A PREDICTIVE MODEL OF VEGETATION DYNAMICS UNDER GRAZING

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ABSTRACT

This quantitative model predicts changes in the species composition of grazed vegetation. It is based on growth equations for each species represented. The three parameters in each equation represent maximum production rate, maximum standing biomass, and the decline of production rate at high total plant density. Parameters may be varied with environmental factors. The model is generic, but is illustrated using values for four taxa growing under red deer (*Cervus elaphus*) grazing on the Isle of Rhum, Scotland: bent/fescue grassland (*Agrostis/Festuca*), purple moor-grass (*Molinia caerulea*), mat-grass (*Nardus stricta*) and heather (*Calluna vulgaris*). The model contrasts the performance of species in monoculture with their performance in mixtures, and predicts the impacts of grazing in both the long and short term. It also predicts the rates as well as the directions of vegetation changes.

KEYWORDS

Competition, grass, heather, model, red deer, Scotland, species composition, upland

INTRODUCTION

Sward species composition is becoming more important in grassland management (West, 1993), especially in the least productive areas, such as uplands and unimproved grasslands. It influences soil fertility and forage quality, as well as alternative sources of income such as tourism. Furthermore, nature conservation and aesthetics are becoming major objectives for the management of large areas. At the same time the environment and the ways we manage grassland are changing. We need to predict the vegetation dynamics caused by those changes.

Predicting the dynamics of natural ecosystems of many species by direct study of every interaction would require hundreds of experiments. Theoretical ecological analyses often only identify the stable states of ecosystems (Anderson et al., 1992). However, pastures are unstable ecosystems maintained by management, in which short term changes are more important than potential eventual outcomes. Here we apply a new approach to a hypothetical mixture of important pasture species from Scottish uplands.

MODEL

The model presented here relies on several simplifications. Production of pasture varies with the amount of vegetation present (Milne and Fisher, 1993). In monoculture, the production rate of a species increases with its density at low densities, remains nearly constant with density when close to the maximum production rate, and declines with density as the species becomes very dense. The relationship between production rate in summer and density can be represented for each species by a characteristic growth curve. We have used a form similar to a logistic curve, but modified to allow the curve to be asymmetric. The growth of any species in a particular environment is represented by three parameter values. These represent the maximum standing biomass density of the species, its maximum production rate, and the rate at which its production declines above the optimum density. These parameters can vary with environmental factors. A fourth parameter represents grazing of the species. The growth equation for a single species is:

$$\frac{dy}{dt} = ay\left[\frac{(K-y)}{K+(c-1)}\right] - gy$$

where y is the biomass density (e.g. kg.m^{-2}), a is the species' maximum relative growth rate at low density (e.g. d^{-1}), K is the maximum density of standing biomass of the species (e.g. kg.m^{-2}), c is a parameter determining growth at high densities (no units), and g is the proportion of biomass removed by grazing in unit time (e.g. d^{-1}).

To predict the dynamics of a mixture, the parameters for all the species are combined in a system of equations and solved by computer. For each species a similar equation to the one above determines its growth, but, within the square brackets, the total density of all species present replaces the density of the individual species (y), and the maximum standing biomass (K) is calculated from a weighted average of all the species present. This relies on several assumptions, for example that each species is equally sensitive to all the other species present, because plants compete for resources such as water, light and nutrients, for which they all have roughly similar requirements. Competition within a species is assumed to be greater than between species. Therefore a parameter is added for each species to limit it to a maximum proportion of total biomass, ensuring species coexistence.

During winter each species loses a proportion of its biomass each day in addition to grazing. This litterfall may be spread evenly through the winter for most evergreen species, or concentrated into a shorter period for deciduous species. Although there is no competition in winter, the differences between species in their winter dieback can be as important as their competition in summer.

APPLICATION AND DISCUSSION

A recent modelling study of red deer grazing Scottish upland vegetation includes four main forage taxa. The most palatable is "bent/fescue", in which common bent and fescues dominate a short, intimately mixed sward. Purple moor-grass is deciduous, with palatable young shoots in early summer. The least palatable grass is mat-grass, whose dead leaves persist for several years. Finally, heather is an ericaceous sub-shrub important for winter forage. All four of these taxa cover large areas as near monocultures, but they often grow together. Their growth and the local climate have been parameterized for the Isle of Rhum, off the west coast of Scotland (Gordon, 1989).

These taxa grow differently in monoculture (Fig. 1). The biomass of heather fluctuates relatively little through each year. Its maximum standing biomass density is much greater than the grasses', but can take decades to accumulate. Moor-grass grows rapidly in early summer, but drops most of its above-ground biomass each autumn. Bent/fescue can also grow fast, but its leaves are short-lived, so it also dies back severely in winter. Mat-grass has the slowest growth and most persistent biomass of the grasses.

When these four taxa are mixed, vegetation change can be slow because of low growth rates (Fig. 2). According to the model, five years of grazing with preferences matching those of red deer restricts the summer growth of moor-grass and causes a steady decline of bent/fescue. The expansion of heather observed in monoculture (Fig. 1) is prevented by a combination of grazing and competition. Only the unpalatable mat-grass increases its presence. When grazing is suddenly stopped, all species increase their biomass for the first one or two seasons (Fig. 2). However, an expansion of moor-grass, with large summer peaks of biomass, soon causes a decline of the other grasses, while the presence of heather remains almost constant. The potential codominance of moor-grass with heather under little or no grazing has been recorded on Rhum (Ball, 1974).

Predictions of the rate and seasonal phenology of vegetation change as well as its direction are valuable information, but also allow more careful development and validation of the model. Although this presentation included only 4 taxa, the model is intended to predict the dynamics of much larger numbers of coexisting species.

REFERENCES

Anderson, H.M., V. Hutson and R. Law. 1992. On the conditions for permanence of species in ecological communities. Am. Nat. **139:** 663-668.

Ball, M.E. 1974. Floristic changes on grasslands and heaths on the Isle of Rhum after a reduction or exclusion of grazing. J. Environ. Manage. **2:** 299-318.

Gordon, I.J. 1989. Vegetation community selection by ungulates on the Isle of Rhum. I. Food supply. J. Appl. Ecol. **26:** 35-51.

Milne, J.A. and G.E.J. Fisher. 1993. Sward structure with regard to production. Grassland Management and Nature Conservation, Leeds University, pp. 33-42.

West, N.E. 1993. Biodiversity of rangelands. J. Range Manage. **46:** 2-13.

Figure 1
The growth of four plant taxa in monoculture for 5 years, starting at the beginning of summer. Each taxon starts from about 1/8 of its maximum standing biomass density. There is no grazing.

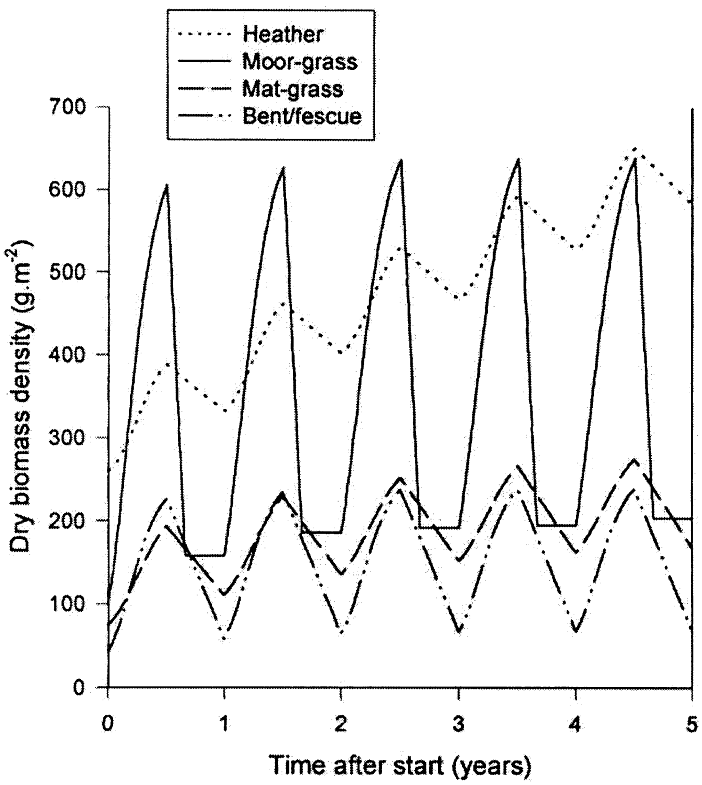

Figure 2
The growth of four plant taxa in an intimate mixture for 10 years. All taxa start from the same initial biomass density as in Fig. 1. For the first 5 years selective defoliation is imposed, simulating red deer grazing, so that bent/fescue loses 1% d^{-1} of its biomass, heather 0.1% d^{-1}, moor-grass 1.2% d^{-1} (summer only), and mat-grass 0.1% d^{-1}. There is no grazing during the the second 5 years.