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Summary

 Natural, semi-natural and artificial grasslands occur extensively around the globe, but successful management for production and biodiversity poses several dilemmas for conservationists and farmland managers. Deriving from three continents (Africa, Australia and Europe), papers in this Special Profile interface three specific issues: plant responses to grazing, plant invasions and the responses to management of valued grassland biota.
Although pivotal in grassland management, plant responses to grazing are sometimes difficult to predict. Two alternative approaches are presented here. The first uses natural variations in sheep grazing around a water hole to model the dynamic population response of a chenopod shrub. The second analyses a long-term grazing experiment to investigate the links between plant traits and grazing response.

3. Linked often crucially with grazing, but also driven sometimes by extrinsic factors, invasions are often cause for concern in grassland management. The invasions of grasslands by woody plants threatens grassland habitats while the invasions of pastures by alien weeds reduces pasture productivity. The papers in this section highlight how a complementary range of management activities can reduce the abundance of invaders. A final paper highlights how global environmental change is presenting new circumstances in which grassland invasion can occur.

4. The impact of grassland management on biodiversity is explored in this Special Profile with specific reference to invertebrates, increasingly recognized both for the intrinsic conservation value of many groups and for their role in ecosystem processes. The potential for manipulating flooding in wet grasslands to increase the soil invertebrate prey of wading birds is illustrated, together with the roles of management and landscape structure in enhancing insect diversity.

5. In the face of climate change and growing demands for agricultural productivity, future pressures on grassland ecosystems will intensify. In this system in which productivity and conservation are so closely bound, there is a need both to raise the profile of the issues involved, and to improve our understanding of the applied ecology required for successful management.

Key-words: climate change, comparative demography, grassland management, insect diversity, invasions, plant traits, population dynamics, population model.

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Introduction

Natural grasslands occur extensively around the globe in areas where there is typically a fairly long dry season. In temperate regions they include the steppes of Eurasia, the prairies of North America, the pampas of South America and the veld of South Africa; in tropical latitudes, savanna is a term applied to a range of tropical vegetation from pure grassland to woodland with much grass (Cox & Moore 1999). Seasonal drought is undoubtedly important in determining the distribution of grasslands, but fire and grazing animals – in removing biomass – often play an overriding role (Peet *et al.* 1999). The role of grazing animals is so marked that semi-natural grasslands now occur extensively in many

© 2001 British Ecological Society Correspondence: Professor Andrew Watkinson (e-mail a.watkinson@uea.ac.uk) 234 A.R. Watkinson & S.J. Ormerod areas of the world where deforestation has taken place, both in temperate and tropical latitudes. However, many natural grasslands have been destroyed by cultivation or extensively modified by grazing from domesticated livestock or by the introduction of alien plant species. Similarly, the pressures to increase animal production have led to many semi-natural grasslands being intensified by reseeding, herbicide and fertilizer application.

With pressures on them so marked, grasslands now pose a number of dilemmas for applied ecologists. From a conservation perspective, they are often important in terms of biodiversity, whether this be the large grazing mammals of the African savannas (Caro 1999) or the plant diversity associated with traditional hay meadows in northern Europe (Smith *et al.* 2000). Both the plant and animal biodiversity depends critically upon the level of grazing. Too much grazing may often lead to land degradation and the loss of biodiversity, while too little grazing may lead to succession from grassland to woodland and the loss of the grassland habitat. Not only is the level of grazing important, but also the timing and the animals species involved (Grant *et al.* 1996; Hulme *et al.* 1999; Humphrey & Patterson 2000).

The range manager, farmer or pastoralist faces a different set of dilemmas. They are typically keen to increase herbage production through, for example, the application of fertilizers, drainage or reseeding (Haugland & Froud-Williams 1999), but such intensification may lead to the loss of diversity (Smith et al. 2000) and increased agricultural run-off with implications for ecosystems downstream (Cresser et al. 2000; Edwards et al. 2000). Farmers are keen to maintain high stocking rates to maximize production but this may result in land degradation and the invasion of weedy species. Balancing stocking rates with herbage production is particularly difficult in arid and semi-arid areas where there is considerable variability in rainfall. Novel insights into the sustainability of semi-arid grazing systems and the debate on equilibrium vs. non-equilibrium dynamics are provided in the Journal of Applied Ecology by Fynn & O'Connor (2000) for semi-arid African savanna and Fernandez-Gimenez & Allen-Diaz (1999) for Mongolian steppe.

Clearly, to resolve these varying dilemmas and to attain what will be an increasingly difficult balance between sustainable production and the protection of grassland biodiversity, there is a need both to raise the profile of grassland issues, and to improve our understanding of applied grassland ecology.

A Special Profile: grasslands, grazing and agriculture

This Special Profile of eight papers on the theme of 'grasslands, grazing and biodiversity' brings together a range of papers that address issues relating to the dilemmas faced by grassland managers. The papers derive from three continents (Africa, Australia and Europe) and address a number of issues.

PLANT RESPONSES TO GRAZING

Grazing is one of the central and pivotal issues affecting grasslands, linking their maintenance, productivity, economic use and management for biodiversity. And yet, plant responses to grazing are difficult to predict. All too often our knowledge of the impacts of grazing on plant populations and communities comes from exclosures. Unfortunately, they are typically an all-or-nothing treatment and tell us relatively little about how grazing impacts on community composition; they are often too small, do not allow for variations in the density or seasonality of grazing and ignore the fact that plant responses are typically non-linear. Grasslands depend critically on the activity of grazing animals, and to understand plant responses to grazing it is therefore imperative to explore the impacts of variation in grazing on community structure. This is very difficult to do.

A modelling approach recently exemplified by Weber et al. (1998) involves addressing both spatial aspects of vegetation dynamics and grazing utilization. Their grid-based model described vegetation in the southern Kalahari in terms of three major life forms, and the grazing of ungulates in terms of a set of rules that govern the distribution, selectivity and memory of the grazing animals. They stress the importance of explicitly quantifying the spatial grazing pattern if the impact of vertebrate grazing on vegetation dynamics is to be predicted. At present we know too little about patterns of vertebrate grazing to predict how varying levels of grazing will impact on the structure and dynamics of the vegetation, but recent studies on red deer and sheep grazing have gone some way to predicting spatial utilization of grass/heather mosaics (Hester et al. 1999; Palmer & Hester 2000).

The challenge to applied ecologists interested in quantifying the impacts of variable levels of grazing on plant populations and communities is therefore to address the question of the considerable temporal and spatial variability in grazing that results from the interaction of environmental factors, resource supply and animal behaviour. How can this be done? In this Special Profile, Hunt (2001) makes use of natural variation in sheep grazing around a watering point (a piosphere) to construct time-varying stochastic matrix models to predict the impact of grazing on a chenopod shrub; other approaches to the modelling of shrub populations in this volume are outlined by McCarthy, Possingham & Gill (2001) and Rees & Hill (2001). The utilization of natural variation in grazing patterns runs the danger of confounding spatial variation in the environment with grazing patterns, but is perhaps the best technique available for animals that range over considerable distances.

It is only possible at present to study the impacts of grazing on the population dynamics of a relatively small number of individual species. There is therefore considerable interest in the response of functional groups of plants (Sternberg *et al.* 2000) to grazing as well as the link with plant traits. Bullock *et al.* (2001) report here,

© 2001 British Ecological Society, *Journal of Applied Ecology*, **38**, 233–237 **235** Grasslands, grazing and biodiversity from a 12-year grazing experiment, on the link between plant traits and grazing, suggesting that it may be possible to predict changes in species composition under grazing through an understanding of the mechanisms of plant responses. An extreme example of the long-term effects of a single defoliation after 20 years is provided by Lee *et al.* (2000) for the alpine tussock grass *Chionochloa pallens* in New Zealand, highlighting how insensitive some grasses are to defoliation.

PLANT INVASIONS

Linked often crucially with grazing, but also driven sometimes by extrinsic factors, invasions of two types are often cause for concern in grassland management. On the one hand, there is the invasion of grassland by woody species with the consequent loss of the grassland system and, on the other, the invasion of grasslands by alien and typically relatively unpalatable species. Shrub encroachment is a serious problem in savanna vegetation worldwide. In South Africa alone it has been estimated that 13 million ha have been subject to thorn bush encroachment (Trollope et al. 1989). In this Special Profile, Roques, O'Connor & Watkinson (2001) report on the relative influences of fire, herbivory and rainfall on shrub encroachment in a lowveld savanna in Swaziland, showing how it can be reversed by the manipulation of grazing and fire.

Within Australia, there is considerable concern over the invasions of pastures by weeds, typically from the Mediterranean Basin. Most of these form only minor components of the flora in the native range, and in this volume Grigulis et al. (2001) provide a fascinating insight into the comparative demography of the pasture weed Echium plantagineum in both Australia and Portugal; the most substantial differences were in seedling establishment and seed bank incorporation. A complementary paper (Sheppard, Smyth & Swirepik 2001) looks at the potential for biological control of Echium by pasture competition and a root-crown weevil; the use of a combination of management techniques for controlling thistles in acid grasslands is similarly explored by Edwards, Bourdôt & Crawley (2000). A previous study in the Journal of Applied *Ecology* on the release of biological control agents has provided guidelines to improve the design and efficiency of release programmes (Shea & Possingham 2000).

Global change will undoubtedly give rise to new opportunities for grassland invasion. Buckland *et al.* (2001) have documented the considerable expansion of populations of the grass *Brachypodium pinnatum* at the northern limit of its distribution in Great Britain in a limestone grassland, 3 years after the termination of experimental manipulations of climate, soil fertility and disturbance. This study highlights the potential effects of climate change when plant traits effective for establishment coincide with the removal of current barriers to dispersal. Earlier studies in the Journal have documented how the grazing of free-ranging cattle impact on the grass invasion of heathlands that has

© 2001 British Ecological Society, *Journal of Applied Ecology*, **38**, 233–237 resulted from increased nitrogen deposition (Bokdam & Gleichman 2000) as a result of anthropogenic perturbation of the nitrogen cycle (Lee 1998).

BIODIVERSITY RESPONSES

Increasingly, cognizance is growing not only of the intrinsic value of biodiversity, but also of the muchdebated link between biodiversity, ecosystem stability and ecosystem processes. As systems in which productivity and conservation are so closely and inextricably bound, interactions between biodiversity, economic production and ecosystem processes are in particularly sharp profile in grasslands. On the one hand, grassland issues demonstrate clearly the effects on biodiversity of adverse management. On the other, as illustrated in this Special Profile and by other recent papers (Orgeas & Andersen 2001), grasslands reveal also the benefits of positive management (Di Giulio, Edwards & Meister 2001) and the trophic role that grassland organisms play in the secondary production of other important groups (Ausden, Sutherland & James 2001).

In a previous Special Profile (Ormerod & Watkinson 2000), we highlighted the impact of changes in agricultural practices on bird populations. Although many compounding changes have taken place, the management of grasslands on farms have undoubtedly affected bird abundance (Chamberlain et al. 2000; Henderson et al. 2000; Siriwardena et al. 2000). Coastal grazing marshes and other wet grasslands are particularly threatened by agricultural intensification (Milsom et al. 2000). They are important both for nesting and foraging birds, particularly in maritime areas such as western Europe (Duncan et al. 1999; Grant et al. 1999). In this volume Ausden, Sutherland & James (2001) investigate the impacts of flooding lowland wet grassland on the soil macroinvertebrate prey of breeding wading birds. Inevitably, the opitimal conditions for different birds vary, and when the different requirements of nesting birds in summer and foraging birds in winter have to be taken into account, there will inevitably be times when the management options conflict on the small remaining areas of habitat that remain (Vickery et al. 1997).

Also highlighted in this issue are the roles of management and landscape structure in enhancing insect diversity in agricultural grasslands, using the Heteroptera as an indicator group (Di Giulio, Edwards & Meister 2001). The influence of grassland management on graminiverous sawflies has also recently been investigated by Barker, Brown & Reynolds (1999) and a previous paper, in our section on *Advances in Applied Ecological Techniques*, examined the adequacy of various collecting techniques for estimating the species richness of grassland invertebrates (Standen 2000).

SYNTHESIS

This sample of papers illustrates that the challenges facing grassland ecologists are considerable in striving

236 A.R. Watkinson & S.J. Ormerod to advise the potentially conflicting needs of agriculture and nature conservation. Across the world, there is clear commonality in at least some of the themes being addressed – such as the issues of grazing, invasion and management for biodiversity illustrated here. New challenges will inevitably intensify the management problems and management pressures: growing agricultural demands, climate change and, more locally, sea level rise, will place further pressure on those natural and semi-natural grasslands that remain.

In some of these cases, the solutions will depend on decisions and actions in the socio-political arena. The loss of natural grasslands and biodiversity within grasslands is, as in many other cases, often associated with the perverse agricultural and forest subsidies that lead to unsustainable land-use practices (Watson 1999). By virtue of their disproportionate contribution to biodiversity and ecosystem processes, those subsidies impacting on wet grasslands in particular need careful scrutiny. But also, with many grassland problems explicitly ecological in nature, the solutions will lie in part in the rigorous science published in periodicals such as the Journal of Applied Ecology that join the perspectives of animal and plant ecologists, agricultural scientists and environmental managers from a wide geographical constituency. For this reason, we are delighted to publish the Special Profile papers in the pages that follow.

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References

- Ausden, M., Sutherland, W.J., James, R., (2001) The effects of flooding lowland wet grassland on soil macroinvertebrate prey of breeding wading birds. *Journal of Applied Ecology*, 38, 320–338.
- Barker, A.M., Brown, N.J. & Reynolds, C.J.M. (1999) Do host-plant requirements and mortality from soil cultivation determine the distribution of graminivorous sawlflies on farmland. *Journal of Applied Ecology*, **36**, 271–282.
- Bokdam, J. & Gleichman, J.M. (2000) Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland. *Journal of Applied Ecology*, 37, 415–431.
- Buckland, S.M., Thompson, K., Hodgson, J.G. & Grime, J.P. (2001) Grassland invasions: effects of manipulations of climate and management. *Journal of Applied Ecology*, 38, 301–309.
- Bullock, J.M., Franklin, J., Stevenson, M.J., Silvertown, J., Coulson, S.J., Gregory, S.J. & Tofts, R. (2001) A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology*, **38**, 253–267.
- Caro, T.M. (1999) Densities of mammals in partially protected areas: the Katavai ecosystem of western Tanzania. *Journal* of Applied Ecology, 36, 205–217.

© 2001 British Ecological Society, *Journal of Applied Ecology*, **38**, 233–237

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, 37, 771–788.

- Cox, C.B. & Moore, P.D. (1999) *Biogeography: an Ecological* and Evolutionary Perspective. Blackwell Science, Oxford.
- Cresser, M.S., Smart, R., Billett, M.F., Soulsby, C., Neal, C., Wade, A., Langan, S. & Edwards, A.C. (2000) Modelling water chemistry for a major Scottish river from catchment attributes. *Journal of Applied Ecology*, **37** (Suppl. 1), 171– 184.
- Di Giulio, M., Edwards, P.J., Meister, E., (2001) Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology*, **38**, 310–319.
- Duncan, P., Hewison, A.J.M., Houte, S., Rosoux, R., Tournebize, T., Dubs, F., Burel, F. & Bretagnolle, V. (1999) Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. *Journal of Applied Ecology*, 36, 11–23.
- Edwards, G.R., Bourdot, G.W. & Crawley, M.J. (2000) Influence of herbivory, competition and soil fertility on the abundance of *Cirsium arvense* in acid grassland. *Journal of Applied Ecology*, **37**, 321–334.
- Edwards, A.C., Cook, Y., Smart, R. & Wade, A.J. (2000) Concentrations of nitrogen and phosphorus in steams draining the mixed land-use Dee catchment, north-east Scotland. *Journal of Applied Ecology*, **37** (Suppl. 1), 159–170.
- Fernandez-Gimenez, M.E. & Allen-Diaz, B. (1999) Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *Journal of Applied Ecology*, 36, 871–885.
- Fynn, R.W.S. & O'Connor, T.G. (2000) Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology*, **37**, 491–507.
- Grant, M.C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., Rodwell, S. & Moore, N. (1999) Breeding success and causes of breeding failure of curlew *Numenius* arquata in Northern Ireland. Journal of Applied Ecology, 36, 59–74.
- Grant, S.A., Torvell, L., Sim, E.M., Small, J.L. & Armstrong, R.H. (1996) Controlled grazing studies on *Nardus* grassland: Effects of between-tussock sward height and species of grazer on *Nardus* utilization and floristic composition in two fields in Scotland. *Journal of Applied Ecology*, **33**, 1053–1064.
- Grigulis, K., Sheppard, A.W., Ash, J.E. & Groves, R.H. (2001) The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *Journal of Applied Ecology*, **38**, 281–290.
- Haugland, E. & Froud-Williams, R.J. (1999) Improving grasslands: the influence of soil moisture and nitrogen fertilization on the establishment of seedlings. *Journal of Applied Ecology*, **36**, 263–270.
- Henderson, I.G., Cooper, J., Fuller, R.J. & Vickery, J. (2000) The relative abundance of birds on set-aside and neighbouring fields in summer. *Journal of Applied Ecology*, **37**, 335–347.
- Hester, A.J., Gordon, I.J., Baillie, G.J. & Tappin, E. (1999) Foraging behaviour of sheep and red deer within natural heather/grass mosaics. *Journal of Applied Ecology*, **36**, 133– 146.
- Hulme, P.D., Pakeman, R.J., Torvell, L., Fisher, J.M. & Gordon, I.J. (1999) The effects of controlled sheep grazing on the dynamics of upland *Agrostis-Festuca* grassland. *Journal of Applied Ecology*, **36**, 886–900.
- Humphrey, J.W. & Patterson, G.S. (2000) Effects of late summer cattle grazing on the diversity of riparian pasture vegetation in an upland conifer forest. *Journal of Applied Ecology*, **37**, 986–996.
- Hunt, L.P. (2001) Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology*, 38, 238–252.
- Lee, J.A. (1998) Unintentional experiments with terrestrial ecosystems: ecological effects of sulphur and nitrogen pollutants. *Journal of Ecology*, 86, 1–12.

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- Lee, W.G., Fenner, M., Loughnan, A. & Lloyd, K.M. (2000) Long-term efects of defoliation: incomplete recovery of a New Zealand alpine tussock grass, Chionochloa pallens, after 20 years. Journal of Applied Ecology, 37, 348-355.
- McCarthy, M.A., Possingham, H.P. & Gill, A.M. (2001) Using stochastic dynamics programming to determine optimal fire management of Banksia ornata. Journal of Applied Ecology, 38 (in press).
- Milsom, T.P., Langton, S.D., Parkin, W.K., Peel, S., Bishop, J.D., Hart, J.D. & Moore, N.P. (2000) Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. Journal of Applied Ecology, 37, 706-727.
- Orgeas, J. & Andersen, A.N. (2001) Fire and biodiversity: responses of grass-layer beetles to experimental fire regimes in an Australian tropical savanna. Journal of Applied Ecology, 38, 49-62.
- Ormerod, S.J. & Watkinson, A.R. (2000) Editors' Introduction: Birds and Agriculture. Journal of Applied Ecology, 37, 699-705.
- Palmer, S.C.F. & Hester, A.J. (2000) Predicting spatial variation in heather utilization by sheep and red deer within heather/grass mosaics. Journal of Applied Ecology, 37, 616-631
- Peet, N.B., Watkinson, A.R., Bell, D.J. & Sharma, U.R. (1999) The conservation of management of Imperata cylindrica grassland in Nepal with fire and cutting: an experimental approach. Journal of Applied Ecology, 36, 374-387.
- Rees, M. & Hill, R.L. (2001) Large-scale disturbances and biological control and the dynamics of gorse populations. Journal of Applied Ecology, 38, 364-378.
- Roques, K.G., O'Connor, T.G. & Watkinson, A.R. (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire and herbivory, rainfall and density dependence. Journal of Applied Ecology, 38, 268-280.
- Shea, K. & Possingham, H.P. (2000) Optimal release strategies for biological control agents: an application of stochastic

dynamic programming to population management. Journal of Applied Ecology, 37, 77-86.

- Sheppard, A.W., Smyth, M.J. & Swirepik, A. (2001) The impact of a root-crown weevil, Mogulones larvatus, and pasture competition on the winter annual Echium plantagineum. Journal of Applied Ecology, 38, 291-300.
- Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P. & Wilson, J.D. (2000) The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. Journal of Applied Ecology, 37, 128-148.
- Smith, R.S., Shiel, R.S., Millward, D. & Corkhill, P. (2000) The interactive effects of management on the productivity and plant community structure of an upland meadow: an 8year field trial. Journal of Applied Ecology, 37, 1029-1043.
- Standen, V. (2000) The adequacy of collecting techniques for estimating species richness of grassland invertebrates. Journal of Applied Ecology, 37, 884-893.
- Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E.D. & Kigrl, J. (2000) Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. Journal of Applied Ecology, 37, 224-237.
- Trollope, W.S.W., Hobson, F.O., Danckwerts, J.E. & Van Niekerk, J.P. (1989) Encroachment and control of undesirable plants. Veld Management in the Eastern Cape (eds J.E. Danckwerts & W.R. Teague), pp. 73-89. Department of Agriculture and Water Supply, Pretoria, South Africa.
- Vickery, J.A., Sutherland, W.J., O'Brien, M., Watkinson, A.R. & Yallop, A. (1997) Managing wet lowland grasslands for breeding waders and over-wintering geese: is there a conflict? Biological Conservation, 79, 23-34.
- Watson, R. (1999) Common themes for ecologists in global issues. Journal of Applied Ecology, 36, 1-10.
- Weber, G.E., Jeltsch, F., van Rooyen, N. & Milton, S.J. (1998) Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. Journal of Applied Ecology, 35, 687-699.

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