

PLANT RESPONSE INDICATORS

KEY INDICATORS: SATELLITES IN MANAGEMENT SPACE

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Abstract

The livestock farmer in the Eastern Cape is faced with an environment and market that has both temporal and spatial variation that does not allow for any single management recipe. The pastoralist must therefore respond to various indicators to achieve his objectives. If the rangeland scientist is to serve the pastoralist, the search for both veld and animal production indicators must be important. This paper investigates the properties and problems of indicators for both veld and animal management and proposes the use of new concepts that might help to isolate management indicators.

disciplines. Any researcher who has to do with animal/plant experiments usually has multivariate data. These data need to be reduced into a few sensible dimensions (gradients) that describe a large proportion of the meaningful variation (pattern) found in the experiment. The next step for the researcher, which is often not done, is the interpretation of these dimensions and models into sensible products that can be used by the land manager. This implies interpreting the dimensions for the land manager. These products for the land user need to be easy to interpret but also informative. Ecologists often deal with ecological space, which is described by Gauch (1981) and is derived from the interpretation of species and samples space into various environmental gradients that explain the changing abundance of various species.

Introduction

The use of satellites to find a position in space, or on the earth's surface is now quite common practice. The accuracy with which a position can be determined is dependent on, among other factors, the number of satellites used and the positioning of the satellites at a specific time. Different satellites are used at different times depending which are available. The pastoralist is faced with numerous management spaces which can be defined by environmental, animal performance and economic dimensions or gradients (Beckerling 1993).

If the pastoralist is to achieve specific objectives then an awareness of the position and movement in that management space is important. The questions therefore are firstly, what management space or spaces should the pastoralist consider and secondly, what management satellites (or indicators) can the pastoralist use to move in the management space? This analogy is the basis of the paper which attempts to describe how veld and animal management spaces can be created and also characterise what could be seen as a veld management "satellite".

Defining management space and creating a management map

This discussion and the examples used will be confined to veld and animal management but the concept can be applied in other

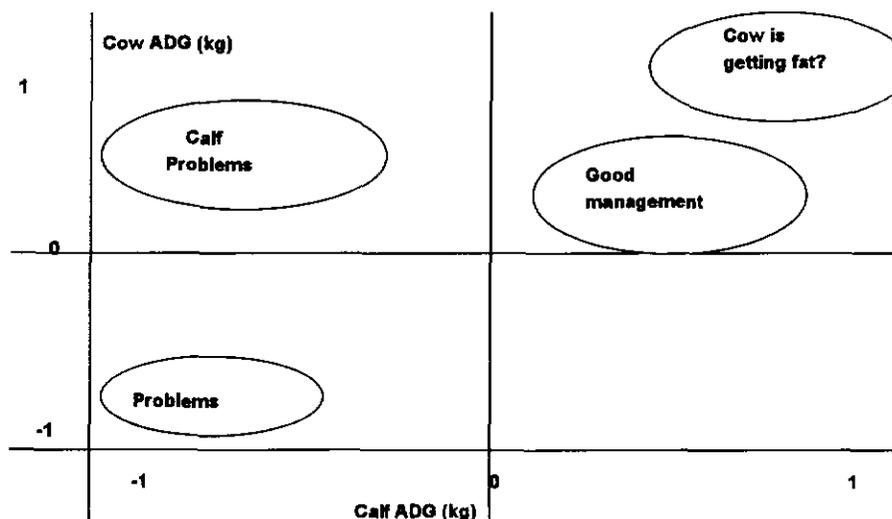


Figure 1 A hypothetical example of an animal management map created by plotting the ADG of a cow and it's calf.

Management space, which is the end product, can be derived from ecological space (Beckerling 1993). In other words, an area with similar ecological space has the same management requirements for a specific objective. However the concept is not confined to species and samples space but can be used wherever there are two or more gradients that can be graphed together and sensibly interpreted in terms of veld and animal management. For example, the average daily gain (ADG) of a cow and its calf could be considered as two gradients (Figure 1). The management implications for each quadrant in this graph will be vastly different for different management objectives but it clearly illustrates the concept.

Each quadrant or some threshold values could be superimposed on this graph to create different management spaces with whole graph then forming a management map. Another example is the veld management map created by two important gradients that have been identified in the Eastern Cape. These are the "edaphic" gradient (gradient 2) and the "altitude" gradient (gradient 1) (Figure 2). These gradients are used to create numerous veld management spaces that describe the different

challenge for researchers because they must be adapted for the end user.

Willis & Trollope (1987), Hurt and Hardy (1989) and Trollope *et al.* (1992) use a weighted key species method for identifying a position on a gradient. These key species are selected because they are closely correlated with the gradients in question. However, simply looking at the statistical properties of the correlation does not always imply a good indicator. Figure 3 gives

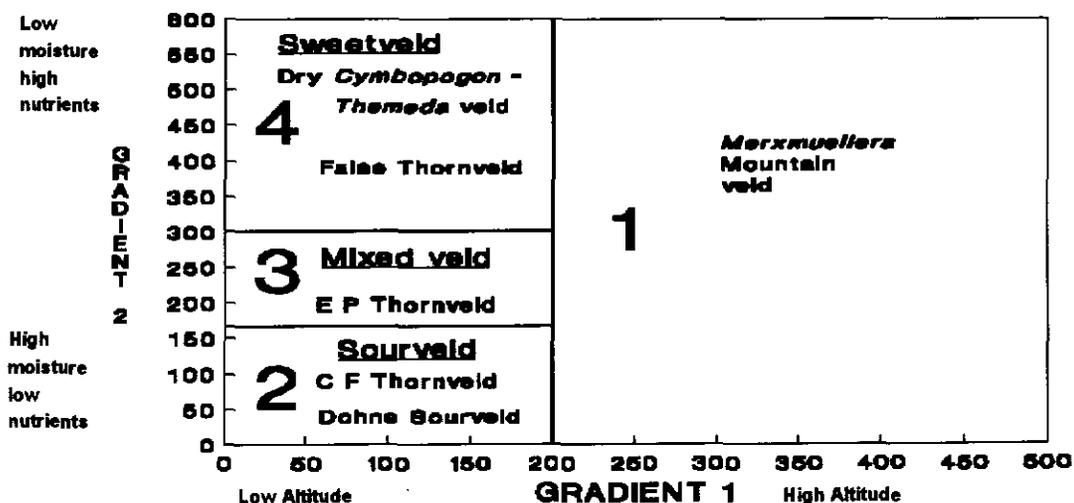


Figure 2 A veld management map for identifying benchmark sites in the Eastern Cape. The values on the axes are generated from the ordination used.

benchmarks in the Eastern Cape, which are the foundation for veld management recommendations (Trollope *et al.* 1991).

The gradients for this management map are a complex of interacting environmental factors created by using indirect gradient analysis. This complex of factors that tend to interact and form one gradient is common in animal and veld research and there are numerous statistical packages available to objectively integrate the individual factors into a few gradients (Gauch 1981, Doledec and Chessel 1991). Average daily gain is a biological gradient where the animal has integrated feed intake and many other factors. Note that a single parameter or gradient used in a management map can often be meaningless on its own but when combined with another gradient relate to important management criteria. For example, fuel load on its own is of little value to determine fire intensity, but is vital information if combined with other variables like fuel moisture (Trollope 1983). This approach to describing multivariate data avoids scientific jargon and focuses on producing a management based product.

Identifying management satellites

The creation of a management map and management spaces is not the final step in the process of producing a management product. The manager must be able to find a "position" in the management space and be able to make decisions that will change his position.

Finding a "position"

The dimensions or gradients that are used to create the management map are often not measurable by the end user so one cannot simply expect the end user to plot the position without knowing the "satellites" which might be removed from the space but indicate the position. The search for these satellites is a

some examples of typical relationships that might be found between an indicator and a gradient.

Themeda triandra represents the first half of the grazing gradient extremely well but does not relate to the second half of the gradient at all. *Sporobolus fimbriatus* represents the whole gradient but can be ambiguous because a change in position from b to a vs. c to d have different directions but the same magnitude along the gradient and differ in changes to the species abundance. There are two ways to overcome these problems:

1. The data can be weighted or transformed in some way. This can be achieved by using co-variate management data which is derived from component research, farmers knowledge or hypotheses generated during the data analysis.
2. More than one indicator can be used to find a position on the gradient. Hence the reason why Willis & Trollope (1987) insist that the key forage species must be selected from different ecological groupings, namely Decreaser and Increaser species.

These problems that can be encountered with indicators are research topics that need clear, scientific investigation. It is the researcher who does the original research who should carry out this task because the task requires familiarity with the data involved.

Moving in management space

Hurt and Hardy (1989) clearly explain how to find a position on the grazing gradient but they fail to describe how a pastoralist can manipulate his management to move on this gradient. Morris *et al.* (1992) points out that knowing a position on a gradient does not always infer knowledge on how to move from that position. For

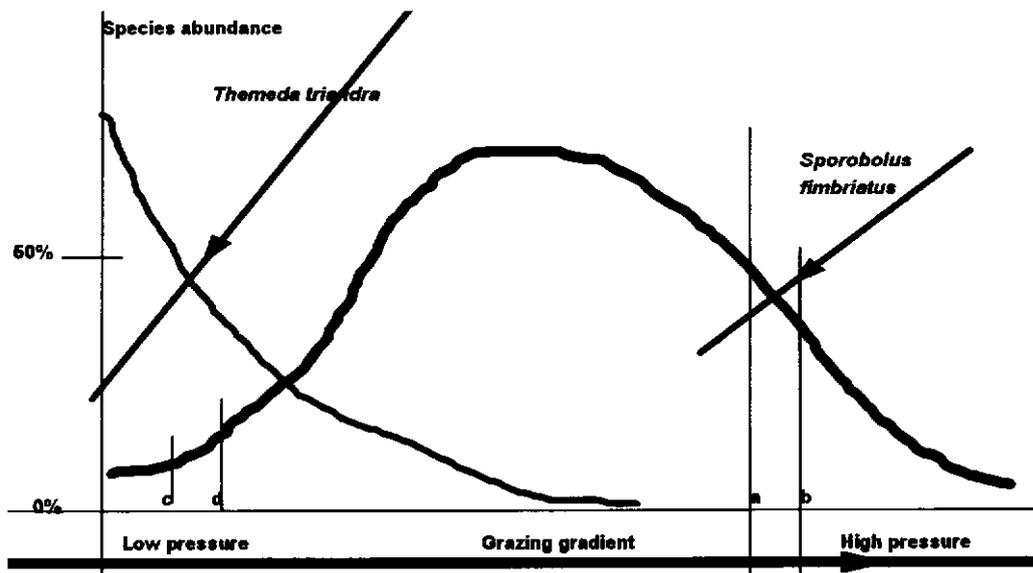


Figure 3 The postulated response curves of *Themeda triandra* and *Sporobolus fimbriatus* to the grazing gradient in the False Thornveld of the Eastern Cape (Acocks 1975).

example, overgrazing can cause an increase in bush in the False Thornveld of the Eastern Cape but resting will not remove the bush. The state and transition model (Westoby *et al.* 1989) does help to explain possible solutions to modelling movement between different management spaces. Trollope *et al.* (1992) use the theory of plant succession and knowledge from good farmers to explain how to move in management space. However, it is quite clear from the literature that scientists have become so involved with describing "Why?" that they have forgotten about the land user who needs to know "What next?". Perhaps this is harsh criticism, but the management space concept does underline the need for clear thinking on management implications of scientific results.

Conclusion

The pastoralist is in urgent need of good indicators to modify his management to achieve his objectives. There are already extensive research results available that could be used to isolate good indicators or management satellites. This task has a unique research component of its own which needs further thought and development. The management space concept together with the management satellite analogy can possibly help to expose certain characteristics of this research.

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INDIVIDUAL, POPULATION AND COMMUNITY RESPONSE OF WOODY PLANTS TO BROWSING IN AFRICAN SAVANNAS

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Introduction

Savannas are the single most extensive vegetation type of southern Africa, covering about 35 % of South Africa and almost all of Zimbabwe, Botswana and Mozambique. By definition, savannas comprise an almost closed herbaceous stratum and a woody component of varying density, and are used extensively for pastoralism, game farming and wildlife conservation. The browse component of savannas is important for pastoralism not only because of widespread goat farming but also the heightened use of browse by cattle (Donaldson 1979; Rees 1974) and sheep (Story 1951) under certain conditions, and support a diverse array of indigenous mammalian herbivores of especial importance to both game farming and conservation.

Previous summaries of the reaction of the browse component of African savannas to herbivory (Trollope 1981; Bergstrom 1992) showed our knowledge to be, at best, fragmentary. The purpose of this paper is to review our current understanding of the effects of herbivory on woody plants at various levels of plant organization, specifically the effects of browsing by large mammals (excluding elephant) on the physiology and growth of individual plants, the population dynamics of individual species, and the structure and composition of plant communities. The intent is not to offer an exhaustive review, but to identify effects which seem important. Browsing does not take place in isolation from other influences on the functioning of a plant, and an attempt is therefore made to identify interactive effects between browsing, climate and fire.

Individual plant level

The response of leaf and shoot growth to defoliation has been relatively well investigated for the genus *Acacia* but almost ignored for deciduous broad-leaved species. All African *Acacia* species studied so far have shown compensatory growth in response to defoliation: *A. nigrescens* (Du Toit *et al.* 1990), *A. karroo* (Stuart-Hill & Tainton 1988; Teague 1988b, 1989a, b; Teague & Walker 1988), *A. tortilis* (Milton 1983, 1988; Pellew 1983; Du Toit *et al.* 1990). Similar responses to moderate browsing have been shown by *Portulacaria afra* (Aucamp 1979). The only example found for which browsing had an inhibitory effect on production was for two West African species, *Combretum aculeatum* (broad-leaved) and *Cadaba farinosa* (evergreen) (Cisse 1980), although in the case of *C. aculeatum* compensatory growth occurred after one year once new shoots were activated from lateral buds (Cisse 1984 unsee, in Hiernaux 1992).

The response of *A. karroo* and *A. tortilis* to defoliation has

been relatively well investigated, and offers a profile of the growth patterns of a browsed woody species. The sensitivity of *Acacia* species to defoliation depends on the frequency and intensity of defoliation, phenophase of the plant, location of browsing within the plant, and type of defoliation agent. Defoliation of *A. tortilis* shoots during winter stimulates shoot production and maintains shoot yields, whereas defoliation during summer depresses shoot yields (Milton 1988), and shoot extension rates can be maintained under long-term browsing pressure (Du Toit *et al.* 1990). By contrast, defoliation of *A. karroo* by goats during growing phenophases stimulates large increases in leaf and shoot production relative to undefoliated plants, although plants are most susceptible to defoliation during spring when carbohydrate levels are lowest (Teague & Walker 1988). This stimulated regrowth takes place within weeks and its effect is carried through the winter dormant period but lost with time. For *A. tortilis*, *A. xanthophloea* and *A. hockii*, clipping stimulates a high rate of forage production (70 %, 48 %, 81 % stimulation after 1 year) which progressively and not immediately compensates for lost material, but high production declines if the stimulus is removed (Pellew 1983). Compensatory increases of *A. karroo* (Teague & Walker 1988) and of *A. tortilis* (Pellew 1983) are due largely to a few dominant shoots in the upper canopy. Increased intensity of pruning of *A. karroo* and *A. tortilis* results in shoots that are individually thicker, longer, have more laterals, and a longer shoot length per branch (Milton 1983). Plants can compensate for defoliation of the lower but not of the upper half of the canopy (Teague 1989c). This finding for *A. karroo* on the effect of location of defoliation within the canopy is noteworthy because it indicates that the effects of defoliation are integrated across the entire plant. Teague (1988b) observed but could not explain that defoliation of *A. karroo* by hand did not result in the stimulation of growth exhibited by goat defoliation. Nor did avian or insect consumption, accounting for 8 % of leaves in the growing period, stimulate leaf or shoot production (Teague & Walker 1988).

Compensatory growth of *Acacia* species in response to defoliation is not without cost to overall growth of the plant. Although all frequencies of defoliation (2, 4, 8, 12 weekly) of *A. karroo* allowed the accumulation of as much leaf as undefoliated controls, this occurs at the expense of carbohydrate reserves, and is not sustainable beyond four years (Teague 1989a). For *A. tortilis*, the frequency of shoot pruning is inversely related to increment of basal area (Milton 1988).

For the succulent CAM species *Portulacaria afra*, season of defoliation influences whether compensatory growth occurs or not (Aucamp 1979). Defoliation during winter results in a decrease of leaf and shoot production, whereas leaf production can increase by 30% following defoliation in autumn, and increased shoot

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production can occur with defoliation during summer and autumn. I could find no papers reporting the effects of herbivory on the biomass or nutrient content of underground parts of woody savanna plants, or on the growth of the complete plant.

Many savanna woody plants possess physical or chemical defences against herbivory (Owen-Smith 1982, 1993), usually interpreted in terms of the resource availability or carbon-nutrient balance hypotheses (Bryant *et al.* 1983; Coley *et al.* 1985). Species growing on nutrient-rich substrates tend to rely on physical defence and rapid growth, characterised by *Acacia* species, whereas species on nutrient-poor substrates, usually unarmed broad-leafed species, invest mostly in carbon-based chemical defences. Some plants are capable of synthesizing extremely toxic secondary metabolites containing nitrogen (mostly alkaloids) in response to herbivore pressure (Harborne 1991), but this is found in only about 20 % of flowering species because nitrogen is usually limiting. However, Fowler & Lawton (1985) have challenged whether the damage-induced changes in foliage chemistry can be considered as induced defences because these changes are small and appear to have negligible effects on the performance of individual herbivores and on herbivore population dynamics.

Although such defence options are known to be important in African savannas (Cooper & Owen-Smith 1986; Owen-Smith & Cooper 1987), this review is concerned only with the inducible response of these defences in individual plants to herbivory. An increased level of spinescence can be induced by herbivory for some *Acacia* species (Young 1987; Milton 1988; Milewski *et al.* 1991). For *A. tortilis*, pruning of shoots increases the thorniness of new shoots (Milton 1988), which can decrease the bite rate of browsers (Cooper & Owen-Smith 1986). These structural adjustments are important because they are irreversible.

The response of condensed tannins, the most commonly evaluated carbon-based defence compound, to defoliation has been varied within woody plants. Heavy long-term browsing by giraffe resulted in a decreased condensed tannin content and an increased foliage nutrient content of *A. nigrescens* but had no effect on *A. tortilis* (Du Toit *et al.* 1990). In contrast for *A. karroo*, 15 days of utilization by goats resulted in an increase of condensed tannins and a decrease of *in vitro* digestibility, especially of young relative to mature leaves and of small compared to large plants (Teague 1989b). Similarly for the CAM succulent *Portulacaria afra*, phenolic content increased in the two weeks following defoliation but then decreased to below that of control trees, or decreased following defoliation if the trees were irrigated (Ras 1990). *Acacia caffra* likewise showed a marked (95 %) increase in condensed tannin within 15 minutes of defoliation, with a concomitant raise in tannin levels of surrounding undefoliated trees (Van Hoven 1984). These varied responses have invariably been interpreted in terms of the resource availability or carbon-nutrient hypotheses, although these studies were not designed as formal tests of these hypotheses.

Inducible defence based on nitrogen compounds is recognized for certain species elsewhere (e.g. *Nicotiana sylvestris* - Ohnmeiss & Baldwin 1994), but is not known for any woody species of African savannas. Such defences are thought to require luxury consumption of nitrogen, and are therefore likely to be rare in systems in which nitrogen is limiting except possibly for legume species which fix free atmospheric nitrogen. Although a number of African legume, especially *Acacia*, species have been confirmed to fix atmospheric nitrogen (Habish 1970; Habish & Khairi 1971;

Hogberg 1986), I am not aware of any work which has investigated the role of nitrogen based defence compounds in African savanna woody species, but the anecdotal recognition of the avoidance of some *Acacia* species when they are small, established individuals, at a stage when believed to be most heavily modulated, raises speculation about its possible importance, or of the extra nitrogen enhancing photosynthesis and thereby promoting carbon-based defence.

The removal of tissue of an individual plant by defoliation may result in a host of altered physiological processes and allocation patterns for that plant. The plant may respond to such lost tissue by increased irradiance and therefore photosynthetic rates in remaining tissue; reallocation of substrates from elsewhere in the plant; prolonging the active life of remaining photosynthetic tissue through reduced leaf senescence; activation of remaining meristems; enhanced conservation of moisture through reduced transpiration loss; increased efficiency of nutrient cycling via animal excretion; direct effects from growth promoting substrates in ruminant saliva (McNaughton 1979).

Some of these physiological responses anticipated by McNaughton (*op cit*) have been documented for African woody species, although information is less than fragmentary. Rate of photosynthesis of fully expanded leaves of *A. karroo* increased markedly following defoliation, although the extent of increase depended on the intensity of defoliation but, surprisingly, depended only slightly on moisture availability (Teague 1988a). Experimental defoliation of the dwarf shrub *Indigofera spinosa* likewise increased the contribution of photosynthate from remaining leaves, increased leaf longevity, and activated auxillary meristems (Coughenour *et al.* 1990).

In turn, some of the physiological changes induced by browsing may influence future browsing patterns. Du Toit *et al.* (1990) propose that heavy browsing of *A. nigrescens* and *A. tortilis* results in positive feedback to give a grazing lawn effect. Specifically, heavy browsing leads to a decrease in intershoot competition, allowing rapid regrowth, which increases carbohydrate demand thereby decreasing carbon based defence chemicals, resulting in a highly palatable tree. Many areas subjected to heavy goat browsing may experience a similar sequence of changes.

In conclusion, it would seem that a clearer understanding of the physiological, defence and growth responses of woody plants to herbivory is only likely to emerge when studies address the complete physiological functioning of the plant, especially the underground component, the nature of available resources, the pattern (continuous versus intermittent) and nature (leaf or structural material taken) of herbivory, and the time frame of interest. The effect of herbivory on patterns of allocation is integral to resolving many of the key questions, but the near impossibility of studying complete root systems of larger shrubs and trees precludes an easy passage forward.

Population level

Mammalian browsers can affect most stages of the life cycle of a plant, including dispersal, germination, seedling establishment, growth and mortality, to a greater or lesser extent. I first examine these individual influences, then consider whether their cumulative effect is reflected in the population dynamics of woody species.

Certain *Acacia* species, characteristically with thick

indehiscent pods, depend largely on mammalian herbivores for the dispersal of their seed (Coe & Coe 1987), although individual plant species may be dispersed by a number of browser species. This lack of species-specificity has resulted in domestic herbivores also operating as efficient dispersers, even of species not normally dispersed in this manner, such as *Acacia karroo* (T.G. O'Connor, unpublished data). Dispersal of seed may be effected by spitting, especially for smaller-bodied ungulates, or by passage through the gut. The critical determinant of which *Acacia* species can be dispersed by a browser is the thickness of the seed testa, and the ability of the seed to therefore withstand molar action while being chewed (Coe & Coe 1987). For adapted species, passage through the gut reduces attack by bruchid beetle and increases germination percentage and rate, although it has been argued that these advantages are irrelevant compared to the advantages of dispersal (Janzen 1981).

While consumption of ripe seed by browsers is readily recognised, there is little data to ascertain the importance of browsers as mortality agents of unripe seed. Certainly, anecdotal account of consumption of fleshy flowers by browsers, particularly goats, is widespread, but similarly not quantitatively supported, nor is it clear to what extent curtailed flower production would result in depressed seed production. For *Acacia*'s, the percentage pollination of their flowers seems to be generally low (Coe & Coe 1987), and it is therefore unlikely that herbivory would have much effect.

Seedling recruitment is suspected to be the life history stage most vulnerable to browsing, but there is little quantitative data to support this. Survival and shoot length of young seedlings of *Acacia senegal* is depressed by simulated browsing for the first 38 days, after which the number of surviving plants increases (Seif El Din & Obeid 1971). *Acacia tortilis* in Manyara National Park, East Africa, has only experienced three recruitment episodes in the last century (Prins & Van der Jeugd 1993). These episodes were correlated with population crashes of impala because of anthrax, which released otherwise heavy browsing pressure for long enough to let a seedling cohort get away. Similarly, sheep are suspected to be important for limiting the seedling recruitment of *Acacia karroo* in eastern Cape grassland (Story 1951), thereby preventing encroachment of this species. It is further suspected that a switch from sheep or mixed cattle and sheep farming to cattle only in this region has resulted in encroachment of *A. karroo*, as cattle do not affect its seedling establishment (Du Toit 1972b). The combined effects of drought and browsing prevented seedling recruitment of woody species in the Sahel, although the relative effect of these two factors was not determined (Gijssbers *et al.* 1994).

Recruitment via vegetative regeneration or propagation can be markedly impacted by browsing. Heavy grazing prevented the reestablishment of *Brachystegia-Julbernardia* woodland (miombo) in Zimbabwe following clear-cutting, initially reducing then finally eliminating coppicing plants (Strang 1974). Cattle may consume a considerable amount of browse of miombo species in the late dry season because miombo species flush early and have high protein content at this time (Rees 1974). Similarly, browsing reduced the number of regenerating shoots of a number of species of parklands in the Sahel region (Gijssbers *et al.*, 1994).

The impact of goat browsing on the vegetative regeneration of *Portulacaria afra* is speculated to have led to the demise of Succulent Valley Bushveld in the eastern Cape (Stuart-Hill 1992).

Mature plants of this species form a 'skirt' of regenerating individuals round their base from drooping branches which root on contact with the ground. Browsing by elephants impacts growth on the top of the plant but does not curtail regeneration, whereas goats feed round the base of the plant and eliminate the 'skirt' of regenerating individuals. Similarly, the negative effect of browsing on seedling recruitment and shoot regeneration is considered to maintain the parklands of the Sahel (Gijssbers *et al.*, 1994).

Trollope (1983) identified that herbivory alone had limited effects on the survival of established plants of *Acacia karroo*, but affected their growth and further influenced survival by means of interaction with fire. The extent of top-kill and complete mortality of woody individuals is inversely related to size. Browsing following fire maintains a coppicing individual in a short state and therefore susceptible to subsequent fires (Trollope 1974). Similarly, browsing by giraffe constrained the recruitment of *Acacia* spp. on the Serengeti plains, which, in conjunction with fire, led to the demise of these woodlands (Pellew 1983). Heavy browsing by small indigenous ungulates (impala, dikdik, grant's gazelle) can also maintain woody individuals <1 m in a short state (Belsky 1984), thereby prolonging the period of susceptibility to fire.

Goat browsing is, however, capable of inducing mortality of coppicing individuals of felled trees of *Acacia karroo* and limiting the regrowth of surviving trees, with continuous browsing having a greater effect than rotational browsing (Du Toit 1972a).

Evidence of the direct effects of ungulate herbivory on the survival of mature plants is unknown, and of the indirect effects is scarce. An example of the kind of indirect effect which might occur is an odd drought event in India which killed many of the mature trees forming the food of Sambar (*Cervus unicolor*), causing them to strip the bark of up to 13 % of the remaining trees (Khan *et al.* 1994). Most of these individuals undoubtedly eventually succumbed. Mortality of adult trees due to complete (Thomson 1974) or partial ringbarking by porcupine in conjunction with fire (Yeaton 1988) has been recorded, but the Sambar example represents a dietary shift dependent on an unusual climatic event.

The following examples show that browsers can markedly alter vegetation structure, but have not identified the affected demographic processes. Goat browsing reduced the amount of browse in the mopaneveld of the northern Transvaal (Donaldson 1979). The absence of browsers on cattle ranches by comparison with mixed game-cattle systems have resulted in far greater density of bush, especially of shrubs, on both *Combretum-Acacia* and *Combretum-mopane* savanna in Zimbabwe (Taylor & Walker 1978; see also Kelly & Walker 1976).

Concluding comment

I have sought to illustrate that browsing by ungulates can have consequences for the physiological functioning, growth and demographic processes of the affected woody plants, and may result in landscape-level changes in vegetation structure. Some of the patterns revealed have implications for the management of the woody component of savannas whether they be used for wildlife conservation or livestock production. Two currently prevailing perspectives on woody savanna species are the maintenance of browse forage flow for production of browser species, and the use of browsers for the partial or complete elimination of the woody

component to enhance herbaceous production. Assessment of these perspectives entails a consideration of different time scales and plant processes. Browsing can exert a considerable influence on the quantity and quality of browse forage in the short term. There is probably sufficient information to formulate guidelines for how to maintain short-term forage flow of some *Acacia* species. However, the maintenance of browse forage flow in the longer term is more likely dependent on influences other than browsing because it is determined by the demographic responses of the constituent species.

The summarized information offers insights for the control or elimination of bush by browsing. Browsers on their own can only affect woodland dynamics at the dispersal and seedling growth stages, the former by promoting increase and the latter by curtailing it. The efficacy of browsers at any other stage is not independent of the influence of fire or climate. Indeed, the use of browsers alone to control mature plants could be counter-productive because seed dispersal by livestock is now recognized as a primary process leading to encroachment (eg Brown & Archer 1989). However, the importance of browsers for limiting seedling establishment, and thereby pre-empting a future problem, warrants consideration (cf Prins & Van der Jeugd 1993). These windows of opportunity are likely to be of short duration because seedlings emerge within a restricted interval and do not seem susceptible to defoliation for an extended period. However, although the combined use of fire and browsing is a well-recognized means of controlling already established woodland, perhaps less attention has been paid to the use of browsers to maintain recently established woody individuals at a height where the occasional use of fire will promote open grassland. The use of browsers at the regeneration phase therefore seems to offer an extremely cost-effective means of pre-empting bush encroachment. Grazing systems and species mixes need to be adapted accordingly.

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PLANT INDICATORS - THE BASIS OF ECOLOGICAL INTERPRETATION

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The principle of the plant indicator

"Every plant is a product of the conditions under which it grows and is, therefore, a measure of environment" (Weaver & Clements 1938). This matching of species and environment is such that it is unlikely that such species as *Festuca costata*, *Urochloa mosambicensis* and *Stipagrostis brevifolia* would be found growing together in the same community. In contrast, one would not be surprised to find *Cymbopogon plurinodis*, *Themeda triandra* and *Digitaria eriantha* growing side by side.

While it is true that the arrival of any plant in an area (through seed or any other reproductive structure) may be purely accidental, the continued presence of that plant in a community will be assured only if it is sufficiently well adapted to the conditions which are imposed on it to allow it to survive in competition with other plants which are present in that area. In other words it will survive in the area only if, in Darwinian terminology, it is *sufficiently fit* to do so. So, therefore, of the large number of species whose seed may be transported by wind into an area and the large number of these whose seed may germinate, only a small proportion are normally able to survive. Those which do are obviously sufficiently well adapted to the conditions imposed by both the biotic (e.g. soil, temperature and moisture conditions) and abiotic (e.g. frequency, intensity and type of defoliation which is imposed) to survive in competition with other plants which already occupy the area or whose seedlings may germinate at the same time.

Through this process, the biotic conditions which exist and the abiotic conditions which are imposed will determine the composition of any community. Therefore, if one understands the biotic requirements of any plant species and the response of such species to biotic factors such as grazing intensity and frequency, or perhaps fire, it is possible to make some judgement of past management on the basis of the mix of species in any community. Also, such understanding allows one to predict what is likely to happen to the species mix given the introduction of any new management procedure.

Such an understanding of plant response to treatment is therefore fundamental to both the planning and the implementation

of grazing management procedures, and forms the basis of adaptive veld management.

Indicators of biotic conditions.

Anyone who is even vaguely familiar with the ecology of any area will appreciate that plants are not randomly scattered across the landscape but that they are distributed in accordance with the diversity of biotic conditions of the habitat.

So, for example:

Wet sites may be occupied by:

- species of *Paspalum* (*P. dilatatum*, *P. urvillei*, *P. vaginatum*, *P. distichum*),
- Acroceras macrum* (Nile grass),
- Leersia hexandra* (Rice grass),
- Phragmites australis* (fluitjiesriet) and many others.

Shallow soils may be occupied by:

- Microchloa caffra*,
- Aristida congesta*,
- Cynodon dactylon* (kweek),
- Eragrostis racemosa*,
- Chloris virgata*,
- Melinis nervigulmis*,
- Eragrostis plana* and others.

These species may occupy such sites more because other plants are unable to tolerate the moisture stress or periods of waterlogging typical of such sites, than because they show any preference for such sites over those which provide better growing conditions.

The same is likely to apply to **compacted soils**, where such species as:

- Eragrostis plana*,
 - Sporobolus africanus*,
 - Eleusine indica*
- and others are able to survive.

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Then one has those species which grow well in the shade of the canopies of trees growing in the bushveld areas, including such species as:

Panicum maximum,
P. deustum and
Karoochloa curva,

or in the even denser shade within forests, such as:

Panicum aequinerve,
Stipa dregeana and
Setaria megaphylla.

And so there are plants which do well in:
acid (*Andropogon eucomis*), or
saline (*Sporobolus virginicus*) soils.

Some species do well in heavy clay soils:

Brachiaria eruciformis,
Sorghum versicolor,
Dicanthium aristatum

while others prefer sands:

Cynodon species,
Stenotaphrum secundatum and others

The list is endless, to the extent that there are few terrestrial environments on earth which are so stressful that no plants are able to survive there. Because of these relationships between the nature of the environment and the species which typically grow there, it is possible to make some assessment of the nature of the habitat given the suite of species which one finds in any area. Our early (pre-computer) ecologists, such as Pentz, Phillips, Acocks, Scott and others were very adept at doing this.

Indicators of biotic conditions

From the veld management point of view it is the indicators of defoliation frequency and intensity and the mode of defoliation i.e. whether it is by grazing or fire and whether it is uniformly applied or is selective, which are important, recognising that the plants response to these factors may vary under different biotic conditions. In this respect, then, it is the adaptation of the grasses to different levels grazing-induced stress which has received a great deal of attention in recent years. The American Dyksterhuis was perhaps the first to formally react to the implied appeal made by Gilbert White in 1778 (to quote from a letter to The Honourable Daines Barrington, June 2, 1778 : "*The standing objection to botany has always been, that it is a pursuit that amuses the fancy and exercises the memory, without improving the mind or advancing any real knowledge : and where the science is carried no farther than the mere systematic classification, the charge is but too true. But the Botanist... should by no means (be) content with a list of names; he should study plants philosophically, should investigate the laws of vegetation, should examine the powers and virtues of efficacious herbs*") (White, 1988). Dyksterhuis, in 1949, proposed a functional (response) classification of range plants into the now well known Decreaser, Increaser and Invader categories. It needs to be said, however, that this type of classification, and the use to which it is put, has been much maligned in recent years although, like the term succession, it seems to be used quite freely, when it is convenient to do so, even by those who malign it. I believe that the reasons for opposition to functional plant classification and the use

to which such classification is being put needs to be analyzed in some depth so that appropriate adjustments can be made, if and where necessary, to its use in South Africa. These, then, I believe to be as follows, and I confine myself here to the response of plants to grazing intensity, since it is this response which is of so much importance in the consideration of grazing management and is the one which has received by far the most attention:

1. *Plants have in practice been assumed to behave similarly to grazing pressure under different ecological circumstances.* The reason for this assumption would seem to be a lack of evidence which shows how plants behave in different circumstances, rather than a failure to recognise that this may occur. It should nonetheless be said that there is no evidence that I can think of which shows that plants indeed react differently to grazing pressure under different circumstances, other than that they may vary in their sensitivity to or tolerance of different grazing pressures.
2. *All species are assumed to respond to grazing intensity.* It is often contended that this is not so. Admittedly, different plants will show different degrees of sensitivity to grazing treatment, but I do not know of any plant species which is totally insensitive to grazing treatment. I might add that if there are indeed such species, and they are palatable, they would no doubt be very useful species indeed.
3. That the response to any assumed gradient is often confounded with responses to other gradients within the environment, and is not purely a function of the gradient to which the change is attributed. If this is so, then it is the research procedure adopted and the interpretation placed on research data which are at fault, and not the principle of classifying plants according to their functional response or of using such a classification to interpret gradients within the community.
4. Perhaps the aspect of using functional species classes in veld condition assessment which has justifiably received most criticism is *the tendency to use a single benchmark community to represent the 'ideal' community within an ecological zone, irrespective of the interests of the user of that community.* Unfortunately the benchmark has been seen by some to be some mystical community with some sort of special powers.

There are three aspects which relate to the use of the benchmark community which deserve comment. The first is that no single community may be best suited to all types of land use. There should be no problem, however, in identifying a benchmark community within any area appropriate to any envisaged production system. The fact that all early work related to that community most suited to beef production was purely a function of the interests of the workers involved. All that is required here is for different interest groups to identify the most advantageous community for their envisaged production system. *This might be expected to be a more profitable venture than the inclination of some to spend their energies criticising others whose interests are different from their own and who have, therefore, proposed benchmarks with other objectives in mind.*

I believe, however, that there should be one constraint to any proposed benchmark. The community type selected needs to provide adequate protection to the natural resources of the area, and particularly to the soil resource. To argue otherwise, as some indeed do, is to argue for short term gain at the expense of long

term sustainability and I find it difficult to justify such an approach, which I consider more appropriate to a miner than to a grazier.

Secondly, there is the problem of applying benchmarks which are *inappropriate to the community in question*. Again this is merely a matter of practical expediency. The ideal would obviously be to match the community currently occupying any site against the known possible benchmarks for that exact site. The problem here is that these are invariably unknown and one is forced to establish, as a benchmark community, one which is derived from ecological conditions as similar to those of the site in question as one can. Unfortunately, there is invariably an element of guesswork here.

Finally, it is argued that *benchmarks are applied across too large a variation in ecological conditions*. This, of course, is merely a matter of scale and can be readily adjusted to meet any scale which is deemed appropriate. The danger is one of producing so many benchmarks that the system becomes unmanageable.

Concluding comments

So where does this leave us? I believe that an understanding of the value of plants as indicators of both biotic and abiotic conditions is of cardinal value to plant ecologists and veld managers.

Indeed, one cannot claim to know anything of the ecology of an

area without an appreciation of the indicator value of the plants growing in such an area. And so, in a Highland Sourveld community, for example, an abundance of *Elionurus muticus* indicates past selective grazing and suggests the dominance of sheep in the livestock mix. An abundance of *Eragrostis plana* suggests extremely intense grazing, often associated with areas where animals congregate to both compact the soil and to deposit large quantities of nutrients. A dominance of *Tristachya leucothrix* suggests a history of lenient use and infrequent fire. And so the potential list is endless.

What we need to do if we wish to make effective use of the resources of the vegetation of any area, is to learn the messages that the plants can give us.

That, after all, is what veld management, and adaptive management in particular, is all about.

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Boer goats demonstrating their potential as browsers for utilizing woody vegetation species (photo WSW Trollope). Some of the work published here investigates feeding preferences and selectivity of the goats as affected by season and time of day.