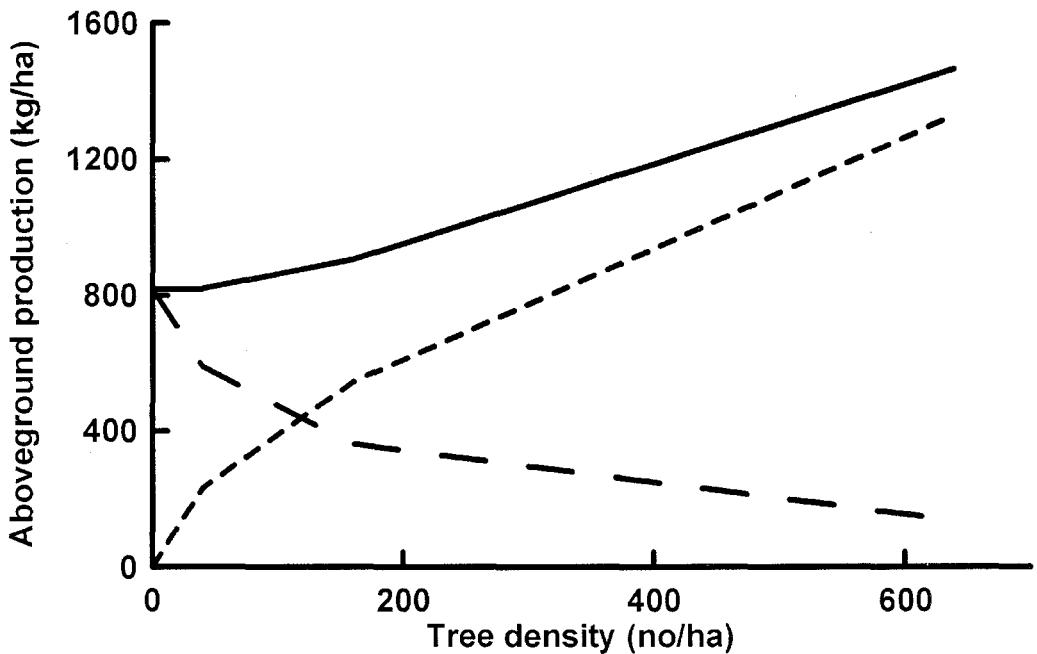
Fig. 3. Simulated aboveground grass (− − −), tree (- - - -) and total production (———) in a mulga woodland in south-western Queensland.

Spatial variability within a landscape

Mature trees tend to be randomly distributed within a landscape unit/patch, whereas seedlings and juveniles show some aggregation (e.g. Scanlan 1984 showed this for eucalypts in central Queensland). The distribution of mature trees will influence the grass production except where the relationship between grass production and tree density/basal area is linear.

This influence of tree distribution on grass production was examined by simulating the grass production in a number of theoretical landscapes within which the mean tree basal area was 8 m^2/ha. The landscapes were made up of a 100 patches, each with a specified tree basal area between 0 and 16 m^2/ha. A variability of zero indicated all patches were 8 m^2/ha; the maximum variability of 8 indicated an equal numbers of patches with 0, 1, 2 …16 m^2/ha (see Appendix 1 for methodology).

In stands with all patches having a tree basal area of 8 m^2/ha, grass production was 356 kg/ha/year. In the patchiest landscape simulated, grass production was 652 kg/ha/year, an increase of 83% over the uniformly distributed case (Fig. 4). The most extreme case would be if there were 50 patches devoid of trees with a production of 2000 kg/ha/year and 50 patches with a tree basal area of 16 m^2/ha producing 255 kg/ha/year, giving an overall mean of 1128 kg/ha/year. As stocking rates are based on grass productivity, there would be a very large difference in safe stocking rate due entirely to variability in tree basal area within a landscape. Failure to account for this variability would result in underestimation of stocking potential and this aspect should be factored into safe stocking rate estimation models like those of Scanlan *et al.* (1994) and Johnston *et al.* (1996). Other management activities may also be influenced, for example, fire is dependent upon fuel load and fuel continuity which both respond to tree density.
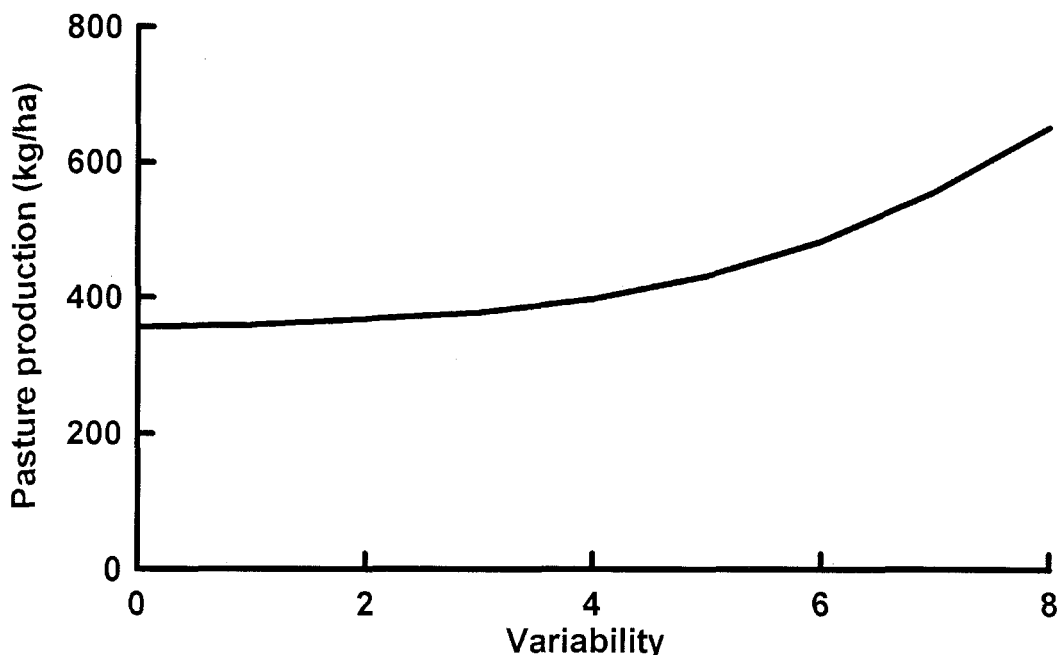
Fig. 4. Simulated pasture production within a patch of eucalypt woodland with a tree basal area of 8m^2/ha but with increasing spatial variability of those trees. (See Appendix 1 for description of variability).

Conclusions

At a regional scale, soils and climate determine what woody vegetation will grow within an area. The amount of woody vegetation, soil characteristics and climate then determine potential grass production.

Grass has little impact on mature woody vegetation. During the stage of woody seedling establishment, competition may have a detrimental effect on survival, and the ability of grasses to carry a fire can lead to death of woody plant seedlings. Some exotic woody weed seedlings do not appear to be adversely affected by grass competition.

The majority of evidence from Queensland indicates that clearing areas of non-leguminous trees gives rise to increased grass production at the canopy and patch/paddock scales. On a regional basis, the increase is least where soil fertility is low, tree density is low and rainfall is high and received during a confined 'wet-season'. The greatest relative increase in grass production

following the removal of woody vegetation occurs: when the initial tree basal area is highest; where rainfall is evenly distributed though the year and on fertile soils with a low water holding capacity.

The key factor that reduces tree density and cover is tree clearing. Landscape structure and its modification by clearing will affect vegetation, livestock and wildlife responses. Some situations exist where woody plant density is increasing, with both native and exotic species showing this increase.

Simulation modelling can play an important role in theoretical and practical considerations of tree-grass interactions. Such studies suggest that total aboveground production (grass plus tree) of mulga woodland increases with increasing tree density. All relationships observed between grass production and tree density at the patch scale (from linear decrease to exponential decrease to initial stimulation and decrease) can be derived by applying the principles of tree-grass interactions at the individual tree scale. The different relationships are due to different relative strengths of competitive and stimulatory effects of trees on grasses. Modelling also shows that patches of low tree density or open areas are very important in determining the pasture production at a property/landscape level. The importance of these is greater in landscapes where the mean tree density is higher.

Acknowledgements

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Appendix 1

Methodology for deriving variability (as per Fig. 4)

To simulate the effect of tree basal area variability on grass production, an area of 100 ha was considered to be made up of 100 sub-units, each of 1 ha. The tree basal area of each of the sub-units was generated as per Appendix Table 1, and the grass production was simulated for each of the sub-units. (The actual areas chosen do not influence the simulation as the main assumption is that within the sub-units, the tree basal area is uniform). The grass production for the patch is the mean production in all sub-units.

Appendix Table 1. Tree basal area of sub-units for which grass production was simulated (refer to Fig. 4).

Variability Level	Description
0	All sub-units 8 m^2/ha
1	33 sub-units with 7 m^2/ha, 34 units with 8 m^2/ha and 33 units with 9 m^2/ha
2	20 sub-units with 6 m^2/ha; 20 with 7 m^2/ha; 20 with 8 m^2/ha; 20 with 9 m^2/ha; 20 with 10 m^2/ha
3	Equal numbers of sub-units with 5, 6, 7, 8, 9, 10 and 11 m^2/ha
4	Equal numbers of sub-units with 4, 5, 6, 7, 8, 9, 10, 11 and 12 m^2/ha
5	Equal numbers of sub-units with 3, 4, 5, 6, 7, 8, 9, 10, 11, 12 and 13 m^2/ha
6	Equal numbers of sub-units with 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13 and 14 m^2/ha
7	Equal numbers of sub-units with 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14 and 15 m^2/ha
8	Equal numbers of sub-units with 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15 and 16 m^2/ha