



Convex Relationships in Ecosystems Containing Mixtures of Trees and Grass

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Abstract. The relationship between grass production and the quantity of trees in mixed tree-grass ecosystems (savannas) is convex for all or most of its range. In other words, the grass production declines more steeply per unit increase in tree quantity at low tree cover than at high tree cover. Since much of the economic value in savannas is ultimately derived from grass, and the main mechanism controlling the tree-grass balance is dependent on the production of grassy fuel for fires, this non-linearity has the effect of creating two savanna configurations. One has a low tree density and supports a viable grazing enterprise, while the other has dense tree cover and a frequently non-viable grazing enterprise. The non-linearity is suggested here to have two main sources: the geometry of the spatial interaction between tree root system and grasses, and the effect of differing phenology (the time course of leaf area exposure) on the acquisition of water and nutrients. The existence of the non-linearity reduces the resilience of the generally-preferred “open” configuration, and increases the resilience of the less-desirable “closed” configuration.

Key words: competition, primary productivity, resilience, savannas

1. Introduction

A large fraction of the Earth’s land surface is covered by ecosystems in which the plant production is generated from mixtures of trees and grasses. The most extensive case is the approximately one-eighth of the surface occupied by tropical savannas (Scholes and Hall 1996). Similar ecosystems occur outside the tropics as well, and in certain cultivated systems.

The key issue in the management of these systems for human benefit relates to the proportions of the mixture, since more tree means less grass. Where the principal benefits are based on the grass component, such as in grazing systems, the strategy seems obvious: maximise grass production. In the short term, maximum grass production is typically (but not always: see Figure 1) achieved at zero tree presence, but since removal of the trees is a significant and recurring expense, and may incur other environmental costs, the objective typically involves finding the level of tree presence that strikes a balance between loss of grass production and loss of other ecosystem services.

The quantity of woody plants in the system can be measured in a variety of ways: tree canopy cover percentage, tree biomass, leaf area, stand basal area or

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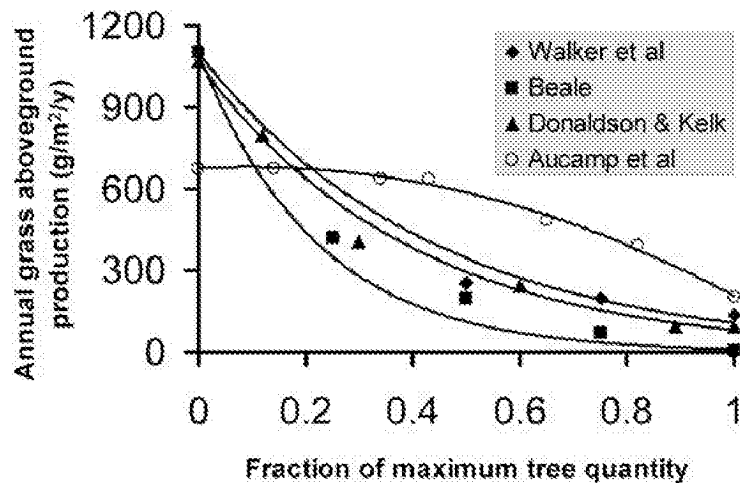


Figure 1. Empirical relationships between the quantity of trees in the system (measured in various ways, and here normalised so that the largest tree quantity reported in the study is equal to 1) and the aboveground grass production.

number of trees per unit area. The last-mentioned is not a good measure, since most systems have many small trees that have little functional impact on grasses. All the other “treeness” measures are highly correlated with one another and with impacts on grass production. Unless otherwise stated, this paper uses stand basal area (i.e., the sum of the cross-sectional area of the stems near the ground level, per unit ground area, m^2/ha) as the index of tree quantity, and it is here given the symbol X . Note that this is a measure of “stock”, whereas in general the grasses are measured in terms of production ($\text{g}/\text{m}^2/\text{y}$), which is a “flux”.

Grass tillers are short-lived (< 1 year), so the useful and grazable stock is more-or-less equal to the within-growing-season production. The use of this mixed terminology has the potential for causing confusion, particularly in graphical analysis where the state of the system is represented by the stocks of the two components. For the key analysis in this paper, the grass production flux is converted to a stock by accumulating it, less losses due to fire, herbivory and decay.

The trade-off curve between the stand basal area and the grass production is central to both the economic use of savannas and their ecological dynamics. In every recorded case it has a strongly non-linear form. The grass production declines as tree basal area increases. In almost all cases this relationship is convex over its entire range; i.e., the grass production declines more rapidly for the initial increments in tree basal area than it does for subsequent increments (Scholes and Archer 1997). In a small proportion of cases, there is little or no impact on grass production (or even a slight increase) for the first increments of tree basal area above zero, followed by a transition to an inverse convex relationship above a certain level of basal area per hectare (Figure 1).

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Savanna systems around the world have been observed to be unstable in terms of the proportions of the mixture, under certain forms of management. In particular, following the introduction of sustained heavy grazing by domestic stock, usually accompanied by reduction in the fire frequency and intensity, the quantity of trees tends to abruptly and apparently irreversibly increase, often to a point where the grass production is so suppressed that pastoralism becomes commercially unviable.

This paper addresses two questions:

- what is the mechanistic basis of the observed convexity in the grass production vs tree basal area curve?
- does the shape of this curve have anything to do with the abrupt transition between different configurations of tree-grass systems?

The analysis presented here is one way of conceptualising savannas. Like all ecosystems, savannas can be viewed through a variety of lenses, whose validity depends on the objectives of the study. The relatively simple and abstracted model presented here aims to explain the widely-observed non-linearity in grass production as a function of tree cover, and to explore its consequences for system dynamics. It does not address species composition dynamics within the grass or tree layers, nor the complexities of grazing behaviour.

2. The Convex Relationship between Tree Basal Area and Grass Production

In the semi-arid to dry subhumid climates that dominate the tropical savanna extent, aboveground grass production, in the absence of tree cover and accumulated over the period of the wet season (i.e., g DM/m²/y, where DM stands for dry matter), has repeatedly been shown to be a linear function of rainfall received during the growing period (equation 1; Rutherford 1980; Scholes 1993). This has been proposed as evidence that grass production in these systems is water-limited; I suggest that it shows that grass production is both water and nutrient limited (Scholes 1997). For instance, fertilisation of these grasslands with nitrogen leads to a relation that is still linear, but with a steeper slope. The simple interpretation is that water availability controls the *duration* of grass growth in these episodically-wetted soils, while nutrient availability determines the *rate of growth* when water is available. The slope of such a linear relationship between Rainfall (R) and aboveground grass production (P_g) is a reflection of the nutrient availability in the system. It is sometimes referred to as the “rain use efficiency” (le Houerou 1984). The intercept of the line, on the other hand, reflects the availability of soil water. For instance, more water is needed to commence production on a clayey soil than on a sandy soil because of the greater initial losses to evaporation and runoff on clayey soils. This is clearer when the equation is written in the form of a slope (a) and an x-axis intercept (c), rather than the more usual y-axis intercept:

$$P_g = a(R - c) \quad (1)$$

A compilation of data from a variety of savanna-climate grasslands provides the following empirical predictors of the slope and x-axis intercept, as functions of the

sand content of the soil (s , as a percentage). For soils between 64 and 92% sand content

$$a = -0.0376s + 3.442 \quad (2)$$

For soils above 92% sand content, a can be given the constant value of 0.1, and below 64%, the constant value of 1.1 g/m²/y/mm. The value of c is a function of the value of a , since they are both ultimately related to soil texture:

$$c = 328 - \frac{142}{a} \quad (3)$$

Measurement of tree radial increment growth (the growth revealed by tree rings, or by measuring the increasing circumference of the stem) shows that wood production is related to both rainfall and “site quality”, a factor that includes soil depth, landscape position and fertility. Primary production by trees is thus also related to water and possibly to nutrient availability, but in less direct ways than in grasses. This is because trees have a greater storage capacity for water, nutrients and carbohydrates than grasses do, and have a greater rooting volume and depth. Thus in many circumstances they are able to carry over a significant quantity of water, nutrients and carbohydrates between years, as well as conserving and recycling a substantial fraction of their nutrients internally at the time of leaf drop. Thus production by trees in a given year needs to consider rainfall not only in the current growing season, but in the previous one as well.

When trees and grasses grow together, several sometimes opposing interactive mechanisms are operative (Scholes and Archer 1997):

1. Competition for water and nutrients between the root systems of the trees and grass;
2. Reduction of the photosynthetically-active radiation and rainfall reaching the grass canopy, through prior interception by a tree canopy;
3. Improved growing conditions for the grasses immediately below the canopy of a tree due to local nutrient enrichment and improved soil water conservation;
4. A risk of scorching for the trees when the flammable dry grass burns.

Although trees and grasses may be occupying the same land area, their root systems are not necessarily occupying entirely the same volume. The grass cover is usually characterised as “continuous” whereas the tree cover is “discontinuous”. Thus, in purely geometrical terms, there may be areas where the grasses are relatively free of tree influence, simply because they are in the interstices of the tree rooting radii (Figure 2).

Since the root reach of savanna trees has been shown to be several multiples of the crown radius (Rutherford 1983; Groot and Soumare 1995), a patch of savanna can be considered to comprise three more-or-less spatially distinct sub-habitats:

1. *the area immediately below the tree crowns*, where the grasses are subject to shading and the interception of water by the crowns, and although exposed to root competition from the trees, generally benefit from the enhanced nutrient status under the crown and a lower evaporative demand;

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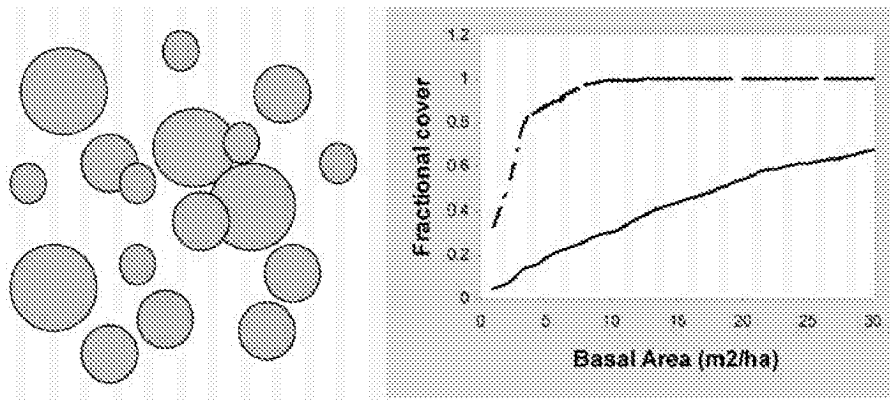


Figure 2. The fraction of the vegetation patch that is beneath tree canopies and between tree canopies can be calculated from knowledge of the tree canopy diameter distribution and the spatial dispersion pattern of trees in the landscape. For simple distributions of both an analytical solution is possible, but for complex distributions, an empirical fit to a numerical solution is more practical. The curves described here assume random spatial distribution, a crown diameter 10 times greater than the stem diameter, and a root diameter 2.5 times the crown diameter.

2. *the area within the reach of tree roots, but beyond the crown*, where shading is minor, but there is competition with trees for water and nutrients; and
3. *the area beyond both the crown and the reach of tree roots*. Grass production here should be the same as grass production in the complete absence of trees. This area is small in savannas with a high tree cover, but can be significant in sparsely-treed savannas.

The aboveground production by grasses (P_g) in a mixed tree-grass situation can therefore be expressed as

$$P_g = P_{g1}A_1 + P_{g2}A_2 + P_{g3}A_3 \quad (4)$$

where A_1 , A_2 and A_3 are the fractions of the patch occupied by the subcanopy, tree root zone and tree root-free subhabitats respectively, and P_{g1} , P_{g2} and P_{g3} are the grass productivities per unit area in each zone.

The area of each subhabitat can be calculated geometrically if the distributions of tree sizes are known as well as their spatial distribution. The tree size distribution in undisturbed, self-regenerating populations follows an “inverse J” distribution, i.e., an exponential decline in the numbers of individuals in each successive size class due to the effect of tree mortality. It may deviate substantially from this ideal form – for instance, many populations show episodic recruitment and mortality, giving multi-modal size distributions. The default assumption regarding spatial distribution is that the location of each tree is random (i.e., independent of every other tree). This assumption is approximated in some naturally-regenerating populations, but not all. Clumping (at several scales, and operating differently for different species in a mixture) is commonly observed, and so is “over-dispersion”

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(i.e., a tendency towards regularity, with its extreme form in the hexagonal spacing of an orchard). Since both the size and location distributions can be quite complex, this paper calculated a family of empirical predictors of A_1 and A_2 , based on the output of a numerical simulation fed with a range of feasible spatial and size-class assumptions. Thus, for a randomly distributed population of trees with an inverse J size distribution, and where the canopy radius is 10 times the radius of the stem (a typical value: Scholes et al. 2002),

$$A_1 = 1 - e^{-0.0379X} \quad (5)$$

Similarly, for trees where the effective root radius is 25 times the stem radius, the area of the subhabitat outside of the canopy but still within the tree root range is

$$A_2 = (1 - e^{-0.4784X}) - A_1 \quad (6)$$

Note that these equations suggest the root reach is about 2.5 times the canopy reach. Researchers who have excavated savanna tree root systems report higher numbers, around 6 times canopy radius (Rutherford 1983; Chin Ong 1996). When these higher values are used in the simulation, effectively no part of the savanna is free of competition with tree roots, which does not accord with field observations. The solution to this apparent contradiction is probably that the roots far from the tree cannot effectively colonise the entire soil volume of the circle described by their most distal reach. The density of roots declines approximately exponentially with distance from the stem (van Noordwijk 1996) Thus an “effective radius” can be described that is smaller than the maximum radius; about 2.5 times greater than crown radius seems to provide satisfactory results. Finally,

$$A_3 = 1 - (A_1 + A_2) \quad (7)$$

In the context of the focus of this paper on non-linearities, the important point is that regardless of the assumptions made about canopy and root dimensions and plant distributions, the fraction of area that grasses have for their exclusive use, and the unshaded area, both decline in a convex form with increasing stand basal area of trees. The degree of convexity increases with dispersed spatial distributions and decreases with clumped distributions.

The grass productivity in subhabitat 3 (where there is no tree root or crown influence) is given by the equation for grass production in the absence of trees (equation 1)

$$P_{g3} = a(R - c) \quad (8)$$

The grass productivity in subhabitat 2 (root competition but no crown influence) depends on the proportion of the available resources in the soil (water and nutrients) that is captured by trees, and is thus unavailable for grasses. The classical hypothesis in this regard is that grasses have preferential access to resources in the topsoil, while trees have preferential access in the subsoil (Walter 1971). Empirical

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evidence (e.g., Scholes and Walker 1993) indicates that the effective rooting-depth niche separation is minor by comparison to the niche separation in time, largely because water and nutrients are both mostly to be found in the topsoil, and thus trees and grass both have most of their roots there. The niche separation in time results from the fact that trees expand their leaf area more rapidly at the beginning of the growing season, and retain them for longer at the end of the growing season, than grasses do. Even though the tree relative growth rate may be slightly less than that of grasses, and in some cases the grass peak leaf area may exceed the tree leaf area in the middle of the growing season, the beginning-and-end of season windows of near-exclusive use provide a strong advantage to trees.

Assuming that the resource being competed for is water, the fractions of the shared water resource acquired by trees and grasses in a mixture can be predicted using the “electrical analog” model for water flow. Water uptake is a good proxy for nitrogen capture as well, since nitrogen is predominantly taken up in the soluble inorganic forms, which require water to be transported to the root. The key “resistance” to water transport through the soil-plant atmosphere system is the leaf resistance (r_{leaf}), which is inversely proportional to the leaf area, $L(r_{\text{leaf}} = L/r_{\text{stomata}}$, where r_{stomata} is the resistance to flow through the pores in a unit area of leaf surface, and has a median value of about 2.5 s/cm in both trees and grasses in savannas). Because the grass leaves are “in parallel” with the tree leaves as a pathway of flow between the soil and atmosphere, the instantaneous fraction obtained by the grass is given by

$$F'_{\text{wg}} = \frac{r_{\text{st}}}{L_{\text{t}}} / \left(\frac{r_{\text{sg}}}{L_{\text{g}}} + \frac{r_{\text{st}}}{L_{\text{t}}} \right) \quad (9)$$

if we assume they are both exposed to the same soil water supply (ψ_{soil}) and atmospheric demand (ψ_{air}).

The fraction of the water resource obtained over the entire growing season is the integral of F_{wg} . There is currently no analytical way of predicting the temporal pattern of tree and grass leaf development (“phenology”), since it depends on the particulars of rainfall and temperature in a given year, in interaction with the soil and any residual water in it. Some generalisations allow a numerical approximation to be made to the time-integral of F_{wg} . Despite a range in mean annual rainfall in savannas between about 300 and 1200 mm/y, in most cases the rainfall is concentrated into a growing season of about 6 months duration. The trees leaf out as soon as the rains begin (or even before, if there is residual water in the soil, provided the air temperature is warm enough) and reach full leaf area expansion within about two weeks. Within the canopy area, the maximum tree leaf area index (one-sided leaf area per unit ground area) is fairly consistent in savannas at 3 m²/m² (Scholes et al. 2002). The grasses, on the other hand, need to grow their leaf area by using current photosynthesis. Once the rains begin, and commencing with a leaf area of about 0.001 m²/m² provided by root reserves, the leaf area grows by about 2% per day. Grass leaf senescence sets in once the accumulated days of water-stress

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exceed about a week. The water deficit is in turn partly determined by the combined tree and grass leaf area. Thus, as the season progresses, the grass leaf area grows exponentially, then peaks and declines. Tree leaf loss only commences after about 14 days of water stress. For the specific climate data of a typical savanna site at Skukuza, South Africa, an empirical representation of the relationship between stand basal area of trees (X) and the fraction of the water resource captured by trees when growing in the same soil volume as grasses is

$$F_{wt} = \frac{X}{2 + X} \quad (10)$$

The grass productivity in subhabitat 2 can then be estimated as

$$P_{g2} = a[(R - c)(1 - F_{w,t})] \quad (11)$$

Again, the key point is that the relationship has a convex shape in relation to tree basal area for all reasonable assumptions regarding tree and grass phenology.

In subhabitat 1, the area directly under the tree canopy, there is in addition to the competition for water, a reduction in water supply and solar radiation due to interception by the tree canopy. About 5% of the rain falling on the canopy is intercepted (de Villiers 1981). The fraction of the incoming solar radiation that penetrates through the tree canopy to reach the grass layer (F_{rg}), assuming a random orientation of the leaves in the canopy, is

$$F_{rg} = e^{-0.5L_t} \quad (12)$$

This has two effects. Firstly, it reduces the rate of photosynthesis, which is a function of intercepted radiation. Secondly, it reduces the rate of evaporation from the soil and vegetation under the canopy, thus prolonging the period for which photosynthesis occurs (Scholes 1988; Belsky et al. 1993). The degree to which the latter effect is expressed depends on what fraction of the energy budget for evaporation in the subcanopy area is provided by radiation, and what fraction by the movement of hot, dry air across the shaded area from the adjacent intercanopy areas. This will vary in a complex way with the relative water availability in the two patches. As a first approximation, I assume that the fraction provided by direct radiation is equal to A_1 . Thus the "effective wetness" modifier of net rainfall (E) is proposed to be

$$E = \frac{1}{1 - A(1 - F_{rg})} \quad (13)$$

The relationship between radiation (I) and photosynthesis (P) can be approximated by a rectangular hyperbola

$$P = \frac{\alpha I P_{\max}}{\alpha I + P_{\max}} \quad (14)$$

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Under the very bright conditions that apply in savanna regions, a large reduction in radiation translates into a smaller reduction in net primary production. The tree leaf area index in the area under the tree canopy is about 3, which reduces radiation by 70%, but production only by half. The shading reduction factor is given the symbol F_L .

The nutrient supply under the tree canopy is enhanced relative to the area between canopies. This is partly due to the fact that nutrients are taken up over the entire tree root extent, but preferentially deposited, by leaf fall and leaching, in the area below the canopy. From the perspective of grass production over the entire savanna plot, this is a “zero sum game” – the gains in the subcanopy habitat are losses elsewhere. The same applies to the additional nutrient input under tree canopies that derives from dust interception and the excreta of birds and animals congregating near the tree. However, a third component, due to nitrogen fixation by microbial symbionts exclusively associated with trees, is additional. If the fraction of the soil nitrogen in the soil under the tree that is derived from symbiotic nitrogen fixation is F_N (this value can be determined by inference from the proportions of isotopes of nitrogen present, and is seldom more than about 0.2), the productivity of grass beneath the tree canopy can be estimated as

$$P_{g1} = F_L(1 + F_n)aW(0.95R - c)(1 - F_{wt}) \quad (15)$$

The P_{g1} component has the potential to account for the observation that sometimes a small quantity of trees in the system leads to increased overall grass production. For high values of F_N and small values of stand basal area, the beneficial effects of nitrogen fixation can outweigh the detrimental effects of competition.

Note that the complementary relationships (the effect of stand basal area of trees on tree production) are generally concave. In other words, tree productivity rises steeply initially, and reaches an asymptote at high levels of X . A simple equation, consistent with the above logic, is that

$$P_t = (A_1 + A_2)F_{w,t}Ra_t \quad (16)$$

where a_t is the “rain use efficiency” of trees, about $0.35 \text{ g/m}^2/\text{mm}$.

3. Some Consequences of the Convexity

3.1. IS PRIMARY PRODUCTION IN TREE-GRASS SYSTEMS A ZERO-SUM GAME?

Historically, the managers of mixed tree-grass systems have tended to focus solely on only one of the components. If they were graziers, their objective was to maximise grass production, and if they were foresters, it was to maximise tree production. The typical solution, in the absence of a model that deals with the interaction of trees and grasses, is to eliminate the unwanted component. If the overall productivity of the savanna mixture was a linear function of the amount

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of tree in the system, then this still remains an “optimal solution”: the system should be driven to whichever endpoint has the highest value. If the outcome of the interaction between trees and grasses is such that the highest productivity occurs at an intermediate level of tree cover, then it is possible that for some combinations of values associated with tree and grass products, a mixed system may be optimal.

The equations outlined above suggest that the only situation where the total production at intermediate tree density is higher than the productivity at either extreme is in the case where nitrogen fixation by trees occurs, and the rain-use efficiency of grasses is lower than that of trees (i.e., infertile soils).

There are cases where the landowner or society require *both* trees and grasses within the same landscape. One example is in ecotourism, where a lightly treed landscape (“parkland”) is deemed more attractive than either a densely wooded one or a treeless one.

3.2. MULTIPLE STABLE CONFIGURATIONS

Historically, there have been two main schools of thought regarding the ecological dynamics of savannas (see review by Scholes and Archer 1996). At present, the schools are tending to converge on a hybrid concept. Both “traditional viewpoints”, here contrasted for clarity, set out to explain the observed widespread coexistence of tree-grass mixtures. The “equilibrium school” posits that the competition between tree and grasses is balanced or limited – for instance by an even stronger competitive effect of trees on trees, or by an exclusive niche enjoyed by the otherwise weaker competitor. The “disturbance school” accepts that trees tend to out-compete grasses, but propose that fire (whose intensity is dependent on grass abundance) acts to keep the trees from completely dominating. The synthesis position argues that a comprehensive model of savanna dynamics requires both a competition mechanism and a disturbance mechanism.

Graphical analysis of the “state space” defined by the quantity of woody biomass (W) on one axis, and grass biomass (G) on the other axis, has been widely used to illustrate the existence of stable configurations (Walker, Ludwig, Holling and Peterman 1981; Walker and Noy Meir 1982). The isoclines where $\Delta G = 0$ and $\Delta W = 0$ (also called “nullclines”) are plotted into this space, and their intersections with one another and with the axes are interpreted as stable or unstable. A recent analysis of resilience in savannas, based on a different model to the one proposed here but reaching similar conclusions, is given by Anderies et al. 2002.

The arguments of neither school are dependent on non-linearities, but the presence of non-linearities of the types described make certain outcomes more likely. For instance, following the “equilibrium school” it is theoretically possible to have a stable tree-grass mixture in a situation where there is a linear relation between grass production and tree amount. It is also possible to postulate a linear system with two stable end-points (complete domination by trees or treeless) separated by an unstable saddle-point. It is not possible, with purely linear forms, to have the

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mostly widely-observed situation, which is alternate configurations of the mixture in which both trees and grasses persist, though perhaps in small amounts (Figure 3). The non-linear effect of trees on grasses described by the equations in the first part of this paper allow the grass biomass to be severely reduced by tree biomass, but never completely eliminated from the mixture.

The production equations presented above make no prediction of an effect of grasses on trees. The empirical evidence on this topic is mixed: in an experiment where the grass cover was physically removed, tree growth was enhanced in one vegetation type but not another (Knoop and Walker 1984). It is clear that the interaction is highly asymmetric: trees have a strong competitive effect on grasses, but grasses have a weak competitive effect on mature trees, although they may have a strong effect on saplings that have not grown above the grass layer.

The system of production equations presented above translates into the diagram shown in Figure 4, with suitable flux-to-stock conversions. The wood nullcline is a vertical straight line, since wood biomass is unaffected by grass biomass. This system has only one stable configuration: a tree-grass mixture, typically at a relatively high tree biomass and low grass biomass.

A quantitative analysis of the predictions of the disturbance school requires the introduction of an equation predicting the effect of grass biomass, via fire intensity, on tree biomass. A simple analysis is that fire intensity is directly proportional to the fuel load in the fire season, which is predominantly dry grass. Fire weather also influences intensity (Trollope and Potgieter 1985), but it is relatively consistent during the main burning season. Fire in savannas seldom kills trees (or grasses), but if the tree crown is in the flame zone, the aboveground parts are killed and must resprout from ground level. The critical threshold for recruitment of trees, and thus the long-term growth of the tree biomass, is whether the tree can grow beyond the flame height in the interval between fires. Flame height is an exponential function of fire intensity (van Wilgen 1986). For many semi-arid savannas, with a fire return interval of three to five years, it is empirically observed that a fire intensity in excess of 3000 W/m/s is required to suppress trees, which translates to a fuel load of around 300 g/m² under average burning conditions and a flame length of about 3 m. Introducing this simple relation into the graphical analysis results in Figure 5, in which two configurations are possible provided that the fuel accumulation over the mean inter-fire interval exceeds the 300 g/m² threshold. The first is the same high tree biomass-low grass biomass mixture predicted with competition alone, and the second has high grass biomass but no trees. The two are separated by an unstable "saddle point": trajectories to the left of this point tend to the treeless state (referred to as the "fire trap").

In practice, the "treeless" configuration usually has a scattering of mature trees that became established, often as a cohort, during a period when the system did not exceed the killing threshold. This can occur, for instance, during a prolonged period of below-average rainfall. In addition, there are typically many suppressed small trees within the grass layer, some of which may be decades old. The resilience

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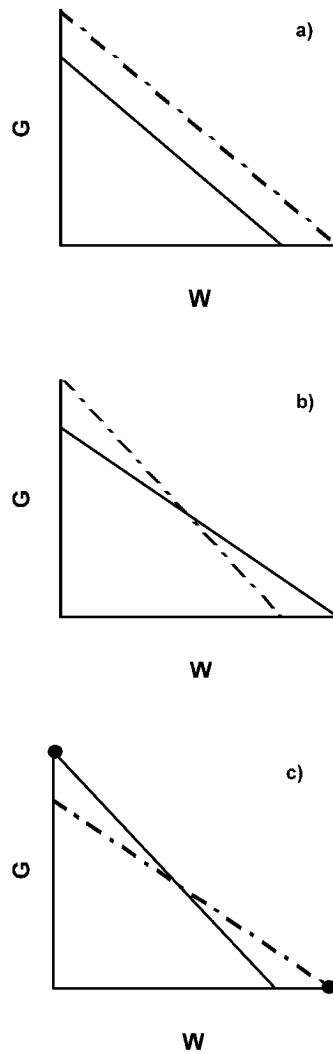


Figure 3. Graphical analysis of “nullclines” in the woody (W) versus grassy (G) state space is a widely used technique for analysing the stability states of savannas. The woody nullcline (dashed line) is the set of values of G at which $dW/dt = 0$, and the grass nullcline (solid line) the set of values of W where $dG/dt = 0$. The linear case is used here to illustrate the method. Where the tradeoffs between woody biomass and grass biomass are both linear, three qualitatively different cases are possible. In case (a) the tree nullcline lies above the grass nullcline over the entire range, and only one outcome is possible: total competitive exclusion of grasses by trees. (An analogous case is theoretically possible but not illustrated, with complete exclusion of trees by grasses.) In case (b) the woody nullcline lies above the grass nullcline at low wood biomass, but below it at high wood biomass. This is equivalent to saying that the competitive effect of trees on other trees is stronger than the effect of trees on grasses, and the same for grasses. The outcome is a stable coexistence of trees and grasses at an intermediate level. Case (c) has the grass nullcline above the wood nullcline at low W , and vice versa at high W . The outcome is an unstable (“saddle point”) equilibrium at the intersection. If perturbed from this point the system will either trend to a treeless or grassless endpoints.

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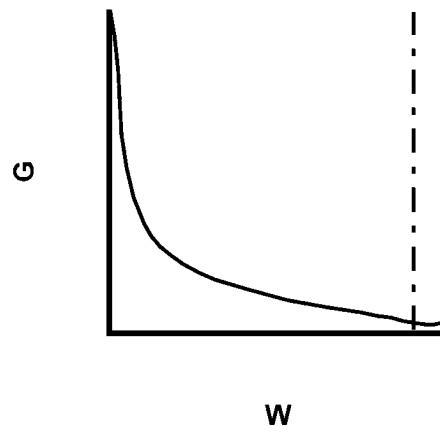


Figure 4. The state-space analysis that would result from the production equations described in this paper would show a strong, convex effect of woody biomass on the grass nullcline, but no effect of grass biomass on the wood nullcline. The wood nullcline would lie at the point where tree-on-tree competition limited further tree growth. The axes have not been quantified because the equations described apply to production at the annual timescale, not the instantaneous production and loss rates of the components. In reality, if the value of G is quantified as, for instance, aboveground green biomass, it shows a strong within-season variation from near-zero in the dry season, to a peak value in the middle of the wet season. The values of W , if expressed as total aboveground biomass of trees, vary slowly between years, but if expressed as tree leaf area (more meaningful for this purpose) show a strong, bounded variation within each year.

of this “open savanna” configuration can be measured as the distance between the treeless stable point and the unstable saddle-point. The effect of strong non-linearity in the effect of trees on grass production is to shift the saddle point to the left, reducing the resilience of the treeless configuration, and increasing the resilience of the high tree – low grass biomass configuration.

3.3. THE DYNAMICS OF BUSH ENCROACHMENT

When the tree-grass ecological system is coupled to a human system (pastoralism), it is commonly observed that the ratio of trees to grasses changes, often very rapidly. When European ranchers colonised the savannas of Africa, Australia, South and North America, the formerly open, grassy configuration frequently switched, within thirty to fifty years, to a densely woody configuration in which there was insufficient grass production, given the size of the holdings, to meet the income requirements of the rancher. Furthermore, the dense bush increases the cost of mustering, and in the extreme case, makes the residual grass physically inaccessible to the cattle. Interestingly, these problems were unknown in the African pastoral system which preceded the colonial period, and are rare on the communal grazing lands in Africa, despite the sometimes high livestock numbers they support. The communal lands often exhibit the opposite problem, “defore-

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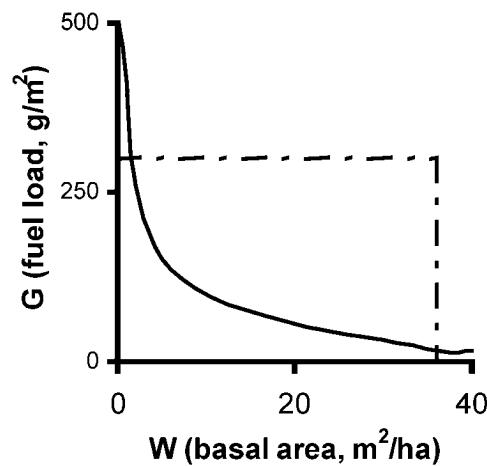


Figure 5. Addition of the effect of fire, largely fuelled by dead grass, on trees allows a state-space analysis based on production equations to be performed. It is assumed, in this case, that a fire of intensity 3000 kW/m/s (equivalent to flames 2.7 m in length, or a fuel load of 300 g/m²) once every three years will prevent tree recruitment. This defines the horizontal portion of the wood nullcline. The vertical section is defined by the limit of woodiness in the absence of fire. An equation resulting from a meta-analysis of global tree cover data in savannas suggest this envelope to lie at $X_{\max} = 1.2(R-300)$. The annual production equations can be used to generate the grass nulcline, by calculating the fuel accumulation over the fire interval (assuming that 60% of fuel carries over between years if not burned or eaten), as a function of woodiness, here represented by the tree basal area. The solution depicted here assumes 600 mm annual rainfall, 80% sand content in the soil and 20% of nitrogen being fixed by trees. At low W, sufficient grass accumulates in three years to exceed the tree mortality threshold. Therefore the system tends to an open state. At high W, insufficient grass fuel accumulates to control the trees, and the system tends to a closed state with a small amount of residual grass.

station”, or a reduction in tree cover to a point where it threatens the supply of tree-based products.

There are several key differences between the two forms of management: ranchers generally suppressed fires, made little direct use of trees, and greatly reduced the numbers of browsers (herbivores that eat trees) in the system. In contrast, communal graziers deliberately set fires, harvest the trees for construction of huts, pens and for fuel, and typically run herds of goats in conjunction with cattle.

In terms of the simple graphical analysis, the effect of increased grazing is to lower the position of the grass nullcline, thus reducing the resilience of the “open” configuration, and eventually eliminating it as a possibility. The effect of long-term fire exclusion is to remove the horizontal segment of the wood nullcline (i.e., a return to Figure 4), which also eliminates the possibility of a stable “open” configuration. Increased fire frequency, up to a point and in the medium term, can lower the position of the horizontal portion of the wood nullcline, increasing the size of the

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fire trap. However, over-frequent fire could, in theory, run down the nutrients in the system or otherwise weaken the grass such that the grass nullcline is also lowered. Browsing and wood harvest have the effect of shifting the vertical portion of the wood nullcline to the left, meaning that the residual grass in the higher tree biomass configuration is increased, and the resilience of the woody configuration is reduced. Under very heavy browsing or wood harvesting the “mixture” configuration can be eliminated. These patterns are at least consistent with observations, even though they do not prove the hypothesis.

The ease and rapidity with which ranchers can tip the tree-grass configuration, and their difficulty in returning to the formerly more open state, is thus strongly related to the convexity of the effect of trees on grass. Following disturbance of the grass sward by grazers and fire suppression, small trees become established. The direct or indirect reduction of fire frequency and intensity and the exclusion of browsers allows them to grow, in a space of about a decade, to the point of being able to suppress grass production. The herd size is not reduced as the rancher begins to feel the economic pinch, resulting in even less grass being available to carry a fire, and the combined pastoralist-savanna system spirals into the encroached condition.

3.4. THE OPTIMAL PATTERN OF TREE CLEARING

A logical consequence of the convexity of the tree-grass relation is that if tree clearing is undertaken for the purpose of increasing grass production, and the amount of money available is insufficient to clear completely (or some trees are desired to be kept in the system for other reasons), the most cost-beneficial pattern of clearing is to remove all the trees in a portion of the landscape, rather than to remove a portion of the trees in all of the landscape. The guideline is to begin with the *least* encroached areas first (rather than the usual “intuitive” practice of tackling the most densely-treed areas first). It is generally easier to manage a “patchy clearing” pattern, since a clear operating rule can be established, fire can be used as a control mechanism, and the dispersal of tree propagules into the cleared area is reduced.

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