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# Changes in the ground flora in Wytham Woods, southern England, 1974-91, and their implications for nature conservation

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# Changes in the ground flora in Wytham Woods, southern England, 1974-1991, and their implications for nature conservation.

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## Summary

1. The ground flora (vascular plants less the 2 m high, excluding trees and shrubs) was recorded in 1974 and 1991 from 163 permanent 10 x 10 m plots arranged on a systematic grid across Wytham Woods, near Oxford (UK). The Woods cover about 320 ha, are predominantly deciduous, but of varying ages and management types.

2. The total number of species found (173, 167 respectively), the mean richness per plot (16.7, 17.2) and the breakdown of the species list between different species types (ancient woodland indicators, other woodland species, non-woodland species) showed no significant differences between 1974 and 1991, but mean ground cover declined from 80% to 64%.

3. Eight species were common across the whole wood in both years and showed little difference in frequency between areas of different histories and management (*Dryopteris filix-mas, Galium aparine, Geum urbanum, Rubus fruticosus, Glechoma hederacea, Hyacinthoides non-scripta, Mercurialis perennis, Urtica dioica*). Ancient woodland indicators as a group were more common in ancient stands, but some ancient woodland indicators had spread widely in the recent woodland.

4. Some species increased in frequency across all types of woodland including *Arum maculatum, Brachypodium sylvaticum, Deschampsia cespitosa* and *Poa trivialis*; while others such as *Ajuga reptans*, *Angelica sylvestris* and *Circaea lutetiana* declined. Mean cover of *Rubus fruticosus* per plot declined from 35% to 6% and of *Mercurialis perennis* from 32 to 24%. Changes in the vegetation were greater in the plantations which showed more species losses than semi-natural stands.

5. Significant differences were found between groups of species in terms of their Ellenberg indicator scores particularly for light, nitrogen and moisture, and in their strategy types (*sensu* Grime 1979). Ancient woodland indicators had the lowest light scores (most shade-tolerant) and tended to have more of a bias towards stress-tolerance in strategy terms. The indicator scores and strategy types were used to interpret the changes observed in the vegetation.

6. The main causes of change were the changing conditions associated with stand growth, particular increased shade in the plantations, and an increase in browsing/grazing by deer. No evidence could be found for an effect of changing soil nitrogen or pH on the vegetation despite known changes in the soil values for these parameters.

7. Changes in the ground flora as well as the woody layers, and in managed as well as unmanaged stands should be monitored, if conservation objectives are to be met.

## Introduction

Nature conservation is an objectives for woodland management in Britain, particularly in ancient and semi-natural woods (Peterken 1977; Forestry Commission 1985, 1994; HMSO 1994). The woodland ground flora is one of the features that has been used to distinguish ancient from recent woodland and to characterise variations in woodland across the country, while ground flora richness has been used to assess the nature conservation value of sites (Peterken 1974; NCC 1989; Rodwell 1991). Therefore woodland managers need to understand how and why the ground flora may change if the special characteristics of ancient woodland are to be maintained.

The cover and richness of the ground flora (the field and ground layers below 2 m high) change during the growth of a stand of trees (Alaback 1982; Brewer 1980). In managed forests both tend to increase during the first few years after a stand has been felled, followed by a sharp decline as the replacement trees grow and form a dense thicket (eg Ash & Barkham 1976; Kirby 1988a, 1990; Mitchell & Kirby 1989; Elliot *et al.* 1997). Cover and richness may increase again in older stands when thinning occurs, although in the southern Appalachian Mountains the richness of the ground flora was still less 80 years after logging than in old-growth stands (Duffy & Meir 1992; Meir, Bratton & Duffy 1995).

Changes under smaller, more natural gaps, following for example windthrow of trees or their death from disease, depend on whether or not there has been disturbance to the ground as well as changes to the canopy cover (Collins, Dunne & Pickett 1985; Collins & Pickett 1987; Moore & Vankat 1986; Peterson & Pickett 1995; Reader & Bricker 1992; Strait, Jackson & Abrell 1987). New species colonise the exposed soil on root plates or in the associated pits, fallen logs may crush locally dominant species to create space for others (Beatty 1984; Buckley, Bolas & Kirby 1994; Thompson 1980). The ground flora also responds to variations in herbivore pressures (eg Bratton 1975; Cooke *et al.* 1995; Gill 1992; Koh *et al.* 1992; Schreiner *et al.* (1996); Tilghman 1989) and to changes of soil pH and in nitrogen availability (Falkengren-Grerup 1990; Falkengren-Grerup & Tyler 1991).

In this paper results from a long-term surveillance system established in Wytham Woods, near Oxford, United Kingdom, are used to assess changes in the ground flora between 1974 and 1991 (Dawkins & Field 1978; Thomas & Kirby 1992). Factors that had the potential to cause ground flora change during the period included increased shade from growth of young stands; opening out of the canopy in other stands; increases in soil nitrogen and decrease in soil pH; increased browsing pressure from deer ( Farmer 1995; Kirby, Thomas & Dawkins 1996). Changes at the plot level might or might not be repeated across the wood as a whole. Different types of 'indicator score' were used to interpret the changes observed.

## Site

Wytham Woods to the west of Oxford (National Grid Reference SP4608) cover about 320 ha and are a mosaic of ancient and recent woodland, semi-natural stands and plantations of various ages and species, with small areas of open grassland and scrub (Elton 1966; Perrins 1989). Ancient and recent woodland were distinguished from historical data and field studies (Gibson 1986; Grayson & Jones 1955). Plantations were recognised using data from the forestry stock map and field observations. The ancient semi-natural areas (36%) are mainly former coppice; the recent semi-natural stands (31%) have grown up on former pasture over

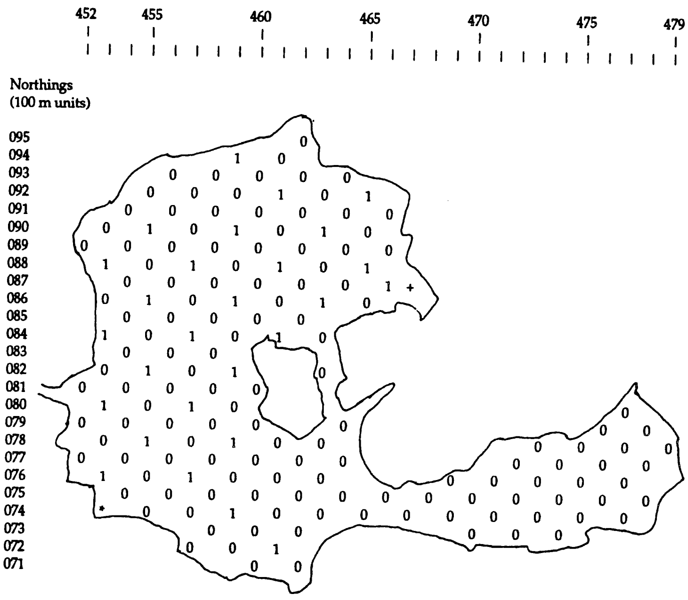



**Figure 1** Distribution of plots (0) through Wytham Woods: 1 plots also recorded in 1984, but data not used in this analysis; *plot not found in 1991; + an extra plot included in both 1974 and 1991 surveys.

the last 100 years; most of the plantations were established in the last 50 years, either within the existing ancient woodland (12%) or on former open grassland (21%). The wood lies on a hill with corallian limestone on the top and heavier clay soils on the lower slopes. The ancient woodland is mainly on the lower slopes. Oak (*Quercus robur)*, ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus)* are the main tree species - even the plantation areas are predominantly broadleaved - and the wood falls within the *Fraxinus excelsior-Acer campestre-Mercurialis perennis* type (W8) of the National Vegetation Classification (Rodwell 1991). The canopy and shrub cover both declined between 1974 and 1991, some shrubs became less frequent, but otherwise there was no major change in the tree and shrub composition of the wood (Kirby, Thomas & Dawkins 1996).

## Methods

*Field survey*

Between 1973 and 1976 (the 1974 survey) 164 10 x 10 m quadrats were established at alternate points on a 100 x 100 m grid throughout the wood (Dawkins & Field 1978) (Figure 1). Each plot was offset to the north-east (true north) from the grid-intersection marker posts by 14.1 m. Two corners of each plot were marked with underground metal markers so that they could be relocated precisely. In 1991 159 plots were re-recorded with a further 4 completed in 1992 (the '1991 data'). The one plot that could not be relocated, on the edge of the wood, has been excluded from the analysis. The recording took place from April to August on both occasions.

Vegetation cover was estimated across the south-west to north-east diagonal of the plot in three height bands: top or canopy cover > 2.5 m high, which was partitioned between species (mainly trees); mid or shrub cover 0.5-2.5 m high; and ground cover < 0.5 m high. Bramble (*Rubus fruticosus*) and some other tall herbs made a major contribution to the mid-cover layer (0.5 - 2.5 m) in places. All vascular plants in the ground flora in the plot were listed but in the analysis seedlings and saplings of woody species were excluded. Nomenclature follows Stace (1991).

In 1974 six common species were chosen (subjectively) which had different ecological characteristics: *Chamerion angustifolium, Hyacinthoides non-scripta, Mercurialis perennis, Pteridium aquilinum, Rubus fruticosus, Urtica dioica*. Their cover was estimated for each plot both in 1974 and 1991 on a six-point scale (0, 1 = 1-5% cover, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-100%) and the mean cover per plot calculated using the mid-point of each cover class weighted by the frequency of that cover class.

*Treatment of the data*

No large set of species records is completely accurate; species may be missed or misidentified. Different recorders have different biases (Sykes, Horrill & Mountford 1983; Kirby *et al.* 1986). When there was uncertainty about whether pairs or groups of species had been recorded consistently on both occasions they were combined prior to the analysis.

Not all species, and not all changes in species abundance, are of equal meaning in nature conservation terms. Three different ways of grouping species were used in the interpretation of the changes found in the Wytham data. Firstly species were classed as either 'ancient woodland indicators' for southern England (Marren 1990; Peterken 1974); other species associated with woodland in Britain (Kirby 1988b); or 'non-woodland' species, mainly those associated with grassland habitats. These three groupings were defined independently of the Wytham surveys and have been widely used in conservation evaluations over the last ten years (NCC 1989).

Secondly the species composition of different areas was analysed using 'Ellenberg Values' for the affinities of individual species for high or low light conditions, high or low soil moisture, nitrogen and reaction (pH) (Ellenberg 1988; Ellenberg *et al.* 1992) . Ellenberg values are on a 1-10 scale (10 high). The distribution of the Ellenberg values and of a weighted mean value (taking account of species abundance) was used to characterise different plot and species groupings using programs kindly provided by Dr D.G. Pyatt (Forestry Commission) (Hawkes, Pyatt & White 1997).

Thirdly the attributes of plot and species sets were analysed using the FIBS programs (Functional Interpretation of Botanical Surveys) developed by the Unit of Comparative Plant Ecology at Sheffield (Grime 1979; Grime, Hodgson & Hunt 1988; Hodgson, Colasanti & Sutton 1995). Attributes for the functional analysis were available for about 95% of species.

The Ellenberg Values and FIBS approaches were used, as possible ways of identifying what lay behind changes in species abundance (increasing openness, higher nitrogen availability, more disturbed conditions etc.) which in turn might be related to the management of the wood.

As well as using these pre-defined groupings of both species and plots the combined 1974 and 1991 data sets were analysed using DECORANA (Hill 1979).

## Results

*Changes in the wood as a whole*

There was little difference in the number of species recorded in the 163 plots on each occasion (Table 1) and Sorensen's similarity index for the two lists was 85%. The fifty species found on one occasion only were infrequent (recorded from less than 10% of plots). There was no significant difference in the mean number of species per plot, but species losses and gains, where a species was recorded in a plot on one occasion but not on the other, were between 40% and 45% of the mean number per plot. Large turnovers of species were generally either mainly gains or mainly losses, rarely both, i.e. plots showed directional change. Mean ground cover (<0.5 m high) declined significantly from 80% (+/-2) in 1974 to 64% (+/- 2) in 1991, although individual plots scattered over the wood showed large increases in cover.

**Table 1. Change in the numbers of species recorded per plot and across the whole wood** (Standard errors in brackets where appropriate)

| | Year | |
|---|---|---|
| (a) | **1974** | **1991** |
| Total no. of species recorded (out of 195 species in combined data-set) | 173 | 167 |
| Mean no. of species per plot | 16.7 (0.8) | 17.2 (0.7) |
| Mean no. only recorded on one occasion | 7.2 (0.5) | 7.7 (0.5) |
| Range in no. of species per plot | 4 - 61 | 0 - 49 |
| Mean no. of species in plots from: | | |
| Ancient semi-natural stands (n=59) | 17.4 (1.2) | 18.8 (1.2) |
| Plantations on ancient sites (n=19) | 17.3 (1.6) | 14.8 (1.6) |
| Recent semi-natural stands (n=50) | 15.2 (1.4) | 18.1 (1.5) |
| Plantations on recent sites (n=35) | 17.7 (1.6) | 14.6 (1.7) |

| (b) | **Plantations** | **Semi-natural stands** |
|---|---|---|
| Mean no. of species gained since 1974 | 6.8 (0.8) | 8.1 (0.6) |
| Mean no. of species lost since 1974 | 9.7(1.0) | 6.0 (0.5) |

*Changes in historical and management-based groupings of plots*

There were no significant differences in the mean number of species per plot between ancient and recent woodland, but the plantations showed significantly higher losses of species present in 1974 than semi-natural stands (t-test, p= 0.001) (Table 1). Plots in ancient semi-natural stands showed a fairly uniform decline in percentage ground cover, whereas recent plantations were more variable with some very large decreases, but large increases elsewhere. Plots that showed little change ( less than 20%) in canopy cover had no change in species richness (Table 2a); those that became more open gained species, those that became more shaded lost species.

**Table 2. Changes in ground flora in plots with different canopy types**

(a) ground flora change in plots showing large increases (>20%) or decreases (>20%) in canopy cover. (Standard errors in brackets).

| Canopy cover type | | Little change | Increase >20% | Decrease >20% |
|---|---|---|---|---|
| No of plots | | 91 | 51 | 21 |
| Mean values (s.e.) for: | | | | |
| Canopy cover (%) | 1974 | 79 (3) | 40 (3) | 90 (3) |
| | 1991 | 83 (3) | 93 (2) | 44 (5) |
| Species no. per plot | 1974 | 15.7 (1.0) | 19.0 (1.3) | 19.2 (1.9) |
| | 1991 | 16.3 (0.8) | 14.9 (1.1) | 23.1 (3.1) |

(b) Change in ground flora cover and species richness associated with plots in different cover change classes (Kirby, Thomas & Dawkins 1996)

| | | Canopy cover % | | Mid-layer cover % | | Ground cover % | | No. of species per plot | |
|---|---|---|---|---|---|---|---|---|---|
| **Canopy change process** | **No. of plots** | **1974** | **1991** | **1974** | **1991** | **1974** | **1991** | **1974** | **1991** |
| Closed, no major change | 78 | 87 | 83 | 45 | 21 | 80 | 63 | 16.2 | 14.8 |
| Open canopy plots | 13 | 41 | 18 | 56 | 41 | 95 | 89 | 17 | 24 |
| Closed, *Prunus* thickets | 6 | 90 | 62 | 54 | 55 | 67 | 51 | 9.7 | 12.3 |
| Young plot growth | 31 | 76 | 81 | 44 | 19 | 80 | 58 | 18.1 | 16.3 |
| Young plots+ thinning | 13 | 81 | 48 | 32 | 21 | 69 | 62 | 18.0 | 20.8 |
| Ride & glade expansion | 9 | 77 | 29 | 21 | 23 | 89 | 86 | 26.2 | 34.6 |
| Wind damage from storms | 10 | 96 | 44 | 54 | 46 | 80 | 54 | 12.2 | 15.6 |
| Dutch elm disease | 3 | 100 | 75 | 40 | 15 | 75 | 55 | 12.7 | 8.0 |

Ground flora changes were compared in more detail to the main changes that had affected the wood between 1974 and 1991. In closed canopy woodland where the leading tree (the largest in the plot) was the same in 1991 as in 1974 (Table 2b) the ground flora cover declined but there was no significant change in species richness. Open plots, mainly on the top of Wytham Hill where scrub had been cleared and the grass cut (to simulate grazing), had high ground cover and species richness increased. Areas that were dense blackthorn thickets (*Prunus spinosa*) in 1974 had less ground flora cover and lower species richness than the closed canopy plots. By 1991 the thickets had become less dense and there was no significant difference between the ground flora under them and the closed canopy woodland category. The plots where ride and glade expansion subsequently took place were richer than most closed canopy plots because they tended to be on the edges of stands; their further opening up led to increases in species-richness and maintenance of a high ground cover against the trend elsewhere in the wood, as also happened in young growth stands where thinning occurred. By contrast in the thirteen plots affected by natural gap-creation processes (windthrow and disease) there was the decline in ground cover seen in most of the wood and relatively little change in species richness. In the windthrow areas there remained a substantial mid-layer cover (sometimes the regrowth from fallen, but living trees); while in the three elm disease plots decline in canopy cover caused by death of elms (*Ulmus* spp) had by 1991 been partly made up by regrowth and expansion of adjacent canopies.

*Species occurrence and turnover*

Eight species of the 195 species recorded were relatively frequent in both years and common in both ancient and recent woodland. semi-natural stands and plantations: *Rubus fruticosus, Mercurialis perennis, Urtica dioica, Glechoma hederacea, Hyacinthoides non-scripta, Geum urbanum, Galium aparine,* and *Dryopteris filix-mas.*

Thirty-three species were classed as 'ancient woodland indicators', ninety-eight as other woodland species and sixty-four as non-woodland plants. The non-woodland component constituted less than 10 percent of all records (Table 3), none were widespread, and they were commonest in recent woodland areas. In Wytham ancient woodland indicators as a group were, as expected, commoner in the plots from ancient woodland. Of the 85 recent woodland plots 18 contained no ancient woodland indicators, and only 12 more than 3 species, whereas just 5 of the 78 ancient woodland plots had no indicators and 30 had more than 3 species. However some 'indicators' , for example *Hyacinthoides non-scripta*, had only a very weak affinity to ancient woodland in Wytham.

**Table 3. No of species and records for different species types**

(a) All plots

| Year | 1974 | 1991 |
|---|---|---|
| No. of species (all plots) | 173 | 167 |
| No. of records (all species) | 2732 | 2804 |
| No. of records unique to each time | 1182 | 1254 |
| No. of species present in more than 10% of plots | 43 | 47 |
| No. of ancient woodland indicator records (no. of species) | 411 (26) | 431 (31) |
| No. of other woodland records (no. of species) | 2075 (92) | 2131 (83) |
| No. of non-woodland records (no. of species) | 246 (55) | 242 (53) |

(b) Distribution of species groups between plots of different types (1974 records only)

| Species type | Ancient woodland | Other woodland | Non-woodland |
|---|---|---|---|
| Records from plots in: | | | |
| Ancient semi-natural stands | 193 | 789 | 43 |
| Plantations on ancient sites | 57 | 258 | 13 |
| Recent semi-natural stands | 87 | 599 | 75 |
| Plantations on recent sites | 74 | 465 | 79 |

Small differences in frequency with which a species was recorded between the surveys may have been due in part to recording errors, but larger ones, particularly of easily recognised species reflected real changes in the plots (Table 4). The wood became more grassy between 1974 and 1991 (increases in frequency of *Brachypodium sylvaticum*, *Deschampsia cespitosa*, *Poa trivialis* and two graminoids *Carex sylvatica*, *Juncus effusus)*. Herb species common in this woodland type (Rodwell 1991) varied in their response: *Ajuga reptans*, *Circaea lutetiana* and *Galium aparine* all declined; *Arum maculatum* and *Glechoma hederacea* increased.

**Table 4. Species showing either a gain to or loss from at least 12 plots between 1974 and 1991**

The last two columns give the frequency of the species in the National Vegetation Classification for the closest sub-communities (I <20% of samples, II 21-40%, III 31-60%, IV 61-80%, nr not listed).

* species that increased in a separate experiment in East Anglia when bramble was removed (Kirby & Woodell 1998).

| Species | Present both years | Present 1974 only | Present 1991 only | Frequency in NVC sub-communities, (Rodwell 1991) of W8 | | |
|---|---|---|---|---|---|---|
| **Species showing major decline since 1974** | | | | **8d** | **8a** | **8e** |
| *Ajuga reptans* | 13 | 28 | 5 | II | II | I |
| *Angelica sylvestris* | 11 | 25 | 8 | I | I | I |
| *Chamerion angustifolium* | 7 | 31 | 6 | nr | I | I |
| *Circea lutetiana* | 80 | 54 | 6 | III | III | II |
| *Dactylis glomerata* | 10 | 26 | 6 | nr | I | I |
| *Epilobium hirsutum* | 0 | 21 | 2 | nr | nr | nr |
| *Epilobium montanum* | 10 | 28 | 12 | nr | nr | I |
| *Equisetum telmateia* | 0 | 12 | 0 | nr | nr | nr |
| *Galium aparine* | 53 | 37 | 14 | I | I | III |
| *Heracleum sphondylium* | 7 | 25 | 0 | nr | I | I |
| *Pteridium aquilinum* | 76 | 23 | 2 | I | I | I |
| *Rubus caesius* | 0 | 28 | 1 | I | nr | nr |
| *Rubus fruticosus* | 120 | 22 | 7 | V | IV | III |
| **Species showing major gains since 1974** | | | | | | |
| **Arum maculatum* | 24 | 11 | 40 | I | II | II |
| *Brachypodium sylvaticum* | 61 | 2 | 75 | II | II | II |
| *Cardamine flexuosa* | 1 | 2 | 24 | nr | I | I |
| *Carex sylvatica* | 25 | 20 | 36 | I | II | I |
| *Cirsium vulgare* | 0 | 4 | 20 | nr | nr | nr |
| *Clematis vitalba* | 5 | 2 | 16 | nr | I | I |
| *Deschampsia cespitosa* | 44 | 5 | 57 | V | I | I |
| *Glechoma hederacea* | 82 | 17 | 28 | I | III | I |
| **Hypericum hirsutum* | 15 | 3 | 44 | I | nr | nr |
| **Juncus effusus* | 3 | 10 | 23 | II | nr | nr |
| *Poa trivialis* | 99 | 11 | 41 | II | III | I |
| *Ranunculus repens* | 9 | 3 | 21 | I | I | I |
| **Rumex sanguineus* | 15 | 14 | 27 | nr | I | I |
| **Scrophularia nodosa* | 4 | 5 | 17 | nr | nr | nr |
| *Senecio jacobea* | 2 | 3 | 17 | nr | nr | nr |
| *Sonchus olearaceus* | 1 | 2 | 20 | nr | nr | nr |
| *Taraxacum officinale* | 5 | 6 | 17 | I | I | I |
| **Veronica chamaedrys* | 13 | 10 | 22 | I | I | I |
| *Veronica serpyllifolia* | 0 | 0 | 13 | nr | nr | nr |

*Changes in cover of major dominants*

There were significant declines in cover of several of the major dominant species (Table 5a). In 1974 many thickets of *Rubus* had been more than 1 m high, but few such stands were found in 1991. For *Pteridium aquilinum* the decline in mean cover is linked to a reduction in the number of plots with more than 50% cover (from 23 in 1974 to 7 in 1991) mainly in plots which were in young plantations and scrub in 1974 that had increased in canopy cover by 1991 against the general trend for the wood (Table 5b). There was a smaller, but still significant decline, in mean cover for *Mercurialis perennis* (24 plots with more than 75% cover in 1974, only 7 in 1991), but the plots showing substantial decline have become slightly more open than the average for the wood.

**Table 5. Changes in mean cover per plot for six major species, 1974-1991**

(a) All plots

| | Frequency (no of plots in which present) | | Mean % cover (SE) (based on weighted frequencies) | | Significance of cover change[1] |
|---|---|---|---|---|---|
| | | | Year | | |
| **Species** | **1974** | **1991** | **1974** | **1991** | |
| *Hyacinthoides non-scripta* | 62 | 63 | 3.6 (0.8) | 4.7 (0.9) | n.s. |
| *Urtica dioica* | 122 | 129 | 12.8 (1.6) | 10.8 (1.2) | n.s. |
| *Mercurialis perennis* | 137 | 132 | 32.2 (2.5) | 24.0 (2.0) | *** |
| *Pteridium aquilinum* | 99 | 78 | 16.6 (2.0) | 9.3 (1.4) | *** |
| *Chamerion angustifolium* | 38 | 13 | 1.8 (0.5) | 0.3 (0.1) | *** |
| *Rubus fruticosus* | 142 | 127 | 35.4 (2.4) | 6.0 (0.8) | *** |

[1] based on paired-sample t-tests, with 163 samples in each case

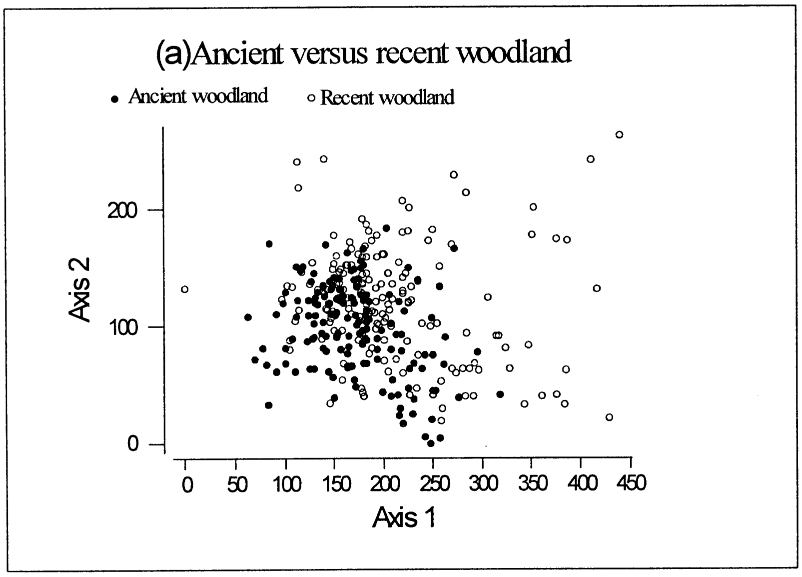
(b) Changes in overall cover of canopy cover (>2.5m), mid-cover (0.5-2.5m) and bottom cover for plots showing substantial declines in *Pteridium aquilinum* and *Mercurialis perennis* 1974-1991. (Substantial decline was set at from greater than 75% to less than 50% cover for the species, or from greater than 50% to less than 25%).

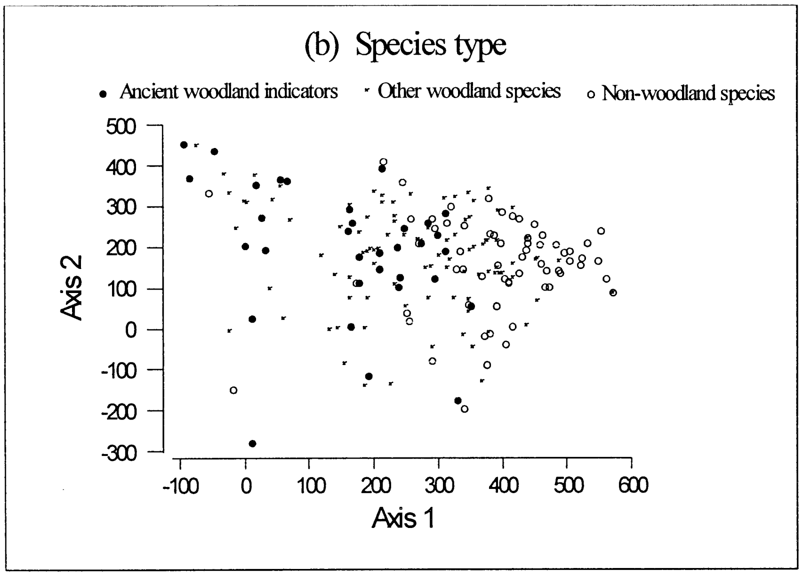
| | Mean % cover (Standard error in brackets) for | | | | |
|---|---|---|---|---|---|
| | **No of plots** | **Canopy layer 1974** | **1991** | **Mid-layer 1974** | **1991** |
| *Pteridium aquilinum* | | | | | |
| Substantial decline | 15 | 59 (8) | 70 ( 9) | 70 ( 9) | 27 (6) |
| Little change | 148 | 83 (2) | 68 ( 3) | 41 ( 3) | 25 (3) |
| *Mercurialis perennis* | | | | | |
| Substantial decline | 17 | 90 (4) | 57 ( 7) | 43 ( 8) | 34 (6) |
| Little change | 146 | 80 ( 2) | 70 ( 3) | 44 (3) | 24 (2) |

*DECORANA analysis*

Axes 1 and 2 of the DECORANA plot show some separation of ancient versus recent woodland plots; and on the species ordination ancient woodland indicators are separated from non-woodland species (Figure 2a,b). The difference in the vegetation between the years is brought out by Axes 1 and 3 (Figure 2c). Movement of individual plots in ordination space between 1974 and 1991 was calculated from the changes in their positions along axes 1 and 3 (Table 6a). This was significantly greater for plots in plantations than semi-natural stands. The 24 plots that showed the greatest movement (more than twice the mean for the wood as a whole) had higher than average species loss, with the losses being particularly of non-woodland species (Table 6b). The changes reflect the increasing canopy cover in these plots (compared to a wood-wide decline). Species that increased in the wood as a whole, such *Arum maculatum, Brachypodium sylvaticum, Deschampsia cespitosa,* also increased in these plots.

**Figure 2.** Distribution on the first three DECORANA axes of ancient versus recent plots, different types of species and 1974 versus 1991 records.




(b) Species type
Ancient woodland indicators
Other woodland species
Non-woodland species
Axis 2
500
400
300
200
100
0
-100
-200
-300
-100
0
100
200
300
400
500
600
Axis 1

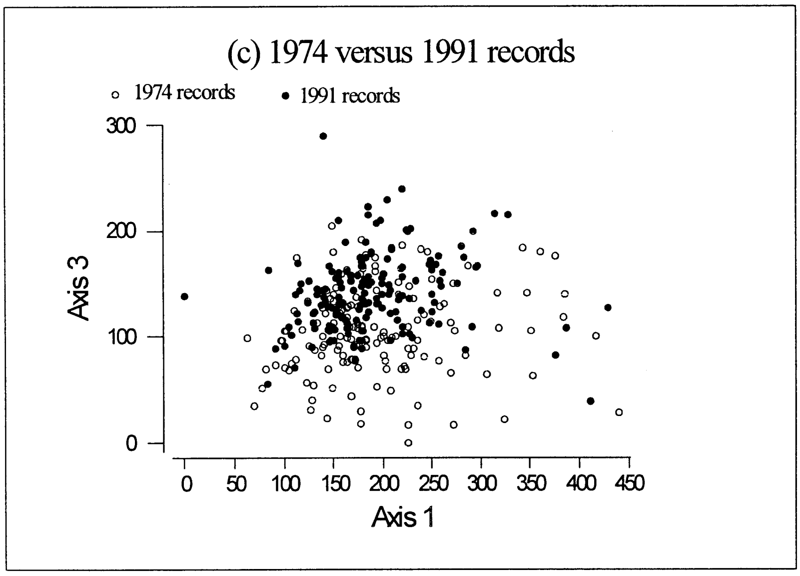

(c) 1974 versus 1991 records
1974 records
1991 records
Axis 3
300
200
100
0
0
50
100
150
200
250
300
350
400
450
Axis 1

**Table 6. (a) Mean distance (standard error in brackets) between plot positions (1974,1991) on a plot of DECORANA axes 1 and 3 (Figure 3) and (b) characteristics of the plots showing the greatest movement.**

(a) Distance moved (all plots)

| Plots in: | Mean distance moved | No in the top 24 for movement |
|---|---|---|
| Ancient, semi-natural stands (59 plots) | 45 (4) | 3 |
| Ancient, plantations (19 plots) | 62 (8) | 4 |
| Recent, semi-natural stands (50 plots) | 55 (4) | 5 |
| Recent plantations (35 plots) | 83 (8) | 12 |

(b) Characteristics of 24 plots showing the greatest distance moved compared to whole wood (standard errors in brackets, where appropriate)

| | | Value for 24 plots | Value for whole wood |
|---|---|---|---|
| Distance moved | | 124 (5) | 58 (3) |
| Mean species no | 1974 | 17.3 (2.2) | 16.7 (0.7) |
| | 1991 | 12.3 (1.7) | 17.2 (0.8) |
| Total no of species recorded | 1974 | 110 | 173 |
| | 1991 | 77 | 167 |
| Ancient woodland indicators | 1974 | 20 | 26 |
| | 1991 | 18 | 31 |
| Other woodland species | 1974 | 63 | 92 |
| | 1991 | 49 | 83 |
| Non-woodland species | 1974 | 29 | 55 |
| | 1991 | 10 | 53 |
| Mean canopy cover (%) | 1974 | 77 (6) | 81 (2) |
| | 1991 | 86 (5) | 69 (2) |
| Mean shrub layer cover (%) | 1974 | 65 (8) | 44 (3) |
| | 1991 | 17 (3) | 25 (2) |
| Mean ground cover (%) | 1974 | 70 (8) | 80 (2) |
| | 1991 | 46 (7) | 64 (2) |

*Use of Ellenberg values in the interpretation the wytham flora*

The Ellenberg light scores per plot for 1974 and 1991 were significantly related to the estimated canopy cover values for that plot, but with a high variation about the regression line ($p=<0.001$, $R^2<30\%$). The mean light scores for plantations were significantly higher than those for semi-natural stands in 1974, but not in 1991, and the declines in light score for plantations between 1974 and 1991 were significant (t-test $p<0.01$) (Table 7b). Increases in the light score were found in the plots where ride or glade expansion took place (Table 7c).

There was a significant positive relationship for the regression between soil pH measured in 1974 and the Ellenberg reaction score for that plot (p<001, $R^2$=22%), but that between total soil nitrogen per plot in 1974 and the equivalent Ellenberg nitrogen score was not significant. The only significant changes in the Ellenberg values for either soil reaction or nitrogen scores were an increase for soil reaction for plantations in ancient woodland. The mean Ellenberg Values for the species that showed major increases between 1974 and 1991 (see Table 4) did not differ significantly from those that showed a major decline (Table 7d).

Light scores were lowest for ancient woodland species, highest for non-woodland ones (Table 7e). All three groups, but particularly non-woodland species showed a bias towards high soil reaction (pH) scores, reflecting the base-rich geology that underlies much of the wood. Woodland species had higher nitrogen scores than non-woodland ones.

**Table 7. Mean Ellenberg indicator values, weighted by species cover, for different plot and species groupings** (Standard errors in brackets)
L light indicator score (non-zero values available for 179 species)
R reaction (pH) score ( " " " " 129 " )
N nitrogen score ( " " " " 163 " )

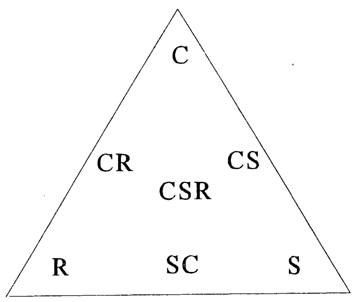
| | | No of plots | L | R | N |
|---|---|---|---|---|---|
| (a) Mean scores for all plots | | | | | |
| All 1974 | | 163 | 4.9 (0.1) | 6.3 (0.1) | 6.4 (0.1) |
| All 1991 | | | 4.7 (0.1) | 6.3 (0.1) | 6.3 (0.1) |
| (b) Mean scores for plots grouped by origin and management | | | | | |
| Ancient, semi-natural | 1974 | 59 | 4.7 (0.1) | 6.3 (0.1) | 6.4 (0.1) |
| | 1991 | | 4.6 (0.1) | 6.3 (0.1) | 6.4 (0.1) |
| Ancient, plantation | 1974 | 19 | 5.1 (0.1) | 5.9 (0.1) | 6.3 (0.1) |
| | 1991 | | 4.8 (0.1) | 6.3 (0.2) | 6.3 (0.3) |
| Recent, semi-natural | 1974 | 50 | 4.7 (0.1) | 6.5 (0.1) | 6.5 (0.1) |
| | 1991 | | 4.7 (0.1) | 6.5 (0.1) | 6.4 (0.1) |
| Recent, plantation | 1974 | 30 | 5.4 (0.2) | 6.3 (0.1) | 6.4 (0.1) |
| | 1991 | | 4.7 (0.2) | 5.8 (0.3) | 6.1 (0.1) |
| (c) Mean scores for plots changing in different ways (Table 2) | | | | | |
| Closed canopy, no change | 1974 | 78 | 4.8 (0.1) | 6.3 (0.1) | 6.3 (0.1) |
| | 1991 | | 4.4 (0.1) | 6.2 (0.1) | 6.4 (0.1) |
| Ride and glade expansion | 1974 | 9 | 4.9 (0.2) | 6.4 (0.1) | 6.4 (0.1) |
| | 1991 | | 5.3 (0.2) | 6.2 (0.1) | 6.2 (0.1) |
| (d) Mean scores for species showing most change (Table 4) | | | | | |
| 19 species showing a major increase | | | 5.5(0.5) | 4.3(0.7) | 6.0 (0.5) |
| 13 species showing a major decline | | | 6.1(0.3) | 4.8 (0.8) | 6.3(0.4) |
| (e) Mean scores for different species groups | | | | | |
| Ancient woodland indicators | | | 4.2 (0.3) | 6.1 (0.3) | 5.3 (0.2) |
| Other woodland species | | | 6.1 (0.2) | 6.1 (0.2) | 6.0 (0.2) |
| Non-woodland species | | | 7.2 (0.1) | 6.8 (0.2) | 4.8 (0.2) |

*Use of functional analysis (FIBS) in the interpretation of the Wytham flora*

The species were biassed towards competitive and stress-tolerant strategies, with only a small contribution from ruderal species (Figure 3b,c). There was no change in the contribution of any of the major FIBS attributes between years for the wood as a whole (Table 8a), nor was there any clear pattern to differences between ancient and recent woodland plots.

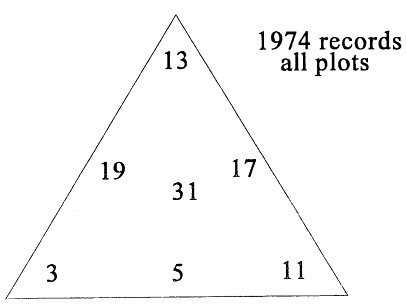
Ancient woodland indicators showed the stronger link with woodland as their most common habitat compared to other woodland and non-woodland species (72%, 31% and 0% respectively) in the FIBS analysis; ancient woodland species also tended towards the stress-tolerant strategy type, whereas the non-woodland species were biassed towards ruderals (Figure 3d-f). The species that showed major increases (Table 4) were slightly less competitive and more ruderal (Figure 3g,h), smaller, less likely to have leafy stems and showed a stronger affinity for pastures and other open habitats than those that declined (Table 8b) but this analysis should be treated with caution because of the small numbers of species involved (19 and 13 respectively).

**Figure 3**. Distribution of Strategy Types (a) amongst (b) the full species list from 1974, (c) the full list from 1991, (d) ancient woodland indicators, (e) other woodland species, (f) non-woodland species, (f) increasing species (from Table 4), (g) decreasing species.

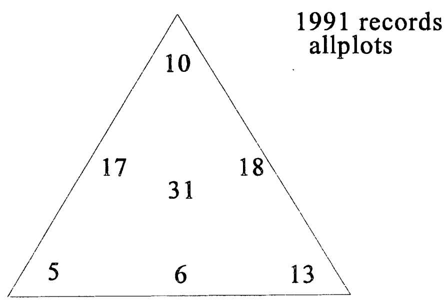



(a)
C competitve
S stress tolerant
R ruderal
CR competitive-ruderal
CS competitive-stress tolerant
SR stress tolerant-ruderal

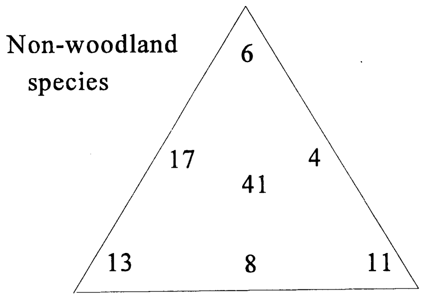
(b)




(c)

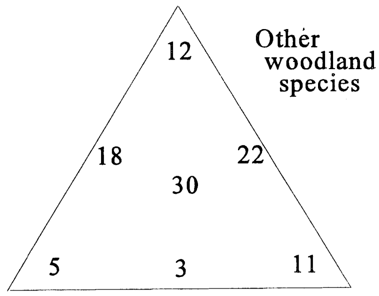


(d)

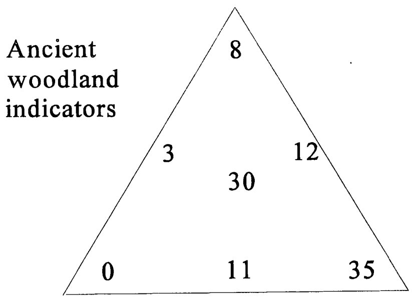


Non-woodland species
6
17
4
41
13
8
11


(e)

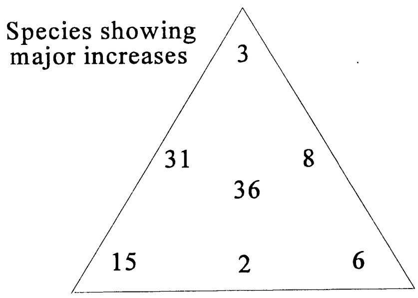


Other woodland species
12
18
22
30
5
3
11

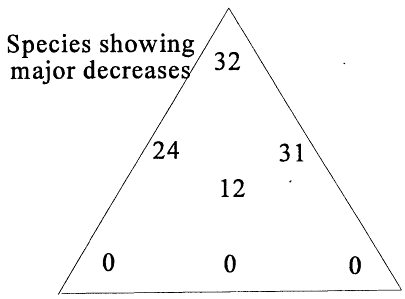



Ancient woodland indicators
8
3
12
30
0
11
35


(f)



Species showing major increases
3
31
8
36
15
2
6

Species showing major decreases
32
24
31
12
0
0
0


(g) (h)

## Table 8. Mean % allocation of species to FIBS attribute types

(a) All species, weighted by their overall frequency (out of 163 plots)

| Common habitat | 1974 | 1991 | Canopy structure | 1974 | 1991 |
|---|---|---|---|---|---|
| Woodland | 41 | 39 | Leafy | 50 | 46 |
| Wasteland | 17 | 15 | Semi-basal | 37 | 40 |
| Spoil | 11 | 11 | Basal | 12 | 11 |
| Pasture | 15 | 18 | **Canopy height(cm)** | | |
| Arable | 10 | 11 | <10 | 10 | 13 |
| Skeletal | 7 | 8 | 10-29 | 27 | 26 |
| Wetland | 10 | 9 | 30-59 | 27 | 26 |
| | | | 60-99 | 10 | 11 |
| | | | 100-300 | 20 | 18 |
| | | | >300 | 6 | 5 |

(b) % allocation to the following attribute types among increasing (19) and decreasing (13) species (Table 4)

| Common habitat | Increasers | Decreasers | Canopy structure | Increasers | Decreasers |
|---|---|---|---|---|---|
| Woodland | 30 | 54 | Leafy | 36 | 65 |
| Wasteland | 10 | 11 | Semi-basal | 57 | 20 |
| Spoil | 29 | 5 | Basal | 1 | 15 |
| Pasture | 27 | 2 | **Canopy height(cm)** | | |
| Arable | 17 | 8 | <10 | 29 | 0 |
| Skeletal | 9 | 7 | 10-29 | 14 | 8 |
| Wetland | 7 | 7 | 30-59 | 15 | 25 |
| | | | 60-99 | 22 | 21 |
| | | | 100-300 | 17 | 30 |
| | | | >300 | 3 | 16 |

## Discussion

Long-term studies allow the detection of changes that take place gradually over decades and may not be apparent to the majority of researchers who seldom remain associated with any particular site for long (Magnuson 1990). Assessing long-term changes in woodland will become more important in future if we are to be able to report on government commitments to maintain forest biodiversity (HMSO 1994) and to understand the impact of exceptional events such as the 1987 great storm (Kirby 1994). In Britain results from permanent transects and plots showing changes in the tree and shrub layers over the last ten to fifty years have become relatively common (eg Backmeroff & Peterken 1989; Peterken & Backmeroff 1988; Peterken & Jones 1987,1989; Peterken & Stace 1987), but less is known about whether changes in the ground flora parallel those of the tree and shrub layers. The Wytham results help to fill these gaps.

*Species turnover at different scales*

The ground flora in Wytham Woods is composed largely of perennial species (85 % classed as polycarpic perennials), some of which can survive for decades (Inghe & Tamm 1985). The poor dispersal ability of many woodland species, particularly ancient woodland species (Peterken & Game 1984) might also be expected to lead to stability in the woodland ground flora over time. This stability was shown at the whole site level, by various measures (total species richness, mean plot richness, number of ancient woodland indicator species, mean Ellenberg Value scores, broad strategy profile) (Tables 1,3,7, 8; Figure 3b,c).

Peterken's (1996) suggestion that small-scale patterns in woodland ground flora are unlikely to last long is reflected in the high turnover of species at the plot level, with all plots showing some gain or loss of species. High turnover in the woodland ground flora has been reported elsewhere (eg. Holland 1978; Falinski 1986). Barkham (1992) found 29% turnover of species from 2 x 2 m plots over 18 years in an ash-hazel woodland in Cumbria (UK) with the least abundant components of the flora being most affected, particularly grassland and ruderal species. However in Wytham even some abundant woodland species such as *Circaea lutetiana* and *Poa trivialis* showed large changes in their frequency (Table 4).

*Variations between blocks of woodland and groups of species*

Ancient and recent semi-natural stands differed in their composition, but not in species richness, and the changes in their vegetation over the period were similar. Many of the plantations were quite young in 1974 and so grew considerably over the following 17 years, leading to more losses from their flora than from semi-natural stands (Table 1). However they also gained species, such as *Brachypodium sylvaticum* and *Deschampsia cespitosa* in common with the rest of the wood.

The species groups used in conservation surveys (ancient woodland indicators, other woodland and non-woodland species) showed differences in the Ellenberg values, functional analysis profiles and separation on the DECORANA axes (Table 7,Table 8, Figure 2,3d-f) and helped to characterise differences in plot composition across the wood. A wider comparison of Ellenberg and FIBS scores for putative ancient woodland indicators and other species recorded in the woodland communities of the National Vegetation Classification (Rodwell 1991) is in hand.

*Stand growth and deer grazing as major causes of changes in species abundance*

The changes at a plot level are complex but overall the effects of stand growth with associated changing light levels for the ground flora, and the direct and indirect effects of increased browsing by deer (mainly *Dama dama* and *Muntiacus reevesii*) can explain most of the patterns seen at a wood level.

Declines in species richness were high where canopy cover had increased most (Table 2,5). The declines in *Chamerion angustifolium* and of *Epilobium* species (both commonly associated with newly-felled or planted areas within forests), and of *Heracleum sphondylium* and *Dactylis glomerata* (species often found in grassy pre-thicket stands) (Table 4) can be linked to stand growth and less forestry activity in the woods during the late 1970s and early 1980s than in the period preceding the 1974 recording.

The decline or absence of *Rubus fruticosus* (Table 5) is a common feature of grazed woods (eg Barkham 1992; Putman *et al.* 1989), where it may thrive only within enclosures; concomitant increases in grasses such as *Brachypodium sylvaticum* or *Deschampsia cespitosa* have been found at other grazed sites such Lady Park Wood (Gwent) and Roudsea Wood (Cumbria) (unpublished data). Similarly, at Monks Wood (Cambridgeshire), heavy grazing by *Muntiacus reevesii* has reduced *Mercurialis perennis* and *Rubus fruticosus* and allowed *Brachypodium sylvaticum* to increase (Cooke *et al.* 1995). Browsing might be expected to affect taller growing species and those with leafy stems more than it would lower growing plants, characteristics that were more common in the species that showed major decreases than in the increasers (Table 8).

The reduction in cover of *Rubus* by browsing permits lower growing species to spread because the competition from the bramble canopy is reduced. Six of the nineteen species that increased at Wytham (but none of the decreasers) (Table 4) were ones that increased following bramble clearance in East Anglia (Kirby & Woodell 1998). Similar competitive effects have been noted elsewhere: an inverse relationship between the cover of *Rubus* and *Pteridium aquilinum* and species richness (Page 1981); reductions in the plant diversity by dense stands of *Allium ursinum* or *Urtica dioica* (Ernst 1979; Hermy, van den Bremt & Tack 1993); increases in *Hyacinthoides non-scripta*, *Primula vulgaris* and other species when the shade of *Mercurialis perennis* was reduced (Pigott 1977). Davison and Forman (1982) reported reductions in diversity and loss of rare species accompanying increased ground flora cover particularly of *Podophyllum peltatum* in a mature oak forest. Meier, Bratton and Duffy (1995) proposed competition with other species as one explanation for the loss of vernal herbs in logged areas and Collins and Good (1987) concluded that interactions within the ground flora could be as important in determining the distribution of species as variation in canopy type.

The numerous deer paths found in the wood may contribute to a slight 'ruderal' tendency among the suite of species showing major increases for example *Cirsium vulgare, Senecio jacobea* and *Sonchus oleraceous* (Figure 3; Table 4), particularly when combined with the reduced canopy cover for the wood as a whole (Kirby, Thomas & Dawkins 1996).

*Soil nitrogen and pH effects*

A decrease in pH and increase in nitrogen content, believed to be caused by atmospheric deposition, have been found in soil samples from the Wytham plots (Farmer 1995). In continental woods similar soil changes have been associated with changes in the flora (Falkengren-Grerup 1990; Falkengren-Grerup & Tyler 1991). Thimonier, Dupouey & Timbal (1992) worked in the Amance Forest (north-east France) with a similar system of plots to that at Wytham Woods. Between 1971 and 1990 they reported small but significant shifts in the mean Ellenberg nitrogen scores for plots and other floral changes indicating eutrophication, particularly along the forest boundary. Species richness increased from 18.9 to 25.2 per sample, unlike in Wytham Woods where no changed occurred. There is some overlap between the species that increased at the two sites (eg *Carex sylvatica, Juncus* spp. *Scrophularia nodosa*) but also differences: for example *Rubus fruticosus*, *Brachypodium sylvaticum*, and *Deschampsia cespitosa* all showed major changes at Wytham but virtually none at Amance. In Wytham species with high Ellenberg scores for nitrogen and pH were found equally among species that have increased and those that decreased. Increasing nitrogen might be expected to favour highly competitive species and yet some of these tended to decrease in Wytham (Table 8, Figure 3h). Any effects of soil eutrophication and acidification on the vegetation have not yet reached a level in Wytham Woods at which they can be separated from other causes of change.

*Implications for monitoring and management for nature conservation*

Any monitoring scheme for woodland ground flora must be set up with the expectation that turnover at plot levels may be high even where there is little overall change in the broad-scale measures such as mean plot richness. If changes in species occurrence are important then a much larger sample is required than if only broad scale measures such as mean species-richness are of interest. Data from this and similar surveys become increasingly unreliable for example as a guide to what is happening to individual species populations as the frequency of species occurrence goes down. *Paris quadrifolia*, an ancient woodland indicator species that attracts much interest (Mabey 1996), was recorded from four plots in 1974 and none at all in 1991. This is not strong enough evidence to say that the plant is definitely declining in Wytham, although it might be sufficient to justify a careful search of the areas where it has occurred in the past to see whether it is still present.

Conservation managers must decide if their concern is with the flora only (the species present on the site) or with the vegetation (the relative abundance and distribution of those species). The flora - the plant list of the site - may be conserved in broadleaved woods that have been partially replanted with conifers even though the vegetation under the plantations is impoverished (Peterken & Game 1984; Kirby 1988a). Similarly the flora at Wytham did not change significantly between 1974 and 1991, but the vegetation did: reduced mean ground cover; changes in the distribution of formerly abundant species, such as *Circaea lutetiana*; a general shift from *Rubus fruticosus* thickets to grasses. However whether the state of the vegetation in 1974 is more or less appropriate as a goal for conservation management than that present in 1991 is debatable. The 1974 vegetation was a product of twenty years of very active forestry work in parts of the wood (associated with the creation and maintenance of the plantations and loss of open grassland). In the century prior to that the vegetation would have been different again since the ancient woodland was being very regularly and heavily disturbed through being cut as coppice (Grayson & Jones 1955).

Conservation-orientated managers must accept therefore that the woodland ground flora is dynamic. However it would seem prudent to seek to moderate changes that lead to a greater homogeneity across a wood and hence a decreased ability for losses in one area to be balanced by gains elsewhere. This leads to the following recommendations with respect to Wytham: a reduction in the deer browsing/grazing pressure to permit some thickets of bramble to re-establish; and the creation of some newly cut areas through felling plantations or coppicing to benefit species typical of the open woodland phase. Since deer management is also needed if young trees and coppice regrowth are not to be seriously damaged by browsing, the two elements are linked, and are reflected in the recent management in the wood.

## Conclusions

The system has fulfilled its originators aims, in that it has survived (both plots and data) and has proved of value in demonstrating the effects of factors that were not a particular concern in 1974, for example the effect of deer on the balance between *Rubus* and grasses. Wytham Woods are now part of a national network of sites set up to look at environmental change, so interest in the scheme and the data that it provides is likely to continue (Sykes & Lane 1996).

Many of the species present when a stand is young are not present later on in the rotation in either unmanaged stands or managed ones (Mitchell & Kirby 1989); change at the stand scale is inevitable and is reflected in the high rates of species turnover at the plot level. Continuity of a range of conditions must therefore be maintained at the wood scale if species are not to be lost, because in lowland England, where woodland exists only as isolated patches, movement between sites is limited for many of the species of highest conservation value (Peterken & Game 1984).

The grid system of plots provides results that suggest this continuity has been achieved at Wytham. Changes in one area eg. species declines were matched by opposite changes elsewhere and even some ancient woodland indicators have spread throughout the wood. At the same time it has been possible to identify some wood-wide trends, and suggest possible causes, using the Ellenberg scores and FIBS attributes.

The Wytham system is not a universal model for setting up long-term plots to study changes in woodland but two of its strengths should be considered in other major monitoring schemes.

a. The range of features that were recorded in 1974 enabled changes in the woody layers, ground flora and soil to be integrated. The Wytham data show that they do not necessarily change in the same way or at the same rate.

b. The samples were representative of the whole wood, not just of unmanaged (minimum intervention) stands. In most British woods minimum intervention areas are unlikely to be large enough to encompass the full range of patch dynamics needed by the flora and fauna associated with different stand growth stages. There will be periods where some species depend for their survival on stands in the adjacent managed woodland. Only if the two treatments are monitored in parallel can the success of either treatment in conservation terms be assessed.

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