

CHAPTER 4A

RESOURCE DISTRIBUTION AND DYNAMICS

Mapping herbivore resources

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Abstract. The distribution of food is an important predictor for the distribution and density of herbivores in an ecosystem. Determining the distribution and densities of resource quantity and quality in space and time is therefore a crucial step towards understanding the spatial arrangement of herbivores. In recent years remote sensing has become the tool of choice for producing high spatial-resolution impressions of the variability of the landscape, and in particular land cover. Remote sensing is slowly moving away from mapping the surface into discrete land-cover classes. More and more, it is now used to produce highly accurate probability maps of presence, depicting the percentage of individual pixels covered with a certain surface element. This more closely represents the continuous nature of natural phenomena. Recent studies have indicated that it is possible to measure the chemical composition of foliage too. Recently a case study in Kruger National Park confirmed that it is possible to measure nitrogen concentration and phenolic compound levels in grass and trees accurately, with a spatial resolution of 4 meters. This opens doors for new lines of research, where the distribution of herbivores can be linked to the actual resource distribution.

Keywords. remote sensing; resource mapping; resource quality; resource quantity; spatial analysis

INTRODUCTION

A herbivore's search for food (vegetation) and its consumption is driven by the spatial and temporal variation in the vegetation resource, and so vegetation is the central resource considered in this chapter. We use the term 'resource' as defined by Morrison and Hall (2002): it is "any biotic or abiotic factor directly used by an organism, and includes food, nutrients, water, atmospheric gas concentrations, light, soil, weather (i.e., precipitation, temperature, evapotranspiration, etc.), shelter, terrain, and so on. For large herbivores, foraging is a central activity and food

(vegetation) is a key resource. Vegetation resource abundance is the absolute amount of a food item in an explicitly defined area. Vegetation resource availability



The focus of this chapter is describing how vegetation resources can be mapped for herbivores at different scales

is a measure of the amount of a resource actually available to the animal. Finally, Morrison and Hall (2002) define resource preference as the likelihood that a resource will be used if offered on an equal basis with others. In the context of herbivory, and specifically vegetation resources, resource preference refers to likelihood that a particular (part of a) plant

will be chosen. In this chapter, resource quantity is synonymous with the definition of resource abundance.

Quality tells us something about how well a resource meets the needs of a herbivore relative to the amount of the resource to be consumed. Resource quality is linked to the concept of resource preference, but also implies that vegetation will have components that both attract and deter an animal. Components of vegetation that are 'attractive' to herbivores include factors such as protein, sugar, starch, etc., while 'deterrents' include factors such as tannin, polyphenols or physical attributes such as thorns. Both the quantity (biomass) and quality (the foliar concentration of nitrogen, phosphorous, calcium, magnesium, potassium and sodium) of grass are important factors influencing the feeding patterns and distribution of wildlife and livestock in savanna rangelands (Drent and Prins 1987; Prins 1989a; 1989b; 1996; McNaughton 1990; 1995). Therefore, mapping the quantity and quality of the vegetation resource is a prerequisite to understanding wildlife distribution patterns.

There is great variation in herbivore resources, and the variation depends on the scale considered. The concept of scale is loosely defined. Traditionally, mapmakers use scale as the ratio of the distance (unit) on a map to the same distance (unit) on the ground. In other words, cartographers define 'large scale' as a small portion of



The concept of scale in ecology and cartography is differently defined

the Earth's surface studied in detail (e.g., a scale of 1:500) while a small scale is large area viewed more generally (e.g., a scale of 1:100,000). With digital maps, the cartographic concept of scale is blurring, as software varies the detail appropriate for the areal extent being viewed. Thus, detail and areal extent have become independent as cartographers turn to

digital media instead of paper media. To confuse matters, the common usage of a 'large scale' implies an approach that covers regional or even wider areas. In other words, in common usage, scale gives a sense of extent, while cartographers define it as a ratio. In the Oxford English Dictionary (OED), this confusion is apparent: scale is defined as "... represent in dimensions proportional to the actual ones ...", which fits the cartographer's definition, while the OED goes on that "... scale up and scale down, make larger, smaller, in due proportions ...", which matches the 'common' use of scale. There have been attempts to match cartographic with ecological scale,

but such definitions are arbitrary and subject to change depending on whim, because the terms have no clear definition and cannot therefore be used comparatively (for example, see Table 4.1 derived from Estes and Mooneyhan 1994).

Other terms have been proposed to define scale in ecology, such as ‘fine’ and ‘broad’ (Levin 1992), but again such terms are inherently imprecise, and their use has not become widespread. Recent research indicates that scale can be precisely defined in ecology and may therefore be used as a tool for comparison as well as understanding of ecological pattern and process.

Table 4.1. Comparative definition of cartographic and ecological scale (Estes and Mooneyhan 1994)

Cartographic scale	Ecological scale
1:10,000 or larger	Site
1:50,000 to 1:250,000	Regional
1:250,000 to 1:1,000,000	Continental
1:1,000,000 or smaller	Global

Another interesting concept related to scale, is that different properties emerge when viewed at different scales. For example, a toadstool may be seen as an individual object in a forest, but may form part of a ‘fairy ring’ when viewed at a distance.



‘Emergent properties’ is an important concept when considering scale

Similarly, a ‘patch’ of grassland which forms part of a heterogeneous habitat for an elephant, may be an unsuitable habitat for a mouse as it is too homogeneous. Thus scale can be defined, scale parameters can define herbivore resources, and through scale, emerging properties may be discovered.

Scale, and its influence on grazing resources, will be referred to throughout this chapter. Box 4.1 explains semivariograms as a tool to describe spatial scale.

Box 4.1. Semivariogram

Curran (1988) defines a semivariogram as a function that relates semivariance to the separation distance of points in space and provides an unbiased description of spatial scale; he goes on to describe the concept of semivariograms in detail. Wavelets partition the variance of a data function, such as a satellite image, on a scale-by-scale basis (Lindsay et al. 1996) and have been described by Ogden (1997) and Bruce and Hong-Ye (1996). Recently, Murwira and Skidmore (2003) developed two new methods to define scale: intensity is the maximum variance exhibited when a spatially distributed landscape variable (such as vegetation cover) is measured with a successively increasing window size or scale, while dominant scale is the scale at which the intensity is displayed. Wavelets and variograms were adapted in order to calculate dominant scale and intensity. Both techniques have been described mathematically and conceptually.

The concept of dominant scale and intensity, as derived from variograms and wavelets, has been proven for the regular landscape of the Netherlands, as well as (semi-)natural areas in northwest Zimbabwe by Murwira and Skidmore (2003). They further showed that 80% of the variation in herbivore (in this case elephant) presence could be explained using intensity and dominant scale. In other words, the patchiness or heterogeneity of the landscape varies according to the object (species) of study (for example, the patchiness relevant to a mouse is clearly different to that of an elephant). The heterogeneity of habitat is clearly relevant to species, and scale in ecology can be treated rigorously using the concepts of dominant scale and intensity.

TOOLS TO MAP ENVIRONMENTAL VARIABLES

Until a decade ago it was virtually impossible to display more than one environmental factor on a single map. The habitat type, defined as a mappable unit of land 'homogeneous' with respect to vegetation and environmental factors, circumvented this problem and was the basis of land-systems (or landscape-guided)



Mapping traditionally uses the concept of land systems. This is being replaced by the concept of landscape continuum

maps developed in the 1980s (Walker et al. 1986; Zonneveld 1988). Land-systems mapping is based on the assumption that environmental factors show an interdependent change throughout the landscape, and that the environmental factors are constant within the 'homogeneous' area (see an example delineating forest types in Figure 4.1). Thus,

the term habitat arose as a way to overcome operational difficulties in species distribution mapping. However, the variation of one environmental factor affecting the distribution of a species tends to be independent of the other environmental factors (Corsi 2000), with the conclusion that 'homogeneity' is seldom the case. If 'homogeneity' cannot be assumed, then the relationship between species and habitat types implied by the land-systems approach requires refinement as we cannot assume that habitat types are homogeneous with respect to the environmental variables that affect the species distribution.

Remotely-sensed imagery has been traditionally classified using computer methods synonymous with the land-systems approach. Each pixel is assigned to a class. The end product is a thematic map of a limited number of classes (Figure 4.1).

Figure 4.1 details land cover and land use classes important for herbivores in the Narok District of Kenya. In these figures, it is possible to detect change in land cover, and relate changes in herbivore abundance and diversity to these changes in land cover.

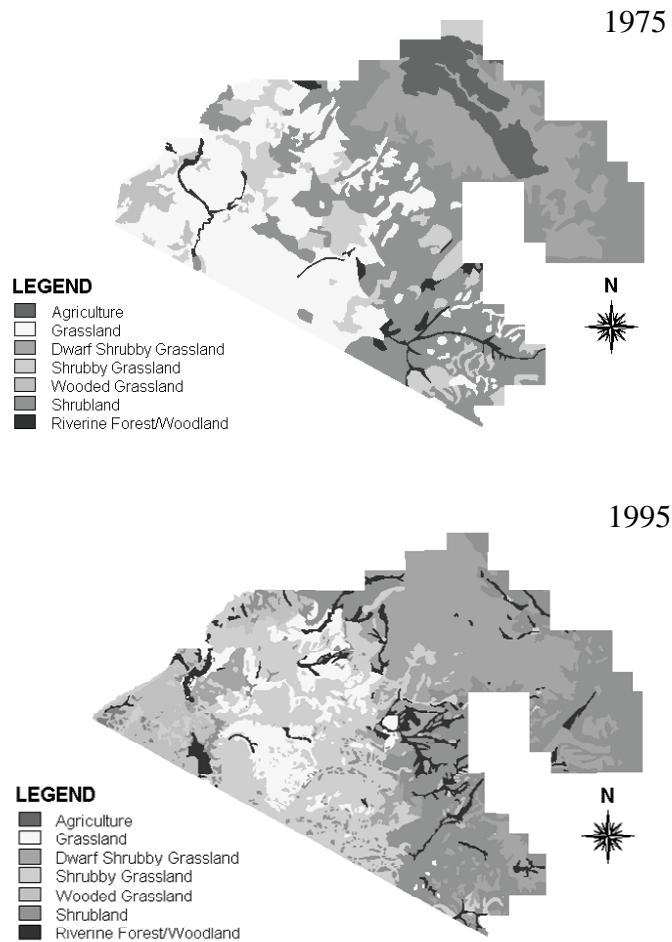


Figure 4.1. Land cover/land use map of the Narok District, Kenya, prepared by computer classification of Landsat imagery from 1975 and 1995

A large number of environmental factors act in concert to determine a habitat. GIS makes it possible to integrate the variation of environmental factors as independent layers of information, and to integrate these independent environmental surfaces into a map displaying the suitability of land as a habitat for a specific species. It is a reductionist approach, where the landscape is viewed as a series of

separate data layers, which are combined by computer models, with features often being managed and displayed as a continuum (Skidmore 1989). Models utilising environmental factors in order to define an 'envelope' of suitable conditions for a species are now standard GIS tools in environmental impact assessment and habitat modeling (e.g., Skidmore et al. 1996).

A new tool to be briefly introduced here is hyperspectral remote sensing. This type of imagery appears to be most promising for mapping vegetation quality and quantity. As pigment concentrations, leaf characteristics, canopy structure, and



Hyperspectral imagery is an important new tool for mapping herbivore forage quality and quantity

biochemical content vary between different vegetation types, so does absorption and reflectance (Knipling 1970; Asner 1998; Martin et al. 1998). Schmidt and Skidmore (2003) summarise the wavelength positions of plant spectral features as calculated by a number of different authors, and conclude that spectral characteristics of vegetation and their

biochemical constituents differ because of different experimental set-ups. However, it is also clear from the summary of (Schmidt and Skidmore 2003) that it is possible to identify common absorption features in vegetation, and that specific biochemicals and physical plant characteristics contribute to each absorption feature.

SPATIAL VARIATION IN HERBIVORE RESOURCES

Quantity of herbivore resource

The production of forage is a key determinant of the suitability of habitat for herbivores. The growth of plants is dependent on their ability to assimilate carbon dioxide as organic compounds using energy absorbed from light during photosynthesis. Factors affecting the rate of photosynthesis include available moisture, temperature, light intensity, nutrients and carbon-dioxide concentration. Other factors affecting plant growth include atmospheric pollutants, defoliation, seasonality, different photosynthetic pathways, i.e., C₃ or C₄, as well as leaf amount, type and duration.

These factors influence plant growth at different scales. At a continental scale, available moisture (derived as a function of rainfall and temperature) and soil



At different scales, various environmental factors determine plant biomass production

fertility have been identified as critical environmental factors explaining resource production (Coe et al. 1976), while geographers classify ecosystems using climatic factors (such as rainfall, temperature, seasonality, latitude and degree of continental influences) (Köppen 1931; Holdridge 1947; Bailey et al. 1996). At a regional scale (a few

hundred km), the influence of topography, geology and soil emerge as key explanatory variables of primary production (Walter 1971; Woodward 1987;

Skidmore et al. 1998). For example, Walter (1971) shows that the vertical profile of soil water depends on soil texture, which is important in determining the distribution of savannas within regions of tropical seasonally (summer) wet climate. At a local scale (i.e., a few kilometres), soil physical and chemical conditions, microclimate (explained by topographic variables such as slope, aspect, elevation and position in the terrain) (Skidmore 1989; Schmidt et al. 2003), as well as indices that integrated microclimatic variables such as total solar-radiation influence (Kumar and Skidmore 2000) influence vegetation type and biomass production.

A number of approaches for measuring productivity have been explored. An important variable explaining canopy primary production is leaf area index (LAI),



LAI and NDVI, measured by remote sensing, can estimate the productivity of ecosystems

which represents the size of the interface between plant and atmosphere for energy and mass exchanges (Kumar et al. 2001). LAI is the ratio of the area of leaf (measured on one side only) to the area of ground beneath (Hutchings 1986). The estimation of LAI from remote-sensing measurements has received much attention. For example, a simplified semi-

empirical reflectance model for estimating LAI of a green canopy was introduced by Clevers (1988, 1989).

A second measure of ecosystem productivity is based on the idea that productivity is the rate at which energy flows through an ecosystem (Rosenzweig and Abramsky 1993). Ecologists usually use a proxy index to measure productivity over larger areas, such as rainfall in semi-arid landscapes (Rosenzweig and Abramsky 1993). Evapotranspiration can be a suitable index of productivity for terrestrial systems where there is a wide range of temperature and precipitation regimes (Rosenzweig 1968). The normalised difference of the red and near-infrared bands (so-called normalised difference vegetation index or NDVI) estimated from satellite remote-sensing systems is closely related to net primary productivity (NPP) as well as actual evapotranspiration for many vegetation types (Box et al. 1989). The relationship between NDVI and net primary productivity can be established through deductive logic.

Net primary production (NPP) is the net amount of carbon captured by land plants through photosynthesis each year. In a series of modelling experiments, Haxeltine (1996) proved theoretically that NPP is roughly proportional to FPAR on a seasonal and annual basis, thereby validating the empirical observations of Monteith (1972, 1977). FPAR (the fraction of photosynthetically active radiation that is intercepted by green vegetation) is a fundamental variable for the prediction of NPP and hence biomass production. It is possible to estimate FPAR using NDVI (Sellers et al. 1994, 1996) and to estimate biome-averaged global FPAR values against observed monthly maximum FPAR, with an explained variance of 76% (Haxeltine 1996).

However, a problem limiting the application of remote sensing to map the quantity of tropical grasses is that NDVI saturates at higher canopy density: the saturation level is usually reached at about 0.3 g cm^{-2} (Mutanga and Skidmore



Only at intermediate biomass quantities, traditional remote sensing can accurately map biomass

2004b). In other words, the widely used vegetation indices (such as NDVI) asymptotically approach a saturation level after a certain biomass density or LAI (Tucker 1977; Sellers 1985; Clevers 1994; Gao et al. 2000), thus yielding poor estimates of biomass during the productivity peak of seasons. Results from Said (2003) used regional data from Africa to

demonstrate that the NDVI response is linear in areas of intermediate rainfall but shows little variation at high and low rainfall (Figure 4.2). In other words, the correlation is low for semi-arid areas as there is little vegetation, and also low for forests as the large amount of vegetation saturates the NDVI response. For intermediate-rainfall zones (such as grasslands and savannas) NDVI can yield reasonable estimates of LAI or biomass.

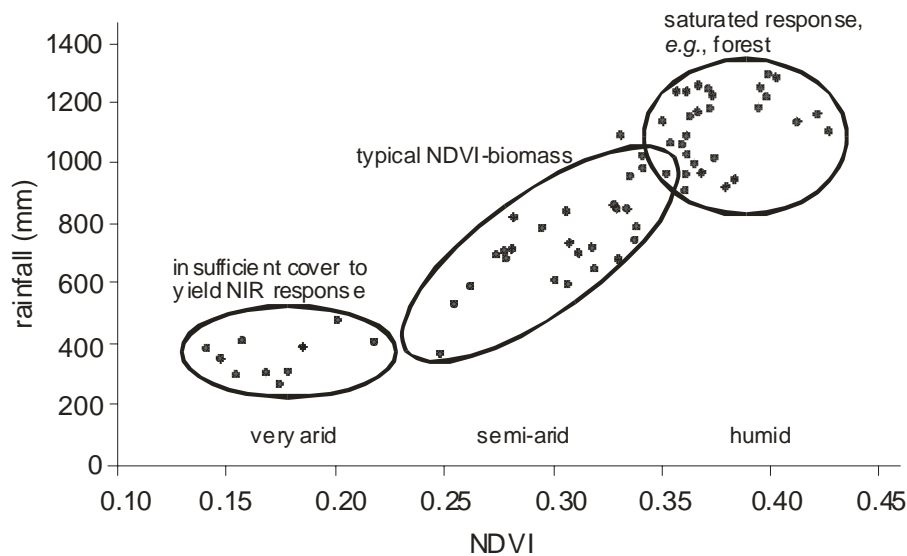


Figure 4.2. Relationship between rainfall and NDVI; results indicate a poor correlation in the very arid and humid regions of East Africa (Said 2003)

In order to improve the estimation of biomass from remotely sensed imagery, Guyot et al. (1988) and Baret et al. (1992) showed that canopy LAI, leaf chlorophyll content and leaf inclination angle may be estimated from the 'red edge' wavelength (see Box 4.2). For grassland in the Kruger National Park, South Africa, Mutanga

and Skidmore (2004b) tested the utility of the widely used vegetation indices for estimating biomass (in particular, NDVIs involving all possible two band combinations between 350 nm and 2500 nm



Using the red edge of hyperspectral imagery, biomass can be more accurately estimated

were tested, in other words also ranging across the red edge). The narrow-band hyperspectral data contained in 647 discrete channels allowed the computation of 418,609 narrow-band NDVIs for biomass estimation. Figure 4.3 shows that a modified NDVI (R755-R746/R755+R746) involving narrow bands located in

the red edge, yielded a higher correlation coefficient with biomass as compared to the standard NDVI (R833-R680/R833+R680).

Box 4.2. *The use of the 'red edge' wavelength in remote sensing*

The red edge is the region of transition in low reflection in the red part of the electromagnetic spectrum, to a region of high reflectance found in the near-infrared region. This transition is a typical element of green-vegetation reflectance spectra. It is suggested that the wavelength shift in the inclination point of the red edge is determined by the brightness of the reflectance in the red and near-infrared, and the variation in this measure is dominated by LAI. Clevers (1994) showed that the red edge seems to be independent of soil reflectance for areas of low LAI and that solar zenith angle appears to have only a minor effect on the position of the red edge. Elvidge et al. (1993) and Clevers and Jongschaap (2001) also demonstrated that the red edge was able to detect changes in the amount of vegetation in areas of sparser vegetation; in contrast, NDVI does not vary in value at low LAI. In other words, evidence from the laboratory and crop fields pointed to the use of red edge for better estimating the biomass of sparse vegetation.

The practical difficulty in utilising the red edge is that traditional broadband satellite sensors such as Landsat or SPOT do not utilise this information. Baret et al. (1992) argued that the small amount of independent information in the broadband two-channel sensors cannot reliably estimate the numerous variables controlling canopy reflectance. In particular, for arid and semi-arid environments, hyperspectral imagery is required to resolve subtle variations in canopy reflectance, in order to estimate biomass-related variables (Asner 1998). In other words, the information contained around the red edge slope appeared to be required for the more accurate estimation of biomass, especially in semi-arid natural landscapes such as found in Southern Africa, which may change from sparse to dense grass biomass depending on precipitation.

The techniques for remotely estimating biomass (or resource quantity) have been steadily improved by using the full information content of hyperspectral imagery, next-generation image pre-processing and calibration image processing algorithms, as well as improved field sampling techniques. In other words, the early results with vegetation indices have been refined and developed to a point where biomass may be reliably estimated, also in areas of sparser and denser grass vegetation.

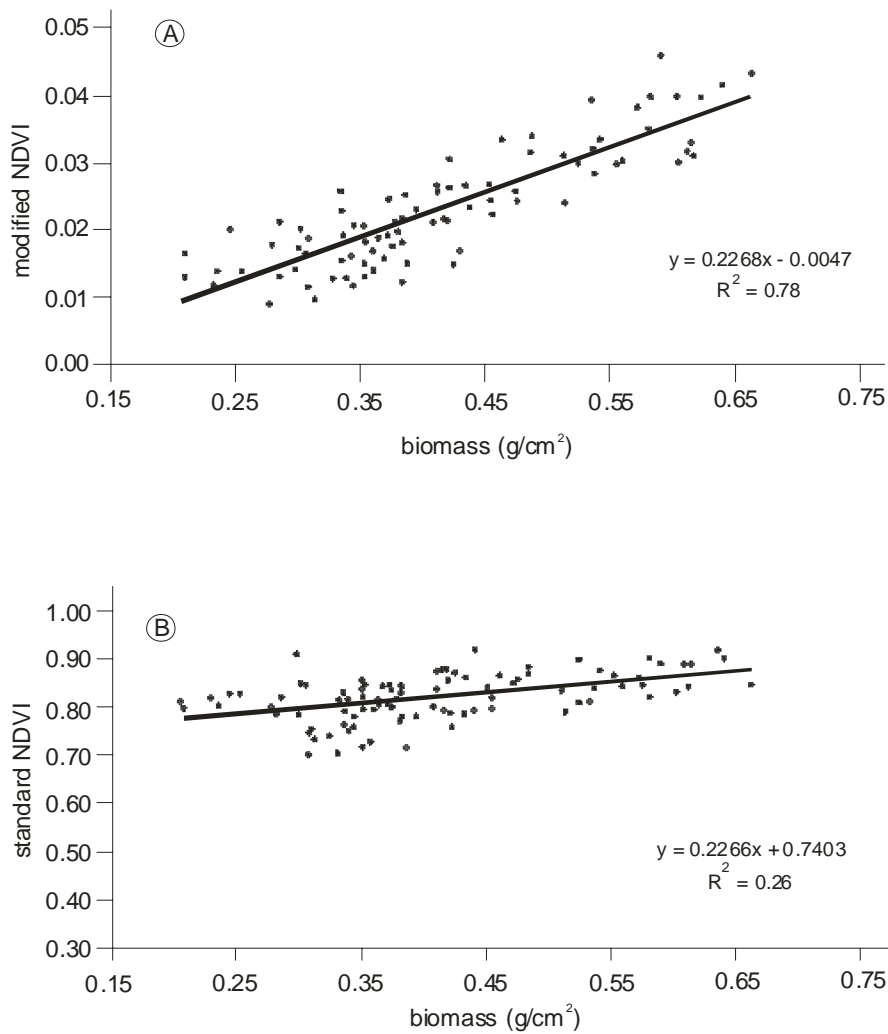


Figure 4.3. Relationship between biomass and the best-modified NDVI (A) as well as the standard NDVI calculated from a near-infrared (833 nm) and red band (680 nm) (B). Note the R^2 improves from 0.26 for the standard NDVI to 0.78 for the modified NDVI. Taken from Mutanga and Skidmore (2004b)

QUALITY OF HERBIVORE RESOURCE

The circulation of nitrogen within ecosystems is a classic example of a nutrient cycle: nitrogen is a nutrient essential for plant and animal survival. By understanding and mapping an important herbivore resource variable such as foliar nitrogen, ecologists may be able to model the distribution of herbivores based on their resource preference, as well as understand and predict the diversity of species across a landscape.

There is generally a strong positive correlation between leaf nitrogen concentration and photosynthesis (as long as other factors such as water availability or light are not limiting) (Field and Mooney 1986; Mooney 1986). Of the nitrogen found in a leaf, a large fraction (over 50%) is contained in the carbon-fixing enzyme ribulose biphosphate carboxylase (Mooney 1986) which is a critical component in photosynthesis. It is therefore not surprising that there is a strong positive correlation between photosynthetic capacity and leaf nitrogen content. The relationships between leaf chlorophyll concentration and leaf nitrogen concentration in petiole sap are strong, and linear (Vos and Bom 1993).

The enhancing effect of increased nitrogen supply on dry-matter production as well as protein (including vitamin-B compounds) concentration is well established in the agricultural literature; see Marschner (1995) for a review. Using artificial media as well as field experiments, insect herbivore growth is positively related to nitrogen content (Lincoln et al. 1982), while significantly higher abundance of large herbivores occurs on nutrient-enriched sites in southern Africa (East 1984; Scholes and Walker 1993; Owen-Smith and Danckwerts 1997; Prins 1996). Foliar nitrogen concentration has been shown to be an important environmental factor (Coe 1983).



By understanding and mapping resources such as foliar nitrogen, ecologists may be able to model and explain the distribution of herbivores

Turning to a food resource that large herbivores in Africa more typically consume (i.e., native grass in Kruger National Park, South Africa), obtaining adequate protein from vegetation is a critical parameter determining the success of herbivores. For example, Dublin (1995) demonstrated that the elephant shifts from a grass diet during the wet season to a woody-species diet during the dry season, as the latter maintains a higher percentage of crude protein (13-17%). In contrast, the crude protein of long grasses declines from about 11% to 3% over the course of the dry season (Dublin 1995). Mutanga and Skidmore (2004b) measured the reflectance of a native grass species *Cenchrus ciliaris* grown under three different nitrogen treatments (i.e., low, moderate and high nitrogen fertilization). They demonstrated that higher canopy nitrogen concentration in African native grass is significantly correlated with a shift of the red edge to longer wavelengths, confirming the results of Clevers and Jongschaap (2001) who had earlier demonstrated this for a ruderal (crop) species.

In another experiment, Mutanga et al. (2004b) tested the utility of using four variables derived from continuum-removed absorption features for predicting canopy nitrogen, phosphorus, potassium, calcium and magnesium concentration: (i)

continuum-removed derivative reflectance (CRDR), (ii) band depth (BD), (iii) band depth ratio (BDR), and (iv) normalised band depth index (NBDI). It was shown that a stepwise regression using normalised bands (calculated from continuum-removed reflectance spectra) could explain the variation of *in situ* grass quality, with R^2 values ranging between 0.43 and 0.80 (Figure 4.4). This is an encouraging result for mapping the distribution of forage quality under natural conditions in Africa.

Recently, Mutanga and Skidmore (2004a) demonstrated that grass foliar chemistry can be successfully mapped. In this case, nitrogen was predicted from



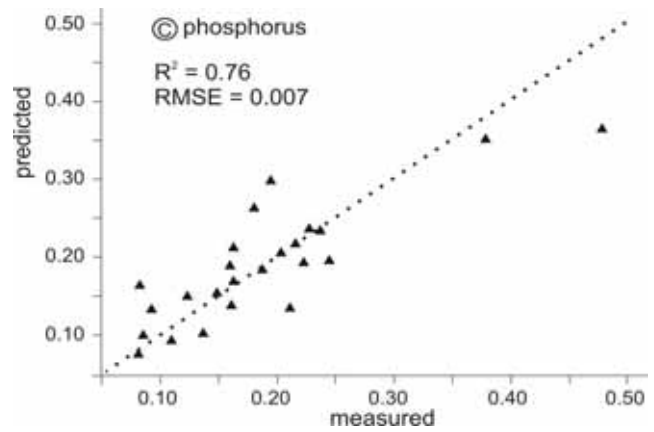
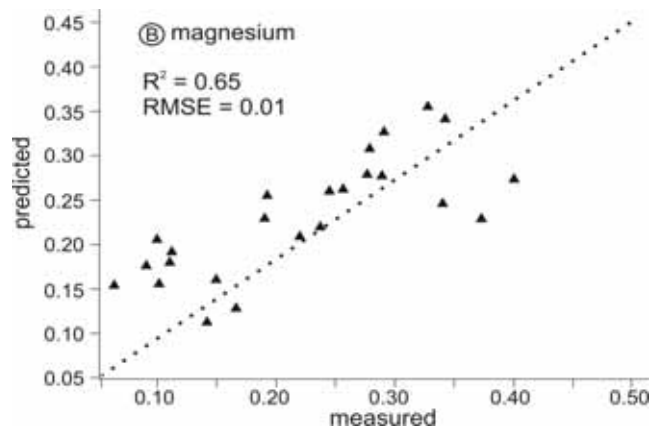
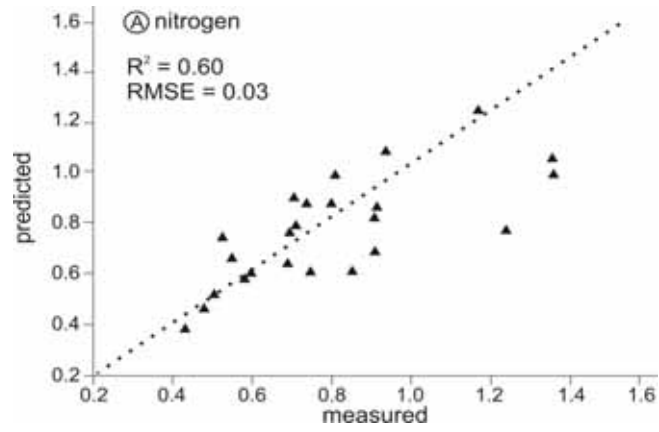
Grass foliar nitrogen can be accurately mapped using hyperspectral imagery

hyperspectral imagery (HyMap) flown over a test area in the Kruger National Park, South Africa. The spatial distribution of foliar nitrogen, and *ipso facto* foliar protein, was for the first time mapped as a continuous variable across a savanna landscape. Mutanga and Skidmore (2004a) further showed that a fenced area (Roan Camp), which had been treated with

fire, had a noticeable difference in foliar nitrogen concentration: the burnt area had significantly higher foliar nitrogen content. This subset of the image (Roan Camp area) demonstrates the utility of mapping foliar nitrogen.

Having established that foliar quality (nitrogen) can be mapped from hyperspectral images, and that large African herbivore strategy is to obtain adequate protein from vegetation, what evidence is there that other herbivores respond to foliar quality? A study of Australian herbivores by Braithwaite et al. (1983) showed that arboreal mammal density varied in response to nutritional quality indicators, as did goose species in the Netherlands (Ydenberg et al. 1983). These results were obtained at a landscape scale, and did not consider intra-specific variations in leaf chemistry, nor the foraging decisions made by individual animals. But the clear message was that nutritional quality determines herbivore density.

Thus far, the discussion concerns foliar 'attractants' such as protein. Can deterrents, plant biochemicals that adversely effect palatability or digestibility, play a role in determining herbivore behaviour? And if so, can deterrents be mapped across a landscape? Studies have highlighted the role of biochemical compounds acting as deterrents for herbivores, and were it not for the widespread and general occurrence of such allelochemical substances, plants would be totally consumed by insect and mammalian herbivores (Boughy 1973). For example, the above results of Braithwaite et al. (1983) were further developed by Lawler et al. (1998), who found that leaf chemicals acting as foraging deterrents (acylphloroglucinol compounds) played a large role in determining which eucalyptus leaves were palatable to herbivores (koalas and ringtail possums), and which leaves they avoided. Those trees with leaves that had higher levels of acylphloroglucinol compounds were virtually ignored by the animals. Interestingly, they hypothesised that acylphloroglucinol compounds are undetectable by the herbivores, but essential leaf oils or terpenes (such as cineole) act as cues to the ultimate deterrent in foliage (Figure 4.5). When viewed from a resource distribution perspective, their results indicate a large variation in secondary metabolite compounds between individual trees within a species.



(cont.)

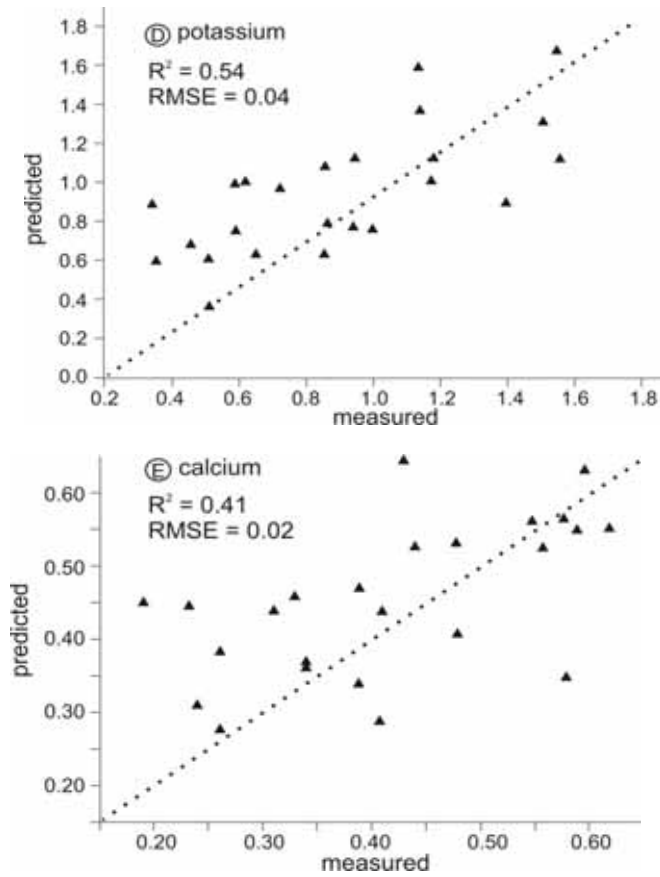
Figure 4.4. (cont.)

Figure 4.4. Measured versus predicted biochemicals for a randomly selected test data set ($n = 24$) using continuum-removed derivative reflectance (CRDR). Regression equations developed from the training data set ($n = 72$) were used to predict biochemicals on an independent test data set. From Mutanga et al. (2004b)

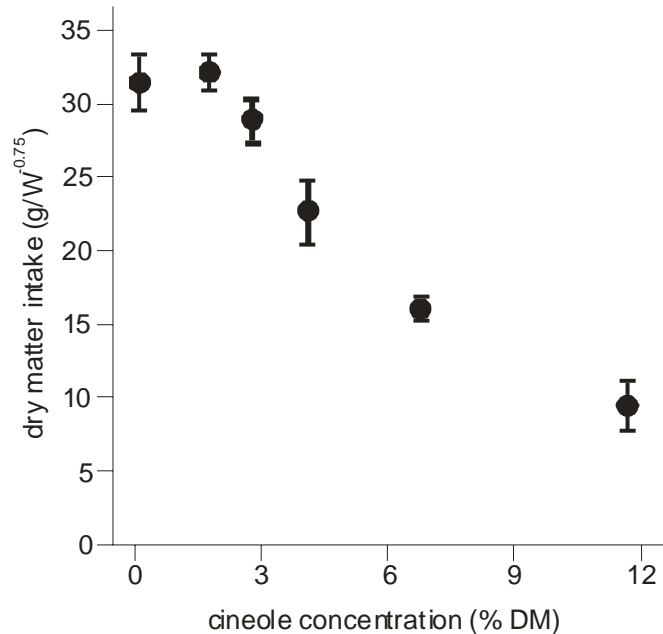


Figure 4.5. Dry-matter intake by koalas decreases as the concentration of terpene (cineole) increases (from Lawler et al. 1998)

Continuing this line of research, Dury et al. (2001) used a spectrometer in the laboratory to estimate the correlation between reflectance of dried and fresh eucalypt leaves and sideroxylonal compounds (R^2 of 0.72 and 0.53 for dry-leaf and fresh-leaf spectra, respectively). It is clear that there may be a number of target compounds (either acylphloroglucinol or essential oils) that perhaps can be detected from aircraft sensors and ultimately mapped using hyperspectral imagery.

Turning to the African savanna, Scholes (1997) summarises knowledge concerning plant defences against herbivores. The fine-leaved savanna trees have developed a physical (thorny) defence system, but are still browsed. The broad-leaved savannas are hardly browsed as a result of tannin in two forms: condensed tannins, which are effective against mammals, and hydrolysable tannins, which are effective against insects (Cooper and Owen-Smith 1986; Owen-Smith et al. 1987; Cooper et al. 1988). Tannins are estimated to be the fourth most abundant group of biochemicals produced by vascular plants (Hernes and Hedges 2000); they have been found to play an important role in several ecosystem processes. Recent studies have shown that condensed tannins may reduce nitrogen cycling in forest ecosystems (Northup et al. 1995; Kraus et al. 2004) and that increased concentrations of tannin forage have a negative effect on browsing herbivores. Condensed tannins in plants may reduce nutrient intake through the alteration of gut efficiency (Robbins et al. 1987; Mangan 1988; Mole 1989; Jones et al. 2001; Kondo et al. 2004; Bailey and Provenza, Chapter 2). By learning from previous encounters,

forage selection may therefore focus on reducing tannin intake levels (Cooper et al. 1988; Belovsky and Schmidt 1994; Clauss et al. 2003b; Matson et al. 2004).

Further, the ratio of condensed tannins to leaf nitrogen is a good predictor of acceptability to browsing antelope (Owen-Smith and Cooper 1987), hinting that in contrast to the Australian findings of Lawler et al. (1998), forage quality attractants (in the form of leaf nitrogen) in combination with deterrents may be important in the African savanna. Ongoing studies are considering the concentration of deterrents (specifically tannin and polyphenols) in mopane shrubs and trees, and assessing whether hyperspectral imagery may be used to estimate these leaf biochemicals (Ferwerda et al. 2002).

Recently, Ferwerda et al. (2006a; 2006b) showed that tree chemical composition can be mapped using hyperspectral remote sensing. By combining data on individual absorption points in the infrared part of the light spectrum with a neural-network



Also deterrents can be accurately mapped using hyperspectral imagery

system, the spatial distribution of condensed tannins and total polyphenol concentration in foliage was mapped with a prediction accuracy (R^2) of 52 % for total polyphenol concentration and 67 % for foliar condensed-tannin concentration. Their calibration routine only considered tannin concentration in mopane (*Colophospermum mopane*) trees and shrubs.

By masking the pixels that were not predominately mopane, they were able to show regional differences in condensed-tannin and polyphenol concentration (Figure 4.6). For this study, a comparison of nutrient and deterrent concentrations in vegetation was possible through utilising the same imagery as Mutanga and Skidmore (2004a). It is clear that regional differences in tannin and polyphenol concentration may be observed at a regional scale, and are related to differences in available nitrogen.

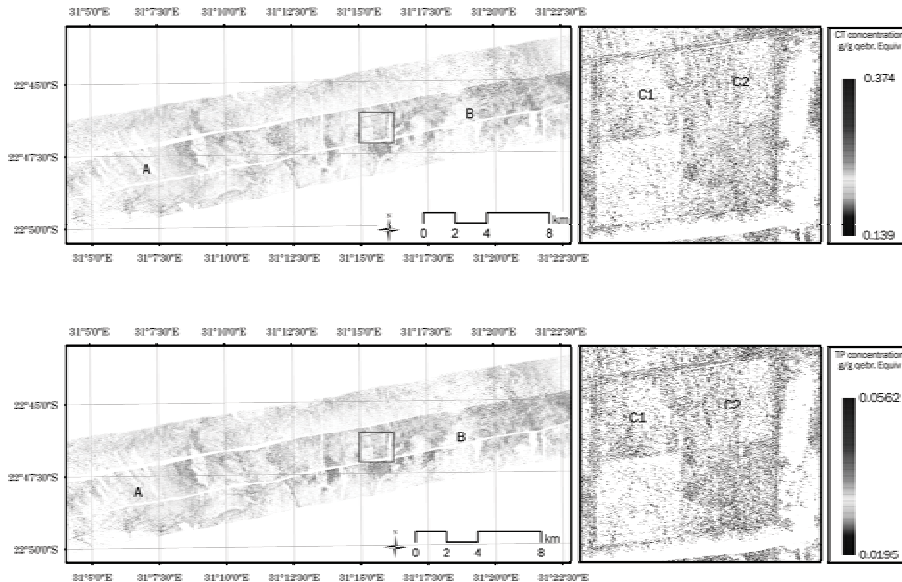


Figure 4.6. Condensed-tannin and total polyphenol concentration in Mopane trees on the Northern Plains of Kruger National Park, as calculated with a neural network from HyMap derivative reflectance images. Tannin concentration is higher on nutrient-poor shales and sandstones (A) than on the basalt-based soils (B), with lower concentration on sites that recently experienced fire (C1) than on the sites that did not recently experience fire (C2) (Ferwerda 2005; Ferwerda et al. 2006a; 2006b)

Forage quality is also related to plant species. The preference for particular plant species (that is forage quality) varies between herbivores (Lawler et al. 1998; Bos 2002). In general, short-growing grass species are favoured by grazers (Aerts et al.



Maps of plant species or groups of species are another interesting indicator of forage quality

1996; Bos 2002). In addition, areas of intermediate biomass have the highest nutritional return (Fryxell 1991). Particular species dominate these broad vegetation types. For example, in the Serengeti, McNaughton (1995) defines short grasslands dominated by species of *Sporobolus*, mid-grasslands by *Themeda triandra*, and tall grasslands by

Loudetia and *Hyperthelia*. The ability to map species may allow the resource component to be defined, and the suitability for herbivores, based on the plant-species occurrence and abundance, to be modelled. Is it possible to map the occurrence of individual plant species?

A number of authors have analysed the spectral difference between plant species and plant communities in the laboratory by visually looking at the shape of the reflectance curves (Elvidge 1990; Vogelmann and Moss 1993) or by statistical analysis of the differences in a more quantitative manner (Gausman et al. 1973; Richardson et al. 1983; Atkinson et al. 1997; Schmidt and Skidmore 2001). The common objective of these studies is to determine whether there is a difference in the spectra between species, as well as whether biochemical or biophysical characteristics contribute to these differences. Some success has been achieved in discriminating between forest species (Franklin 1994; Gong et al. 1997), as well as major physiogonomic categories (i.e., tree, shrub, grass) (Kalliola and Syrjanen 1991). For grasses, there have been few successful mapping exercises using remote-sensing imagery (Lewis 1994; Fayaerts and Van Gool 2001), though recent results prove it is possible to discriminate between African grassland species based on their hyperspectral reflectance spectra. Schmidt and Skidmore (2001) successfully discriminated 10 grass species for a rangeland in the Masai Mara, Kenya. At the herbaceous and grassland level, Schmidt and Skidmore (2002) demonstrated that 27 salt-marsh vegetation types in the northwest of the Netherlands could be discriminated.

A link between the salt-marsh vegetation types and herbivores (Schmidt and Skidmore 2002), is explored by Bos (2002), who showed that geese and hare herbivory modified the vegetation types, and also that grazing intensity was in turn influenced by the vegetation types and species. In fact, there are a number of empirical studies that show that short-growing plants characteristic of early succession are favoured by grazing (Aerts et al. 1996). Ungrazed high marshes are dominated by tall *Elymus* (Bakker 1989; Andresen et al. 1990; Olf et al. 1997). Based on similar published results, interviews with expert ecologists, as well as additional field work, an expert system using knowledge from expert ecologists was developed to map and monitor salt-marsh vegetation (Skidmore et al. 2001; Schmidt and Skidmore 2003), with accurate maps of herbivore resources being produced at the vegetation type level. These expert-system approaches can be modified to generate wildlife habitat maps directly, or wildlife habitat may be deduced from the vegetation map.

Another example of ecological (point-based) research being linked to resource availability affecting herbivores is formed by local hotspots of resident animals existing in the Serengeti in Tanzania (McNaughton 1995), these hotspots being associated with high sodium concentration in the vegetation. Sodium is particularly important to herbivores during late pregnancy and lactation. Mutanga et al. (2004a) demonstrated that vegetation with high sodium concentration may be differentiated from low-sodium-concentration vegetation using hyperspectral remote sensing. Again, ecological knowledge about large-herbivores resources can potentially be mapped over extensive areas and linked to animal behaviour, providing information for management.

TEMPORAL VARIATION IN HERBIVORE RESOURCES

As discussed in the section on “Quantity of herbivore resource”, there are a number of methods to estimate resource quantity spatially. For example, the biomass available in Kenya has been estimated by analysing the time series of advanced very high-resolution radiometer (AVHRR) images normalized using the difference vegetation index (NDVI). High positive values of NDVI correspond to dense vegetation cover that is actively growing, whereas negative values are associated with bare soil or sparse vegetation, clouds and snow. In Figure 4.7, the average NDVI for Kenya was calculated over a 12-month period and plotted every year for 4 years. 1982 was a dry year with low average biomass, and 1985 a wet year with much higher mean biomass.

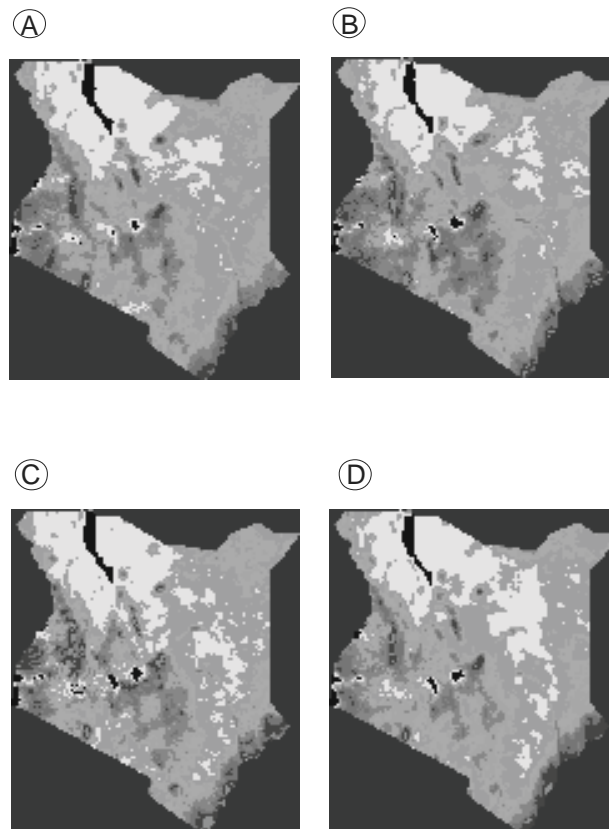


Figure 4.7. Average Normalised Difference Vegetation Index calculated from NASA AVHRR imagery for Kenya for (A) 1981, (B) 1982, (C) 1983 and (D) 1984. Dark tones are high biomass, light indicates low biomass. Note that images were prepared for this chapter using a NOAA AVHRR data set for Africa (processing involved calculating the highest NDVI value per 10-day period in order to remove cloud and other artefacts, and then averaging the 10-day periods over the whole year)

Oindo (2003) used a 20-year time series of NDVI processed by the Global Inventory and Monitoring and Modeling Studies (GIMMS) at NASA, and re-sampled to a pixel size of 7.6 km. The inter-annual maximum NDVI used in this study was considered to represent the NDVI at the height of the growing season



Satellite imagery can be used to map the change in biomass over time using NDVI

(Lewis et al. 1998). The data were corrected for cloud and atmosphere contamination as well as variations in sensors over the period (Los 1998). Morin (2000) suggested that temporal variation in productivity may be a factor that generates diversity. The results produced by Oindo (2003) suggested that a greater number of herbivore species and individuals coexist in

more seasonal environments, in other words, environments that have a greater variability in maximum NDVI. In contrast, for bird species in Kenya, Oindo et al. (2001) found that the standard deviation of maximum NDVI represents the amount of woody vegetation, and this factor limits the distribution of birds. High bird species diversity was also shown by this time series analysis to occur in stable and predictable environments in Kenya (Oindo et al. 2001).

The study by Said (2003) also used time-series data to estimate the ungulate-species richness in East Africa, and proved that time-series climatic indices (based on rainfall and potential evapotranspiration) are a better predictor of species richness than time-series NDVI indices (69% versus 55% of the variance explained). Ottichilo (2000a) used long-term animal census data from the Department of Resource Surveys and Remote Sensing (DRSRS) in Kenya and showed that the total of all non-migratory wildlife species in the Masai Mara ecosystem in Kenya declined by 58% in 20 years as a result of land use change, drought effects and poaching. Said (2003) confirmed that loss of wildlife wet-season range and habitat fragmentation through land use changes has a much wider impact on large herbivores than do the effects of climatic variations. This was caused by signs of competition between large herbivore species during non-migratory periods mainly associated with intra-specific competition (i.e., wildebeest and buffalo) for food.

The above results, generated using NDVI and climatic surfaces and analysed over extended time periods, show that spatial patterns of variation in resources are clearly impacting on large herbivores. Classical ecology, using point-based observations, has built up a large body of knowledge demonstrating the influence of time on ecological processes. For example, Dublin (1995) showed that there is a change in elephant feeding from grass to trees during the dry season as a response to reduction in the resource quality (foliar nitrogen) of grasses through the dry season. Such results may be combined with spatial-temporal models to better understand the resources available to large herbivores and assist in their management.

Since 1988, the Environment and Natural Resources Service of the UN FAO has been operating the Africa Real Time Environmental Monitoring Information System (ARTEMIS) (see <http://metart.fao.org/default.htm>). The system acquires and processes routinely hourly estimates of rainfall and vegetation index (NDVI) images, using Meteosat and NOAA data. The system covers the whole of Africa, and the outputs are produced on a 10-day and monthly basis for use in the field of

'early warning for food security' and 'desert locust control'. An example of the type of output that may be generated from these data can be found at the FAO website. A vegetation index was generated by calculating the difference between the 1997 and 1982-1996 average NDVI, and the difference sliced into 5 classes. For each class, a moving average-NDVI difference through a growing season or other period can be calculated, and used to estimate whether the biomass production is less than, or exceeding, the long-term average biomass production.

SYNTHESIS

In this chapter, we advocate that determining the distribution and densities of resource quantity and quality in space and time is a crucial step towards understanding the spatial arrangement of herbivores. In recent years remote sensing has become the tool of choice for producing high-spatial-resolution impressions of the variability of the landscape, and in particular land cover. Remote sensing is slowly moving away from mapping the surface into discrete land cover classes. More and more, it is now used to produce highly accurate probability maps of presence, depicting the percentage of individual pixels covered with a certain surface element. In this chapter, we presented several examples to illustrate the progress in remote sensing supporting resource ecology. These examples showed that biomass and nutrient concentrations in the vegetation may be monitored. The consequences for large herbivores from such approaches are obvious in terms of modelling resource quantity and quality over time. Some hypotheses for future research are formulated in Box 4.3.

Box 4.3. *Testable hypotheses for future research*

Hypothesis 1. Spatial variation of resources as charted by remote sensing can be used to test herbivore-foraging models.

Hypothesis 2. Although regional forage quality patterns can be mapped using remote sensing, local variation cannot accurately be captured with current-day sensor systems.

Hypothesis 3. Nutrient levels in forage as measured with hyperspectral remote sensing can be as accurate as nutrient levels measured using traditional lab-based techniques.