

A community and population perspective of the possible role of grazing in determining the ground flora of ancient woodlands

A.R. WATKINSON, A.E. RIDING* AND N.R. COWIE†

Centre for Ecology, Evolution and Conservation, Schools of Biological and Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, England

* Present address: ADAS Woodthorpe, Wergs Road, Wolverhampton WV6 8TQ

† Present address: Royal Society for the Protection of Birds, 25 Ravelston Terrace, Edinburgh EH4 3TP

Summary

The ground flora in ancient woodlands is affected by a wide range of factors at a range of scales. In an analysis of 495 sites of ancient woodland throughout Great Britain, regional trends in ground flora species composition were explained primarily by climatic and soil variables, while the most important variable determining species richness was soil pH. In this analysis, ~85 per cent of the variation in ground flora composition could not be accounted for and was probably a result of local variation in a range of ecological processes including grazing by vertebrates. Within sites, the use of exclosures indicates that large herbivores may have a dramatic impact on vegetation structure and composition, but it is a very crude tool. The exclosures are often too small, and measurements do not allow for variations in the density or seasonality of grazing and ignore the fact that plant responses are typically non-linear. Manipulation of grazing levels is critical if we are to understand the impact of grazing on vegetation structure and composition. Individual species vary in their responses to grazing. A population approach is used to illustrate how it is possible to explore how individual species respond to grazing. This is illustrated with reference to *Anemone nemorosa* and how intermediate levels of grazing are expected to favour this species. Complex, and as yet poorly understood, feedback mechanisms between the plant and the grazing animal will contribute to the spatial structuring of grazing impacts on the woodland ground flora. A major challenge for predicting the impact of grazing on plant populations and communities is the quantification of the spatial grazing pattern.

Introduction

A wide range of factors determines the structure and composition of woodlands. However, our understanding of the way these factors interact to

determine woodland composition depends critically on the question of scale. At a regional level the influences of climate and geology are overriding (Rodwell, 1991), but it is the interaction between tree species and ground flora (Beatty,

1984; Whitney and Foster, 1988), topography (Pigott and Taylor, 1964), management (Ash and Barkham, 1976; Kirby, 1990), soil (Rackham, 1975; Cowie, 1992) and grazing (Rackham, 1980; Kirby, 2001) that influence the plant communities at a particular site.

It is the aim of this paper to examine some of the factors influencing the structure of the ground flora of ancient woodlands in the British Isles from both a community and population perspective, with particular reference to grazing. Ancient woodlands are considered to be relics of the primeval forests that covered the country after the last glaciation, but in reality most are only documented to have been present since around AD 1600 (Peterken, 1981). Currently, ancient woodland occupies 2.6 per cent of the land surface in England and 2.7 per cent in Wales (Spencer and Kirby, 1992). These woodlands are consequently highly fragmented; 83 per cent of them are smaller than 20 ha and <2 per cent of sites are greater than 100 ha. However, Rackham (1993) considers that the chief threat to present-day ancient woodland is grazing. The influence of grazing on the ground flora, however, remains poorly understood.

A community perspective

In temperate woodland, two main vegetation layers are found which can almost be thought of as independent communities. The tree/shrub layer nevertheless has a large effect on the environmental conditions that are experienced by the field layer, which is composed of a ground flora of small shrubs such as *Rubus fruticosus*, ferns such as *Pteridium aquilinum*, herbs such as *Anemone nemorosa*, *Hyacinthoides non-scripta* and *Mercurialis perennis*, and bryophytes. Many of the ground flora species are typically spring-flowering herbs; flowering takes place from March to April and senescence of aerial parts occurs in the late summer at the peak of tree canopy cover (Peterken, 1981). The nature of the ground flora communities varies immensely between ancient woodlands and has been quantified by Peterken (1981) and Riding (1995) using data collected across Britain by Peterken between 1971 and 1981. The resulting data set contained 495 sites with information on the percentage

cover of 302 ground flora species and 45 tree species.

The vegetation data were analysed using detrended canonical correspondence analysis (DCCA), a method of direct gradient analysis that produces an ordination of species and sample sites that is constrained by external variables (ter Braak, 1987–1992). The analysis indicated a clear relationship between trees and ground flora (Riding, 1995) and a regional trend (Figure 1 and Table 1) from warm, sunny conditions in lowland Britain typified by *Acer campestre* and *Fagus sylvatica* with ground flora species such as *Carex sylvatica*, *Galium odoratum*, *Glechoma hederacea*, *Lamium galeobdolon*, *Mercurialis perennis*, *Poa trivialis* and *Urtica dioica* to wetter, windier sites in northern Britain and Scotland characterized by *Quercus petraea* and *Alnus glutinosa* with ground flora species such as *Anthoxanthum odoratum*, *Holcus mollis*, *Lysimachia nemorum*, *Oxalis acetosella*, *Potentilla erecta*, *Pteridium aquilinum*, *Ranunculus repens* and *Teucrium scorodonia*. The data show that the most extreme sites in Scotland are associated with *Pinus sylvestris* and *Betula pubescens* and with ground flora species such as *Agrostis capillaris*, *Deschampsia flexuosa* and *Vaccinium myrtillus*. These variations in community distribution, and in particular the regional trend from lowland Britain to northern England and Scotland, bear much resemblance to those described in the National Vegetation Classification (Rodwell, 1991), although the analysis here emphasizes the continuous nature of the variation.

While the DCCA indicates that climatic variables are the most important in determining the composition of the ground flora, soil variables and in particular pH were also shown to have an impact (Table 1). pH was also particularly significant in terms of its impact on species richness across the sites (Figure 2) accounting for 22 per cent of the variation in the data. Other variables such as coppice management were found not to have a significant impact upon community structure, but this reflects the coarse nature of the data and the lack of recently coppiced stands within the data set. Other studies (e.g. Ash and Barkham, 1976; Cowie, 1992) have reported significant changes in ground flora species composition and richness following coppicing, with effects peaking between 2 and 5 years after coppicing.

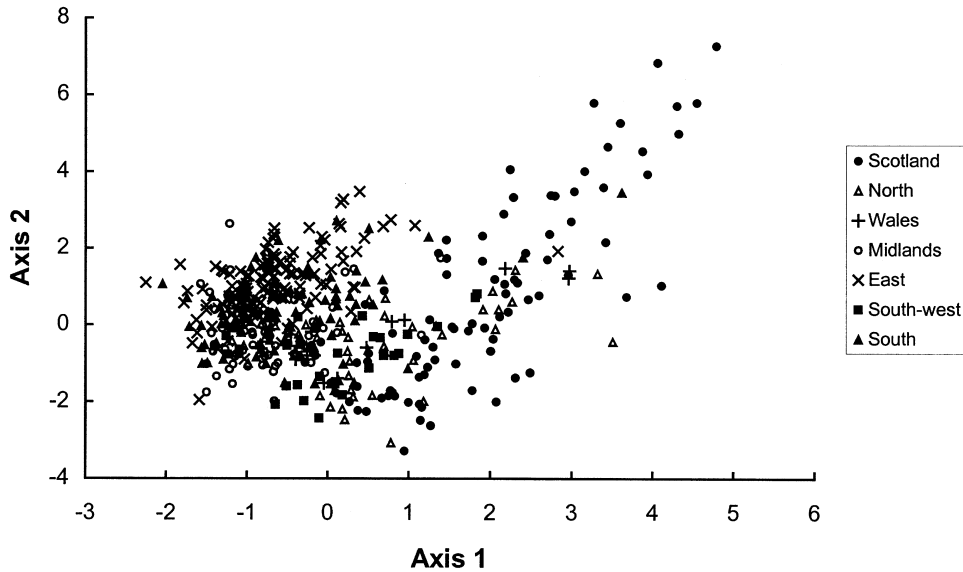


Figure 1. DCCA ordination of the ground flora species composition in British woodlands constrained by environmental variables with the site scores annotated by region.

The variation in ground flora composition (amounting to ~85 per cent) not accounted for by the analysis of Riding (1995) is most likely the result of local variations in ecological processes such as vertebrate grazing, invertebrate herbivory, competition, fungal interactions, and past and present disturbances. It is clear that their potential impact is considerable. Many of them

are difficult to quantify and are not usually done so in surveys where there is typically a concentration on abiotic factors. This is unfortunate. Quantification of the grazing damage to plants or simple dropping counts could provide a rapid assessment of grazing pressure, inexact though they may be. In the case of dropping counts, variation in the decomposition rate of droppings between sites and the difficulty in matching the scale at which the vegetation is monitored with the spatially and temporally variable scale at which grazing operates are just two of the problems likely to be encountered. This should not, however, deter people from making some assessment of grazing pressure.

Table 1: Correlations of environmental variables with the first two axes of a DCCA ordination of ground flora from a range of ancient woodlands across Great Britain

Variable	Axis 1	Axis 2
% Canopy cover	-0.576	-0.344
pH	-0.505	0.339
% Clay	-0.383	0.033
% Sand	0.345	-0.039
% Silt	-0.113	-0.008
Drainage	0.019	-0.333
Wind speed at 10 m	0.699	-0.295
Mean temperature	-0.772	0.033
Rain days	0.845	-0.426
Days of grass frost	0.584	0.260
Sunshine hours	-0.805	0.246

Grazing can be considered to have two effects on woodlands. First, it can cause problems with regeneration of the tree species (e.g. Pigott, 1983; Hester *et al.*, 1996). Deer eat shrubs, young trees, and in coppice woods the spring growth is either eaten right down or nibbled at the tip and caused to grow crooked (Rackham, 1980). Secondly, grazing has direct effects on the ground flora species composition through the grazing of palatable species, trampling and the redistribution and concentration of nutrients in dung and urine.

Two primary methods have been used to assess

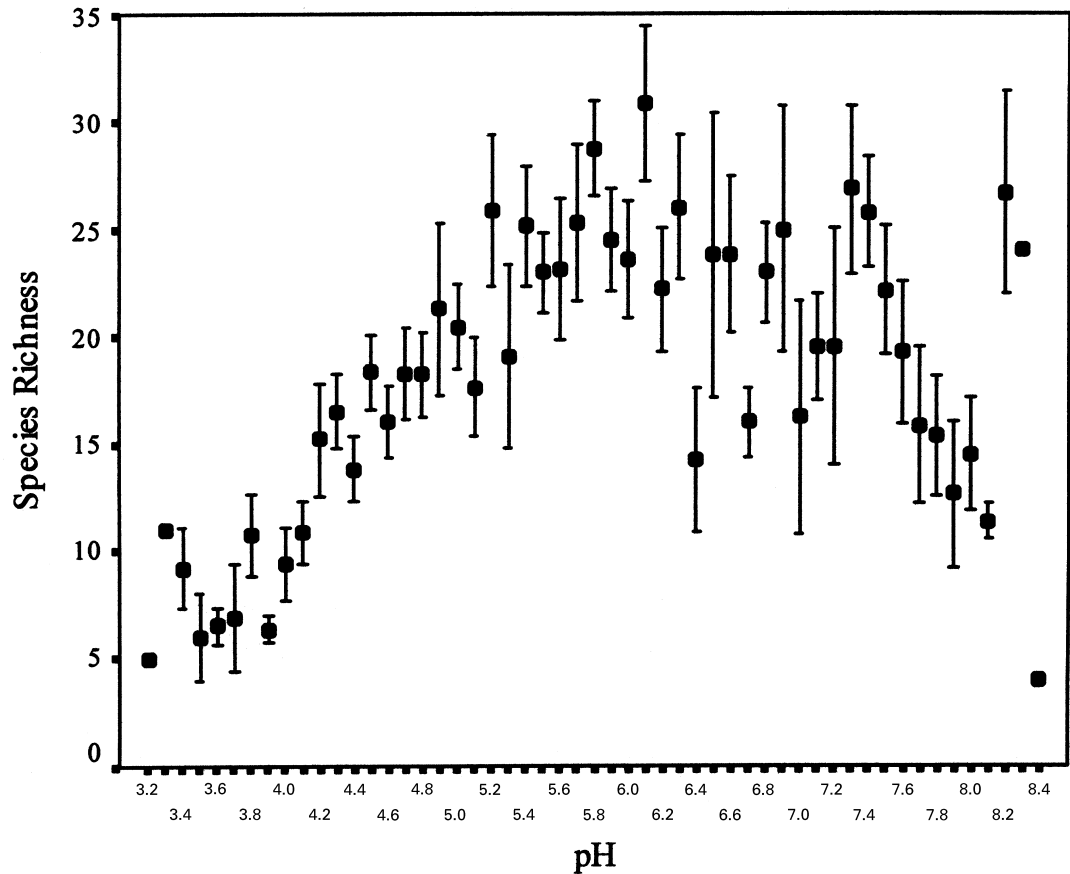


Figure 2. Variation in ground flora species richness with pH. Mean species richness is given with standard error bars.

the impact of grazing on community composition. The first involves monitoring the changes in vegetation at a site following the cessation of grazing or as grazing pressure increases. For example, myxomatosis, and the reduction in rabbit numbers that occurred as a consequence of the disease, provided the opportunity to assess the impact of rabbit grazing on grassland structure in the 1950s (Harper, 1977). It is, however, insufficient to record the changes at individual sites, interesting as these are (Cooke and Farrell, 2001; Perrins and Overall, 2001), in that changes in grazing are almost bound to be compounded by changes in other variables. In an analysis of the impacts of grazing on bush encroachment in savanna, Roques *et al.* (2001), for example,

found that the impacts of grazing were strongly correlated with those of fire.

The second method that is used to assess the impact of grazing on community structure involves the erection of exclosures (Cooke and Farrell, 2001; Morecroft *et al.*, 2001), although these are often not replicated or reported. Barkham (1992) reports that plots fenced against deer and rabbits at Monks Wood National Nature Reserve changed within 12 years from domination by *Hyacinthoides non-scripta* and *Mercurialis perennis* to domination by *Rubus fruticosus*, which is extremely palatable to deer. *Rubus fruticosus* often shades out other ground flora, so the effect of light grazing at least may be to increase species diversity. Barkham suggests

that coppice woods dominated by *Rubus fruticosus* may be those in which deer grazing is absent or where rabbit populations have not recovered since the introduction of myxomatosis and/or canopy re-establishment is slow. Furthermore, he suggests that the characteristic ancient woodland ground flora dominated by low growing vernal perennials with showy flowers is the product of intensive selective grazing over hundreds and probably thousands of years. Crude exclosures are insufficient to demonstrate the appropriate level of grazing for maintaining such diversity.

Ecologists never cease to marvel at the impact of exclosures on plant community composition. Unfortunately, they are typically an all-or-nothing treatment and tell us relatively little about how grazing impacts on community structure; 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. Few woodlands in the British Isles would have ever had no large grazing mammals, and a non-linear response of plant population growth rates to grazing might mean that even light grazing would have a considerable impact on community structure (see Law and Watkinson (1989) for an analogous and more detailed discussion on the role of competition in determining community structure where plant responses are non-linear). It is therefore imperative to explore the impacts of variation in grazing on community structure.

Manipulating grazing pressure is obviously very difficult to do as grazing intensity varies both in time and space depending upon the numbers and behaviour of the grazing animals concerned. Experiments with livestock have shown how variations in stocking rates and also the seasonality of grazing impact on community composition (Hester *et al.*, 1996; Hulme *et al.*, 1999; Fynn and O'Connor, 2000; Bullock *et al.*, 2001), but it is difficult to envisage how such experimental manipulations can be carried out with deer in a realistic manner that manages to take account of their different behaviours. In semi-arid regions, water holes and the natural grazing gradients that surround them (piospheres) provide the opportunity for investigating the impacts of varying grazing intensity by ungulates on plant community structure (Andrew and Lange, 1986; Hunt, 2001). Such experiments can often be carried out over large areas – but in ancient

woodlands the areas are much smaller, although shooting does provide one mechanism whereby grazing intensities could be varied across sites. Utilizing temporal, in addition to spatial, variation in grazing adds another dimension to exploring the impact of grazing alongside the other variables driving vegetation structure. For example, Roques *et al.* (2001) utilized variation in grazing patterns, resulting from land-use contrasts and quantified through livestock units, to quantify the relative impact of grazing on bush encroachment in savanna. Moreover, this study allowed the impacts of grazing animals to be contrasted with those of browsers. Studies modelled along such lines need to be carried out if we are to understand the relative impacts of grazing on woodland ground flora.

A population perspective

The responses of plant species to grazing are inevitably individualistic: some species increase in abundance while others decrease (Kirby, 2001). Grazing is not bad for all species! In order to understand how key components of the vegetation respond to grazing, it is necessary to take a population perspective recording how individual stages of the life cycle respond to grazing. A number of species that are members of the woodland ground flora have been studied from a demographic perspective (Falinska, 1985; Kawano, 1985). These include *Mercurialis perennis* (Hutchings and Barkham, 1976), *Narcissus pseudonarcissus* (Barkham, 1980a, b; Barkham and Hance, 1982) and *Anemone nemorosa* (Shirreffs and Bell, 1984; Cowie *et al.*, 1995). While a number of these studies, for example that on *Erythronium japonicum* (Kawano, 1985), mention that grazing animals may be responsible for the loss of seeds and the death of vegetative plants, and it is intuitively obvious that grazing animals must have an impact on the ground flora, directly or indirectly, hard evidence for this remains fairly scarce (Evans and Barkham, 1992). Here we examine a demographic approach that can be used to quantify the impacts of grazing on plant abundance with specific reference to *Anemone nemorosa*.

Anemone nemorosa is widespread in the British Isles and is most frequent in deciduous woodlands

(Shirreffs, 1985). It is particularly suited to coppice management, and flourishes in *Corylus-Quercus* coppice where *Arum maculatum*, *Hyacinthoides non-scripta*, *Mercurialis perennis* and *Rubus fruticosus* are frequent associates. Although mammals usually avoid grazing the plant because of its bitter, burning taste (Shirreffs, 1985), roe deer (*Capreolus capreolus*) have been reported as including the plant in their spring and summer diet, preferring the leaves to the flowers (Voser-Huber and Nievergelt, 1975). This indicates that the direct effects of grazing on survival and fecundity may be relatively slight. However, the indirect effects of grazing on competition are likely to be considerable, as are the effects of disturbance through trampling and digging. Shirreffs (1985) indicates that *A. nemorosa* is susceptible to shading from taller species such as *H. non-scripta* and *M. perennis* and that it tends to become a subsidiary species in the ground flora when those species are present. In contrast, it is thought to be more tolerant of grazing, trampling and coppicing than those species and consequently disturbance is likely to be an important factor enabling *A. nemorosa* to survive in sites containing those two species. Unfortunately, there is very little information on either the effects of competition or of disturbance on *A. nemorosa*. Nevertheless one might predict that it would be favoured by intermediate levels of grazing that remove competitors but which do not create too high a level of disturbance. Inferences about its response can be made from what we know are the impacts of canopy shading and density-independent mortality.

The growth dynamics of clonal plants such as *A. nemorosa* can frequently be described using a few simple growth rules (Bell, 1986), the most important being internode or spacer length, branching angle and branching probability. However, most of such models are only used to examine the growth dynamics of isolated clones (e.g. Shirreffs and Bell, 1984; Cowie *et al.*, 1995). In order to understand how population size is determined, it is necessary to integrate such growth models with information on how a range of density-dependent and density-independent factors impact on the numbers of births, deaths, immigrants and emigrants in the population (Watkinson, 1996). Cowie (1992) presents an adaptation of a standard growth model for *A.*

nemorosa (Cowie *et al.*, 1995) that incorporates (1) variation in growth rules through the coppice cycle, (2) the observed density-dependent control of growth and (3) a range of levels of density-independent mortality. From this model, it is clear that the plant performs better in a coppice rotation than in the permanent shade of unmanaged woodland (Figure 3). The simulations of Barkham and Hance (1982) also show that stable populations of daffodil *Narcissus pseudonarcissus* may occur under the alternating shade and open environments that occur with coppice management, whereas many populations in unmanaged woodland can be expected to decline to extinction. The relatively poor performance of the plants under canopy shade most probably reflects the low light levels, but lower soil water levels (Cummings and Cook, 1992) and nutrient availability (Pigott and Taylor, 1964) have also been recorded in unmanaged stands. Competition from taller-growing members of the ground flora might be expected to have a similar impact to that of canopy shading on the dynamics of *A. nemorosa*, although the time scales over which competition takes place are inevitably different. It would nevertheless be interesting to see how the growth dynamics of *A. nemorosa* varies in different species assemblages. The key to understanding the impact of competition on the abundance of *A. nemorosa* is a quantification of the effects of interspecific competition on both rhizome and shoot growth and survival (Cowie *et al.*, 1995).

If increased shade from competitors that might

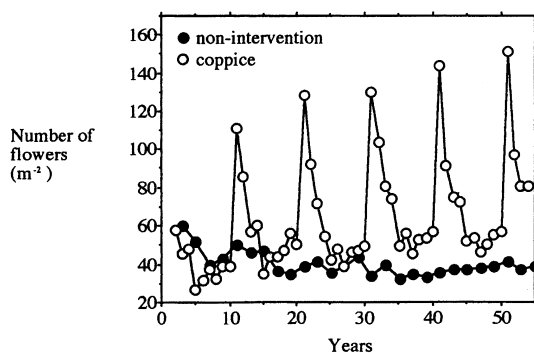


Figure 3. A model simulation of the density of flowering shoots of *A. nemorosa* in non-intervention and coppice woodlands. Coppicing takes place every 5 years. From Cowie (1992).

flourish under low grazing pressures might be expected to reduce the abundance of *A. nemorosa*, what are the likely impacts of increased disturbance from higher grazing pressures? Mortality levels of rhizome segments that have been recorded in relatively undisturbed ancient woodland are typically less than 10 per cent (Cowie, 1992). Simulations incorporating a range of levels of density-independent mortality indicate that populations will persist at such levels of mortality, but that the viability of populations is much less secure if mortality rises above 15–20 per cent (Figure 4). Moreover, Cowie (1992) also showed that recovery of populations over a number of years can typically be expected to be very slow following past high rates of mortality. As with competition, we unfortunately do not have data on the impacts of grazing animals on the mortality of *A. nemorosa*. It would nevertheless appear feasible that *A. nemorosa* may respond positively to light grazing, which removes competitors, but that heavy trampling and disturbance from grazing animals may severely reduce populations, which will be slow to recover even if the disturbance is then removed.

We believe that the demographic approach has

the potential to allow a much greater understanding of the response of individual species to variations in grazing pressure. However, there remains the problem of how to understand the impacts of varying levels of grazing in time and space on plant abundance. It must be remembered that the heterogeneous distribution of plant populations may in part reflect variable levels of grazing, but that the patchy distribution of plants will also impact on the behaviour of vertebrate herbivores. The system is interactive and it is therefore important to understand not only how the plant responds to the herbivore but also how the herbivore responds to the plant. This entails understanding the way in which consumers distribute themselves in relation to resource density (Rowcliffe *et al.*, 1998, 1999) and this will inevitably depend upon a range of factors: the social behaviour of the grazing animal; the spatial distribution of different plant communities (Hester *et al.*, 1999; Palmer and Hester, 2000); the functional and aggregative responses of the herbivore both in relation to individual species and the general availability of food (Rowcliffe *et al.*, 1998); and also disturbance (Gill *et al.*, 1996). Kay (1993), for example, in a study of deer browsing, found that the major factors relating to

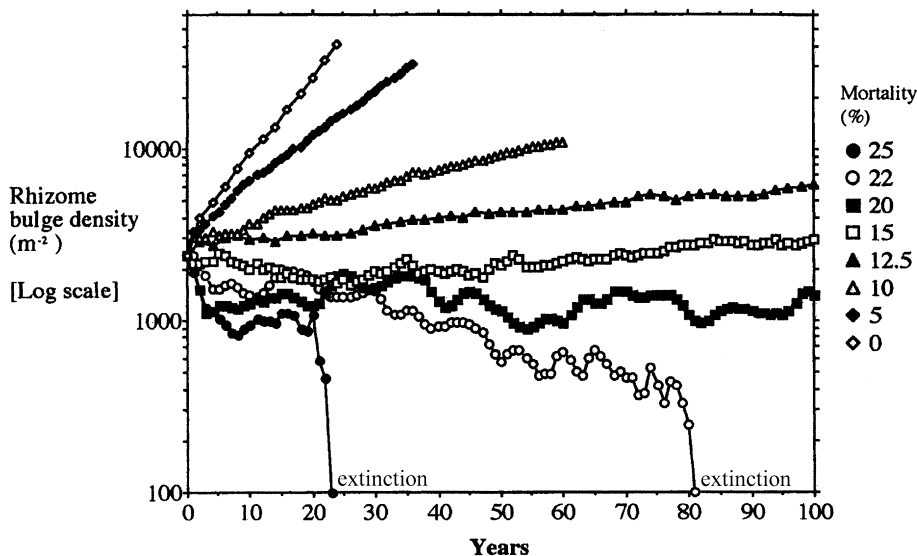


Figure 4. A model simulation of the effect of increasing density-independent mortality on the population density of simulated clones of *A. nemorosa* growing under constant shade in non-intervention coppice. From Cowie (1992).

the amount of damage inflicted by roe deer were tree species present, size of the coppice block and the quantity of surrounding cover.

Weber *et al.* (1998) have recently developed a modelling approach that addresses spatial aspects of both vegetation dynamics and grazing utilization. Their grid-based model described vegetation in the southern Kalahari desert 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 in woodlands to predict how varying levels of grazing will impact on the structure and dynamics of the vegetation. The challenge to conservationists 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 (Hunt, 2001). Exclosures will not provide the answer, as they can only tell us what will happen when large vertebrate grazing ceases altogether. Such a scenario would be as undesirable from the perspective of the conservation of the woodland ground flora as some of the current heavy levels of grazing.

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