

## Rangelands as dynamic systems — structural and functional diversity in rangelands: integrating different scales in rangeland functioning

Conveners: Willy Stock  
University of Cape Town, South Africa

Many rangelands exist as dynamic systems where structural and functional diversity of the community is a function of several interacting factors. Understanding the effects of these factors in rangelands requires an understanding of component functioning at different scales. Integrating the range of levels from ecophysiology of individual organisms, populations, communities and systems is required if the dynamic nature of rangelands in response to driving forces is to be understood.

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### Invited Papers

#### The role of nitrogen in grasslands: from ecophysiology to ecosystem and competition to herbivory

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Assembling a unified theory of how grasslands work requires understanding how organisms work at multiple process levels, how organisms interact, and how state factors such as soil type and climate affect the functioning and interaction of ecosystem components. Nutrients in many grasslands are a resource that links functioning at many scales and serves as a major constraint that simplifies the potential diversity of ecosystem functioning. Natural selection for growth in humid, low nutrient supply environments have produced a plant strategy that includes low nutrient concentrations, low activity rates, and long lifespan for leaves and roots. These low-N traits serve as the basis for vertical integration of ecosystem processes as they are tightly linked to whole-plant morphology and serve to reinforce low N availability. High root length density that results from thin, long-lived roots minimises inter-root distance and decreases soil solution N concentrations. The low N concentrations of biomass strongly increase microbial N immobilisation. Also, plant N concentrations are too low to support mammalian grazers and these humid grasslands burn instead of being grazed, removing a potential source of N return and adding an additional loss factor. These broad patterns notwithstanding, it is important to note that there is tight coupling between plant traits and ecosystem processes and many traits such as N concentrations and activity rates are derived from a plant's effect on N availability, not necessarily causing them. Other factors serve to alter ecosystem functioning away from this low-N state. As N inputs increase from N<sub>2</sub>-fixation or deposition, N availability increases, species shift away from species with the low-N strategy, grazing increases, and fire decreases. At low water availability, nutrient availability becomes less limiting and the N cycle becomes more open with higher plant N concentrations (possibly to increase water use efficiency), increased grazing, and decreased fire. Differences in mean temperature do not seem to affect the N-state of ecosystems, but do affect the manner in which plants are built and N cycles. Although many important differences in plants and ecosystems are independent of N status, such as the differences between monocots and dicots, arraying plants and ecosystems along an N gradient is a powerful explanatory and predictive tool for understanding ecosystem function.

#### Ecological sustainability and changing land use in the Pilbara region of Western Australia — a question of scale and dynamics?

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Australian semi-arid rangelands are complex owing to spatial and temporal variability at a range of scales. Ecological dimensions (e.g. species diversity and abundance, rates of nutrient cycling, productivity) are typically dependent on a combination of factors (e.g. competition from nearest neighbours, nutrient and water holding properties of different soil types, landscape position) and disturbance events (e.g. fire, grazing, cyclonic rainfall and drought), all of which display spatial heterogeneity at varying scales. As yet, there are no satisfactory methods that either qualitatively or quantitatively describe the relative importance of spatial and temporal factors in driving ecosystem dynamics. Indicators of the ecological condition of arid ecosystems, variously described as 'health' (De Soyza et al. 2000) or 'function' (Ludwig and Tongway 1997), are traditionally based on vegetation characteristics, which in turn are often heavily dependent on the impacts of grazing and fire on plant response to change in the temporal and spatial availability of water and nutrients (Noy-Meir 1985, Stafford-Smith and Morton 1990). Hence, assessment of ecological condition for sustainable management and rehabilitation is hindered by a lack of quantitative information on ecological processes. We outline here some of our approaches to improving understanding of the dynamics of semi-arid systems in rangelands of north-western Australia including:

- De-stocking of rangeland, to assess the likely increases in woody vegetation
- Assessment of the effects of removal of woody vegetation — can we restore perennial grasslands?
- Measurements of roads, railways and stock movement on the decline of mulga (*Acacia aneura*) communities.
- Devising ways of measuring and understanding the functional significance of root systems to productivity, water and nutrient cycling

- Examination of the nature of heterogeneity in nutrient and water availability in relation to vegetation patterns and regrowth after disturbance
- Testing the response of soil resources to disturbance
- Describing and quantifying resource capture and distribution in the arid zone including measurement of vegetation distribution and its dimensions in terms of patch size and patch perimeter over multiple scales and in response to disturbance.

### Foraging strategy of cattle in Pantanal rangeland, Nhecolândia sub-region, Brazil

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The objective of this paper was to evaluate the foraging strategy adopted by cattle on grazing and to determine the relationship between patch biotic features and grazing time, from October 1997 to September 1999, in an area in the Nhecolândia sub-region, Pantanal, Brazil. All observations were made in an area of 151ha, under continuous grazing and light stocking conditions, so that the cows had the opportunity to be selective in their grazing. The grazing time (min ha<sup>-1</sup>) in each patch was verified by continuous sampling. In the area, spatial scales were identified based on functional use by cattle: nine feeding stations, nine landscape units and 29 feeding sites. Based on foraging hierarchy theory, the foraging decisions at spatial scales presented the following order: feeding station, landscape unit, feeding site, patch, species, plant part and bite. The main grazing patches represented 25% of the total area. With no constraints caused by abiotic factors, cows spent more time on the patches that allowed maximisation of the intake, obtained through the presence of a greater number of 'preferred' species. These species provided greater levels of crude protein and lower levels of neutral detergent fiber. However, not all patches selected for grazing presented a greater quantity of dry matter. Intake rate also appeared to be maximised by increasing the daily grazing time. The animals used spatial memory and social learning to choose the patches for grazing. Thus, the foraging decisions can be explained by determinist and analytic theories, both complementary to each other.

### The importance of ecosystem dynamics in managing the bush encroachment problem in southern Africa

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In southern African savanna the phenomenon of increasing woody plant abundance is commonly referred to as bush encroachment. Many savanna areas are water-limited ecosystems and bush encroachment is considered a major factor contributing towards the low occurrence or even total absence of herbaceous plants in severe cases. The presence of woody plants in savanna is associated with both positive and negative aspects, which is closely related to tree density. Any bush control program (chemical, mechanical or biological) should thus focus on tree thinning rather than clearing of all woody plants. The rapid establishment of woody plants after the removal of some or all of the mature woody plants may reduce the effective time span of bush control measures. In many cases the resultant re-establishment of new woody plants may in time develop into a state that is worse than the original state. It is hypothesised that a more stable environment can be created, which is not as prone to the rapid regeneration of new woody plants

by making use of system dynamics. Here the natural functioning of the savanna system is allowed to stimulate the development of an open savanna comprised mainly of larger trees. It is based on the principle that the distance between a tree and its nearest neighbour of the same species is not determined purely by chance, but that tree spacing is normally distributed. The larger the individual, the greater is the distance between it and the nearest individual of the same species.

### From individual scale to population and community scale: modelling community dynamics of the semi-arid grasslands of South Africa

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Community dynamics of rangelands is highly complex and characterised by the interaction of several interacting factors at different scales. Understanding the effects of these factors requires an understanding of component functioning at different scales. In this paper we present an individual-based spatially explicit community model for the semiarid grassland in South Africa which integrates data ranging from the scale of individual grass tufts to that of long-term population and community level responses to climate. While long-term population level changes in basal cover, species composition, and phytomass production to climate are well documented for the semiarid grasslands, knowledge on the demography of grasses is sparse. The specific aim of the model is to identify the specific demographic conditions of the grassland in different compositional states which were likely to have produced the observed population level pattern.

The model combines information on germination, establishment, growth, competition, fragmentation and mortality of grasses of four functional groups represented by three perennial grasses (*Cymbopogon plurinodis*, *Themeda triandra* and *Eragrostis curvula*), and the annual *Aristida congesta* with moisture availability and long-term rainfall data to simulate ecosystem dynamics over several decades. We calibrate model parameters and processes on the tuft scale using long-term data of population scale responses of phytomass production and basal cover changes to climate, and data on establishment and mortality collected during selected years. We find that monthly variation in rainfall and carry-over from previous months and years explains >80% of the observed variability in production. The grassland in good compositional state shows little change in the number of large tufts of dominant *T. triandra*, (mean mortality is below 10%) but a high variability in establishment and mortality of small tufts.

### Posters

#### Invasibility of pastoral vegetation in dry areas of New Caledonia by native and exotic plant species A1.1

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Rangeland and grassland stretch over 11% of the Island of New Caledonia characterised by a high degree of endemism and susceptible to biological invasion. Therefore the benefits of livestock systems from an economic and social point of view must be considered as well as the reduction of harmful environment and territory. Our research aims to produce a set of diagnostic tools for a bet-

ter management of pastures in order to improve animal feeding, while conserving the rangeland environment.

To succeed, it is essential to understand the processes responsible for the dynamics of these 'complex ecologic systems managed by man', particularly the proliferation of pasture weeds that threaten their sustainability.

Concepts and methods of systemic ecology, phytosociology and landscape ecology are used to assess the effects of environmental factors and management practices on the vegetation dynamic. These combinations of approaches allow exploration of the complexity of these ecologic grazing system at different time and space scales (population, communities, farming system, landscape, territory). We've studied particularly, the distribution and the factors responsible for the presence and the abundance of invasive species through the different types of pastoral vegetation. More than 300 spots have been described (botanical composition, environmental parameters, management practices) in 25 cattle stations.

We have selected two species as a model to study the invasive process and the reproductive and spatial strategies (vegetative/sexual reproductive strategy). Spatial extension of both species is extremely facilitated by the most widely used technique of control, the crushing machine and by overgrazing.

At the landscape level, the spatial distribution of patches of these invasives was related to field history, physical environment (soil, slope and geomorphology) and wild and domestic herbivore behaviour.

#### Impact of long term fire regime and herbivory on the structure of the woody component of the *Colophospermum mopane* shrubveld in the Kruger National Park A1.2

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The objectives of this study were to determine the effect of the current interaction of herbivory and season and frequency of burning on the overall condition of the woody component in the *Colophospermum mopane* shrubveld on basalt in terms of: the species composition, density, the structure, root development and the survival of *C. mopane*.

The study was conducted in the Kruger National Park (KNP) situated in the eastern lowveld of South Africa. The data collection was carried out in the Letaba Experimental Burning Plots (LEBPs) situated in the *C. mopane* veld. The mean annual rainfall of the veld type is 420mm. The LEBPs comprise four sets of 14 rectangular savanna plots, each measuring 180m x 360m, located at four different sites in the central section of KNP. The replicates were spread out within this veld type, in an attempt to achieve representivity. A partly randomised block design was laid out in which each of the 14 plots at each site was subjected to one of 14 burning treatments. KNP management since 1958 has applied these treatments continuously. Intensively maintained double strip firebreaks were used to prevent unplanned fires.

Mopani veld that is burned too frequently reaches a stage where bush structure is severely affected. Lower frequency fires at a stage when vegetation is still dormant affects the bush more than the grass. Medium to high intensity fires in spring after rain at a low frequency, results in fairly open bush and good quality forage. Low intensity fires and less frequent fires create a good balance between bush and grass.

#### Plant effects on soil N pools and dynamics in the Patagonian Monte, Argentina A1.3

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We hypothesised that in patchy ecosystems of the Patagonian Monte the main plant groups (perennial grasses and evergreen shrubs) would exert different effects on local soil N which would be enhanced with increased time span of soil colonisation. We selected four canopy types: 1. bare soil, 2. areas recently colonised by evergreen shrubs or perennial grasses, 3. small/incipient plant patches of perennial grasses and evergreen shrubs and 4. large plant patches with a long-time span of soil colonisation formed by both plant groups. We assessed N and C concentration, potential N-mineralisation and flush of microbial-N in the soil of each canopy type and N and C in senesced leaves of each plant group at each canopy type. We found lower N in senesced leaves of grasses than in those of shrubs (4.1mg g<sup>-1</sup> and 9.7mg g<sup>-1</sup>, respectively). C in senesced leaves did not vary between plant groups. Soil N and C were lower in bare soil than in the soil beneath all plant canopies, and higher beneath shrubs than grasses in small/incipient and large plant patches. Soil N accounted for 94% of the total variance in potential N-mineralisation and both soil N and C explained 89% of the variance in flush of microbial-N. Our results suggest that positive feedbacks between plants and soil N may be initiated by plant colonisation but are clearly noticeable after some time span of soil colonisation. In these interactions shrubs play an important role in the maintenance N-soil pools and dynamics.

#### Morphogenesis, phenotypic plasticity and adaptation to grazing of *Dactylis glomerata* L. in pastures of Buenos Aires Province (Argentina) under persisting water stress conditions A1.4

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The efficiency of the herbage use in grazing systems has to take into account not only the short-term maximisation of the ratio between forage production and consumption, but also the long-term persistence of the resources. In this context, the research aims to assess the response to grazing of *Dactylis glomerata* L. in pastures — Fertilised (F) with 103kg ha<sup>-1</sup> year<sup>-1</sup> of N and Not Fertilised (NF) — of a dairy farm of the Pampean region of Argentina during the spring of 1999 characterised by persistent dry conditions. The experimental design adopted was a completely randomised block with three replicates. During the re-growing periods after each defoliation, the following morphogenetic characteristics were assessed weekly by means of labelling techniques: LER (Leaf Elongation Rate); TLER (Total Leaf Expansion Rate); LAR (Leaf Appearance Rate). The phenotypic plasticity and the adaptation to grazing of *Dactylis glomerata* L. were assessed at the beginning and the end of each re-growing period: NPA (Number of Plants per Area unit); NTA (Numbers of Tillers per Area unit); NTP (Numbers of Tillers per Plant), growth forms (erect, semi-prostrate, prostrate) and death of the tillers of the central part of the tussock. Compared to the F treatment, the persistence of strong water stress conditions determined higher values of leaf expansion and appearance of *Dactylis glomerata* in the NF pasture. On the contrary, the major vigour of the plants growing in the F pasture determined a higher density of tillers of taller size and, even if of limited intensity, a better adaptation to grazing.

## Dynamics in herbivore aggregation resulting from seasonal changes in forage resource quality and production — a modelling approach A1.5

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We are investigating the interaction of large grazing herbivores with their seasonal forage resource. In our model, grasslands show strong seasonal variation in forage quality and production. In the beginning of the growing season, forage mass is low, but is increasing fast because production is high. At this time, forage quality, which is a negative function of forage mass, is high, too, because of the high quality of young plant material and little differentiation between plant parts. In the course of the growing season forage mass increases continuously while the production slows down. Plant tissue aging causes forage quality to decline and progressive differentiation of plant parts causes an increase in the variation of quality between plant parts. In the dormant season forage production ceases. The variation in quality between plant parts lessens as all plant material turns moribund and forage quality becomes low. The density of resident herbivores in our model is limited by the low dormant season forage availability and therefore is too low to check overall growing season biomass build-up. Herbivores select for plant parts of a minimum quality. The functional response has the shape of an asymptotic Holling's type II curve. The slope and maximum of the response curve depend on the density of the preferred plant parts. Feeding sites are selected by the herbivores on the basis of a nutrient intake maximising trade-off between quality and quantity of ingested forage. Our findings show seasonal dynamics in the spatial aggregation of herbivores. These dynamics are the result of intra-specific facilitation being the temporally limited benefits of herbivore co-operation in controlling forage resource quality.

## Patch grazing in an African semi-arid savanna: 1. Separation of patches and non-patches A1.6

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Patch grazing by domestic livestock was studied in a semi-arid savanna in the Eastern Cape, South Africa. With a mean annual rainfall of 515mm, the vegetation comprises a Themeda triandra dominated grass sward, and an Acacia karroo woody layer. Five grazing treatments were studied:

- Sheep stocked continuously at a conservative stocking rate (SC)
- Sheep stocked rotationally at a conservative stocking rate (SR)
- Cattle stocked rotationally at a conservative stocking rate (CR)
- Cattle stocked rotationally at a heavy stocking rate (CH)
- Cattle stocked continuously at a conservative stocking rate (CC)

Two techniques for separating patches (short grass) and non-patches (tall grass) were tested.

In the first technique frequency histograms, generated by estimating sward height with a falling plate disc-meter, were analysed using a Maximum Likelihood Estimation technique. Contrary to expectation, distributions were often unimodal, not bimodal, especially in treatments grazed by cattle. Bimodal distributions were evident only in the SC treatment. This technique was unsuitable, therefore, for estimating patch structure, and was rejected.

In the second technique, both species composition (estimated using a modified Dry Weight Rank method) and sward height were considered. DCA and TWINSpan analyses revealed that species were associated according to their ecological (Increaser/Decreaser) status. *Cymbopogon plurinodis* (Inc I) and *Eragrostis obtusa* (Inc II) were least likely to be associated. Patches and non-patches were clearly separated in ordination space based on species composition.

There was little inter- or intra-treatment variation in species composition for patches and non-patches. Based on species composition associations in ordination space, patches separated from non-patches at a height of 6cm. This technique was adopted.

## Patch grazing in an African semi-arid savanna: 2. Treatment effect on patch geometry and susceptibility to degradation A1.7

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An objective technique for separating patches (short grass) and non-patches (long grass) was used to describe the geometry of the grass sward of grazing trials in a semi-arid savanna. (See '1. Separation of patches and non-patches' for a description of treatments.)

The extent of patch grazing (defined as the area patch grazed as a proportion of the total area) was affected by stocking rate and grazing system. A 50% increase in stocking rate increased the extent from 32–68%. Animals that were stocked continuously grazed 50% of the area, while those stocked rotationally grazed 29% (cattle and sheep results combined). Animal type had relatively little effect on the extent of patch grazing, although sheep grazed patches more intensely.

Animals at heavy stocking rates and stocked continuously formed patches comprising a wide range of sizes (1–40m in length). Cattle and sheep stocked rotationally at conservative rates formed patches only less than 20m and 7.5m in length respectively, with the majority of patches being in the smallest size class (2.5m).

Densities of *Themeda triandra* were estimated across all treatments by measuring the abundance of plants in 1m x 1m quadrats on patches and non-patches. The density of *Themeda* on non-patches did not differ between treatments. On patches, densities were significantly lower ( $P = 0.012$ ) on treatments stocked rotationally at conservative rates (cattle and sheep) than on treatments stocked continuously or at heavy stocking rates. It was hypothesised that *Themeda* dies out in small patches due to relatively more competition with ungrazed neighbours than is found in large patches.

## Effects of fire regime on soil microbial community composition and activity A1.8

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Soil microbial communities and fire play major roles in nutrient cycling in savanna ecosystems. However, little is known about the long-term effects of fire regime on soil microbial community composition. By examining changes in broad level microbial community composition through the use of single carbon source utilisation assays (BiOLOG™) and changes in the activity and numbers of nitrifying bacteria and mycorrhizae, we hope to answer the question 'How does the fire regime affect the functional biodiversity of soil micro-organisms?' The second question to be answered in this study is 'How does the fire regime affect the activity of soil micro-organisms?' This will be examined by measuring 'soil respiration' as an indication of the activity of the soil microbial communities and by measuring *in situ* nitrogen mineralisation as an indication of the activity of nitrifying bacteria in the soil. The study will be conducted on the KNP burn plots, sited on the nutrient rich clay soils and the nutrient poor sandy soils. With this research we hope to gain an understanding of the effects of fire on the below ground biological processes involved in nutrient cycling in savanna ecosystems.

## Does soil chemistry influence vegetation change with time since fire? An example from semi-arid Western Australia

A1.9

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Through soil heating and ash deposition, fire alters soil chemistry. Fires burn through the landscape heterogeneously such that edaphic properties vary spatially in response to fire characteristics. Consequently, post-fire vegetation patterns can differ from pre-fire patterns at small spatial scales (~0–10m). Fires in semi-arid systems are often characterised by an increase in  $\text{NH}_4^+\text{-N}$  in the immediate post-fire period. This short-term increase may be important in re-establishment of vegetation, but little is known about how time since fire affects soil N resources and N uptake by plants. We examined changes in amounts and ratios of soil  $\text{NH}_4^+\text{-N}$  and  $\text{NO}_3^-$  after fire at five sites in the semi-arid Pilbara region of north Western Australia. Sites ranged with time since fire from 1–12 months. Spinifex (*Triodia* spp.) was dominant at all sites with a mixed *Acacia* or *Eucalyptus leucophloia* overstorey. Burnt sites were enriched in  $\text{NH}_4^+$  and  $\text{NO}_3^-$  compared to adjacent unburned areas. In both burnt (regenerating vegetation) and unburned treatments, ( $\text{NH}_4^+$ ) was significantly higher under spinifex tussocks than in open spaces. Burnt sites 6–11 months old had significantly less  $\text{NH}_4^+$  than sites more recently burnt. These results suggest that increases in soil N after fire occur mostly in relation to existing nutrient pools, and while time since fire appears to deplete  $\text{NH}_4^+\text{-N}$ , the relative difference between 'under tussock' and 'open' soil  $\text{NH}_4^+\text{-N}$  is maintained. Residual nutrient patterns following fire suggest that post-fire vegetation patterns are similar to pre-fire patterns.

## Seedling establishment under livestock pressure in succulent karoo systems: an impossible scenario?

A1.10

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Overgrazing in many farming systems in South Africa leads to the reduction of palatable plant species and their replacement by unpalatable species. In the succulent karoo we do not understand when and how grazing has the greatest impact on community composition. The effects of livestock on the establishment of perennial seedlings were tested in an arid winter rainfall region characterised by succulent karoo vegetation. Three sites, near different stockposts and with similar vegetation cover and soils were selected. Two treatments, grazing and microhabitat were studied. For each treatment combination, seedlings of five species indigenous to the study site, *Cheiridopsis denticulata*, *Leipoldtia schultzei*, *Ruschia robusta*, *Hirpicium alienatum* and *Tripteris sinuata* were transplanted in August 2000. At each site seedlings were transplanted inside and outside an enclosure, the unfenced seedlings being exposed to grazing by goats and sheep following their normal daily patterns of movement. Seedlings were transplanted in open areas and under *Galenia africana* (dominant plant species in heavily grazed areas) to provide two different microhabitats to test what affects the shrubs may have on seedling recruitment. The effects of grazing and microhabitat on seedling establishment, as well as grazing intensity were monitored over 16 months. Most species showed greatest mortality of seedlings in unfenced treatments. This was ascribed to grazing. However, seedlings in both fenced and unfenced treatments showed high mortality during the drier summer months. Nearly all asteraceous seedlings had died by the end of the study. Significantly more mesemb seedlings survived.

## Effect of different levels of browsing in the nutrient content of three shrubs

A1.11

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Game and extensive grazing are forestry uses affecting more than 80% of the Spanish forest area. Forest grazing and long-term maintenance in optimal conditions requires a knowledge of the nutritional characteristics of plants, feeding source for the animals, as well as their nutrient dynamics under grazing. Our objective was to determine how different levels of browsing affect the nutrient content in three very common and abundant shrub species of Galician forests: *Pterospartum tridentatum* (carqueixa), *Ulex gallii* (gorse) and *Calluna vulgaris* (heather).

Significant changes in the Na, K, Ca and N content in the plants under browsing conditions occurred during periods of less active vegetative growth. Different browsing levels applied did not affect P and Mg content. Although the highest level of browsing seemed to stimulate Na content in *C. vulgaris* during the winter, this mineral will be deficient generally for browsers feeding on these three shrubs. Potassium content in *C. vulgaris* and *P. tridentatum* was favoured by browsing during spring and fall respectively. We could expect deficiencies in K for vegetation communities containing predominantly these three shrubs. The highest intensity of browsing on *U. gallii* and *P. tridentatum* decreased this nutrient in the fall and in the winter respectively. Ca content was favoured by a moderate browsing in *P. tridentatum*. Different levels of browsing did not significantly affect N content, except for *U. gallii* that was affected negatively by the first level of browsing, although under the highest level of browsing applied N was stimulated.

## Scientific value of research on the experimental burn plots in the Kruger National Park

A1.12

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The Kruger National Park (KNP) has a long documented history of fire management. However in the 1950's it became clear that the knowledge about whether, where, when and how often to burn within KNP was lacking. In 1954, a series of long-term experimental plots (EBP's) to help answer such questions was undertaken in four of the major rangeland types in KNP. The initial experimental design aimed to investigate the influence of season and frequency of burning on the landscape, although the plots have also been widely used to also study the type and intensity of fires. Plots of 7 hectares in size, consisting of 12 treatments comprising a combination of frequency and season of burning were replicated four times in each of the four major landscapes. This long-term experiment has been ongoing for almost half a century and throughout this time numerous surveys, research projects and experiments have been undertaken. This poster serves to give an overview to the scientific community of the type of surveys conducted on the plots, the different research thrusts and updates a 1998 report on the EBP's in the light of recent research activities on the plots. The scientific and management implications are also discussed.

Root hydraulic architecture and water use by the riparian species *Melaleuca argentea* W.Fitz. in rangelands of north Western Australia A1.13

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*Melaleuca argentea* is a large tree common to permanent creeks of semi-arid zones in northern Australia. *M. argentea* is in declining condition downstream of mining activity where sites have been de-watered with subsequent lowering of the water table. This study identified sources of water utilised by *M. argentea* as well as factors influencing water fluxes within trees, particularly root hydraulic architecture. We studied root function by assessing vulnerability to cavitation and measured root sap flow in response to diurnal variation and change in Vapour Pressure Deficit (VPD). Roots of *M. argentea* were highly susceptible to cavitation (~0.1MPa) and cavitation is likely to contribute to sudden decreases in heat pulse velocity (cm hr<sup>-1</sup>) in most roots at midday. However, sap flow rates increased rapidly in the afternoons as vessels re-filled under negative pressure. Root architecture of *M. argentea* was quantified using topological and fractal approaches. Structural roots of *M. argentea* complied with fractal principles for estimating root length, biomass and link length, and confirmed that 75% of structural roots were as surface laterals. Placement of laterals was critical in determining water supply, where roots extending in to the stream always had greater rates of sap flow than roots in dry areas (stream bank), regardless of VPD. Deuterium analysis (δD) confirmed that the primary water source for *M. argentea* was stream and soil water, and not groundwater. This study highlights the lack of information regarding water use and adaptations by different species in semi-arid and arid rangelands.

Determining the scales at which nutrients act as drivers of herbivore distribution in the Kruger National Park A1.14

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Two of the main drivers of savanna function are soil moisture and soil nutrients. These drivers are governed globally by climate and regionally by the underlying geology. In the Kruger National Park, total K, Ca, Na, organic C and N concentrations in soil were significantly higher in the basalt-derived soils and total K, Ca, Na and P were significantly higher in soils in the lower rainfall areas. However, significantly more N was available in soils derived from granite, and total N was significantly higher in soils in the higher rainfall landscapes. Higher numbers of herbivores were recorded on the more nutrient-rich basaltic, and higher rainfall landscapes, but utilisation of these landscapes was not random. On the habitat/patch scale, grass tufts in certain areas were significantly more utilised. In the KNP, termite mounds and sodic sites are the best examples of such highly utilised patches, representing the only grazing lawns like those described for the Serengeti. Soil nutrients did not define differences at this scale but forage nutrients did. Significantly higher concentrations of nitrogen and lower C:N ratios were recorded in the leaves of tufts collected in the more utilised areas. Tufts collected on termite mounds had significantly higher concentrations of Ca, P, K and Mg, while tufts from sodic sites had significantly higher Na concentrations. Since these patches seem to be key resource areas, it is suggested they be well represented in vegetation and eco-system monitoring programmes in savannas.

Dynamic analysis of landscapes and landcovers for the knowledge and the evolution of the pastoral ecosystems in the Ferlo, Senegal A1.15

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For the past three decades, the pastoral ecosystems of the Ferlo have been undergoing severe and repetitive droughts. This coincides with an increase in the livestock and the concentration of pastoralists and agro-pastoralists around drillings and pools. Besides, the development of the rice fields in the Senegal River valley to the north of the Ferlo and the expansion of the 'peanut basin' in the south has led to the reduction of the pastoral areas and consequently to socio-spatial competition for access to and management of the natural resources.

To apprehend these changes and their impact on the environment and to better understand the dynamics of its evolution, a 'diachronic' and 'synchronic' study of landscape and land cover has been done with the help of aerial photography and satellite imagery and site research on three characteristic regions. The results show two opposite zones: the east and north Ferlo against the south Ferlo. The east and the north Ferlo are characterised by a relative increase of the vegetal cover between 1980 and 1999, after a phase of recession between 1978 and 1980. In the population sphere, we can note a decrease in settlement and agricultural areas. On the other hand, in Ferlo south, though vegetal cover is thicker, it is less dense than it was in 1969. In return, the settlements and the agricultural areas are spreading to the detriment of the rangelands.

This paper will first deal with the spatial analysis and then with the results obtained and finally the inferences that stand out.

Determination of the role of each independent variable (soil factor) in the distribution of plant species in Tabas Kavir, Iran A1.16

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The study area is located at a longitude of 56°42'–57°02'E and a latitude of 32°17'–33°45'N. The western limit of the study area is Kal shor Tabas; the 700m altitude line in the east; Dehshor and Feiz Abad villages in the north and Moazum Abad village in the south. In order to determine and study the effect of each independent variable (soil factors) on plant species distribution in the studied area, soil and vegetation studies were carried out.

Results of these studies were soil maps, a classification map of land irrigation capability, a land use map and a vegetation map. We selected and made grids in four areas that included all soils and vegetation types. We considered soil distribution, vegetation and land use of the studied areas. Consequently in considered to percent of different vegetation types, least necessary samples calculated in order to validate statistical calculations at 95% level. A double of highest value for calculated samples was selected and sampled in random systematic method. Finally, 310 points were selected and sampled. Statistical calculations were carried out on the observations and soil attributes at each point sampling. Then by converting the independent variables to standardised variables and unifying range variety of all variables, and calculating BETA value at multiple regression, the effect of each variable clarifying variance of dependent variable were determined.

## Nutrient dynamics and inventory in a tropical grazing land ecosystem at Maramalai, southern India A1.17

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The present study deals with the distribution of three elements (N, P and K) in vegetation compartments and soil (top 30cm) in a tropical grazing land at Maramalai, southern India. The live shoot s contain the highest amounts of N, P and K. Nitrogen in live shoots varied from 4.63–24.02g m<sup>-2</sup> and in roots the nitrogen content ranged between 1.74 and 8.73g m<sup>-2</sup>. The monthly changes of live shoot nutrients (N, P and K) showed a significant relationship with a linear combination of rainfall, ambient temperature and soil moisture.

Inventory of the nutrients indicates that, of the three elements studied, annually 526.1kg ha<sup>-1</sup> of N, 27.6kg ha<sup>-1</sup> of P and 538kg ha<sup>-1</sup> of K was taken up by the vegetation while 70.7kg ha<sup>-1</sup> of N, 2.9kg ha<sup>-1</sup> of P and 40.8kg ha<sup>-1</sup> of K were released. Less than 6% of the nutrients entered the vegetation, except potassium (15%).

## Classification of vegetation ecological groups and their relations with physiographic characteristics A1.18

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In order to identify the plant ecological groups and determine their distribution pattern with physiographic characteristic, this research was carried out in an area of 124ha at altitude of 80–1200m from sea level, in Bousher province, southern Iran. To identify and classify vegetation cover, 248 grid permanent plots with 256 square meter for tree-shrub layer and 64m<sup>2</sup> for herbal layer were chosen on the basis of the Brun-Blanquet combined cover-abundance scale. The phytosociological study was carried out in the last parts of the growing season (March and April 2002) in two distinct layers (tree-shrub and herb cover). A clustering method was used for the vegetation analysis. Classification analysis was done using TWINSPLAN to identify plant ecological groups. GIS application was used to develop mapping plant ecological groups and Digital Elevation Model (DEM). Comparison among plant ecological groups, slope, aspect and elevation maps showed a significant relation between vegetation and elevation, but there was not a significant relation between-vegetation and slope and aspect.

## Landscape approach to understanding water use by trees in the Pilbara region of north Western Australia A1.19

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Extraction of groundwater by government agencies, mining industry and pastoralists in the Pilbara region of north Western Australia may have significant impacts on vegetation health. However, the role of groundwater in maintaining/supporting ecosystems is poorly understood throughout semi-arid Australia and limited to presumptions based on descriptions of plant communities. Studies of the natural abundance of deuterium ( $\delta D$ ) within soil water, groundwater and plant sap are useful in determining sources of water used by a range of plants species growing in deserts, savannas and riparian systems. Stable isotope techniques used in

combination with 'heat pulse' methods for measuring amount and direction of sap flow can be used to estimate the amount of water used by trees and the dominant factors affecting flow of water through different species. Such information is essential for predicting the response of semi-arid vegetation to change in water supply. We used a landscape approach to assess responses of Eucalyptus and Acacia species to a gradient of water availability, where depth to groundwater increased with distance from creek-lines. Species growing in creek-lines used both soil and groundwater, but the source was dependent on season. For example, after winter rains the  $\delta D$  of xylem sap of all species reflected the  $\delta D$  of soil water ( $\sim -25\%$ ) while in drought periods  $\delta D$  of many species reflected  $\delta D$  of groundwater ( $\sim -49\%$ ). Species growing on floodplains or hill slopes had little access to water at any time. All species had fast rates of respiration ( $\sim 7\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) except *Acacia aneura*.

## Architectural models of branching of *Kochia Prostrata* (L.) Schrad. and *Salsola orientalis* S.G.Gmel under the influence of shoot clipping A1.20

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The growth of shoots is a physiological and morphological indicator. This character determines the general structure and habit of a plant. The plants possess regenerative power, that is they can grow under grazing or cutting and give new green mass. The study of morphogenesis after clipping part of the annual shoots in various periods and to different lengths will allow us to show some peculiarities of shoot formation and the reserve potentialities of organisms, that will promote an understanding of biormorph formation and can be used in the practice of pasture science. The aim of the present investigation is to reveal the influence of clipping on architectural models of 4, 9 and 12 year old plants of *Kochia prostrata* (L.) Schrad. and *Salsola orientalis*. The investigations were carried out on experimental plots of Uzbek Scientific Research Institute of Karakul Sheep and Ecology of Deserts in south-west Kizilkum and in the foothill semi-desert at the foot of the Nurata hills. The annual shoots were cut in spring (the end April to the beginning of May) and in summer (in the middle of June) to 60–70% (a moderate grazing) of their length. *Kochia prostrata* refers to the vital form — it is a semi-bush, the characteristic features of which are the presence of quickly growing generative shoots and dying away on 50–60%, the presence of rezid. This is an evolutionary advanced biormorph, transitive between bushes and grasses (Khokhryakov 1975, 1981). *Salsola orientalis* is a semi-bush with a shorter shoot length and more intensive dying away (up to 80% of shoot length). In control for four year plants of *Kochia prostrata* and *Salsola orientalis* characterised by the presence of one rezid of the order with the length 4–5cm, II order in *Kochia prostrata* — 6 in *Salsola orientalis* 4–6, with the length of 2–4cm. The rezids of III order *Kochia prostrata* has 8–12, *Salsola orientalis* has 8–11, with the length 1.5–4cm. 9, 12 year plants have the number of skeleton axes — 6, with the length of 4–5cm in *Kochia prostrata* (L.) Schrad. in *Salsola orientalis* — 4–7cm. The system of shoots forms a stretched, conic form of bush. The clipping of plants influences their general habit, changing the height, bush diameter, the number of shoots, the correlation of their types. After clipping in spring the bush acquires a spherical form, the number of generative shoots increases and the plant rejuvenates. Summer clipping has the same influence on the habit of the bush, the bush becomes spherical, the number of shoots increases, amount which the brahiblusters are prevailed. In old age plants a weakening of root-leaf connection occurs (according to Kazaryan 1969), the necrotic processes are developing. That is why the clipping of shoots in the stress period of vegetation leads not to the mobilisation of merysystems, but to their exhaustion and activity stopping and at the end, to the plant extinction from the grass stand.

## Nutrient partitioning in herbaceous biomass in savanna zones of Nigeria A1.21

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Nutrient partitioning in herbaceous components of natural rangelands in Nigerian savanna was studied. The aim was to determine the nutrient elements content of herbaceous components (forb; grass) at peak biomass and changes in nitrogen and structural constituents in forb and grass species in Nigerian savanna. Nigerian savanna lies within latitudes 6–14°N and longitudes 2°44'–14°42'E. The mean maximum herbaceous yield ranged from 130.67–407.18g m<sup>-2</sup>. Grass biomass contributed 71.7–93.2% and forb biomass 6.8–28.3% of this. Forb biomass has higher concentrations of the nutrient elements (N, Ca, Mg, K, Cu, Zn) than grass biomass at peak growth. The order of concentration of these elements in the herbaceous components is forb Ca>K>N>Mg>Zn>Cu and in grass K>N>Ca>Mg>Cu>Zn. Grass accumulated higher quantities of the nutrient elements than forb. At peak growth, nitrogen content of grass species decreased by 57.0–69.4% while that of forb decreased by 22.0–33.1%. There was also a higher percent increase in structural constituents (fibre, lignin) with age in grass than in forb species. These findings indicate the contributions of the different herbaceous components especially forb component can make in animal nutrition on natural rangeland. It is advocated that in managing savanna as rangeland effort should be made to increase the proportion of forb species in grazing lands.

## Looking down below for what lies up above: ignoring higher level processes severely limits our understanding of rangeland dynamics A1.22

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Traditional range ecology based on plant community dynamics (especially Clementsian Plant Succession Theory) has been widely criticised and to varying degrees replaced by more realistic models that emphasise hysteresis and non-linearity. More recently, landscape function has also gained international currency and offers great promise in linking on-ground observations to satellite-based observations.

However, we contend that our development of models has still not addressed another failing of traditional range ecology: its focus on what can be observed by the human eye. We have not kept pace with technology; in many ways we are still asking the same old questions at the same old scales. We have added some new questions (e.g. biodiversity), but even this opportunity to take a more holistic, hierarchical approach seems to have been passed up largely. This limited view of the rangelands precludes diagnosis of higher-level, off-site (out of sight) factors that may need to be recognised to achieve local management objectives.

We explain these criticisms using examples of scrub encroachment, remote sensing and biodiversity research from both Australia and southern Africa. We present an alternative approach that includes hierarchical salience analysis, including driving land succession processes and explain how the approach is being used in a participatory catchment restoration project.

## How do ruminants survive on arid rangelands? Modelling the effects of plant-animal interactions A1.23

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In the semi-arid tropics rainfall is seasonal and varies widely between years. Consequently, grazing animals are subjected to short or long periods of moderate to severe undernutrition.

Undernutrition in young ruminants affects their chances for survival and the time required to reach the weight and body composition at which they are suitable for slaughter or able to work as draught animals or, if female, to conceive and rear offspring. Animals can adapt to undernutrition by differential mobilisation of tissues. Initially the weights of the liver and small intestine decrease rapidly which leads to a reduction of the animal's energy expenditure. Fat and protein are catabolised to meet the requirements for maintenance. When the nutritional restriction is removed, animals may respond in different ways. Partial or complete compensation may occur if previously restricted animals increase their growth rate relative to that of their unrestricted contemporaries. However, there may be no compensation. The ability to predict the probable short- and long-term consequences of undernutrition will support the planning and evaluation of measures to ameliorate undernutrition in a specific environment. A mechanistic model was developed to simulate voluntary intake, rumen digestion and nutrient utilisation during continuous growth, undernutrition, and realimentation for growing cattle. The model also simulates changes in the weights of ash (bone), muscle, adipose tissue, liver and small intestine and the relative effects of these changes on the maintenance expenditure. The model may be used to predict energy expenditure, liveweight changes and the probability of survival due to the variation in herbage quantity and quality.

## Interaction of tannins and saponin in herbivore diet A1.24

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Sheep and goats were allowed to choose between Mediterranean shrubs containing tannins and other Mediterranean shrubs containing tannins and saponins. Twelve sheep and goats offered tannin-containing shrubs consumed less biomass than animals offered shrubs containing tannins and saponin. Simultaneous consumption of shrubs that contain tannins and saponin may promote chemical interactions that inhibit toxin absorption from the intestinal tract. This type of interaction is likely to have influenced the evolution of herbivore feeding behaviour.

## The effect of the sub-habitat below savanna trees on soil, grass and grass utilisation by cattle A1.25

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The relationship between savanna trees, the grasses growing in the sub-habitat beneath their canopies and grass utilisation by beef cattle was investigated in the semi-arid camelthorn tree savanna of eastern Namibia, an area that supports an economically vital beef exporting industry. In each of eight long-term experimental treatments, consisting of combinations of four cattle stocking rates (15, 25, 35 and 45kg cattle biomass ha<sup>-1</sup>) and two beef cattle types (large-framed Simmental x Afrikaner crossbred and small-framed Sanga purebred cattle), three sub-habitats were studied: the sub-habitat underneath leguminous *Acacia erioloba* trees, the sub-habitat underneath non-leguminous *Terminalia sericea* trees and a sub-habitat in the open, not covered by a tree canopy. In each sub-habitat, representative soil samples taken at mid-canopy level were analysed for physical and chemical soil properties, grass population density and composition was determined by individual counts, grass yield was measured by clipping, the nutritive value of grasses was determined by subjecting a representative sample to standard laboratory analyses and the utilisation of grasses was established by bite-counting during diet selection observations on foraging cattle. Results indicate that the density of grasses underneath tree canopies increases with an increase in cattle stocking rate, but that

total grass yield declines. Grass species react differently to grazing pressure, but in general, grasses become more numerous, smaller and less productive as grazing pressure increases. This effect is particularly obvious under leguminous trees and may be the result of cattle utilising grasses growing under leguminous trees preferentially. As grazing pressure increases, cattle tend to find an ever-increasing proportion of their most preferred grass species underneath tree canopies, in particular underneath leguminous trees, rather than in the open, especially the large-framed cattle type. Severe grazing at high stocking rates leads to a change in the grass population under trees, where *Eragrostis lehmanniana* and *Stipagrostis uniplumis* displace grasses more common at lower stocking rates, such as *Anthephora pubescens* and *Schmidtia papophoroides*. Laboratory analysis of the nutritive value of grasses suggests that, even though the proportion of grasses taken underneath trees seldom exceeds 20% of all grasses taken by cattle, these grasses may contribute an extraordinary amount of nutrients. This is due to differences in the chemical properties of the soil of each sub-habitat: soil underneath trees contains noticeably higher levels of organic matter, significantly more N, P and K and is slightly more acid than soil in the open sub-habitat. Results indicate that the soil–tree–grass association in arid tropical savannas has a profound and beneficial effect on the dietary preferences and nutritive intake of free-ranging livestock and ultimately, on animal productivity.

#### Stability of Pilbara grasslands in relation to management and ecological events

A1.26

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Quantitatively assessing the stability of grassland systems for management purposes has been made more tractable in the last decade because of:

- 1 Increasingly robust monitoring of rangelands over time through digital data capture;
- 2 Large improvements in available computational power;
- 3 Developments of Bayesian statistical theory leading to Markov Chain Monte Carlo methods.

Markov Random Fields (MRF) are used to simulate vegetation patterns from a time series of photographic images of vegetation cover in Pilbara grasslands, Western Australia. The probabilities used in defining the MRF are then taken as functions of site-specific and temporal factors. In effect, different transition probabilities that quantify system change can be estimated for given time intervals and different system events. These conditional probabilities lend themselves to stability analyses, based on the work of Li (1995). In principle, the stability of a mathematical system should mirror the resilience of the ecosystem being studied. This is because mathematical stability and ecosystem resilience both refer to the ability of a system to return to an 'attracting' or 'stable' pattern after that pattern has been perturbed by some event. Different patterns of system events can then be compared, thereby identifying patterns of events that lead to stability, and patterns that lead to instability and which management should avoid. This approach of analysing spatio-temporal changes in ecological processes using a series of digital images could easily be generalised to any ecosystem for which regularly collected image data exists.

#### Constraints to productive and sustainable grazing systems in temperate southern Australian grasslands

A1.27

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A national experiment, undertaken as part of the Sustainable Grazing Systems Program, collected data over 5 years from 6 grassland sites in temperate Australia with the aim of improving profit from livestock while reducing land degradation caused by surplus water. Sites were located in New South Wales, Victoria and Western Australia and included both sown and native pastures in high rainfall zones (>600mm annual rainfall) varying from winter to summer dominant. Site data were collected according to a common protocol and a unifying concept of themes for pastures, animal production, water, nutrients and biodiversity were used to identify the major factors influencing production and sustainability. Across-site data were analysed using both experimental data and modelling.

Much of the variation in herbage mass accumulation was accounted for by pasture type (native or sown), soil P level, legume density, stocking rate and plant available water. Perennial grass persistence varied according to stocking rate, grazing management, soil pH, fertility, standing herbage mass and plant available water. For animal production, the most significant factor affecting carrying capacity were rotational grazing, annual legume and perennial grass content, soil pH, soil P and plant available water. The probability of generating winter excess runoff and drainage was highest (>80%) on duplex soils in the winter dominant rainfall zone. Overall, the impact of perennial grasses on the quantity of water used was not large when compared with the effect of trees.

#### The effect of twenty years of burning on the species diversity and basal cover of a moist montane grassland in KwaZulu-Natal, South Africa

A1.28

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The Drakensberg mountains in Lesotho and South Africa are an important reservoir of biodiversity. Fire is an integral part of management in the landscape, but the long-term effects of fire on plant diversity have been insufficiently studied. The species composition and basal cover of a twenty-year burning trial in a conserved area of the Drakensberg were measured with a point-based survey. Grassland protected from fire for 20 years had significantly lower basal cover (12.8%) than burned plots (17.2–20.9%). Annual winter burning had significantly lower species richness (14.7) than annual (19.0) or biennial (17.3) spring, quintennial (five-yearly) spring (18.0) or unburned (18.3) plots. Mean Shannon's diversity indices ranged from 1.9 to 2.3, and evenness values from 0.69–0.81; neither showed significant differences. Ordination showed a shift upward along axis 2 (eigen value of 0.148) with time. Unburned plots shifted to the right along axis 1 (eigen value 0.503) to a region dominated by *Hapochloa falx*, while annually and biennially burned plots stayed close to the origin. The exception was annual winter burning, which shifted the plots to a region dominated by *Themeda triandra*. Quintennially burned plots were most heterogeneous in composition, and unburned plots changed the most in composition relative to burned plots.

#### The influence of sub-habitat differentiation on the soil under varying competition regimes in mopane savanna in South Africa

A1.29

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The investigation was conducted on a densely wooded area in the mopane savanna of South Africa dominated by the tree species *Colophospermum mopane* interposed with a few individuals of *Salvadora australis*. Seven plots were subjected to different intensi-

ties of tree thinning, ranging from a totally cleared plot (0%) to plots thinned to the equivalent of 10%, 20%, 35%, 50% and 75% of the leaf biomass of a control plot (100%). Distinction between five sub-habitats was made. These included the following: between tree canopies, under *C. mopane* trees, where *C. mopane* trees have been removed, live *S. australis* and where *S. australis* have been removed. Ten topsoil samples (to a depth of 150mm) per sub-habitat were randomly taken in each experimental plot, bulked, thoroughly mixed and one subsample taken for analysis. Differences between sub-habitats were large and significant. Soil under *C. mopane* canopies had a significantly ( $P < 0.001$ ) higher % total N, % organic C, P, Na, K, Mg and pH in comparison to soil from between tree canopies, while Ca and electrical resistance did not differ significantly ( $P > 0.05$ ). The soil from the *S. australis* sub-habitats differed radically from that of the *C. mopane*-subhabitats in respect of all the investigated soil variables with the exception of P. Few of the investigated soil variables, on the short term (3 years), changed significantly as a result of the various tree thinning treatments.

### Recovery capacity of *Poa ligularis* after defoliation in Patagonian grasslands: auxiliary buds and biomass production

A1.30

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*Poa ligularis* is one of the dominant species in Patagonian grasslands that decreases under grazing. We investigated the defoliation effect on the number and position of viable axillary buds, and biomass production during one growing season. Experiments were arranged in a randomised complete block design and conducted in a natural stand. Treatments included one defoliation height (10cm), one to five times a year, in addition to undefoliated controls. Bud respiratory activity was examined using tetrazolium test and the vital stain Evan's blue. At the end of the growing season, plants that have been defoliated more than three times showed significantly ( $P < 0.05$ ) lower number of respiratory active buds than unclipped controls. Both defoliated and undefoliated plants produced more ( $P < 0.05$ ) axillary buds at the periphery than at their centre. Mean production of dry matter on plants defoliated one, two, three, four, and five times a year was 14.02g, 13.32g, 10.98g, 16.63g and 10.56g, respectively, compared to 11.34g on undefoliated controls. Defoliation treatments increased shoot weight by 13.4% on average compared with undefoliated controls. Although grass biomass was higher when plants were defoliated four times a year, the number of active buds was reduced with more than three defoliation events. Therefore, it appears that *Poa ligularis* could tolerate moderate grazing intensity without compromising its potential regrowth capacity in the following season. Longer-term studies of the effects of defoliations on biomass production and bud metabolic activity are needed to exactly understand the effects of grazing in natural grasslands.

### Tree influence on grassland in the Paraguayan Chaco

A1.31

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A common problem for grasslands in the semi-arid central Chaco is the competition exerted by invading woody species. There is, however, an increasing awareness of positive influences of individual trees on the associated grassland, beyond the recreational

and esthetical values of a park like woodland and the offer of shade and protection for livestock. In this study, soil and grass cover was analysed under the canopy and in a 30m distance from the canopy, at three consistent directions, of 65 randomly selected isolated trees belonging to seven different species, *Aspidosperma quebracho-blanco*, *Astronium fraxinifolium*, *Bulnesia sarmientoi*, *Chorisia insignis*, *Schinopsis heterophylla*, *Schinopsis quebracho-colorado*, *Prosopis alba*. Tree canopy influence on grassland characteristics was highly dependent on the prevailing soil type, even though at both, loamy (luvisol) and sandy (regosol) sites, soil organic matter and grass crude protein contents were significantly higher under the canopy than in the open area. Canopy influence on grass dry matter yield and water content of fresh grass was only significantly positive at sandy sites. No tree influence was found as far as the metabolisable energy content of the grass is concerned. Equally, no significant and consistent differences between tree species were observed. It is concluded that, wherever excessive grazing and treading of animals seeking shade is avoided, a generally positive canopy influence of individual trees on grassland characteristics occurs in the Paraguayan Chaco.

### Interaction of rainfall, nutrients and topography limits growth of native and introduced plant species in Australian semi-arid grassland

A1.32

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Arid ecosystems that experience pulses of primary production related to variable rainfall may shift between water and nutrient limitation of plant growth. I tested this hypothesis by adding several levels and combinations of nutrients to a semi-arid South Australian grassland at the start of the growing season following a severe drought in the previous year, with rainfall only 42% of the long-term annual mean of 257mm. The two growing seasons immediately after the drought received 122% and 88% of the long-term mean annual rainfall. Nutrient limitation developed rapidly on a claypan, but the adjacent ridge remained water-limited, probably due to the small soil volume. Nitrogen was more limiting than phosphorus, but nitrogen plus phosphorus caused a greater increase in above-ground plant biomass on the claypan than nitrogen alone. Nitrogen amendments increased the percent nitrogen in plant tissue on both the claypan and ridge. Introduced species were more common on wetter, more fertile claypan and responded more strongly to nutrient additions than native grasses and forbs. Thus, both species and site-specific characteristics influenced the response of the plant community to nutrient amendments. Increasing nitrogen inputs might have significant effects on the species composition and ecosystem function of these oligotrophic semi-arid Australian ecosystems.

### Interpreting plant-level spring growth of tufted perennial grasses using the model TILLER

A1.33

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The dominant plant forms in humid grasslands are caespitose perennial tufted grasses. Seed recruitment in these environments is probably restricted to rare events so tufted grasses persist through vegetative reproduction of secondary tillers, which are able to develop into independent rooted plants. It is hypothesised that morphology differences between species are at least partly responsible for the field-scale changes in species composition in response to defoliation by fire and grazing. The mechanistic object-orientated model, TILLER, which has been designed explicitly to evaluate growth of tufted grasses, is used to explain the spring growth pattern exhibited by some tufted grass species in the species-rich Southern Tall Grassveld of South Africa in response to various defoliation regimes of fire and grazing. Initial results suggest that only a very small amount of stored carbohydrate is critical to restart spring growth, but the actual growth rate of plant organs

depends on the availability of carbohydrate through the middle of spring, which depends on photosynthate production and organ sink demands. Critically sink demand depends on tiller recruitment at the beginning of spring, a characteristic of species.

### Nitrogen and phosphorus allocation as affected by grazing in a riparian community A1.34

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Decomposition, mineralisation and nutrient allocation are not well understood in riparian ecosystems. The purpose of this study was to assess sources and sinks of nitrogen (N) and phosphorus (P), and decomposition of leaf litter, in grazed and protected treatments in a montane riparian ecosystem in Colorado, USA. Forage samples of water sedge (*Carex aquatilis*) and planeleaf willow (*Salix planifolia*) were collected monthly throughout the growing season and analysed. Nitrogen was greater in water sedge from grazed areas than from exclosures during most of the growing season. Phosphorus was only higher in previously grazed forage of water sedge during one sampling period. Nitrogen, P and digestibility were greater for plants of planeleaf willow from short-term grazed paddocks than from protected areas. Digestibility of water sedge during the latter part of the growing season was also greater for previously grazed plants than similar plants in exclosures. These data indicated that uptake of N and P by plants in grazed areas may exceed uptake by plants in ungrazed exclosures. There were no significant differences in litter decomposition rates for either species between grazed and protected areas throughout the growing season. However, higher nitrate availability and plant uptake in grazed paddocks may indicate more rapid mineralisation with grazing disturbance. Through a better understanding of soil–microbe–plant interactions in nutrient uptake, utilisation and distribution, we should be able to better manage these riparian ecosystems to be an efficient sink of nutrients for plant uses and maintain stream water quality.

### Patterns of forb diversity in the southern African grasslands A1.35

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Southern African grasslands represent a wealth of floral diversity, yet to date this has been poorly investigated. Forbs constitute most of this diversity, but have largely been ignored in favour of the dominant grasses that are important for livestock production. To gain a better understanding of patterns of floral diversity across our grasslands, we examined forb life history strategies and growth forms from 14 sites along a rainfall gradient ranging from ~650mm to ~1 600mm pa. Across this range perennial dicot forbs form >70% of the taxa. A major compositional shift in life form and history strategies was, however, noted around 800mm MAP. In drier grasslands (<800mm MAP), infrequent burning and regular droughts favour reseeding life history strategies; there are few monocots and the proportion of annual species rises from ~5% to ~25% around 650mm MAP. In the wetter grasslands (>800mm MAP), the proportion of monocots increases, annuals are seldom encountered and frequent burning and infrequent drought favour resprouting, as indicated by a greater proportion of perennating organs. The increase in monocots in the wetter grasslands corresponds to an increase in flat and upright basal leaved growth forms. While the proportion of upright cauline leaved growth forms was not strongly affected by rainfall, creeping cauline taxa increased in the drier grasslands. Thus it appears that the forbs, like the dominant grazing grasses, are divided into two distinct floras along this rainfall gradient.

### Litter cover in sagebrush steppe-types and patterns of occurrence A1.36

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Litter is a dominant ground cover variable in sagebrush steppe ecosystems. Litter includes fallen herbaceous material; humic material; animal feces; woody parts of sagebrush and other shrubs; sagebrush leaves; leaves of other shrubs and forbs; flowers and seeds of sagebrush; flowers, fruits, or seeds of other shrubs and forbs; and dead portions of cushion plants. Grasses and sedges (45%), humic litter (15%), and fallen sagebrush leaves (13%) were the predominant litter types in high-elevation sagebrush steppe in southern Wyoming, USA. On windy sites, litter layering only occurs under and on the lee sides of sagebrush plants. Layers consist of grass/sedge litter or woody parts of sagebrush on top of sagebrush leaves, which in turn cover humic litter. Litter plays an important hydrologic role by protecting the soil surface from raindrop splash, promoting infiltration, and providing opportunities for both water detention and retention. The woody portions of shrubs are the most effective litter type for watershed protection.