

- Helle, P. 1984. Effect of habitat area on breeding bird communities in northeastern Finland. *Annales Zoologici Fennici* 21: 421–425.
- Helle, P. and Jarvinen, O. 1986. Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. *Oikos* 46: 107–115.
- Holling, C.S. 1992. The role of forest insects in structuring the boreal landscape. In: Shugart, H.H., Leemans, R. and Bonan, G.B. (eds), *A Systems Analysis of the Global Boreal Forest*, 170–192. Cambridge University Press, Cambridge.
- Jarvinen, O. and Vaisanen, R. 1977. Long-term changes of the North European land bird fauna. *Oikos* 29: 225–228.
- Jarvinen, O. and Vaisanen, R. 1978. Long-term population changes of the most abundant south Finnish forest birds during the past 50 years. *Journal of Ornithology* 119: 441–449.
- Jarvinen, O., Vaisanen, R. and Kuusela, K. 1977. Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975. *Silvae Fennica* 11: 284–294.
- Johnston, C.A. and Naiman, R.J. 1990. Aquatic patch creation in relation to beaver population trends. *Ecology* 71: 1617–1621.
- MacDonald, G.M., Edwards, T.W.D., Moser, K.A., Pienetz, R. and Smol, J.P. 1993. Rapid response of tree-line vegetation and lakes to past climatic warming. *Nature* 361: 243–246.
- Mattson, W.J. and Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37: 110–118.
- Mladenoff, D.J. and Pastor, J. 1993. Sustainable forest ecosystems in the northern hardwood and conifer region: Concepts and management. In: Aplet, G.H., Johnson, N., Olson, J.T., and Sample, V.A. (eds), *Defining Sustainable Forestry*, 145–180. Island Press, New York.
- Olson, J.S., Watts, J.A., and Allison, L.J. 1983. Carbon in live vegetation of major world ecosystems. *Oak Ridge National Laboratory Technical Report ORNL-5862*. Oak Ridge, Tenn.
- Pastor, J., Bonde, J., Johnston, C.A. and Naiman, R.J. 1993b. Markovian analysis of the spatially dependent dynamics of beaver ponds. *Lectures on Mathematics in the Life Sciences* 23: 5–27.
- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F. and Cohen, Y. 1993a. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74: 467–480.
- Pastor, J. and Johnston, C.A. 1992. Using simulation models and geographic information systems to integrate ecosystem and landscape ecology. In: Naiman, R.J. (ed.), *Watershed Management: Balancing sustainability with environmental change*, 324–346. Springer-Verlag, New York.
- Pastor, J. and Mladenoff, D.J. 1993. The southern boreal–northern hardwood forest border. In: Shugart, H.H., Leemans, R. and Bonan, G.B. (eds), *A Systems Analysis of the Global Boreal Forest*, 216–240. Cambridge University Press, Cambridge.
- Pastor, J. and Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139: 690–705.
- Pastor, J. and Post, W.M. 1988. Response of northern forests to CO₂-induced climate change. *Nature* 334: 55–58.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R. and Bonan, G.B. (eds), *A Systems Analysis of the Global Boreal Forest*, 144–169. Cambridge University Press, Cambridge.
- Payette, S., Fillion, L., Gauthier, L. and Boutin, Y. 1985. Secular climate change in old-growth tree-line vegetation of northern Quebec. *Nature* 315: 135–138.
- Post, W.M. (ed.) 1990. Report of a Workshop on Climate Feedbacks and the Role of Peatlands, Tundra, and Boreal Ecosystems in the Global Carbon Cycle. *Oak Ridge National Laboratory Technical Monograph ORNL/TM-11457*, Oak Ridge, Tenn.
- Roulet, N.T., Ash, R. and Moore, T.R. 1992. Low boreal wetlands as a source of atmospheric methane. *Journal of Geophysical Research* 97: 3739–3749.
- Shugart, H.H., Leemans, R. and Bonan, G.B. (eds) 1992. *A Systems Analysis of the Global Boreal Forest*. Cambridge University Press, Cambridge.
- Telfer, E.S. 1992. Wildfire and the historical habitats of boreal forest avifauna. In: Kuhnke, D.H. (ed.), *Birds in the Boreal Forest*, 27–39. Northern Forestry Centre, Edmonton, Alberta.
- Updegraff, K., Pastor, J., Bridgman, S.D. and Johnston, C.A. 1995. Environmental and substrate quality controls over carbon and nitrogen mineralization in a beaver meadow and a bog. *Ecological Applications*, (in press).
- Virkkala, R. 1987. Effects of forest management on birds breeding in northern Finland. *Annales Zoologici Fennici* 24: 281–294.
- Virkkala, R. 1991. Population trends of forest birds in Finnish Lapland in a landscape of large habitat blocks: consequences of stochastic environmental variation or regional habitat alteration? *Biological Conservation* 56: 223–240.
- Wein, R.W. and El-Bayoumi, M.A. 1983. Limitations to predictability of plant succession in northern ecosystems. In: Wein, R.W., Riewe, R.R. and Methven, I.R. (eds), *Resources and Dynamics of the Boreal Zone*, 214–225. Association of Canadian Universities for Northern Studies, Ottawa.

6.1.7 Temperate grasslands

6.1.7.1 Introduction

Grasslands are the potential natural vegetation on approximately 25% ($33 \times 10^6 \text{ km}^2$) of the land surface of the Earth (Shantz 1954), although estimates of their current extent range from 16% (Whittaker and Likens 1975) to 30% (Ajtay *et al.* 1979).

Three aspects of grassland environments distinguish them from other ecosystem types (Anderson 1982; Milchunas *et al.* 1988): these are drought, fire and grazing by large ungulate herbivores. All three factors provide selection pressures favouring high turnover of above-ground plant organs, location of perennating organs near the soil surface, and location of a large fraction of plant biomass and activity below ground. Drought is a frequent influence on dry grasslands: fire is a much more significant force in shaping grasslands in humid regions than it is in dry regions. Grazing can be an important evolutionary force across the moisture gradient but its specific influence depends upon the moisture status of the site (Milchunas *et al.* 1988). Adaptations that enhance survival in arid and semi-arid environments may promote tolerance or

avoidance to grazing (Coughenour 1985). Therefore, grazing should have a larger effect on the species composition in humid than in arid and semi-arid grasslands (Milchunas *et al.* 1988).

6.1.7.2 Human impact on biodiversity

The most common use of grasslands is for grazing by domestic animals to produce mainly meat, milk and fibre. The first management action in most cases has been to replace native grazers and their predators with a few species of domestic animals. In an attempt to enhance animal production, humans have tried to increase primary production and/or animal consumption. Techniques aimed at increasing primary production, such as fertilization and irrigation, are all practices that raise resource availability for plants. Given that domestic animals have a selective intake, a large fraction of management techniques attempts to change species composition to match domestic animal preference. By their selective grazing behaviour, livestock tend to modify species composition in opposition to the efforts of managers. Even minimum husbandry has resulted in significant increases in animal biomass density in vast grassland regions (Oesterheld *et al.* 1992).

Grazing does not necessarily reduce plant biodiversity although overgrazing can result in losses of diversity at the population, species, ecosystem and landscape levels. The lack of grazing in some grassland types also results in biodiversity losses (Sala *et al.* 1986; Sala 1988). In general, ecosystem enrichment via fertilization or irrigation results in a decrease in diversity at the population and species levels (Tilman 1993). The replacement of animal or plant species by introduced species has a clear and direct negative effect on biological diversity. Changes in ecosystem and landscape diversity occur as a result of habitat selection by livestock (Smith *et al.* 1992) and replacement of native ecosystems by cultivated grasslands and croplands (Burke *et al.* 1991).

6.1.7.3 Productive capacity

Human impact on biodiversity. Primary production is most often manipulated by the addition of water or mineral nutrients. Both kinds of resource additions directly and indirectly modify biodiversity (Rosensweig 1971; Mellinger and McNaughton 1975; Lauenroth *et al.* 1978; Tilman 1993).

Ecosystem consequences of the impacts. A decrease in species richness, with initial deletion of the rarest species, results in no change in primary production until a threshold is reached beyond which there is a steady and substantial decrease in production (Figure 6.1-2). Removal of rare species in the Serengeti grasslands resulted in full compensation of production by the remaining species (McNaughton 1983). Deletion of species of intermediate

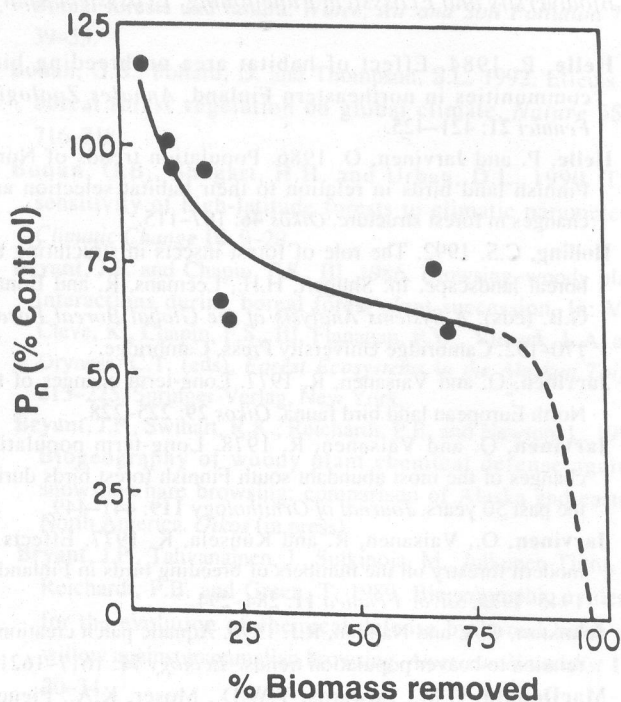


Figure 6.1-2: The effect upon primary productivity (P_n) of removing species that have different biomass in the intact ecosystems. In each case, all the individuals of a different species were removed. Remaining species were able to compensate for the removal of species with small biomass but were not able to compensate for the removal of the most abundant species (From: McNaughton 1983).

abundance resulted in production being only partially compensated. Finally, removal of dominant species resulted in a significant decrease in production.

Grasslands provide several examples in which the relationship between diversity and primary production has been assessed experimentally. The sites studied are geographically diverse and include California annual grasslands, old fields in New York, and grasslands in the Serengeti (McNaughton 1993). Results are contradictory: a negative relationship was observed between productivity and biodiversity in the annual grasslands of California and in the old fields of New York, whereas no relationship between productivity and diversity was found in the Serengeti. The effects of species diversity on production should be assessed with reference to which species have been deleted, and with respect to the driving forces behind the observed changes in diversity, rather than the diversity itself. In the case of the Serengeti, differences in diversity resulted from differences in grazing regime, while in the old fields in New York the diversity differences were a consequence of a successional process.

The diversity–stability hypothesis (McNaughton 1977) suggests that perturbations will result in a larger change in

ecosystem functioning in simple systems than in diverse systems. There is experimental evidence to test this hypothesis in grasslands. McNaughton (1993) analysed the response to a perturbation caused by fertilization along a diversity gradient which emerged as a result of a successional process. Similarly, Tilman and Downing (1994) analysed the response to a perturbation caused by a severe drought along a diversity gradient resulting from an experimental nitrogen fertilization where diversity was maximum in the native system and decreased as fertility increased (Figure 6.1-3). In both cases, the effect of perturbation on production was at a maximum in the simple systems and a minimum in the most diverse systems. The conclusions emerging from the experiment which used a diversity gradient created by differential fertilization has been criticized because greater soil fertility generally favours plants with lower root: shoot ratio, higher leaf conductance, and greater photosynthetic capacity (Givnish 1994). These characteristics also result in lower drought resistance. Therefore, the largest effect of drought observed in low diversity plots could have been the result of those plots being dominated by drought sensitive plants. The critical experiment to address this question has not been done yet: it would compare the response to similar perturbations of ecosystems with different levels of natural or experimentally created diversity, and should disentangle the effect of diversity from the effect of individual species.

6.1.7.4 Decomposition and soil structure

Human impact on biodiversity. Range managers use chemical, fire and mechanical means to modify plant species composition by deleting those species that are least preferred by domestic animals or by adding those that are highly preferred. Selective grazing by domestic herbivores also modifies plant species composition.

Ecosystem consequences of the impacts. The effects of biodiversity on decomposition in grasslands can be viewed from the plant perspective or the microbial perspective. Microbial diversity is not well documented in grasslands and its effect on decomposition is even less clearly understood. The effects of plant species diversity on decomposition result mainly from differences in litter quality among species. Several experiments have demonstrated the importance of species characteristics to total soil nutrients, nutrient availability and the rate of decomposition (e.g. Wedin and Tilman 1990; Matson 1990; Hobbie 1992; Vinton and Burke in press).

6.1.7.5 Water distribution and balance

Human impact on biodiversity. Management manipulations and foraging behaviour may change biodiversity. Large areas of grasslands in North America and Africa have slowly changed into shrublands and savannahs presumably as a result of grazing (Buffington

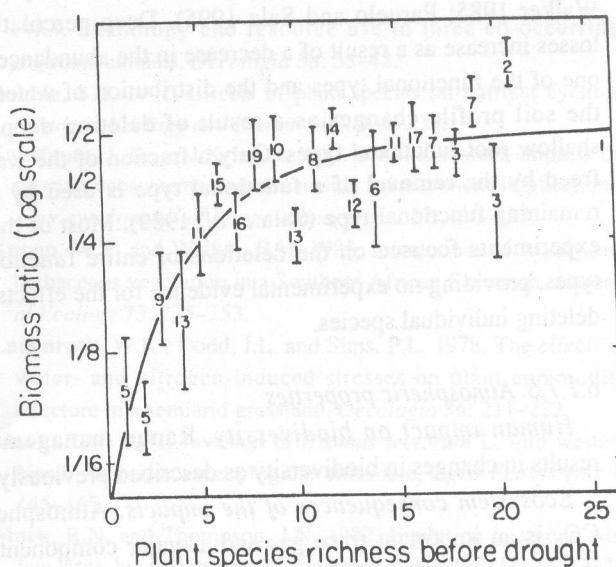


Figure 6.1-3: The effect of plant species richness before a severe drought on above-ground biomass during the drought year expressed as a fraction of previous year biomass. Standard error and number of plots with a given species richness are shown. The gradient of species richness was experimentally created by fertilization (from: Tilman and Downing 1994).

and Herbel 1965; Walker *et al.* 1981; van Vegten 1983; Neilson 1986; Archer 1989).

Ecosystem consequences of the impacts. Important input and output flows, which determine water balance and distribution of water, change with the scale of the unit under consideration. At the ecosystem level, the major flows are transpiration, bare soil evaporation, deep percolation, run-on, run-off and precipitation. At the plant level, transpiration is the only relevant flow but at higher levels of organization, watershed variables become dominant. All the output flows of water at one scale are intimately related, and although the biotic components directly affect mainly absorption and transpiration, they affect all other components of the water balance indirectly.

Reduction of transpiration as a result of species deletions is related to species-specific characteristics that affect water dynamics. Rooting depth, phenology, maximum transpiration rate, drought resistance or avoidance are all species characteristics that affect water balance. Species with deep roots are able to absorb water from a different part of the soil profile than species with shallow roots. Species with different phenological patterns (early vs late season) are able to use water available at different times of the year. In addition, many of these characteristics are self-associated. For example, late season phenology is associated in several systems to xerophytism or deep root systems (Gulmon *et al.* 1983; Golluscio and Sala 1993).

Experiments and associated models of grassland water dynamics have shown how removal of functional types such as perennial grasses or shrubs results in profound

alterations of the ecosystem water balance (Knoop and Walker 1985; Paruelo and Sala 1995). Deep percolation losses increase as a result of a decrease in the abundance of one of the functional types and the distribution of water in the soil profile changes as a result of deleting deep or shallow root functional types. Only a fraction of the water freed by the removal of a functional type is used by the remaining functional type (Sala *et al.* 1989). Most of these experiments focused on the deletions of entire functional types, providing no experimental evidence for the effects of deleting individual species.

6.1.7.6 Atmospheric properties

Human impact on biodiversity. Range management results in changes in biodiversity as described previously.

Ecosystem consequences of the impacts. Atmospheric CO₂ is an important trace gas and a major component of the carbon cycle. We have described how biological diversity at scales ranging from species to landscapes affects production and decomposition which are the major processes driving the carbon cycle. We are not aware of any studies relating species diversity to atmospheric properties. However, Burke *et al.* (1991) calculated the effects on the carbon balance of converting a large fraction of the North America Central Grassland Region into cropland. Cultivation resulted in a net release of carbon from soil organic matter larger than the expected loss as a result of climate change. The current increase in atmospheric methane is not related to an increase in the number of grazing mammals (Crutzen *et al.* 1986).

6.1.7.7 Landscape structure

Human impact on biodiversity. Croplands have expanded dramatically during this century, from 9.1×10^6 to 15×10^6 km² (Richards 1990). This expansion has altered landscape heterogeneity in grasslands. Habitat selectivity by domestic livestock has differentially influenced riparian ecosystems and therefore altered landscape diversity. Domestic livestock, and especially cattle, tend to congregate in the topographically lowest portions of the landscape (Senft *et al.* 1985; Pinchak *et al.* 1991). Such habitat selectivity has negative effects on the plant and animal diversity of riparian ecosystems (Kauffman and Krueger 1984; Smith *et al.* 1992).

Ecosystem consequences of the impacts. The reduction in diversity of streamside vegetation and its productivity have negative effects on both physical and chemical indicators of water quality (Kauffman and Krueger 1984). Reduction in the diversity and productivity of the herbaceous vegetation layer can change the velocity and erosive energy of the stream flow, while losses of the woody overstorey have large effects on water temperature. Both the overstorey and understorey vegetation layers have important effects on the rates and kinds of aquatic

processes that occur in a stream (Kauffman and Krueger 1984), and the diversity and productivity of invertebrates and fishes are profoundly influenced by the diversity of the streamside vegetation.

6.1.7.8 Biotic linkages and species interactions

Human impact on biodiversity. Invasions in grasslands are common and in some cases have been associated with changes in grazing regime. Examples of grasslands that have been invaded by exotic species are the California grasslands and the intermontane west of North America, the pampas in South America, and the savannahs in tropical South America (Sala *et al.* 1986; D'Antonio and Vitousek 1992).

Ecosystem consequences of the impacts. Invasions in grasslands have usually occurred in association with an increase in grazing intensity and/or a change in dominant grazer. Vulnerability to invasions associated with grazing appears to be related to moisture availability and the grazing history in evolutionary time (Milchunas *et al.* 1988). Grasslands that evolved under light grazing conditions and under mesic conditions are more vulnerable to invasions than those that evolved under heavy grazing in xeric environments. Semi-arid grasslands of the northwest USA and southwest Canada have a short evolutionary grazing history, and before the introduction of cattle they were dominated by perennial tussock grasses (Tisdale 1947; Daubenmire 1970). The inability of these grasses to cope with heavy grazing resulted in the invasion and dominance of many areas by Eurasian weeds (Daubenmire 1940, 1970; Ellison 1960; Mack 1981; Mack and Thompson 1982). Invasions often disrupt competitive interactions (D'Antonio and Vitousek 1992) which result in changes in species composition with the ecosystem effects described above.

6.1.7.9 Microbial activities

Human impact on biodiversity. See discussion of decomposition and soil structure above.

Ecosystem consequences of the impacts. The effect of changes in plant species diversity on microbial activity as a result of changes in litter quality and quantity are described in the decomposition section above.

6.1.7.10 Summary and relevance to human activities

On a world-wide basis the response of grasslands to the major human use – domestic livestock grazing – has been variable (Milchunas and Lauenroth 1993). In some areas where the native vegetation is well adapted as a result of evolution, changes in biodiversity have been very small (Milchunas *et al.* 1988). In other areas changes have been very large. In some cases and especially in tropical and subtropical grasslands, the large changes have involved a shift from a grass-dominated vegetation to one dominated

by woody plants (Walker *et al.* 1981; vanVegten 1983; Archer 1989). In other cases the large changes have involved invasions of exotic plants which have profoundly altered the ecosystems. Conversion of grasslands to croplands or seeded pastures has also had a major influence on biodiversity and ecosystem functioning. In many cases these converted grasslands have become net sources of carbon and nutrients accelerating global change. These major transformations of grasslands and their effects on biodiversity modify the water, carbon and nutrient cycles to an extent that significantly contributes to altering the Earth's life support system.

References

- Ajtay, G.L., Ketner, P. and Duvigneaud, P. 1979. Terrestrial primary production and phytomass. In: Bolin, B., Degens, E., Kempe, S. and Ketner, P. (eds), *The Global Carbon Cycle*, SCOPE edition. Vol. 13. 129-182. John Wiley, Chichester.
- Anderson, R.C. 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands. In: Estes, J.R. and Tylr, R.J. (eds), *Grasses and Grasslands: Systematics and ecology*. 312. University of Oklahoma Press, Norman.
- Archer, S. 1989. Have southern Texas savannahs been converted to woodlands in recent history? *American Naturalist* **134**: 545-561.
- Buffington, L.C. and Herbel, C.H. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* **35**: 139-164.
- Burke, I.C., Kittel, T.G.F., Lauenroth, W.K., Snook, P., Yonker, C.M. and Parton, W.J. 1991. Regional analysis of the central great plains. *BioScience* **41** (10): 685-692.
- Coughenour, M.B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden* **72**: 852-863.
- Crutzen, P.J., Aselmann, I. and Seiler, W. 1986. Methane production by domestic animals, wild ruminants, other herbivorous fauna and humans. *Tellus* **38B**: 271-284.
- D'Antonio, C.M., and Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**: 63-87.
- Daubenmire, R. 1940. Plant succession due to overgrazing in the *Agropyron* bunchgrass prairie of south-eastern Washington. *Ecology* **21**: 55-65.
- Daubenmire, R. 1970. *Steppe vegetation of Washington*. Washington Agriculture Experimental Station Technical Bulletin Edition. Vol. 62. Washington State University, Pullman.
- Ellison, L. 1960. Influence of grazing on plant succession of rangelands. *Botanical Review* **26**: 1-78.
- Givnish, T.J. 1994. Does diversity beget stability? *Nature* **371**: 113-114.
- Golluscio, R.A., and Sala, O.E. 1993. Plant functional types and ecological strategies in Patagonian forbs. *Journal of Vegetation Science* **4**: 839-846.
- Gulmon, S.L., Chiariello, N.R., Mooney, H.A. and Chu, C.C. 1983. Phenology and resource use in three co-occurring grassland annuals. *Oecologia* **58**: 33-42.
- Hobbie, S.E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* **7**: 336-339.
- Kauffman, J. B., and Krueger, W.C. 1984. Livestock impacts on riparian ecosystems and streamside management implications: a review. *Journal of Range Management* **37**: 430-437.
- Knoop, W.T. and Walker, B.H. 1985. Interactions of woody and herbaceous vegetation in a Southern African Savannah. *Journal of Ecology* **73**: 235-253.
- Lauenroth, W.K., Dodd, J.L. and Sims, P.L. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* **36**: 211-222.
- Mack, R.N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro Ecosystems* **7**: 145-165.
- Mack, R.N. and Thompson, J.N. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* **119**: 757-773.
- McNaughton, S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* **111**: 515-525.
- McNaughton, S.J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* **53**: 291-320.
- McNaughton, S.J. 1993. Biodiversity and function of grazing systems. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 361-383. Springer-Verlag, Berlin.
- Matson, P. 1990. Plant-soil interactions in primary succession at Hawaii Volcanoes National Park. *Oecologia* **85**: 241-246.
- Mellinger, M.V. and McNaughton, S.J. 1975. Structure and function of successional vascular plant communities in central New York. *Ecological Monographs* **45**: 161-182.
- Milchunas, D.G. and Lauenroth, W.K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **63**: 327-366.
- Milchunas, D.G., Sala, O.E. and Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* **132**: 87-106.
- Nelson, R.P. 1986. High resolution climatic analysis and Southwest biogeography. *Science* **232**: 27-34.
- Oesterheld, M., Sala, O.E. and McNaughton, S.J.. 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature* **356**: 234-236.
- Paruelo, J.M., and Sala, O.E. 1995. Water losses in the Patagonian steppe: a modelling approach. *Ecology* **76**: 510-520.
- Pinchak, W.E., Smith, M.A., Hart, R. H. and Waggoner, J.W. 1991. Beef cattle grazing distribution patterns on foothill range. *Journal of Range Management* **44**: 267-275.
- Richards, J.F. 1990. Land transformation. In: Turner, B.L., II, Clark, W.C., Kates, R.W., Richards, J., Mathews, J.T and Meyer, W.B. (eds.) *The Earth as Transformed by Human Action*. 161-178. Cambridge University Press, Melbourne.
- Rosenzweig, M.L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* **171**: 385-387.

- Sala, O.E. 1988. The effect of herbivory on vegetation structure. In: Werger, M.G.A., van der Aart, P.J.M., During, H.J. and Verhoeven, J.T.A. (eds), *Plant Form and Vegetation Structure*. 317–330. SPB Academic Publishing, The Hague.
- Sala, O.E., Golluscio, R.A., Lauenroth, W.K. and Soriano, A. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81: 501–505.
- Sala, O.E., Oesterheld, M., León, R.J.C. and Soriano, A. 1986. Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio* 67: 27–32.
- Senft, R.L., Rittenhouse, L.R. and Woodmansee, R.G. 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. *Journal of Range Management* 38: 82–86.
- Shantz, H.L. 1954. The place of grasslands in the earth's cover of vegetation. *Ecology* 35: 142–145.
- Smith, M.A., Rogers, J.D., Dodd, J.L. and Skinner, Q.D. 1992. Habitat selection by cattle along an ephemeral channel. *Journal of Range Management* 45: 385–390.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179–2191.
- Tilman, D. and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363–365.
- Tisdale, E.W. 1947. The grasslands of the southern interior of British Columbia. *Ecology* 28: 346–382.
- van Vegten, J.A. 1983. Thornbush invasion in a savannah ecosystem in eastern Botswana. *Vegetatio* 56: 3–7.
- Walker, B.H., Ludwig, D., Holling, C.S. and Peterman, R.M. 1981. Stability of semi-arid savannah grazing systems. *Journal of Ecology* 69: 473–498.
- Wedin, D.A., and Tilman, D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84: 433–441.
- Whittaker, R.H. and Likens, G.E. 1975. The biosphere and man. In: Lieth, G.E. and Whittaker, R.H. (eds), *Primary productivity of the biosphere*. Ecological Studies Edition. Vol. 14. 305–328. Springer-Verlag, New York.
- and Sainz Ollero 1993). The five regions have markedly different biogeographic characteristics, histories and current patterns of human habitation and use, and markedly different patterns of biodiversity. These differences are most clearly obvious between the Mediterranean region, which has a long history of human habitation, and some of the areas more recently settled by Europeans, such as Australia. Mediterranean-type ecosystems consist of a variety of vegetation types, including forest, woodland, shrubland and grassland. A feature of many of the vegetation types is their sclerophyllous nature, and high levels of secondary compounds such as terpenes. Floristic diversity and degree of endemism are high in most Mediterranean areas, and shrublands in Australia and South Africa are particularly noted for their high floristic diversity.
- Human impacts on biodiversity vary between regions, and include both positive and negative components. In the Mediterranean Basin, where human activities have modified the landscape for thousands of years, current levels of biodiversity are in part maintained by continued human influence. Where traditional human activities cease, plant and animal diversity can be reduced (González Bernáldez 1991; Naveh 1994) and susceptibility to disturbances, especially fire, can be increased (Moreno 1989). This in turn can promote landscape homogenization, with resultant negative effects on biodiversity (Faraco *et al.* 1993; Pérez *et al.* in press). Landscape homogenization can also result from the abandonment of agricultural/pastoral land (Fernández-Alés *et al.* 1992). Human activities have also played an important role in determining the distribution of vegetation and ecosystems in Chile, and may be important in the retention of components of the biodiversity within these ecosystems (Fuentes and Muñoz 1994; Fuentes *et al.* 1995).

6.1.8 Mediterranean-type ecosystems

6.1.8.1 Introduction

Mediterranean-type ecosystems share a climate of cool wet winters and a distinct summer drought, and are found in the Mediterranean Basin, California, Chile, the Cape Province of South Africa and southwestern and southern Australia. Estimates of biome cover vary depending on the climatic classification used, but are approximately as follows, given as 10^6 km² (estimates of numbers of plant species in each region are given in parentheses where available): Mediterranean Basin 1.87 (c. 25 000), California 0.32 (5050), Chile 0.14 (c. 2100), Cape Province 0.09 (c. 8550), Southwestern Australia 0.31 (c. 8000) (Quézel 1981; Cowling *et al.* 1992; Fuentes *et al.* 1995; Hobbs *et al.* 1995; Keeley and Swift 1995). The last four regions are listed as 'hot spots' for species diversity by WCMC (1992), although parts of the Mediterranean Basin also possess high plant diversities, as estimated on a species per km² basis (Davis *et al.* 1986; Valdés *et al.* 1987; Moreno Saiz

In South Africa and Australia, and in California, human impacts are largely negative. These include reductions in population size and/or distribution of sensitive species which have occurred as a result of land-use changes and fragmentation (Saunders 1989, 1993; Hopper *et al.* 1990; Cowling and Bond 1992; Hopper 1992). Reduced age structure diversity of dominant species results from altered disturbance regimes (Yates *et al.* 1994); genetic diversity is reduced through habitat loss (Rebelo 1992), and loss of species diversity is caused by introduced predators, herbivores, plants and diseases (Mooney *et al.* 1986; di Castri *et al.* 1990; Groves and di Castri 1991; Scougall *et al.* 1993; Wills 1993).

Reduced structural complexity can occur because of management practices such as post-fire re-seeding (Barro and Conrad 1987) or deforestation, but this is countered in some cases by local increases in complexity through reforestation (Blondel 1976). Human activities can maintain structural diversity where vegetation patterns are