1.2 Modelling

1.2.1 Simplification of a complex system

Antagonistic to any generalized piosphere modelling effort is the range of responses that have been found for vegetation and soil properties with distance from water across different study sites. That is to say, the piosphere effect is a multivariate system response, further complicated by its particularity to the site of interest. The spatial extent of vegetation impact is largely determined by soil and vegetation type (*e.g.*, Kalikawa 1990 and Section 1.1.6). However, within the detectable extent of impact for any given site, characteristic zones of compositional change in the vegetation and particularly in the tree-grass ratio may be recognised. This has enabled the representation of the individual piosphere as annuli in the form of conceptual models in the presence (Collinson 1983) and absence (Perkins *&* Thomas 1993a) of woody layer mediation by browsers.

1.2.2 Conceptual models

Whilst being parsimonious treatments of a complex system, the conceptual models do provide a reasonable basis upon which to design an improved understanding of the piosphere response (*e.g.*, one that includes temporal dynamics). Changes in composition with time depend on the life histories of individual plant species present, the selectivity of animals, the plant response to that grazing pressure, and on the plant location along the gradient of grazing pressure (Lailhacar *et al*. 1993). A notional pattern displaces less hardy (centrifugal) species, from the centre, outwards, towards the perimeter, and replaces them with hardier (centripetal) species (*c.f.* Fig. 1.5). This is a rule of thumb, an aid to the conceptual models, for which some studies are in good agreement (*e.g.*, Friedel 1988, Thrash *et al*. 1993), and others contradict

wholly (*e.g.*, Stroleny & Mentis 1989, Perkins 1991, van Rooyan *et al.* 1994), or at least in part (*e.g.*, Foran 1980; Andrew & Lange 1986b). Why all piospheres do not conform to the concept may be due to complicating factors such as grazing-induced vigour (Andrew & Lange 1986b), implying a complex community response to disturbance (Perkins & Thomas 1993b).

1.2.3 The use of conceptual models in rangeland management

Further abstraction allows these models to be used as units of landscape management (Foran 1980, Collinson 1983). Incorporating knowledge about livestock behaviour and patterns of home-range use (*e.g.*, dietary preference, wind direction) and paddock design, will highlight areas most susceptible to impact (Pickup & Stafford Smith 1987). Consideration of these areas allows the construction of management strategies for optimal rangeland use and minimal degradation (Cridland & Stafford Smith 1993). Application to wildlife areas involves additional levels of complexity. These include notions regarding the stabilising qualities of heterogeneity on system dynamics (Goodman 1982), wet and dry season ranges (*e.g.*, Funston *et al.* 1994), and the importance of maintaining rare species refugia in the landscape (Owen-Smith 1996).

1.2.4 The general logistic model

The piosphere effect that underlies the conceptual models is the pattern that results from the amalgamation of animal impacts and the separate graded responses of vegetation and soil characteristics. The separate responses fall into two categories; those in which there is a concomitant increase in the level of the variable with distance from water, and those that decrease. Graetz & Ludwig (1978) recorded vegetation and soil data that appeared sigmoid when plotted against distance from water. This led them to suggest that a generalised regression model could be used to describe both the increasing and decreasing variable response types in terms of a logistic curve (Fig. 1.6). The parameters of this model lend themselves well to mathematically describing the shape of the piosphere pattern depicted by the conceptual models. The upper asymptote, K, and the slope parameter, b, are easily measured in the field and therefore supply us with a convenient way to assess the

impact of water provision for a single site but also to make comparisons across sites. The sacrifice zone is described by the lower asymptote.
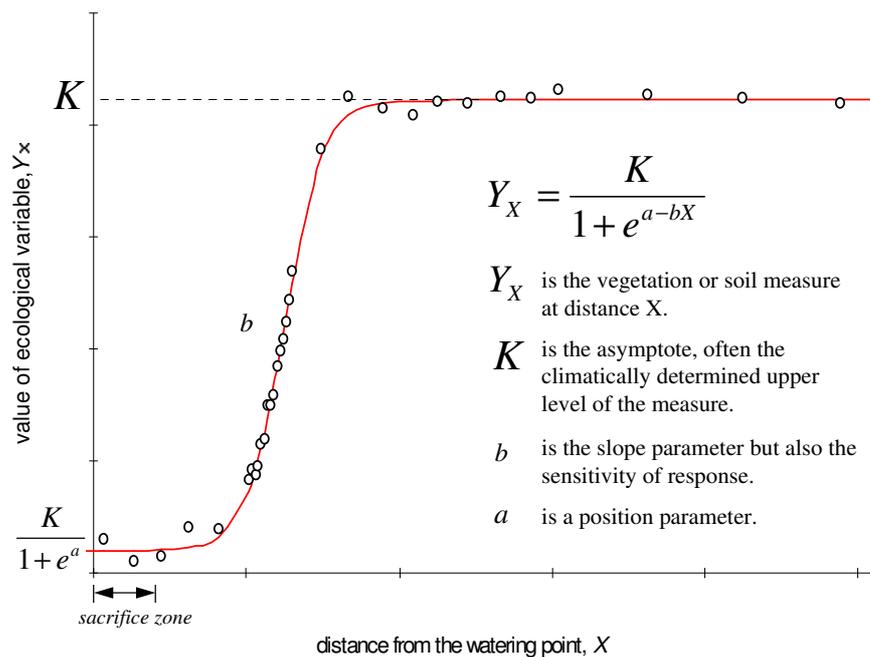

Fig. 1.6: The logistic curve adopted from population biology can be used to describe the piosphere effect. The parameters of the curve are convenient for representing the response of variables to the decrease in stocking pressure with distance from water. Positive relationships are modelled by negative values for parameters *a* and *b*. Adapted from Graetz & Ludwig (1978).

In addition to proving to be an acceptable fit for their own data collected in the Australian chenopod shrubland of New South Wales, the generality of Graetz and Ludwig's model is supported by examples collected for studies in southern and central Africa (Table 1.3). These include an additional term to account for nonzero y-intercepts (Thrash 1998b; Verlinden *et al.* 1998). However, it can be seen that large negative values for parameters *b* and *a* typically result for left-hand truncated forms of the positive relationship of a variable with distance. Also, because truncation produces a curve with no upper asymptote, values for *K* exceed the maximum value of 1 for the normalized data. "Forcing" the logistic model in this way can also give rise to nonsensical values for y_0, although a significant fit does indicate the piosphere pattern. Therefore, while the logistic model is useful for the affinity of its parameters to the real world, its universality is questionable (see Section 1.2.5). Also, there is no apparent variation due to climate, site age or stocking history, although more work is necessary to carry out a valid meta-analysis and one that includes a measure of piosphere extent.

Location	Vegetation	Rainfall	Animals	SR	Age	y_0	K	a	b	SE	R^2	F	P	Data	n	Source
Mallangwe Nature Trust, S.E. Zimbabwe	Limpopo lowveld	300-500	Wildlife[1]	57 ha/head	Unknown	-	0.96	1472.64	-319.95	0.101	0.90	37.05	<0.0001	Canopy distance	115	Unpublished. S. & B. Clegg & J.F. Derry.
Gonarezhou, S.E. Zimbabwe	Limpopo lowveld	300-500	Wildlife[1]	90 ha/head	Unknown	-	0.91	59.03	7.90	0.090	0.96	23.86	0.0402	Tree density	50	Rodriguez 1995
						-	1.02	501.61	-114.98	0.006	0.99	1168.0	0.0009	Tree damage	50	
Tierberg, South Africa	Karoo Dwarf Shrublands	167	Sheep	6 ha/ssu	Closed 20 yr	0.09	25.12	-26.16	-6.96	0.164	0.12	3.52	0.0187	Total cover	84	Unpublished. S.J. Milton,
Sandrivier, South Africa	Karoo Dwarf Shrublands	167	Smallstock[2]	6 ha/ssu	1/2 yr rotation	-	0.48	174.80	-127.54	0.198	0.15	6.07	0.0038	Total cover	70	Percy FitzPatrick Institute, University of Cape Town.
						0.08	3.34	-6.50	-17.04	0.062	0.95	74.82	<0.0001	Dung cover	16	
Kgatleng District, S.E. Botswana	Kalahari sandveld	350-400	Cattle	475 head	29 yr	-	0.85	31.20	19.43	0.108	0.89	32.35	0.0001	Tree cover	88	Moleele 1994
						0.47	2.34	-56.50	-48.64	0.071	0.92	28.19	0.0003	CEC[3]	88	
						0.57	0.32	86.83	-8.73	0.068	0.89	18.10	0.0011	Soil organic carbon	88	
						0.68	0.20	164.01	-48.46	0.070	0.71	5.79	0.0260	Plant nitrogen	88	
						-	11.35	-48.51	-20.68	0.077	0.96	87.19	<0.0001	Bare ground	88	
						0.70	0.51	14.98	-53.38	0.023	0.97	85.92	<0.0001	Soil pH	88	
						-	0.76	50.06	-6.99	0.123	0.91	39.26	<0.0001	Soil phosphorus	88	
						0.20	3.52	-35.78	-29.24	0.064	0.96	61.46	<0.0001	Soil calcium	88	
						0.21	13.64	-84.05	-29.76	0.065	0.96	52.56	<0.0001	Soil magnesium	88	
						-	48.20	-133.03	-34.06	0.084	0.95	76.59	<0.0001	Soil potassium	88	
						0.08	44.72	-50.48	-13.06	0.027	0.99	354.06	<0.0001	Soil sodium	88	
						0.42	0.60	92.80	-28.61	0.037	0.99	172.54	<0.0001	Plant phosphorus	88	
Makgadikgadi Basin, E. Botswana	Kalahari sandveld	400-500	Cattle	17 ha/LU	25 yr	-	1.11	19.46	-12.17	0.056	0.94	228.18	<0.0001	Grass composition[4]	34	Perkins 1991
						-	2.32	-10.08	-21.97	0.049	0.95	418.12	<0.0001	Shrub composition[4]	46	
						-	1.08	18.97	-7.47	0.002	1.00	76467	<0.0001	HUI[5]	56	
						-	0.98	45.04	-2.05	0.029	1.00	447.52	0.0002	Soil sodium	64	
						-	0.97	46.64	-2.05	0.073	0.98	71.50	0.0029	Soil potassium	64	
						-	0.99	48.47	-2.05	0.079	0.98	64.91	0.0034	Soil phosphorus	64	
						-	0.87	177.56	-11.68	0.183	0.91	14.58	0.0285	Soil nitrogen	64	
Makhi, N. Botswana	Kalahari sandveld	451	Cattle	12 ha/LU	21 yr	0.72	1.05	-223.21	-210.52	0.033	0.93	21.13	0.0029	Soil pH	41	Mphinyane 2001
						0.53	19.12	-965.35	-257.81	0.073	0.87	11.51	0.0111	Soil magnesium	41	
						-	0.93	438.94	556.16	0.080	0.94	24.57	0.0138	Phytomass[6]	100	
						-	79.57	-5749.99	-1299.03	0.109	0.94	23.18	0.0150	Utilisation[7]	400	
						0.42	25.87	-639.26	-168.85	0.029	0.99	116.02	<0.0001	Soil phosphorus	41	
						0.45	1.40	-107.40	-246.82	0.031	0.98	106.40	<0.0001	CEC[3]	41	
						0.27	42.82	-1264.23	-309.42	0.038	0.99	113.27	<0.0001	Soil calcium	41	
Tierberg, South Africa	Karoo Dwarf Shrublands	167	Unknown	Unknown	Unknown	-	5.72	137.67	50.57	0.164	0.32	8.654	0.0008	Total cover	40	Stokes & Yeaton 1994
Worcester, South Africa	Karoo Dwarf Shrublands	150	Unknown	Unknown	Unknown	0.44	0.27	18.26	-1.11	0.124	0.54	12.15	<0.0001	Canopy cover	35	Thrash 1993
Kruger National Park, South Africa	Transvaal lowveld	530	Wildlife	35 LSU/km²	28 yr	-	1.77	6.57	-15.72	0.046	0.98	607.07	<0.0001	Grass composition[8]	23	van Rooyen et al. 1994
Kalahari Gemsbok National Park, Botswana	Kalahari sandveld	209-230	Wildlife	Unknown	Unknown	-	7.98	-28.69	-14.75	0.027	0.99	1937.7	<0.0001	Grass composition[8]	44	Morris 2002
Eastern subalpine and alpine mountains, Lesotho	*Themeda Festuca* Alpine Veld	900-1100	Smallstock + cattle	Unknown	Unknown	-	0.57	389.98	267.30	0.194	0.11	5.46	0.0057	*Festuca caprina*	94	
						-	0.58	-23.26	-52.58	0.135	0.16	8.83	0.0003	*Bromus unioloides*	94	
Ceel Dhere, Somalia	Coastal grassland	275	Wildlife + livestock	9 ha/AU	Unknown	-	0.95	11.50	10.77	0.106	0.90	53.83	<0.0001	Range condition	15	Barker et al. 1989
						-	0.90	3.12	2.11	0.072	0.93	76.20	<0.0001	Bare ground	15	

[1] especially elephant [2] sheep and goats [3] cation exchange capacity [4] Detrended Correspondence Analysis [5] herbivore use intensity [6] dry weight [7] biomass removed [8] Canonical Correspondence Analysis

Table 1.3: Regression of generalised piosphere model (Graetz & Ludwig 1978) for variables measured in Africa. Site age and location, vegetation and animal types, annual rainfall (mm/yr.), regression statistics (standard error, SE; R^2; F and P), sample size (n) and data source are given, along with model parameters (K, a and b) plus adjustment term y_0 introduced by Thrash (1998b) for non-zero lower asymptotes, equivalent to $K/(1+e^a)$. These regressions were carried out for this thesis. To enable comparisons, each variable was normalised with respect to its maximum value. Only significant fits are presented. Model selection between 3- and 4-parameter versions was based on SE, R^2 and PRESS (Press 1992, *not shown*) statistics.

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1.2.5 The use of the logistic model in rangeland management

Although the logistic curve is a convenient tool to estimate piosphere dimensions, by adopting the logistic equation and not selecting a more complex empirical model that may better satisfy statistical selection criteria for a piosphere data set, the loss in estimator precision may outweigh the logistic curve's usefulness. Conversely, the process of selecting the most suitable model will have some bearing on what we may infer from the analysis (Buckland *et al*. 1997). For example, one dimension of a piosphere that may be estimated using this graphical model is the distance to the extent of its impact as measured by the abscissa upon negligible change in the asymptotic gradient (*e.g.*, Thrash 2000). This value would be useful to managers when trying to assess the spacing of watering points. Keys of 3 models, exponential, logistic and Gompertz, were fitted to compositional vegetation data collected at nine sites in Kruger National Park (Thrash *et al*. 1993). Whilst there was no overall effect on estimating the impact extent by selecting the logistic curve in favour of a 'best-fit' alternative if one existed ($t_{0.05,8}$ = -0.16; p>>0.05), the error in doing so for individual sites ranged between approximately a fifth (0.18) and nearly four times (3.91) the distance estimated by selection of the 'best-fit' model, and on average the distance estimated by the logistic equation was over twice (2.06) that estimated by the 'best-fit' model (J.F.Derry & C.D.Morris, *unpublished*). Alternatives have been used: an exponential decay model, offering similar interpretation by its parameterization, was favoured for the change in cover with distance from water for a site on the Nullarbor Plain, Australia (Cridland & Stafford Smith 1993).

1.2.6 Regression models

Semi-arid environments exhibit high temporal and spatial variability (Ellis *et al*. 1993), this spatial heterogeneity being found at a range of spatial scales; locally, within plants, through the whole plant communities and up to landscape and regional scales (Kotliar & Weins 1990). Foraging animals respond to the spatial heterogeneity of their environment by making diet selection decisions that need to account for the distribution of their forage resource (Laca & Demment 1991). A grazing gradient occurs where there exists a relationship between foraging behaviour and a trend in this spatial distribution. At the landscape scale, animal distributions are the simplest

method we have to study the behavioural response. Relating direct measurements of animal density to watering point location can show species interaction, especially wildlife displacement by livestock (de Leeuw *et al.* 2001). If measurements are analysed using statistical modelling techniques (*e.g.*, kriging), they can also highlight the impact zones associated with animal distributions along grazing gradients (Verlinden *et al.* 1998).

1.2.7 The prediction of animal densities

A large number of models have been developed, each an attempt to shed some light on the behavioural response underlying what appears to be a complex grazing pattern. Techniques that have been employed include, regression analysis (*e.g.*, Senft *et al.* 1983), probability densities (*e.g.*, Arnold & Maller 1985) and GIS (*e.g.*, Wade *et al.* 1998). Disquietingly, Stafford Smith (1990) achieved realistic results from an elementary random-walk model of sheep movement. The only adjustments made were to keep animals within the scope of the paddock, motivate them through previously utilised areas, and probabilistically tailor their movement with respect to wind direction.

1.2.8 Looking for gradients from outer space

More analytically, the flux of animal movements to and from watering points has been captured by using a convection-diffusion process calibrated with remote-sensing measurements (Pickup & Chewings 1988, Pickup 1994). Remotely-sensed Landsat images of vegetation cover are typically translated into animal distributions via the design of a filter that accounts for vegetation growth and temporal variation in vegetation cover. The filter incorporates growth, originally modelled as an exponential decay of a growth peak following satisfactory rain, however since then more sophisticated rainfall-driven growth models have been devised (Pickup 1995). Additional terms account for natural decline in vegetation cover, and species gradient effects (compositional changes) assumed to reduce forage quality under heavy stocking. Animal density is then assumed to be proportional to the depletion of vegetation cover and can be modelled using families of inverse Gaussian distribution functions. The approach is effective in extrapolating information from satellite

imagery and linking animal densities to range utilisation. Animal densities were shown to be highest at intermediate distances from water (Pickup & Chewings, 1988).

Landsat data has proved useful for the prediction of herbage production and the subsequent distribution of animals along a grazing gradient. It is also effective for the monitoring of rangeland (Pickup *et al*. 1994) and estimation of rangeland degradation (Pickup *et al*. 1998). To date the approach lacks a two-dimensional treatment, and requires further development of the biological component for application to other sites (Stafford Smith 1990). It is noteworthy that this remote sensing technique uses defoliation as a predictor of animal distribution. Heterogeneity in rangeland utilisation is assumed to be equivalent to spatial difference in the removal of vegetation cover related to distance from the nearest watering point.

1.2.9 Productivity gradients

General relationships between animal densities and primary production (*e.g.*, Coe *et al*. 1976, Fritz & Duncan 1994) might imply an alternative predictor of animal distribution and thus herbivore impacts. Gradients may be found in standing crop biomass, as well as vegetation cover (Cridland & Stafford Smith 1993), and appropriately, herbage production may be estimated using remotely-sensed data (Pickup 1995). However, animal responses to gradients of primary production do not fully reflect large-scale dependencies. Functional responses may be complex (Spalinger & Hobbs 1992). van de Koppel *et al*. (1996) detected reduced foraging efficiency in tall, dense grasses at the upper end of a productivity gradient. To model this, negative relationships between plant density and consumption rate, and plant density and digestion efficiency were introduced into a typical predator-prey formulation to reduce the herbivore numerical response. The model predicted a maximal grazing pressure at intermediate levels of standing crop. Under these conditions, multiple stable states may occur for systems of intermediate productivity. Under high productivity, there is a potential for unchecked domination by vegetation. Utilisation thresholds in tall, dense swards are due to dietary and other factors.

Reduced digestibility and preference of plant material, reduced intake of structural tissues and increased vertical resource partitioning constrain diet quality and quantity. Other effects are physical impediment (*e.g.*, impenetrable swards of *Cenchrus ciliaris*, Tuli Block, South Africa, *pers. obs.*), increased threats of predation through obstructed vigilance (Lamprey 1963), and substitution of foraging time to heightened vigilance (Illius *&* Fitzgibbon 1994).

1.2.10 System models

Simulation models seek to emulate ecosystem behaviour by the integration of system components (sometimes packaged in submodels) by various means (*e.g.*, Starfield *&* Bleloch 1991, Balzter *et al.* 1998, Derry 1998), allowing independent dynamics (*e.g.*, growth) as well as interaction (*e.g.*, competition). The representation of the need, to differing degrees, for animals to drink water, depends largely on a model's iteration interval and the nature of the animal component. At one extreme, highly mechanistic, spatial models that attempt to predict foraging behaviour within small time steps may simulate animal movements that are responsive to physiological stress. Constraint within a home range as a function of water requirement becomes a model output. Simpler models that are not so concerned with the fundamentals of foraging behaviour and its associated spatial impacts may simply superimpose a grazing gradient over the modelled region.

1.2.11 Patterns in forage production and utilisation

Adler & Hall (*subm.*) have produced similar results to Pickup *&* Chewings (1988) and van de Koppel *et al.* (1996), also predicting a peak in grazing intensity at intermediate distances, but with a dedicated piosphere systems model. An accompanying field study provided real examples of higher utilisation at intermediate distances for subhumid and semi-arid biomes. In a parallel arid case study, utilisation was highest close to water. There is a shortage of other real world examples, however, Western (1975) measured peak biomass of water-bound livestock for his middle distance class.

For their model, Adler & Hall (*subm.*) coupled an individual-based herbivore foraging submodel to a two species vegetation submodel of Lokta-Volterra plant growth and competition. Versions were developed to test four foraging strategies: maximization of forage biomass intake, equivalent to time minimization (TMin); probabilistic movement away from water (MaxDist); maximization of energy intake adjusted for distance from water (EMax-Dist) and energy intake maximization based on forage quality (EMax-Q). Animals began each day at the water source and then foraged independently until reaching their daily intake requirement.

If a 'start-eating' rule was satisfied, a single bite was taken from each position before progressing to the next position. The 'start-eating' rule for TMin, MaxDist and EMax-Dist allowed consumption if the current location held more biomass than a fraction (ET) of the environmental mean, for which the environmental mean was calculated globally, across the length of the piosphere gradient.

Animals moved from each position in the direction with highest mean available intake within their range of perception. MaxDist introduced probabilistic movement away from water. EMax-Dist goes someway to account for travel costs by dividing the intake rate at each position by the distance to water. Emax-Q used a 2nd order quadratic function to relate forage quality (digestibility) to forage biomass for substitution in the 'start-eating' and movement rules. Simulations were run for each version of the model on two types of landscape, one with a point water source in a square grid and another linear water source in a rectangular grid. The linear system presents a constant available foraging area at any position, in contrast to the increasing area with distance from water for the square grid.

All versions of Adler & Hall's model (*subm.*) produced patterns in grass biomass that were strongest near water and decreased with increasing distance from water. For the square grid, TMin and MaxDist gave the most recognizable piosphere responses, while EMax-Dist and EMax-Q curves indicated abrupt increases to background vegetation levels beyond the range of animal foraging (Fig. 1.7a).
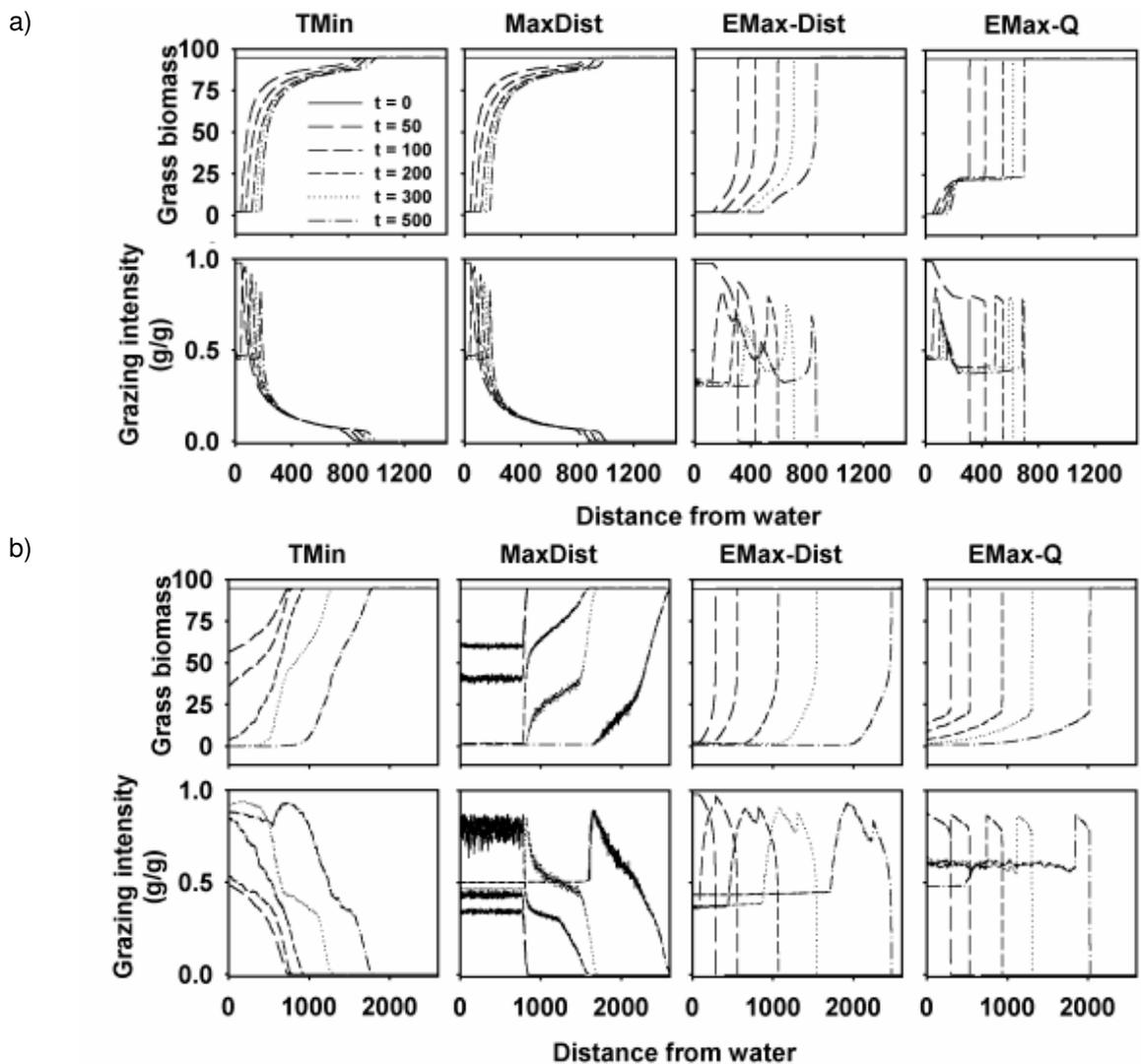
Fig. 1.7: Simulated temporal changes in patterns of grass biomass and utilisation (grazing intensity) under different foraging models run on a landscape with a) a point water source, and b) a linear water source. Lines correspond to patterns at different days (t = 0, 50…500) during the simulation. Results for the MaxDist model at doubled time intervals (t = 0, 100...1000) because the patterns were much slower to develop. Utilisation was calculated for the 50 day period preceding each output time for all models. ET=0.2 for purposes of model comparison. (Adler & Hall *subm.*).

In the linear landscape, responses for all versions of the model were abrupt beyond the range of animal foraging (Fig. 1.7b). All responses showed an increase in the extent of the severely degraded sacrifice zone over time. Utilisation initially decreased with distance from water and then developed a narrow peak at an intermediate distance that shifted away from water over time. So, intermediate peaks develop only after forage abundance nearest to the water source had been decreased

to very low levels. Larger sacrifice zones and broader utilisation peaks were seen for the linear system than for the point water source.

Adler & Hall (*subm.*) were able to moderate the strength of the piosphere response in their TMin model for both landscapes by manipulation of ET (Fig. 1.8). Effective suppression of the gradient formation was achieved for ET equal to 1 which meant that only sites with biomass in excess of the environmental mean could be utilized. Lowering ET produced utilisation patterns with increasing degradation of grass biomass nearest water.
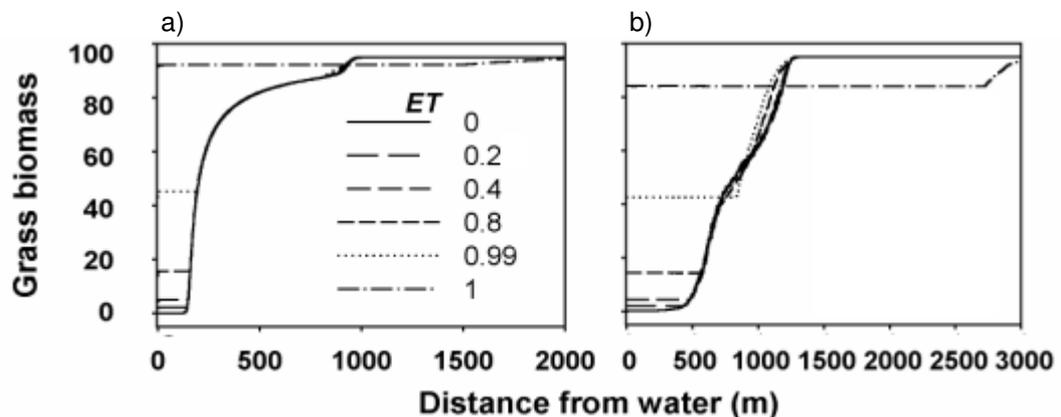

Fig. 1.8: The influence of ET on simulated grass abundance across a distance from water gradient, using using the TMin model on a landscape with a) a point water source, and b) a linear water source. For each simulation, grass biomass is shown at day 300. (Adler & Hall *subm.*).

Adler & Hall's model (*subm.*) is the most comprehensive systems model of piosphere development reported outside this thesis. They do not assume a utilisation gradient but integrate animal foraging behaviour with vegetation dynamics to evolve the piosphere pattern without a predetermined distribution of animal spatial foraging. However, the strength and shape of the responses may be attributable to assumptions in their model. Their 'start-eating' rule is a derivative of the Marginal Value Theorem (Charnov 1976), that predicts that animals should move to more profitable sites once resources at the current location have been depleted to the environmental mean (G^*). This defines the theoretical giving up density (GUD) for the resource. An extension

of this is Ideal Free theory (Fretwell & Lucas 1970) which predicts that herbivore densities should reflect resource distribution in a heterogeneous environment. Although Adler & Hall (*subm.*) assume that animals have perfect ("ideal") knowledge of resource profitability and are "free" to move between resource sites, using levels of ET below 1 is a manipulation of Marginal Value Theorem assumptions.

With ET=1, animals remove a single bite from locations with resource levels above $G*$. The model does not include energy expenditure nor does it limit available foraging time, so they are able to move freely between sites without constraint, until daily intake requirements are met. Utilisation patterns are consequently diffused (*not shown*). Reducing ET below 1 improves the profitability of all sites relative to $G*$, and the animals do not need to travel as far from water to find a comparatively resource-rich location. Further reducing ET emphasizes local profitability and the sacrifice zone is reduced to lower resource levels (Fig. 1.8). Because animals are held local to water, the majority of foraging activity occurs to extend the sacrifice zone, and the rise beyond this to background resource levels is artificially abrupt.

The model fails to capture the essential control on animal spatial foraging behaviour exerted by dry season conditions. Arditi & Dacorogna (1988) described how food patchiness could be a function of the critical food density equal to the animal GUD. Increasing the GUD tends towards the continuous food supply that may underlie a patchy distribution. Using a fraction of $G*$ will effectively increase the size of patch, and reduce inter-patch distance, in spatially heterogeneous distributions of resources.

Adler & Hall (*subm.*) are correct to conclude that the response shapes in their results "indicate that other factors not included in the models have important influences on animal movement". It is reasonable to speculate that these factors include time and energy. Animal movement is moderated by energy travel costs, which must restrict the distances travelled when resources are dispersed, (*e.g.*, for increasing ET). Thus energetic constraints would act in parallel with limitations on the available foraging time to compromise daily intake for insufficient local resources. Simply put, animals

do not have time to fully exploit their environment, whilst any additional energy expended during travel needs to be offset by equivalent energy intake.

Further discussion of forage digestibility, energy intake maximization, travel costs and spatial foraging strategies and other issues relating to Adler & Hall's work (*subm.*), and a comparative study, also contrasting a square grid with a linear system, can be found in Chapter 3.

1.2.12 A grid-based model of a single piosphere

Jeltsch *et al*. (1997) considered the question of piosphere reversibility and spread using a grid-based simulation model of 2 separate borehole sites in the Kalahari thornveld. They succeeded in generating similar variability in piosphere size, as determined by changes in grazing pressure, to that observed by Perkins (Perkins *&* Thomas 1993a). Fundamental piosphere responses are recognizable in their model's output for herbaceous and woody cover. While this exercise provides invaluable insight into the generation and maintenance of piosphere responses in vegetation cover, the rule-based algorithms comprising the model do not extend to include foraging behaviour. This means that the grazing pressure was constantly levied according to location along the extent of a preconceived, exponential grazing gradient. Reduction of phytomass in random grid cells conforms to this grazing pressure. Perhaps then, accumulated depletion is likely to give rise to a herbaceous layer that reflects a deterministic gradient. Possibly more impressive is the model's simulation of bush encroachment. The location and depth of bush encroached zones in the near vicinity of the "virtual borehole" are similar to those measured by Perkins (1991), and were found to be stable for simulation times in excess of a century after removal of grazing pressure. The bush dynamics are a product of increasing the grazing pressure upon nearing the water point, leading to extinction of herbaceous cover within local grid cells, and subsequent colonization of those grid cells by a woody species. Perkins (1991) carried out his experiments in the eastern Kalahari, where precipitation levels (~450mm/yr) might be expected to generate rooting patterns that seek to partition the water resource (Mordelet *et al*. 1997). Deep surface sands proffer a low storage capacity for infiltration (Mazor 1982) which allow

shallow herbaceous roots access before percolation to the deeper placed roots of the woody vegetation. It is reasonable, therefore, that the foundation for bush encroachment is considered to be the depletion of grasses by the high herbivore utilisation intensity near the borehole. Fire (included in the model as a function of fuel load) was previously identified as having an important influence on the model's results (Jeltsch *et al*. 1996). Perkins (1991) originally identified the exclusion of fire by the continuous grazing of the herbaceous layer, which reduces the available fuel load, along with seedling establishment following favorable rainfall patterns, as cofactors in the promotion of the woody layer (Perkins 1991).

1.2.13 Grid-based models of animal densities

Another Kalahari-based model (Starfield *et al*. 1982) moves 3 species of wildlife between blocks along a section of river according to an index of attractiveness that captures diet preferences and water dependence, including drought tolerance. The model was successful in predicting basic animal movements and population dynamics in response to water location and accumulated defoliation in blocks hosting a watering point, but is not configured to model piosphere patterns. The *Paddock* utility in RANGEPACK (Stafford Smith 1988, Stafford Smith *& Foran 1990, Cridland & Stafford Smith 1993) provides a user interface for the specification of paddock characteristics, such as watering point location, fencelines, and wind direction (an influence on sheep movement). The exponential decay model is used to impose a grazing gradient, the slope of which is determined by watering point salinity and a vegetation preference index, also influenced by watering point salinity, thereby introducing an element of animal physiology. The model can be used to test sketched paddock designs against predicted spatial impacts for multiple watering point systems, and is being developed to accept real paddock data via GIS input.

1.2.14 Modelling the physiology of foraging behaviour

Mechanistic models move away from the grazing gradient approach towards predictions of animal movement whilst accounting for physiological constraints. To model animal movement with respect to water requirements, the balance between acquirement via drinking and dietary moisture content, and losses via respiration,

sweat, urine, and fæces need to be considered. Loza *et al.* (1992) include all of these factors in a physiological submodel, and specify the location of a watering point and shade in a landscape submodel. An hourly iteration interval sees animals making daytime decisions conditional on their physiological status, derived from thirst, respiration and hunger indices. Animals are mobilised towards water or shade according to the strength of the corresponding index, and if sufficiently hungry, will forage *en route*. A priority is set for drinking, over shade, over eating. During winter, animals were predicted to spend roughly a half of each day near water. During warmer months animals were predicted to suffer higher water loss, spend longer drinking, and spend more time near shade. Increasing the distance between water and shade reduced the time spent near water in favour of travelling to shade after drinking requirements had been satisfied. The representation of the landscape is course. Water and shade are located in, and separated by, adjacent kilometre-wide blocks with movement in 0.5 km units. Forage growth is not dynamic, daily growth being input as a value independent of consumption. Hence, impacts are not recorded.

1.2.15 Distance to water versus animal energy expenditure
SAVANNA (Coughenour 1993) does not simulate animal water balance but does take account of energy expenditure in travel undertaken to satisfy water requirements. The iteration interval is a week. Animals are distributed across the grid-based landscape in relation to an index of habitat suitability, assessed in terms of distance to water along with forage abundance and tree cover. Watering points may either be seasonal wells, permanent wells or perennial streams, each classifiable as either a mineral or fresh quality. The level of seasonal wells are dependent on the previous three months' rainfall, whilst loss from permanent wells is dependent on the previous 12 months' rainfall. Discharge rates and distance to water are input as maps. Animals that cannot be supported at current discharge rates disperse to other areas containing excess water. A maximum animal density may be set for each grid cell. Plant growth is related to soil moisture and transpiration rate. Trees are classified into size classes. Grazing and browsing impacts are registered on the corresponding phytomass in each cell. Whilst, the model has been successfully applied to predicting large-scale vegetation dynamics and animal distributions (Kiker 1998), an

assessment of the model's capacity to simulate piosphere dynamics has yet to be carried out.

1.2.16 Piospheres and the socio-economics of livestock production

An additional dynamic component important to sustainable rangeland management arises from market forces. Piosphere dynamics in the Kalahari are inextricably linked with socio-economic (Perkins 1991) and political factors (Perkins 1996). A benefit function in ORIA (Optimal Rangeland Integrated Assessment model, Duraiappah & Perkins 1999) is used to encapsulate the income from livestock sales, the cost of shipment from the cattlepost to the abattoir, the gain of milk, draught power, hides and prestige by retaining animals and the loss of these benefits by selling animals. The analytical model also includes the cost of restocking, the provision of supplementary food, labour costs and effort. Borehole density for the modelled region is limited within bounds to avoid overlap of neighbouring piospheres. The cost of borehole establishment and maintenance are also charged. Additional boreholes are drilled if the current quantity of boreholes cannot support the current head of livestock. Stock numbers fluctuate with available forage. Vegetation dynamics are modelled for grass and browse within 2 concentric zones surrounding the boreholes, and a grazing reserve beyond the outer annuli. The level of bush encroachment is assumed to be an exponential function of distance from a borehole once grass levels fall below a threshold. Forage intake is balanced against energetic requirements for maintenance and travel. Vegetation is trampled in proportion to animal density and affects grass more than browse. Substitution of herbaceous forage with browse is constrained to reflect digestive constraints in cattle. The model seeks to maximise the benefit function net costs limiting sales to levels that do not result in a smaller herd size than the initial herd. The model manages to simulate various aspects of Kalahari piospheres; including, temporal dynamics such as bush encroachment, spatial effects such as essential winter grazing being limited to the outlying grazing reserve, and animal behaviour such as mixed diets during summer. It also provides a test of optimal herd sizes and national agricultural policy, finding in support of an 8 km spacing of boreholes. Ecologically sustainable stocking rates (carrying capacity) were found in excess of economically sustainable stocking rates,

dependent on cattle prices and borehole costs. Losses from trampling were found to be large enough to justify investment in more boreholes to diffuse herd intensity.

1.2.17 Miscellaneous models

Aspects of other models lend themselves to solving some of the problems envisaged during development of a comprehensive piosphere model. A few examples are parsimoniously given here. Fryxell (1998) has generated a central-place foraging model of beaver resource depletion that effectively generates a piosphere pattern. The model accounts for the effects of forage abundance and nutritional quality on beaver forage preference and subsequent handling and retention times. The pitfall with beaver foraging behaviour, when comparing it to *e.g.*, livestock, is that beavers restart their foraging excursions from a central position on each occasion. Each food item is located relative to the central point rather than with respect to the previous food item, lending itself well to the Markovian Chain approach adopted, but requiring modification if to be applied in a piosphere modelling context. Pennycuick (1979) provided a useful allometric energetics model of animal mobility to calculate the foraging radius, the determinant of piosphere extent and the dry season (home) range of the free-ranging animal. Effective and economical artificial water provision is partly dependent on the type and dimensions of the water container (Zambatis 1985), and this could be included in bioeconomic system models of watering points. Evaporation is related to surface area, therefore, water loss from rectangular troughs is proportional to the length of their perimeter, whilst water loss from circular pans increases exponentially with their diameter. Insufficiently sized pans (<10 m diameter) tend to become mud wallows. This deters drinking. Sufficiently sized pans (>25 m diameter) lose 16.7 times more water to evaporation (919.8 m^3 *per annum*) than that lost from a 15 m trough (55.1 m^3 *per annum*) holding 6300 litres, deemed a minimal capacity for daily wildlife water provision.

1.2.18 Conclusions and gaps in knowledge

The location of animal drinking water has been identified as an important factor in determining patterns of rangeland use, and yet models of the piosphere response are scarce. Ecosystem modelling efforts tend to concentrate on the prediction of animal