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Chapter 12

Grazers and Browsers in a Changing World: Conclusions

Iain J. Gordon and Herbert H.T. Prins

12.1 Introduction

The world on which we live is constantly changing, slowly through geological and evolutionary change and rapidly as the result of rainfall events or droughts, storms, hurricanes and cyclones, cold snaps or heat waves, and diurnal changes in light levels. Some of these changes have only local effects but others have global effects. In recent times the world has undergone a dramatic global change in form of the levels of CO₂ in the atmosphere, much of it derived from anthropogenic sources (King 2005). Currently, the level of CO₂, 380 ppm, has not been experienced by the biota on the planet for over 650,000 years (Siegenthaler et al. 2005). This increased CO₂ level is leading to changes in climate with consequences for rainfall and temperature patterns across the globe (IPCC 2001) with knock-on effects for vegetation community composition, and plant chemistry. For example, it is predicted that there will be a shift in the balance from grass to tree dominance in many savanna systems (Higgins et al. 2000; Bond et al. 2003). These changes in tree/grass ratios are happening rapidly (e.g., Lewis 2002) and will provide both opportunities and constraints both for humans in managing their domestic livestock species and also for wild herbivores. Much of this change is also brought about because of changes in land use over the last century with much land being taken out of agriculture, particularly in the temperate regions of the northern hemisphere (e.g., Ford 1971; Kjekshus 1977; Prins and Gordon, Chap. 1 this book). Whatever the exact causes or the interaction between them, an increase in the amount of browse in the landscape clearly will increase the amount of food available for browsers, whilst a reduction in the amount of grass, because of competition with woody species, will reduce the amount of food available for grazers. However, the system responses are unlikely to be that simple, because of such effects as non-linearity in the system and positive and negative feedbacks (e.g., Van de Koppel et al. 2002, van Langevelde *et al.* 2003). As a consequence systems responses will be difficult to predict at the scale at which they are managed and managers, therefore, need to be able to manage systems for unpredictable dynamics; that is, adopting risk averse, adaptive management principles (see Convention on Biological Diversity 2001). Scientists will have to

work with managers to develop modelling frameworks that incorporate both hard and soft (expert opinion) knowledge. Scientists will also have to use what knowledge we currently have to make 'best bet' predictions as to what the responses of systems might be to changes in management, and not fall back on the 'we don't yet know enough' argument to continue to collect data before giving advice.

Putting our money where our mouth is, in this chapter we will outline the likely biophysical responses of vegetation systems to CO₂-induced climate change, in terms of the quantity and quality of plant material available to grazers and browsers. We then assess the ways in which browsers and grazer populations are likely to respond to these changes in food quantity and quality and the consequences for the large herbivore community structure. Finally we give some advice as to how browsers and grazers might be managed in changing landscapes with particular emphasis on the collaboration that has to be built between managers and scientists to support the development of adaptive systems levels management approaches.

12.2 Responses in Plant Species Composition

Increases in CO₂ allow shrubs and trees to grow more quickly, and increase their water use efficiency (Drake et al. 1997; Ehleringer et al. 1997), relative to grasses, leading to shrub and tree encroachment into areas that have long been grasslands (Bond et al. 2003). Elevated CO₂ levels may cause higher allocation of carbohydrates to the roots of woody species. This results in, for instance, larger stores of starch resulting in faster regrowth after the dormant season (Bond et al. 2003). Because of this faster growth, woody species have an increased chance to escape a fire trap (Higgins et al. 2000) where fire can kill saplings before their vulnerable growing points have reached a height above the flames. Once saplings and young trees or shrubs are outside this zone, they are not reset by every fire to a prostrate post-fire form again, and can start expanding their crown, thus suppressing grass growth. This in turn leads to a reduced fire frequency and fire intensity, which feeds back into expanding woody cover.

Grasslands comprise approximately 30% of the global vegetation communities (Parton 1995), savannas about 20% (Sankaran et al. 2005), whilst forests cover 30% (FAO 2005). With changes in the circulating CO₂ levels in the atmosphere there will be changes in the balance of trees and grass in many terrestrial ecosystems leading to a reduction in the area of the globe covered by grassland and an increase in the area covered by forest. Two types of systems are most prone to change; the first are savannas because in these systems woody species are interspersed with grass at all possible scales, and transition from mixed grass–tree systems to tree-dominated ones can thus happen over large areas very fast (e.g., Stuart-Hill and Tainton 1999). Moreover, many savannas appear to have an unstable balance between woody species and grasses (Sankaran et al. 2005). It is noteworthy that contrary to the generally believed notion that forests are decreasing in the tropics, they are in fact spreading again in West and Central Africa. Two wet years in a row are often

enough to allow forest margins to expand into an area that was under savanna before. Only an increased disposal of manpower can keep secondary forests at bay. The second system type prone to change, is man-made agricultural grassland that has been converted from original natural forest. Large parts of the eastern United States, nearly the whole of Europe and also Japan have been cleared of forest in the service of agriculture. De-intensification of agricultural practices, then, can lead to the rapid re-emergence of woody species and forest (see Chap. 1, this book).

It has been predicted that the C4 grasses will not respond as effectively as C3 grasses to changes in atmospheric CO₂ (Bowes 1993; Ainsworth and Long 2005; and see Wand et al. 1999). However, the extent to which C3 and C4 grass species will respond to changes in atmospheric CO₂ levels will depend upon the water availability. Under well-watered conditions, C3 plants show increased photosynthesis and growth. Well-watered C4 plants exhibited increased photosynthesis in response to increasing CO₂, but total mass and leaf area were unaffected (Ward et al. 1999). In response to drought, C3 plants drop a large amount of leaf area and maintain relatively high leaf water potential in the remaining leaves, whereas C4 plants retain greater leaf area, but at a lower leaf water potential, which suggests that C4 species may have an advantage over C3 species in response to increasing atmospheric CO₂ and more frequent and severe droughts.

12.3 Responses in Plant Chemistry

Plant metabolism is centred around carbon, oxygen, and water. Plants get their carbon and oxygen primarily from the air; thus the concentrations of carbon and oxygen in the atmosphere play a major part in the chemistry of plants, most particularly in the photosynthesis rates. Increased CO₂ levels potentially leads to increased levels of photosynthesis (called the CO₂ fertilisation effect) and improve their water-use efficiency (because plants can restrict stomata, reducing transpiration, while fixing the same amount of CO₂) but the extent to which this potential is realised depends on the effects of other limiting factors, such as water and nutrients, including N and P. Therefore, the response of plants to elevated CO₂ will depend on local climatic circumstances, e.g. the degree of aridity and soil nutrient status (Kimball 1983; Nowak et al. 2004).

Increased CO₂ in both grass and browse plants generally leads to increases in C/N ratios and sugar concentrations, and to decreases in nitrogen and phosphorus concentrations (Kinney et al. 1997; Coley et al. 2002; Goverde et al. 2004; Hattas et al. 2005). Thus, whilst nitrogen concentration is reduced, the concentration of soluble carbohydrates is increased. Other responses are less predictable, with some authors describing no changes in plant secondary compounds to increases in CO₂ (Goverde et al. 2004), whereas others find an increase in concentrations of certain secondary compounds (tannins and ellagitannins, Kinney et al. 1997; leaf phenols, Coley et al. 2002) and, depending on the species, even variation in response (Kinney et al. 1997; Coley et al. 2002).

Since concentrate selectors tend to be energy limited while bulk or roughage feeders are nitrogen limited (Sinclair 1977; Prins and Beekman 1989; Prins 1996), the changes in vegetation quality associated with elevated levels of atmospheric CO₂ are likely to lead to improved levels of nutrition for browsers but not for roughage grazers. All other things being equal, increased overall levels of browser populations are to be expected. If the ratio of nutrients/secondary compounds increases, a relative increase in the nutritional value of browse is likely, resulting in an increase in the nutritional ecology of browsers relative to grazers.

Within the class of roughage grazers there is likely to be a difference in response between ruminants and hind-gut fermenters; roughage hindgut-fermenting grazers (equids, white rhinoceros) are perhaps less severely nitrogen limited than ruminant bulk grazers (many bovids and some cervids). Hindgut-fermenters are often seen as a sort of evolutionary dead end; but as Janis pointed out in Chapter 2 of this book, this opinion is not supported by analysis of the fossil record. We believe that within the class of bulk or roughage grazers, elevated CO₂ levels may even tip the balance of herbivore community composition towards hindgut-fermenters and away from the large ruminant roughage grazers.

It does not appear there will be any great differences between browse and grass in their response to the increased CO₂, in terms of quality, and so we might expect similarities in the nutritional responses among browsers and populations of selective grazers. Yet, in areas where C3 and C4 grasses co-exist, we expect a shift towards vegetations dominated by C4 grasses. Such a shift counterbalances a trend towards increased soluble carbohydrates in the plants, making the vegetation as a whole less attractive to both selective grazers and roughage grazers.

12.4 Responses in Terms of Population Dynamics

With changes in vegetation community structure, that is, the evolving dominance of ecosystems by shrubs and trees, there may be a shift towards browsers dominating the majority of herbivore communities. In turn, there is a possibility that browsers may limit the degree to which shrubs and trees survive in systems, counteracting the CO₂-generated propensity for shrubs and trees to increase. Ultimately, the response will depend on the degree to which the large herbivore/plant ecosystems are food or predator limited. To date there is little evidence for large herbivores being predator limited (Mduma et al. 1999), even where they are confined to islands (Vucetich and Peterson 2004), and there is ample evidence for a relationship between vegetation biomass/productivity and herbivore population growth rates/density (Coe et al. 1976; Fritz and Duncan 1994). There is a great deal of evidence that herbivore population size is positively correlated with the quantity of vegetation biomass available (Coe et al. 1976; Fritz and Duncan 1994). There is also much evidence that herbivores are bottom-up controlled (Drent and Prins 1987).

However, whilst herbivore populations may respond positively to increases in vegetation productivity and nutritional quality, it is not clear whether this will result

in top-down control of vegetation composition by herbivores (Bond 2005). As such, it is unlikely that any increase in herbivore population size will have an overall effect on vegetation composition other than on a local scale (Palmer et al. 2003). It is most likely, therefore, that vegetation composition will change towards one that is dominated by trees and shrubs and away from grasses. What effect is this likely to have on the structure of the large herbivore community?

This will depend on the degree to which herbivores are coupled to the dynamics of the vegetation. Where the coupling is strong (e.g., in temperate systems) the potential exists for herbivores to control vegetation structure and composition. Arid and semi-arid grazing systems, however, are prone to the effects of highly variable rainfall, with droughts causing frequent episodic mortality in herbivore populations. This has led to the suggestion that these are actually nonequilibrium or decoupled systems, in which animal impacts on plants are strongly attenuated or absent (Behnke and Scoones; 1992; Scoones 1994). Illius and O'Connor (1999) argued that even in arid and semi-arid systems animal numbers are regulated in a density-dependent manner by the limited forage available in key resource areas, which are utilized in the dry season, but this re-emphasizes the point that herbivores and vegetation are decoupled (not linked through density dependent effects) in the biggest part of the population's range.

12.5 Responses in Herbivore Community Structure

So, worldwide we expect forests to expand in those areas where people do not actively suppress its regrowth. We thus predict that the wetter parts of the tropics (with more than 600 mm annual rainfall: Sankaran et al. 2005), and the wetter parts of the temperate zone (with more than about 400 mm/yr rainfall, which demarcates the natural steppe formation) will experience this tendency towards increased forest cover. Browsers will benefit from this trend; mixed feeders may benefit too, roughage grazers will not.

It appears easier to make predictions about trends in the types of food than about the chemical composition of the different food stuffs for the different classes of herbivores. We predict that for browsing concentrate selectors, food quality will increase. We also predict that in areas that are dominated by C4 grasses (steppes and tropical savannas), roughage grazers will not benefit from elevated CO₂ levels. Because they are nitrogen-limited; for this class of grazers the situation will become even less favourable. This will also apply to grazers in C3-grass-dominated vegetation (in montane tropical areas and mesic temperate areas). It might be that selective grazers, such as hares or oribi, will be favoured by increased CO₂ levels because of elevated soluble carbohydrates. However, in the contact zones where C4-grass-dominated vegetation borders on C3-grass-dominated vegetation, we predict an expansion of C4 grasses to the detriment of all grazing species that are adapted to using C3 grasses (see Table 12.1).

It makes sense to suggest that selective grazing species of the Ruminantia are energy-limited as are their browsing counterparts. Not many herbivores with a

Table 12.1 Predicted changes in the numerical abundance of classes of mammalian large herbivores in response to increased carbon dioxide levels. Two effects are foreseen, namely changes in food quality and changes in the balance between woody species and grasses. Browsers in grassland may appear a contradiction in terms, but browsers may be living on herbs or make use of small pockets of woody species in a generally grass-dominated biome

	Species typical for tropical open forests	Species typical for tropical grasslands	Transition from C4 to C3 grasslands	Species typical for temperate grasslands	Species typical for temperate forests
Roughage grazers	Rare, and will become rarer	Dominant, but will decrease	Rare (since the beginning of the Holocene), and will further decrease but 'southern species' could invade	Rare (since the beginning of the Holocene), and will further decrease	Extinct (European wild 'forest' horse and aurochs are extinct). Remaining species are rare, and will become rarer
Selective grazers	Rare, but could increase	Common, but could increase	Rare, but could increase and 'southern species' could invade	Will increase	Absent
Mixed grazers	Common and can further increase	Common, but could increase	Rare, but could increase and 'southern species' could invade	Will increase	Will increase
Browsers	Common and will further increase	Rare, but could increase	Rare, but could increase and 'southern species' could invade	Will increase	Will increase

mass greater than that of rodents fall into that group, but the oribi is a candidate. Large non-ruminant concentrate selectors do also exist and most of these are either browsers that include fallen fruits in their diets (like the tapiroids) or mixed-feeders with a strong leaning towards omnivory (suids and tayassuidae). In this respect, lagomorphs (hares, picas, and rabbits), warthogs, and hippos deserve special interest as to whether they are energy-limited or nitrogen-limited. The evolution of coprophagy in lagomorphs may indicate that they have 'solved' nitrogen limitation (Hirakawa 2001). If this is true, then with rising CO₂ levels we predict an increase of the densities of lagomorphs and duiker antelopes; we keep our powder dry for the warthog and the hippo. We predict that, everything else being equal, suids, tayassuidae, tapiroids, and browsing rhinoceroses will increase.

As pointed out already, roughage-eating hindgut-fermenting grazers (equids, white rhinoceros) are less severely nitrogen-limited than ruminant bulk grazers (many bovids and some cervids). On the basis of that, we cautiously predict a shift in the class of roughage grazers from artiodactyls towards equids and rhinos. However, such a shift in numerical abundance will possibly be hampered by lack of sufficient biological variety within the group of hindgut-fermenters remaining for a future renaissance of this group of animals. Indeed, the northern white rhino (*Ceratotherium simum*) went extinct in 2005, and all wild equids except for the Burchell's zebra (*Equus burchellii*) are vulnerable or threatened. But other grass-eating rhinos went extinct before, like the steppe rhinoceros (*Dicerorhinus kirchbergensis*) and the woolly rhino (*Coelodonta antiquitatis*). North American horses went extinct recently, and so did *E. mauritanum* in North Africa and *E. hydruntinus* in Europe. There is thus much less variety left than in the artiodactyl group.

The same lack of potential may apply to the rebound we predict for browsers or for that most versatile group, the mixed feeders. In the temperate zone, there is a definite lack of biological variation to capitalise on the more favourable circumstances. Not only did the North American cameloids go extinct, but perhaps the animal whose all-round adaptations are missed most sorely is the extinct straight-tusked elephant (*Loxodonta atlanticum* / *Palaeoloxodon antiquus*) of the last interglacial of the temperate zone. In the tropics there are two species that typically may benefit from both trends (increase of woody cover and soluble carbohydrates). These are the Asian elephant (*Elephas maximus*) and the African elephant (*Loxodonta africana*). Ironically, through their desire for ivory and their need to protect their crops, humans keep elephant population numbers low, but through their use of fossil fuels, people probably create better conditions for elephants. We do not believe that in the modern world we will quickly see new elephant populations from either African or Asian stock taking an abode in the new forests of Europe, Siberia, or North America. The northern forests thus will lack bulldozer herbivores to facilitate a secure livelihood for smaller species, necessitating perhaps continued management. In Table 12.2 we have summarized our predictions about changes in community structure as a result of the trends we discern.

Table 12.2 Predicted changes in community structure as a result of an increased tendency towards woody encroachment and expanse of forests, and to increased availability of soluble carbohydrates

Predicted community trend		Typical for the tropics	Typical for the temperate zone
Browsers will increase		Greater kudu, lesser kudu	Moose
Concentrate selectors will increase	Browsers	Duiker antelopes	Mountain hare
	Grazers	Oribi; perhaps warthog and hippopotamus	Rabbits, picas, other hares
	Omnivores	Pigs, peccaries, tapirs, browsing rhinoceroses	Wild boar
Mixed feeders will increase or stay the same	More typical grazer will stay the same	Asian elephant, impala	White-tailed deer, red deer
	More typical browser will increase	African elephant	Roe deer
Bulk or roughage grazers will decrease or increase	Ruminants will decrease	Asian buffalo, African buffalo, wildebeest,	American bison, European wisent, fallow deer, Père David's deer
	Hind-gut fermenters will increase	Zebra species, white rhino	Kiang

12.6 Ways of Managing Browsers and Grazers

12.6.1 *Managing for Variability Rather than Stability*

Natural grazing systems are typified by dynamic herbivore populations (Prins and Douglas-Hamilton 1990 and Saether 1997; Clutton-Brock and Pemberton 2004). The present management ethos which advocates managing herbivore populations for stability (du Toit et al. 2003), often at levels well below carrying capacity, is, therefore, 'unnatural'. For example, for over 50 years the management of the Kruger National Park in South Africa was predicated on the basis of culling large herbivore populations to maintain predetermined levels. This management strategy does not reflect the natural dynamics of this semi-arid grazing system where climatic variability, predator/prey interactions, and disease would have meant dramatic annual, decadal, and centurial fluctuations in the numbers of large herbivores (Owen-Smith and Ogutu 2003). This would have lead to increased diversity of vegetation in the park, reflecting periods of low grazing pressure when tree recruitment, for example, would have been high, and periods of high grazing pressure when trees and shrubs would be been rare in the system and grasslands dominant (e.g., Prins and van der Jeugd 1993). In an area the size of the Kruger National Park it should be possible to restore this temporal variation in herbivore grazing pressure by using spatially variable population management policies.

However, in many other parklands, especially in Europe, this management opportunity does not exist. In the European context, the management of large herbivore populations will require cooperative management policies which link groups of (national) parks together allowing the build-up of large herbivore densities in some parks whilst reducing densities in others. This situation could be reversed at specific time intervals to allow ecosystem dynamics to mimic natural boom and bust cycles, with movement of animals between parks maintaining genetic integrity of the metapopulation (Hanski and Gilpin 1997). Whilst this strategy would require human intervention, it mimics the natural cycles of interactions between plants and herbivores, allowing plant adapted to both severe and lax grazing pressures to coexist.

12.6.2 *Gardening Versus Laisser Faire*

The European and American models of nature conservation differ in that the latter views a natural area as one that is left alone to reach some hypothesised wilderness equilibrium, whereas the former takes a much more interventionist approach in which nature has to be managed primarily for specific interests, e.g., birds, biodiversity, habitats of conservation importance, Scottishness! Each of the approaches has its benefits and drawbacks. In East Africa, the *laissez faire* policy has been for years the dominant one, while in southern Africa the interventionist ‘gardening’ approach was dominant for many decades. In West Africa, the *laissez faire* approach was a matter of fact, not of choice. It is poignant that with the abolishment of apartheid, the interventionist gardening approach has been imported into East Africa; specialists from South Africa and Zimbabwe now take up practice there. On the other hand, in Germany, France, and the Netherlands there is increased public interest in applying the American ‘wilderness’ concept to local nature management. Even in Japan, in the northeastern corner of Hokkaido Island, the management is keenly interested in cooperating with Yellowstone National Park to apply management principles for increased ‘wilderness’—as is also happening in Russia’s Far East.

With changes in land use occurring in both the developing and the developed world, there may be opportunities for both approaches since land abandonment in the developed world may allow large areas to be left to nature, whereas in the developing world, where the populations of rural areas are likely to expand dramatically over the next 50 years, there can be expected to be a requirement to strictly manage wildlife to reduce interactions with human agricultural interests. However, it may also be the case that in developed countries urban populations will call for strong control of wildlife as contact is made with predators in the countryside (on weekend visits), or as wildlife comes into conflict with people in peri-urban areas (e.g., traffic accidents, diseases such as Lyme disease). Incongruously, it may be that places such as Europe and North America will become the bastions for predators whilst in Africa and Asia predators are extirpated from much of their range as they come into conflict with ever expanding human populations.

12.7 Where Do We Go From Here?

As we have outlined in previous sections of this chapter, there are likely to be major changes in the structure and composition of the vegetation communities across large parts of the globe over the next 50 years. In turn this will lead to changes in the population densities and community composition of the large herbivores that rely on the vegetation. What can we do, as scientists to help managers to make decisions in this changing world? Firstly, we will have to make predictions about what is likely to happen. This can be at the qualitative level such as we have described above, however, we are likely to be asked to make more quantitative predictions in order to inform decisions about such things as what is the vegetation composition likely to be in a certain area in 20 years, what population levels of herbivores could these changed landscapes hold, what culling policies might need to be adopted in order to manage vegetation composition/structure to meet other biodiversity objectives?

A large number of models are available that predict different components of the system response, from those dealing with changes in plant growth in relation to CO₂ levels, through changes in tree/grass ratios, to herbivore population dynamics models (Illius and O'Connor 1999). However, given the complexity of the responses of these multi-dimensional systems it is our view that complex mechanistic models are likely to be too unwieldy to provide realistic quantitative outputs for management. We advocate the use of relatively simple Bayesian approaches that take into account the levels of understanding of system linkages and the strength of those linkages. This will allow scientists to work with managers to develop models of systems with the degree of certainty associated with the quantitative predictions.

12.7.1 *Landscape Scale Experiments*

Some exciting new initiatives have recently been taking place in Russia and the USA; parks are being established where the extinct large mammal communities are being replaced by functionally similar species (Zimov 2005; <http://www.faculty.uaf.edu/ffsc/park.html>). We have to use the kinds of predictions we provide in Tables 12.1 and 12.2 if we, as ecologists, are to help the developers of these parks decide how to introduce and manage species in a changing world. The predictions we have made about the changes in population density and community structure as a result of changes in CO₂ are not amenable to classic replicated experiments, however, the need remains to provide management advice at the landscape scale. This often forces a paradigm shift where the ecologist has to adopt a logical stance closer to that of the forensic scientist and address questions more closely aligned to the particular management issue at hand rather than any general scientific posture. We would suggest that model-based approaches, including Bayesian methods, offer powerful ways of addressing such questions,

but the status of the conclusions is different from those that a truly replicated and scientifically controlled experiment would provide (Hobbs and Hilborn 2006). In cases where only observational data are available, some model-based approach is inescapable. We see no clear demarcation between model-based approaches and classical experimental approaches, particularly in ecology, since both rely on underlying assumptions about repeatability in the natural world, which in practice may not be entirely correct. In the end, the new “Pleistocene” Parks offer us a great opportunity to test hypotheses and provide guidance for adaptive learning management where scientists and managers work hand in hand to manage our natural resource for the future.

12.8 Conclusions

The world in which we live is changing rapidly. Rising levels of CO₂ and changes in land use patterns will lead to changes in vegetation productivity and vegetation community composition and structure. Herbivore populations and communities will respond to these changes. Unless society is going to adopt a *laissez faire* attitude to these changes (in which case there could be significant societal and economic consequences) then managers will be expected to make decisions which will affect landscapes in the long term. If science is to play a part in determining the decisions that are made, then we have to develop partnerships with managers in which we work in collaboration to use our knowledge to develop predictions of how systems will change and to gather data to improve our understanding of how these systems operate. This is a challenge facing us all—and scientists must meet the challenge if they want to remain relevant and valued by society.

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