Impacts of deer herbivory on ground vegetation at Wytham Woods, central England

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Summary

Between 1974 and 1992 there were declines in bramble (*Rubus fruticosus* agg.) and several woodland forbs and an increase in grasses at Wytham Woods. These changes have been explained as effects of increasing deer populations. We set out to test this by establishing exclosure experiments in the summer of 1997. Comparison of permanent vegetation monitoring plots inside and outside the exclosures, showed that forbs tended to increase inside exclosures whilst decreasing in the wider wood, supporting the hypothesis that deer herbivory was responsible for the change. Changes in individual species were not, however, significant and it may take many years for the vegetation in the exclosures to reach a new equilibrium. In contrast to exclosures under the woodland canopy, additional exclosures in a clearing have been rapidly colonized by bramble. It appears there is an interaction between solar radiation and herbivory and the decline of bramble at Wytham may reflect canopy closure as well as deer herbivory. Faecal pellet counts made in Environmental Change Network monitoring plots between August 1998 and April 1999 indicated different habitat use by fallow (*Dama dama*) and muntjac (*Muntiacus reevesi*) deer. Grasslands in proximity to the woodland tended to accumulate proportionally more fallow deer faeces, whilst dense ancient woodland areas tended to accumulate more muntjac faeces. There was, however, little evidence of an association between particular species of plant and differential habitat use by deer.

Introduction

Wytham Woods, Oxfordshire, is a well-known site for ecological research, owned and managed by Oxford University. Since 1992, the woods have been used by researchers from the Natural Environment Research Council's (NERC) Centre for Ecology and Hydrology (CEH) for the long-term monitoring of a wide range of variables under the Environmental Change Network (ECN) programme. Specific studies on deer have only recently commenced, but the background of other research does allow a good insight into their impacts.

Since the mid-1970s, rising populations of deer (fallow *Dama dama*, muntjac *Muntiacus reevesi* and, to a lesser extent, roe deer *Capreolus capreolus*) have been reported (Perrins and Overall, 2001). Over this period there have been major changes in the vegetation of the site, which are believed to be caused by the rising deer populations. These changes can be identified and quantified with a high degree of confidence as a system of 163 permanent plots was established in 1974 by staff of the Commonwealth (now Oxford) Forestry Institute (Dawkins and Field, 1978). These plots, or subsets of them, have subsequently been recorded in 1984/85, 1991/92 and 1999 (Kirby *et al.*, 1996a, b; Kirby and Thomas, 2000; Hall and Kirby, 2000). Of those changes which can be attributed to deer herbivory, the major ones have been a decrease in the shrub layer, a decline in bramble, a decrease in a number of characteristic woodland forbs (e.g. dog's mercury *Mercurialis perennis,* enchanter's nightshade *Circea lutetiana*) and an increase in grasses, particularly wood brome (*Brachypodium sylvaticum*).

Although deer do provide a good explanation for these trends in vegetation, other changes have also taken place at Wytham in recent decades, including those associated with succession and management, as well as wider scale changes such as increasing atmospheric nitrogen deposition. In order to test whether the observed impacts could indeed be attributed to deer, an exclosure experiment was established by CEH in collaboration with Oxford University in 1997. Exclosure experiments carried out at other sites with high deer populations have shown changes in species composition, including increases in *M. perennis* and *R. fruticosus* and decreases in grasses (Putman *et al.*, 1989; Cooke *et al.*, 1995; Cooke and Farrell, 2001). Vegetation has been recorded in the Wytham exclosures in successive years and compared with a series of controls drawn from existing ECN vegetation recording plots. The main exclosures are within closed-canopy ancient woodland (henceforth they will be referred to as 'woodland exclosures') but a further series of small exclosures in a clearing ('clearing exclosures') offered the opportunity to look at interactions between canopy closure and herbivory.

Exclosure experiments provide an experimental test of deer impacts (or at least the impact of release from deer herbivory) by comparing grazed and ungrazed areas. Impacts are, however, likely to be more subtle than this all-or-nothing sort of comparison. In particular, some vegetation types may be grazed preferentially by some species, leading to uneven impacts across a site. To try to pick out areas with the greatest impact by different species, we have made dropping counts in permanently marked plots and tested for correlations with vegetation characteristics. Dropping counts, following a preliminary clearance of old droppings, are particularly useful for assessing medium to high deer populations in sites with poor visibility (Mayle *et al.*, 1999).

Our aims can then be summarized as follows:

1. To test whether the removal of deer grazing reversed changes in vegetation recorded between 1974 and 1991 at Wytham.
2. To identify the vegetation types that are most heavily used by different deer species.

Methods

Site description

Wytham Woods (Figure 1) is an area of mixed woodland with semi-natural grasslands, 5 km north-west of Oxford (1°20′W 51°46′N; UK national grid SP462082). A deer fence encloses a total of 389 ha at Wytham; most of it is woodland but ~65 ha are covered by agricultural land, semi-natural grassland and rides. Some woodland lies outside the deer fence, but this paper only addresses areas inside it. The woodland can be divided into the following types:

1. **Ancient** abandoned coppice, mostly of hazel (*Corylus avellana*) with oak (*Quercus robur*) standards. This area is largely W8a the *Primula vulgaris–Glechoma hederacea* sub-community of *Fraxinus excelsior–Acer campestre–Mercurialis perennis* woodland in the National Vegetation Classification (NVC; Rodwell, 1991).
2. Naturally regenerated **secondary** woodland, mainly W8e, the *Geranium robertianum* sub-community of *Fraxinus–Acer–Mercurialis* woodland. Ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus*) are the principal tree species in these areas, which are mostly high forest, though there has been a little coppicing in the past.
3. **Plantations**, mainly of oak (*Q. robur*) and beech (*Fagus sylvatica*). The oak plantations

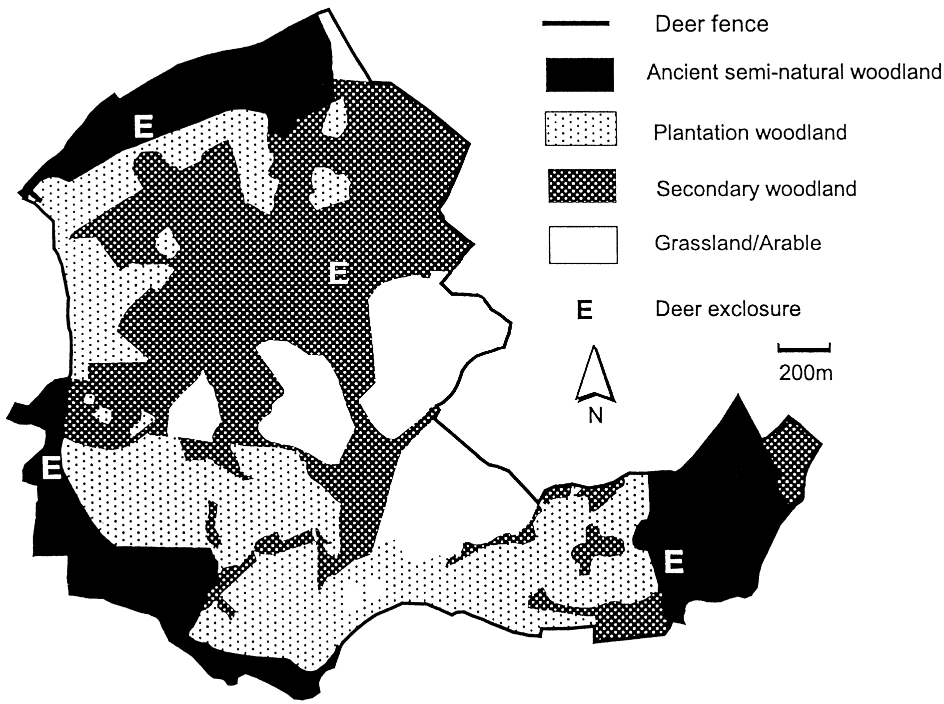

Figure 1: Map of the area enclosed within the deer fence at Wytham Woods, showing main areas of different habitat types. The 'secondary woodland' includes some areas with both planted trees and natural regeneration and some with small fragments of ancient woodland. About one-third of the plantations (those in the northern half of the site) were on ancient woodland sites.

tend to be W8 communities in the NVC; most of the beech plantations are W12 and W14. Most of these areas have been planted since 1945.

Exclosures and vegetation recording

Three large exclosures of ~0.3 ha each were set up in the summer of 1997, using 2 m high deer fencing. All were located in areas of ancient abandoned coppice woodland. Fence lines were located along rides and through existing gaps between trees, to avoid having to fell trees or remove branches. Care was taken to ensure that disturbance of the soil and ground vegetation did not take place within the exclosures. In each exclosure, three permanently marked monitoring plots were established, as described below. In addition, three exclosures, each measuring 10 × 10 m were set up in a clearing in the spring of 1998. These were intended to test whether differential exclosure of fallow and muntjac was possible, so one exclosure used standard, 2 m tall, deer fencing, one was lower, using 1.25 m fencing and the third used 2 m fencing raised ~0.2 m above the surface of the ground.

In 1993, 45 vegetation monitoring plots were established using the ECN 'coarse-grain' protocol (Sykes and Lane, 1996). These plots were chosen randomly from all potential positions on a regular 100 m grid (remaining grid points received a more superficial, base-line survey). Ground vegetation was recorded in a 2 × 2 m quadrat, which was subdivided into 25 'cells' of 0.4 × 0.4 m. Each 2 m quadrat was nested within a 10 × 10 m plot used for monitoring trees and pellet counts (see below). Three plots of the same sort were established in each of the woodland exclosures and vegetation was recorded in 1997, 1998 and 1999. In 1998 and 1999, nine plots from the 1993 survey were re-recorded to provide unexclosed controls. These nine plots were selected as being those closest to the exclosures with the most similar vegetation.

Between late March and early May 2000, bramble plants – defined as points at which the brambles rooted – were counted in the woodland exclosure monitoring plots and controls, the clearing exclosures and a control plot adjacent to the exclosures in the same clearing. Percentage cover was also estimated visually.

Faecal pellet counts

In total, 52 plots, each 10 × 10 m, were used for faecal pellet counts. Of these, 43 were the ECN 'coarse grain' plots described above; the other nine had initially been established for ECN 'fine grain' vegetation recording (Sykes and Lane, 1996). A clearance method was used: all deer faeces were removed from each plot and the number of pellet groups counted after a period of ~1 month. Faeces were attributed to species and a dropping accumulation rate calculated for each species for each plot. The counts for roe deer were very low and were not included in the analysis. Counts were carried out in August/September 1998, December/January 1998/99 and March/April 1999.

All statistical analyses were carried out using SYSTAT 8.0 (SPSS, 1998).

Results

Changes in vegetation after exclosure

A comparison of the number of species increasing and decreasing inside and outside the woodland exclosures showed that most herbaceous dicotyledons (forbs) increased inside the exclosures, but most decreased outside, between 1998 and 1999 (Table 1). This difference was significant at the $P < 0.05$ level (χ^2 test). This measure gives equal weight to common and rare species and to large and small increases. Tests for differences in the mean number of plants of the different groups per cell showed no significant effects of exclosure. The more common species (including bramble) were also individually tested, but no significant effects of exclosure were found.

Brambles

Percentage cover in the woodland exclosure and control plots and the clearing control plot was <1 per cent. In the clearing exclosures, the estimates were: complete exclosure 35 per cent, low fence exclosure 5 per cent, raised fence exclosure 3 per cent. When the numbers of individual bramble plants were compared between the woodland exclosure plots and their controls within the wood, no significant difference was found (P = 0.57, t test) (Figure 2). The number of brambles in the control plot at the open site was slightly higher, but there were many more plants in all of the clearing exclosures, particularly the complete exclosure (Figure 2). The partial exclosures with lower fences or raised fences had 190 and 273 plants each, respectively – lower than the 593 in the complete exclosure but still an order of magnitude higher than the 20 found in the neighbouring control plot. The lack of replication of the clearing sites constrains interpretation, but the differences are very large and strongly suggest that bramble regeneration is favoured by the

Table 1: Species increasing and decreasing in exclosure and control plots between 1998 and 1999 (increase or decrease refers to the total number of cells with a species present across all plots)

Plant group	Exclosures		Controls		Probability*
	Increasing	Decreasing	Increasing	Decreasing	
Dicotyledons	8	2	3	8	0.016
Monocotyledons	4	5	4	4	0.82
Woody seedlings/suckers	4	7	5	6	0.66
Bryophytes	9	5	5	6	0.35

*Significance was determined using a χ^2 test.

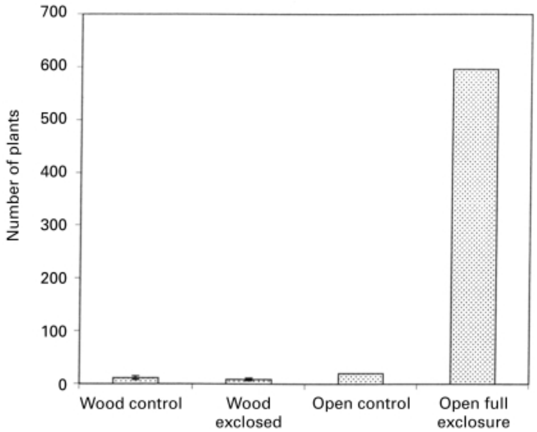

Figure 2: Number of bramble plants counted within 10 × 10 m plots, in woodland and clearing exclosures with unexclosed controls. The woodland data are means and standard errors of nine plots. The clearing data are from a single control plot and the single complete exclosure (2 m fence from ground level).

combination of both an open site and exclosure of deer. If the exclosure plots in the woods are compared with the three clearing exclosure plots taken as a group (which substantially underestimates the effect of complete exclosure), using a Mann–Whitney *U* test, a significant difference was found ($P = 0.012$).

Associations between faeces accumulation and vegetation

There was a significant correlation ($r^2 = 0.12$, $P = 0.013$) between fallow pellet accumulation rates in August–September and those in December–January, implying that there was a degree of consistency in deer usage of different vegetation. Correlations were not, however, significant for muntjac or between the last two counts for fallow. When the plots were grouped according to broad habitat categories (ancient woodland, grassland, secondary woodland, plantations) mean dropping accumulation rates were found to vary between habitats (Figure 3). Fallow appeared to have preferentially used grasslands and avoided ancient woodland. With muntjac, the reverse is true, with ancient woodlands being preferred and grassland avoided. Broadly similar results were found when counts from different times of year were analysed separately, although there was no evidence for preferential use of the grasslands by fallow in the spring.

No significant correlations were found between the frequencies of the most common woodland plant species and the pellet accumulation rates of either fallow or muntjac deer averaged over all three counts (transformed data were used where appropriate). There was a significant ($P = 0.02$) positive relationship between *Mercurialis perennis* frequency and fallow pellet accumulation

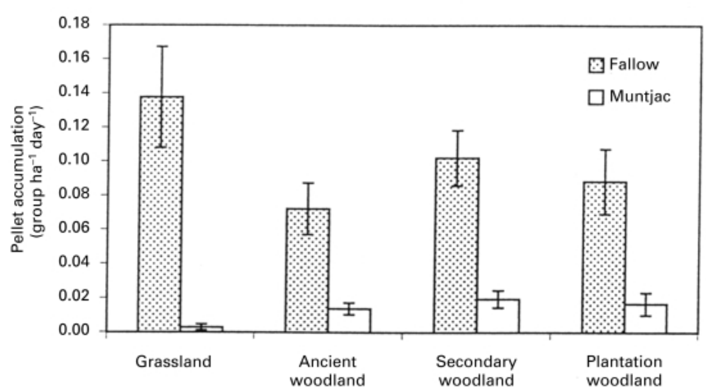

Figure 3: Accumulation rates (means of three surveys) of groups of faecal pellets in contrasting habitat types for fallow and muntjac. Error bars are ± 1 standard error.

rates in August–September only. This may indicate preferential grazing in areas with *M. perennis* during the summer but in view of the number of comparisons with all combinations of species (11) and counts (3), it would be unwise to place too much weight on this.

Discussion

After 2 years of exclosure there had been no dramatic change in the appearance of exclosure plots in closed canopy woodland; in particular bramble cover remained low. There were, however, the first signs of change taking place, in that the forbs increased between 1998 and 1999 inside the exclosures but not outside them (Table 1), in contrast to a lack of response of the monocotyledons. It does therefore seem likely that changes of the sort found in exclosures by other authors (Putman *et al.*, 1989; Cooke *et al.*, 1995; Cooke and Farrell, 2001) are starting to occur. This supports the proposition that deer have been an important factor in the changes at Wytham since the mid-1970s. However, the lack of any significant change in individual species frequencies shows that recovery from the effects of deer herbivory will be a slow process under the woodland canopy.

The exclosures in the clearing were intended as a test of an experimental technique rather than a properly replicated experiment in their own right and have not been fully surveyed for vegetation. The dramatic increase in bramble cover was very visible and prompted the recording that is presented here. The contrast with the woodland exclosures is all the more dramatic for the clearing exclosures having been functional for ~6 months less time. Although we would ideally establish exclosure plots in other clearings to establish the generality of the phenomenon, it does seem that the interaction between canopy closure and herbivory is an important factor in bramble regeneration. This is not surprising in view of the fact that bramble is not a specialist shade plant. Hill *et al.* (1999), in their adaptation of Ellenberg's indicator values to the UK, give *R. fruticosus* a 'light value' of 6, from a range 1 (most shade-requiring) to 9 (most sun-requiring); for comparison *Mercurialis perennis* is rated 3. Could an interaction between deer herbivory and canopy closure have had a role in the decline of bramble at Wytham? Kirby *et al.* (1996b) actually found that tree canopy cover, particularly in semi-natural areas, was higher in 1974 than in 1991/92 (because of thinning, removal of sycamore, and windthrow). However, inspection of aerial photographs from 1953 and 1977 reveals a substantial increase in forest cover. This is because during the period 1945–1965 some open sites were planted and others were colonized by natural regeneration, especially by sycamore. It is likely that the dense bramble cover built up when the site was relatively open, in the years prior to 1974. Some decline in bramble was probably inevitable in the years following 1974, although the extent of the decline must have been increased by deer grazing.

The woodland exclosures may never attain the same degree of bramble cover as was seen in 1974 and is seen today in the clearing exclosures (unless large trees fall or thinning takes place – which is not planned). From a conservation point of view, this is not necessarily a bad thing – other components of woodland ground flora may decline under a very dense bramble cover. What is important is that management history of a site is well understood when designing management plans. The number of well-designed exclosure experiments in Britain is low relative to the variety of woodland types and conditions; care is needed in extrapolating between situations.

The counts of faecal pellets suggested that different parts of the site are not used evenly (assuming that high defecation rates are a reasonable indication of the areas where deer spend the most time). The regular use of grasslands and rides by fallow deer is supported by anecdotal evidence from Wytham and has been described by other authors (e.g. Chapman and Putman, 1991), although the presence of domestic stock may discourage use by deer. Grasslands are potentially most important in winter when little ground vegetation is available in the woodland (Chapman and Putman, 1991). In contrast to the fallow, muntjac appear to use the ancient woodland preferentially at Wytham. Chapman (1991) notes that muntjac often prefer areas with dense cover and the ancient woodlands at Wytham tend to be the densest parts of the sites, especially where there are blackthorn (*Prunus spinosa*) thickets. The abundance of hazel (*Corylus avellana*) in the ancient woodland at Wytham may also be attractive; Chapman *et al.* (1985) detected selection for areas with nut-bearing trees (although they were working in largely coniferous woodland).

There is little evidence for patterns of association between particular plant species and deer. This perhaps reflects density-dependent herbivory within the woodland area. Intensive grazing of a preferred species in one location would lead to its decline and the deer would tend to move to a different patch, allowing the sensitive species to recover to the point where it became attractive once again. At the regional scale, however, this approach may yield information on preferentially grazed species by comparing flora in whole woods with different levels of deer populations.

This study has added to the weight of evidence that rising deer populations have been changing the ground vegetation of British woodlands in recent decades. It has, however, also demonstrated that interactions with other factors such as site management and the availability of grassland may play an important role in determining outcomes of grazing at particular sites.

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