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The development of beech woodland at Dendles Wood National Nature Reserve, Devon

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Preface

English Nature is grateful to the authors for the opportunity to include this report in its research report series. This should help to ensure that knowledge of the permanent vegetation plots at Dendles Wood is maintained. The work was however done independently of English Nature and any views expressed are not necessarily those of English Nature and its staff.

Keith Kirby, English Nature

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Summary

- The development of mixed beech stands in the southern part of Dendles Wood National Nature Reserve were quantified using several data sets collected between 1967 and 1998. The records related to a range of stands and included data on tree size, survival, growth, stratification, mortality, regeneration, storms, mammal damage, canopy gaps and dead wood.

- The majority of trees grew up on pasture around 150 years ago. It is not clear how many were derived from natural regeneration or planting, though sweet chestnut, silver fir, European larch, and Scots pine were certainly planted widely. Beech and oak trees set in the original pasture provided local seed sources and, along with other locally occurring native species, probably produced some natural regeneration. The status of beech in this outlying site remains uncertain.

- By the 1960/70s, all stands were high forest with beech dominant or co-dominant with oak. A minority of sweet chestnut, silver fir, European larch, and Scots pine remained, along with a few large old beech and oak. The presence of small trees, especially of beech, suggested that there had been some recent regeneration, possibly following silvicultural thinning. Birch remained only as snags in one stand. A few understorey holly and very few rowan were present, along with a few ash, elder, hazel, hawthorn, sallow and sycamore that were possibly marginal to the main stands.

- Over the next three decades most areas remained as maturing high forest. A long-term trend from oak-beech to beech dominance was apparent, with beech proving more competitive than oak and most minor species. Nevertheless, some surviving oak and sweet chestnut remained healthy, commanded dominant canopy positions, and appeared capable of remaining locally prominent indefinitely. Although competitive exclusion remained predominant, storm-damage increased, removing some large beech, silver fir, and oak from the canopy, damaging several sub-ordinate oak, beech and holly, and leaving 20% of the transect under gaps. Grey squirrels debarked many and killed some beech stems, though fast-grown medium-small poles proved most vulnerable to severe debarking. Holly and rowan remained infrequent and suffered damage and losses due to debarking by deer/sheep. Regeneration remained limited, mainly of beech, and mainly restricted to gaps. Despite some vigorous beech and a few birch, silver fir and rowan recruiting in one well-lit gap, consequent debarking by grey squirrels left most beech severely damaged or dead. Grazing and debarking by deer/sheep inhibited regeneration of beech, rowan and silver fir, and prevented the development of a holly underwood. Dead wood increased to high levels: accumulations occurred where storms had damaged beech, oak and fir, and where exclusion had left large, slowly decaying, oak trunks.

- The general development of the stands is discussed. This most closely resembled observations in similar untreated wood-pasture stands in the New Forest. Recommendations for future research and monitoring are suggested.

Contents

1. Introduction

This report is based on various records of stand change in a semi-natural woodland in south-west England. The site has been left untreated as a minimum intervention woodland reserve, and provides an interesting case of beech woodland growing on the edge of its native range. Scientific research is a fundamental reason for the establishment of minimum intervention reserves (Peterken 1996, 2000; Hall *et al* 1999, Parviainen *et al* 1999, 2000). It often aims to show what features develop in such 'natural' woodland and what processes and factors are responsible for these. Such information provides ecologists and policymakers interested in natural woodland and nature-based management with an important reference-point, particularly in the absence of any surviving truly-natural woodland in Britain. With this in mind, a representative series of minimum intervention woodland reserves and programme of long-term monitoring therein has been proposed (Mountford 2000, Peterken 2000).

2. Site details

This study was carried out in Dendles Wood National Nature Reserve (Figure 1) (national grid reference SX 615620), which covers 29ha and lies on the southern slopes of Dartmoor and in the upper valley of the River Yealm, 2½km, north of the village of Cornwood. It has been a nature reserve since The Nature Conservancy purchased it in 1965, and an archive of unpublished information on the site is held by English Nature and summarised in the site management plan (Lamboll & Page 1997). Apart from semi-natural woodland, the site supports rare insects (including the rare blue ground beetle *Carabus intricatus*), mosses, ferns, and lichens (including 150 species). It is crossed by a steep-sided valley cut by the River Yealm and includes some floodplain areas. Annual rainfall is high at about 1900mm. Most of the ground is dominated either by beech *Fagus sylvatica* (9ha), oak *Quercus robur* (6ha), mixed broadleaved (9ha), or conifer woodland (1ha). The vegetation corresponds mainly to woodland types W15b/c *Fagus sylvatica-Deschampsia flexuosa*, W10e *Quercus robur-Pteridium aquilinum-Rubus fruticosus,* or W11a *Quercus petraea-Betula pubescens-Oxalis acetosella* in the National Vegetation Classification (Rodwell 1991).

Much of the scientific interest in Dendles Wood is related to its beechwood component. It may be an outlying native population, since it includes several large, spreading (pollard) beech, which would pre-date their widespread planting in Devon (Jones 1961, Rackham 1986) if there age is confirmed as 300 years (Table 1). Oaks at least up to 300 years are also present (Table 1), and a few extant oak coppice stools and charcoal hearths show that parts of the wood were once treated as (oak) coppice. However, most extant trees originated in the mid-late 19th century and show a general relationship between girth and age (Tables 1 and 2). The 1842 Tithe Map records much of the site as pasture, and various ruined internal walls in Fernfires Wood and elsewhere mark old enclosures. Although heavy grazing must have stopped and facilitated natural regeneration soon after the mid-19th century, many trees were certainly planted, with 19th century sweet chestnut, silver fir, European larch, and Scots pine widespread and in places frequent (Table 1). Grazing resumed in the 20th century and, although the wood was ring-fenced when it became a reserve, fallow and more recently roe deer have become abundant, and sheep and sometimes cattle and ponies have regularly gained access. Stumps with felling marks indicate that some stands were thinned several decades ago, with at least some pine, fir and oak being cut and removed. In the 1980s the

reserve was nominated as an area of beech-oak woodland suitable for management by minimum intervention and long-term monitoring.

3. Study area

Recording took place in the southern part of the reserve where the vegetation composition varies according to the topography (Figure 1). In the River Yealm floodplain areas of Fernfires Wood and Clam Flat, the vegetation corresponds to type W15 *Fagus sylvatica-Deschampsia flexuosa* woodland of the National Vegetation Classification (Rodwell 1991). Beech *Fagus sylvatica* is the dominant tree, along with some pedunculate oak *Quercus robur* and a minority of ash *Fraxinus excelsior*, elder *Sambucus nigra*, European larch *Larix deciduas*, hazel *Corylus avellana*, hawthorn *Crataegus monogyna*, holly *Ilex aquifolium*, sallow Salix *cinerea/caprea*, Scots pine *Pinus sylvestris*, silver fir *Abies alba*, sweet chestnut *Castanea sativa*, and sycamore *Acer pseudoplatanus*. By the river a few downy birch *Betula pubescens* and rowan *Sorbus aucuparia* occur. The ground vegetation under the closed beech canopy is sparse, with some bryophytes present, mostly *Dicranum* spp., *Leucobryum glaucum, Plagiothecium undulatum, Polytrichum formosum,* and *Rhytidiadelphus loreus*. Gaps are, however, invariably filled with bracken *Pteridium aquilinum*, bramble *Rubus fruticosus* agg., soft rush *Juncus effusus*, great wood-rush *Luzula sylvatica*, foxglove *Digitalis purpurea*, and various grasses. The soils are typically well-drained, acid, brown earths with signs of incipient podsolisation. An example from under beech gives 5cm of leaf litter, pH at 3.9, and a dark brown-grey, silt loam upper soil, grading to a sandy clay loam (Ling 1991).

To the east of the floodplain is Elvan Bank, an area of higher, sloping ground above the floodplain. On the lower 30° steep slopes, beech and pedunculate oak remain dominant, whereas on the upper 15° slopes there are changes towards W10e *Quercus robur-Pteridium aquilinum-Rubus fruticosus* and W11a *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland of the National Vegetation Classification (Rodwell 1991). Beech becomes less and chestnut and oak more prominent, and grow in mixture with a minority of ash, fir, hawthorn, hazel, holly, larch, pine, rowan and sycamore. The ground vegetation includes bluebell *Hyacinthoides non-scripta*, bilberry *Vaccimium myrtillus*, bracken, bramble, great wood-rush, honeysuckle *Lonicera periclymenum*, ivy *Hedera helix*, wood sorrel *Oxalis acetosella*, and various grasses. Soils are shallower, stonier, and bedrock is exposed in places. An example from under beech on the lower slopes gives 7-8cm of leaf litter, pH at 4.2, 10cm of dark brown-grey, sandy clay loam upper soil, 10cm of stony, brown-orange, blocky clay loam mid soil, and a mid-orange becoming browner, sandy clay loam, stony subsoil (Ling 1991).

4. Recording

4.1 Total stand enumerations

In January 1967 or November 1968 and April 1977 all live stems ≥7.5cm diameter at 1.3m breast height (dbh) were measured in all compartments in the wood, including Fernfires Wood (4.09ha), Clam Flat (1.3ha), and Elvan Bank (2.25ha) (Figure 1). All live stems ≥7.5cm diameter at 1.3m breast height (dbh) were measured with callipers and assigned to 5cm classes sub-divided for each species. In the second recording dead stems were also

measured. The first recording survived only in aggregate form, and could not be sub-divided by species.

4.2 Sample stand enumeration

Live trees around a pair of permanent seedling plots (see below) in Fernfires Wood were plotted and measured in June 1975. Their position was drawn onto 1:200 scale A4 charts, the species identified, and the quarter-girth at 1.3m height measured to the nearest quarter inch. No minimum threshold for inclusion was given, but the smallest tree measured was 4 inches quarter-girth (41cm girth), and more than one stem measured on low-forked individuals. The limit of recording was not defined, but appeared to be about 5m out from the edge trees, which therefore amounted to 0.122ha.

4.3 Permanent seedling plot

In 1975 seven near-by pairs of 10m x 10m plots were established to record long-term changes in tree and shrub seedlings under contrasting grazing regimes. These were scattered throughout the wood and one of each pair was fenced with 1m tall netting to exclude sheep and inhibit deer. Two plots were located at the north end of Fernfires Wood (Figure 1). In 1976, 1982 and 1988 live seedlings were counted in each plot, sub-dividing them into <15cm or >15cm height-classes. In 1995 seedlings >15cm were counted in 25 regularly spaced 0.5m x 0.5m sub-plots, which covered 1/16 of the plot area. Photographs were taken of the plots at each recording.

4.4 Permanent transect

In October 1988 a permanent transect was established to monitor long-term changes in trees and shrubs. This ran across Fernfires Wood, the River Yealm, Clam Flat, and up Elvan Bank (Figure 1). It was 20m-wide, 331m-long, included 0.6455ha of woodland, and was marked by galvanised posts. Within the transect the following details were recorded and drawn onto 1:100 scale A3 charts that covered 30m-long sections of the transect:

- Species, status (standing and alive ≥1.3m height, fallen and alive ≥1.3m height, or dead) and location (to nearest 10cm) of all tree and shrub individuals that attained 1.3m height. Stems on multi-stemmed individuals, and large stumps, dead fallen trunks, and dead branches were sketched. Some trees just outside the transect were included.
- Girth at 1.3m breast height (gbh) to nearest cm of all live and dead standing stems ≥5cm gbh
- Location of patches of established tree and shrub seedlings, several years old, ≥30cm and <1.3m height, were sketched.
- Miscellaneous notes of some trees recording abundant ivy, uprooting, snapping, height and condition of dead standing stems, patches of abundant ground vegetation, old paths and other salient features.

The transect was recorded again in October 1998, with the following details overwritten onto the 1988 charts or tabulated:

- Species, status and location as in 1988, but dead standing stems were distinguished from those only alive <1.3m height.
- Gbh as in 1988, but to nearest 5mm and including low forks ≥10cm gbh
- Location of each established tree and shrub seedlings, several years old, ≥20cm and <1.3m height, was mapped.
- Brief descriptions of live stems noting their stature, vigour, crown condition, damage, debarking, and other salient features. These were also assigned to a strata, size and dieback category based on crown position, spread, and loss due to competition, debarking, damage and other factors: *canopy layer* = crown in uppermost layer and not overtopped; *sub-canopy layer* = crown just below and mostly overtopped by the canopy layer; *understorey layer* = crown below sub-canopy layer; *ground layer* = crown mostly <2m height; *very large crown* = spread of more than 10m diameter; *large crown* = spread about 6-10m diameter; *medium crown* = about 3-5m diameter; *small crown* = about 2m diameter; *very small crown* = <1m diameter; *very severe dieback* = >90% crown loss; *severe dieback* = 60-90% crown loss; *moderate dieback* = 30-60% crown loss; and *part dieback* = <30% crown loss.
- Grey squirrel bark-stripping to the trunk and main forks of beech stems scored using a five-point scale (Mountford 1997): 0 = *none* = no bark removed; 1 = *limited* = one or few small patches with <10% bark circumference removed; 2 = *moderate* = one large or few medium and/or many small patches with 10-50% circumference removed; 3 = *severe* = few large and/or many medium and many small patches with >50% circumference removed; 4 = *very severe* = as for severe but ring-barked. Bark-stripping was recorded first for the lower trunk (<2m height) and then for the upper trunk (>2m height), with the maximum score used to categorise overall damage, i.e. scores of 1/3, 3/3 and 3/1 were all categorised as severe damage.
- Heights of dead stems (and those only alive <1.3m height) ≥1.3m height and ≥10cm gbh to nearest 0.5m if <6m and nearest metre if ≥6m.
- Extent of gaps in the upper canopy layer as viewed from the ground.
- Miscellaneous notes on the cause of stem death, patches of abundant ground vegetation, origin and infilling of canopy gaps, and other salient features.
- Location, species, length (to nearest 10cm), and mid-girth (to nearest cm) of fallen dead logs ≥1m length and ≥40cm mid-girth or girth below main trunk fork. Where logs extended outside the transect, only the part inside the transect was considered. Mid-diameter was taken on some trunks.

4.5 Dead wood line transects

In October 1998 the amount of fallen dead wood was estimated in Fernfires Wood, Clam Flat, and Elvan Bank compartments (Figure 1). In each, six equal length line transects covering 150m in total (t) were laid out using random start points and directions. The number (N) of fallen dead wood stems attaining 5cm diameter and intersecting the line was counted, their diameter (d) measured in centimetres at the intersection, and the species identified. The

length (L) (m ha^{-1}) and volume (V) (m^3 ha^{-1}) of fallen dead wood were estimated using the formulae, $L = N\pi 10^4/2t$, and $V = \Sigma(\pi^2 d^2/8t)$ (Warren & Olson 1964).

5. Analysis

The analysis aimed to identify development in beech and mixed stands at southern end of Dendles Wood. The data available from Fernfires Wood, Clam Flat, and Elvan Bank amounted to about 5,200 records, which were entered on to a Microsoft Excel spreadsheet to facilitate sorting, statistical analyses, and long-term storage. Development prior to the first recordings was reconstructed based on surviving features. The total stand enumerations from 1967/8 and 1977 were used to assess stand characteristics in Fernfires Wood, Clam Flat, and Elvan Bank, as was the 1975 sample stand plot from Fernfires Wood. The pair of seedling plots in Fernfires Wood was used to assess seedling development and understorey regeneration under grazed and non-grazed conditions from 1976 to 1995. The permanent transect provided information on stand characteristics in Fernfires Wood, Clam Flat, and Elvan Bank, and on tree and shrub survival, growth, stratification, damage, mortality, and regeneration. Along with the line transects, it provided information on standing and fallen dead wood.

The permanent transect was sub-divided into six stands based on structure and topography (Figure 2). Four were mature beech-oak stands; (1) 0.1535ha on the floodplain of Fernfires Wood; (2) 0.058ha on the riverside terraces of Fernfires Wood; (3) 0.1235ha on the floodplain of Clam Flat; and (4) 0.0615ha on the steep lower slopes of Elvan Bank. The other two were (5) 0.036ha of regenerating beech stands on the riverside terraces of Clam Flat, and (6) 0.213ha of mature beech-oak-chestnut stands on the moderate upper slopes of Elvan Bank. Most stems shown on the transect charts were confidently relocated, but some anomalies in the record were detected and these had to be adjusted for. A few individuals were misidentified, misplaced on the charts, or omitted. It was difficult to decide where girth measurement had been taken on stems that had fallen or had forks, kinks, bulges, bosses or damaged bark at 1.3m height. Where stems had not been drawn on multi-stemmed individuals, the largest stem in the first survey was assumed to have remained so. In dealing with size anomalies, amendments were made where records were missing or the difference was considered implausible by interpolating from the known performance of similar stems located nearby. Live individuals/stems included those standing or fallen and with live leaves at or above 1.3m from the base. Snags included dead standing stems ≥1.3m height.

Stem density and basal area values included stems ≥5cm gbh. Basal area was calculated for the enumerations and permanent transect by assuming stems were circular in cross section, and, for the total enumerations, using the mid-class dbh. Snag volume included stems ≥10cm gbh and was calculated by assuming that it approximated a cylinder based on the gbh and height measurements. Stem growth was assessed by examining changes in the basal area of stems that remained alive and upright at the end of each period. Stems whose size was 'adjusted' for errors (see above) were excluded. The relationship between annual increment (change in size ÷ 10 growing seasons) and initial size was tested using linear regression. Differences in average growth rates were tested using single-factor Analysis of Variance (ANOVA) and pinpointed by Tukey Honestly Significantly Different tests. Chi-square (χ^2) analysis was used to test the significance of associations between frequency counts. The true annual mortality rate (m) and half-life rate ($t_{0.5}$) were calculated using the formula

recommended by Sheil *et al* (1995): $m = 1-(N_0/N_1)^{1/t}$, $t_{0.5} = -\log_e 2/\log_e(1-m)$, where N_0 and N_1 were population counts at the beginning and end of the census interval $t = 10$ years. Statistical procedure followed Zar (1984) and calculations were carried out using *Microsoft Excel Version 7.0* computer package.

6. Results

6.1 Stand enumerations in 1967/8 and 1977

The compartments enumerated in 1967/8 were all high forest (Table 3). Stem basal area and density was highest in Fernfires Wood, where 32.5-62.5cm dbh trees were abundant, moderate on Elvan Bank, and considerably lower on Clam Flat where many stems were small. The size-class distributions suggested all contained a few large old trees and possibly a cohort of smaller-sized stems that established during the last few decades. A cohort of medium mid-aged stems was most clearly defined in Fernfires Wood, the distributions in Clam Flat and Elvan Bank being more irregular.

Changes between recordings might have been imprecise because the compartments were large and boundaries unmarked, but they suggested that Fernfires Wood remained relatively unaffected by disturbances. Moderate gains were made in basal area and density, apparently through limited in-growth, moderate mortality of smaller stems due to competitive exclusion, and moderate growth of larger stems. Clam Flat decreased in basal area and density and apparently had several large trees die. Shifts in the size-distribution suggested many smaller stems were excluded, whilst many surviving medium trees, and some small stems that grew into the smallest-class, were released into growth. The increase in basal area and decline in density on Elvan Bank suggest undisturbed growth and mortality due to competitive exclusion, which was evidenced by changes in the small and medium size-classes. However, change in the larger classes shows some mortality and very rapid growth of the largest tree, which are best explained by imprecise recording.

The species breakdown recorded in 1977 provided more details of stand composition and trends (Tables 4, 5 and 6). Fernfires Wood was dominated by beech and oak, beech being most abundant. The largest trees were beech and oak, whilst the group of medium trees was mainly beech, with numerous oak, and a few sycamore, ash, fir, larch, chestnut and pine. The smallest trees were also mainly beech, along with a few oak, sycamore, ash, and chestnut. Shrubs were mainly holly, along with some hazel and few hawthorn and rowan. Snags were concentrated in the smaller size-classes reinforcing the view that competitive exclusion had been dominant. Beech snags were scarce, along with a few sycamore, chestnut, ash and pine, and oak most abundant, indicating that beech had increased in dominance during the past decades. Birch had been completely excluded from the stand remaining only as snags.

Clam Flat had a similar composition, though beech accounted for a higher percentage of the basal area, nearly all medium and large trees were beech or oak with sycamore, larch, chestnut and pine absent, whilst fir was a scarce medium and small tree, and the understorey was more mixed with less holly, more hazel, and a few sallow and elder. The low basal area in 1965 and 1977 and abundance of hazel, sallow and elder ties in with the inclusion of Wellbrook mire in the compartment: this area of boggy ground supported scrub vegetation rather than high forest. Snag basal area was high mainly because a few large beech and fir

snags were present, probably those that appeared to have died during 1965-77. These most likely arose due to other causes than exclusion, perhaps storm-damage, in contrast to the other snags which were small. With fir snags outnumbering live firs, and oak snags being relatively more abundant than beech, the trend was a decline in fir and an increase in beech dominance.

Elvan Bank was quite similar in composition to Fernfires Wood, though beech was less abundant in the medium and small size-classes, no large oaks were present, sycamore was less and ash much less abundant, pine was absent, but medium chestnut and larch were more abundant, and fir was present as a few small and medium trees. Snags were predominately small-sized indicative of exclusion. Beech snags were scarce, oak and fir were relatively abundant, and some larch and sycamore occurred, indicating that in recent decades beech and chestnut had survived best.

6.2 Sample stand enumeration in 1975

The sample plot from Fernfires Wood recorded in 1975 (Table 7) was in an area of closed high forest that was more beech-dominated and less species rich than the compartment as a whole (Table 4). Beech included a few large old trees up to 244cm gbh and dominated the medium-large trees. Oaks were mainly medium-small trees and these appeared to have been out-grown by similar aged but somewhat larger beech. The understorey was poorly developed, including only a few suppressed beech trees and a single holly. Although the size-distributions for beech and oak were somewhat truncated, they reflected patterns observed in the compartment as a whole (Table 5). These patterns reinforced the suspected trend of increasing beech dominance.

6.3 Changes in the permanent seedling plot 1976-95

The number of tree and shrub seedlings in the two plots in Fernfires Wood increased from 1976 to 1995 (Table 8). Holly accounted for 96% of all recorded seedlings, the others being beech (3%), sycamore or ash. Holly numbers started low, with a slightly higher total and slightly more >15cm high in the fenced plot. By 1982 both short and taller seedlings had increased in both plots. However, in the fenced plot most (81%) were >15cm high and in the unfenced plot most (72%) were <15cm. Fencing had prohibited grazing and allowed most large saplings to grow to 1m or more in height, whilst in the unfenced plot the effect of grazing was obvious and the largest saplings were <30cm height. Changes by 1988 were limited and both plots made slight gains in taller seedlings.

In 1995 only taller seedlings were counted. Holly made large gains in both plots, and for the first time a few beech and sycamore grew above 15cm height in the fenced plot. Although holly increased much more in the unfenced plot, it remained 27% more abundant in the fenced plot. Moreover, it was noted that holly in the unfenced plot was generally under 15cm due to grazing by sheep or deer, and photographs showed no tall seedlings in the fenced plot and a cohort of steadily rising saplings to about 2m high covering the fenced plot.

6.4 Permanent transect in 1988

The permanent transect crossed a variety of stands (Figures 1-2). Most were mature high forest with beech and, sometimes, oak dominant (Tables 9-11). Trees were present in all size-classes up to 360cm gbh, including large >200cm gbh beech, oak, chestnut and silver fir. Only on the riverside terrace east of the river was the canopy broken and regeneration of beech plentiful. Chestnut and fir were prominent on the upper slopes only; birch, larch, rowan, pine and sycamore were localised minor species; and holly was widespread but infrequent.

The west floodplain stand in Fernfires Wood was a mainly closed, high forest stand with a moderate basal area and density of live trees, and small number of snags (Tables 9-10). Live trees were mainly oak and beech, with chestnut and holly making a minor contribution. The size-distribution (Table 11) revealed a few large oaks growing amongst some medium-large beech, oak and a few chestnut. Descriptions made in 1998 noted the large oaks included several old pollards: two were live trees at 250 and 345cm gbh (one was just outside the transect), and two were snags at 171 and 240cm gbh. The smaller size-classes, which were dominated by beech, either represented a younger cohort or a group of suppressed, slow-growing trees. Whichever, a change from oak-beech to beech dominance was evident, and this was reinforced by the presence of 11 medium-large dead oaks: two were snags at 172-240cm gbh, and nine were fallen trunks/stumps at 111-152cm gbh, which contrasted with two similar beech stumps. Most of the fallen oaks appeared to have been excluded, but at least one at 152cm gbh had been windblown. When this fell it apparently crushed two or three more 111-148cm gbh oak, two 60-87cm gbh beech, the smallest of which remained alive, and the top of 41cm gbh beech. Another extant c.170cm gbh beech was also wind-damaged, with a large central old split in the trunk from 4m to crown top. The understorey comprised a few, scattered, shade-tolerant holly. All of these were older individuals, the largest stems on each being 44-78cm gbh Four holly stems at 40-58cm gbh were snags: debarking had apparently killed two, and the others had apparently died after being struck and damaged by a oak bough. The only other recorded holly was a 77cm gbh stem that been crushed by the 152cm gbh windblown oak.

The transect crossed a small section of riverside terrace in Fernfires Wood. This had a similar structure to the adjacent floodplain stand, but beech dominated the basal area, oak made a moderate contribution, and fir, holly and rowan were minor species (Tables 9-10). The largest tree was a live beech at 266cm gbh (Table 11), which forked low-down into two trunks suggesting it may have been an old-pollard. The other live trees, three beech and three oaks between 132-153cm gbh, appeared to be younger infill around the old beech and contemporary with the medium-large cohort in the adjacent floodplain stand. Exclusion had apparently killed the four dead trees recorded: two beech snags at 48 and 122cm gbh, and two oak stumps at c.75 and 137cm gbh. The few understorey individuals grew within a few metres of the riverbank, presumably where conditions were better lit. These included two small rowans, a poor fir sapling, and an old holly with its largest stem, which was just outside the transect, at 68cm gbh.

The small section of riverside terrace on Clam Flat, east of the River Yealm, had a different structure and composition (Tables 9-11). The canopy was broken and basal area was mainly in snags because the two main 243 and 432cm gbh beech trees survived only as 7-10m snags.

Descriptions in 1998 recorded that these had been windsnapped, probably whilst alive and, judging by their decay state, probably in the 1980s. Despite these losses, live stem density was the highest of all stands. Apart from three 34-95cm gbh beech and a 34cm gbh fir, which survived on ground close to the floodplain stand, several beech and a few downy birch and rowan had developed along the riverbank into individuals up to 30cm gbh, and on slightly higher ground originally occupied by the large beech snags, several sapling beech had grown above 1.3m height. The only holly recorded was an old 98cm gbh understorey tree located just outside the transect and towards the edge of the floodplain stand.

The east floodplain stand on Clam Flat was similar in structure to the other floodplain stand, but live stem and snag basal area were higher, and beech dominated the living trees and silver fir the snags (Tables 9-10). The bimodal size-distribution of live trees suggested two age groups (Table 11). Beech dominated the larger trees and included two large, 250 and 272cm gbh, old pollards. Large beech dominated the higher ground up to the base of the lower slopes, but immediately adjacent to the riverside stand, the stand was more diverse and had a part-broken canopy due to storm-damage. Here, most of the 49-113cm gbh beech were recorded, along with two live 107 and 189cm gbh oak, and three large 142, 264 and 300cm gbh fir snags. The latter had been killed by storms, with the largest two windsnapped at 2-8m up and the smallest tipped over. When they fell they bent over a 62cm beech, broke the tops in two 94 and 101cm gbh beech, uprooted a 100cm beech, and uprooted and killed a 100cm gbh beech. Only three dead tree stumps were recorded: a small excluded beech, an old cut out oak in the area close to the riverside stand, and a similar oak close to the base of the slope in the next stand. Only two holly were recorded at 30 and 60cm gbh, with the smallest having died after being smashed by a canopy bough. However, in the centre of the stand there were signs that holly would regenerate, having established a sizeable strip of low-growth.

The stand on the lower slopes of Elvan Bank was similar in structure to the floodplain stand below, though basal area and density of live stems were slightly higher, mainly because oak and holly stems were better represented, and snags were only oak and beech (Tables 9-10). Beech was the dominant tree, with a wide-range of stem sizes (Table 11) and 3 out of 9 live individuals having two or three stems/forks. Based on the largest sized stem on each individual, seven individuals at 128-211cm gbh appeared to be older than the two at 28 and 50cm gbh. The multi-stemmed individuals were possibly derived from coppice or low cut pollards, but equally they could have been low-forked maidens having grown low down on the slope and out towards an old track at the slope base. The two live oaks at 155 and 186cm gbh were also amongst the older individuals, as were the two snags, a beech 161cm gbh and an oak at 213cm gbh. The later had been windsnapped at 6-11m, possibly in the same incident that uprooted a dead fallen c.75cm gbh oak. The only recorded dead tree stump was of an excluded smaller-sized oak. Three understorey holly individuals were present, two of which had two or three live stems present. Based on the size of the largest stem on each, the individual at 80cm gbh appeared to be older than the two at 34 and 38cm gbh.

The upper slopes of Elvan Bank differed from the other stands (Tables 9-11). Although it was mainly closed high forest with beech and oak prominent, chestnut and silver fir made a moderate contribution to the stand, and along with holly, larch, pine and sycamore were included as minor species. The basal area was the highest recorded, mainly because large trees were abundant. Most individuals were single-stemmed maiden trees, but some coppice, pollard and other multi-stemmed individuals were present, including; four single- or twin-

stemmed coppice oaks with snags of 29-64cm gbh; a fallen chestnut with a fallen dead 179cm gbh trunk that had developed a replacement 135cm gbh stem at the base; two probable coppice beech with close-grown stems of 119, 65 and 62cm gbh and 46 and 25cm gbh; and three old pollard beech at 257, 266 and 350cm gbh and four beech at 206-233cm gbh that were possibly old pollards. Live trees of all sizes were present. Based on the largest stem on each individual three groups could be identified: (i) older trees, larger than about 200cm gbh, and mostly of beech with some oak and a few chestnut and fir; (ii) possible mid-age trees, about 100-200cm gbh, and mostly of beech and oak with some chestnut and a few larch; and (iii) younger trees, less than about 100cm gbh, and mostly of beech with a few sycamore and fir. One oak at 154cm gbh had been windsnapped at 4m up but remained alive. Snags were numerous, and for analysis were combined with an oak snag just outside the transect and the stumps of 11 dead trees. All the main species were represented, though only one dead beech was recorded and all oak, larch and chestnut <100cm gbh had been lost. The snags and stumps were divided into four groups: (i) 21 excluded stems <100cm gbh, 8 oak, 4 fir, 4 larch, 3 chestnut, 1 beech and 1 holly; (ii) three larger excluded trees between 111 and 151cm gbh, 2 oak and 1 fir, (iii) a toppled chestnut at 179cm gbh and a windsnapped pine at 122cm gbh; and (iv) five felled trees, 1 larch at 50cm gbh, and four pine at 50, 50, 60 and 200cm gbh. Only two live understorey holly were recorded, both being older individuals with largest stems of 91 and 122cm gbh. A strip of low-growing holly was recorded suggesting the understorey might increase.

6.5 Changes in the permanent transect 1988-98

Much of the transect remained as beech or beech-oak dominated high forest in 1998 (Tables 12-14). Density and basal area of live stems increased slightly, despite 12 out of 186 stems ≥5cm gbh dying (Table 15). The latter helped create several large openings and in 1998 canopy gaps covered 1315m^2 or 20% of the transect area (Figure 3). Recruitment amounted to 26 new individuals and established seedlings to 243, most of which were beech or holly (Table 16). Growth trends were similar in the main species with larger girth trees tending to have increased most in basal area (Figure 4). Generally these had larger crowns located in the upper strata and thus intercepted more sunlight than smaller-crowned, sub-canopy and understorey stems.

Beech increased its overall dominance as reflected by changes in the basal area and density of live individuals and stems ≥5cm gbh (Tables 12-13). In 1998 beech formed the majority of crowns in all canopy layers, including 67% of canopy trees (Table 14). Most survivors made moderate-good growth, though a few large trees made slow basal area growth (Figure 4). Surviving trees were benefiting from localised opening of the canopy, with 36 trees located around canopy gaps showing signs of release through new crown growth and/or branch or trunk sprouting. However, numerous beech trees had been debarked by grey squirrels either at the base, or on the trunk/crown branches (Table 17). 65% of recorded live stems in 1998 were affected, including 28 stems with severe or very severe debarking, and another nine sized 10-16cm gbh had been killed due to ring-barking by squirrels. 12 surviving trees had snapped boughs or trunk out following debarking. Combining all standing live and dead stems, and by comparing size-class numbers with none, limited or moderate damage against those with severe or very severe damage, the worst damage was associated with stems <120cm gbh, with 36 out of 95 having been severely or very severely debarked ($\chi^2 = 19.54$, $p<<0.001$). Within this vulnerable size, most rapid grown stems up to 90cm gbh had been badly damaged (Figure 5). Although both beeches toppled in 1988 survived, the more

vigorous, which was layering well at 5m along and at the end, had most of the several vigorous erect trunk sprouts debarked at the base by squirrels. Beech mortality during 1988-98 was low, but included four, 118-266cm gbh, wind-damaged trees located on the west riverside terraces, east floodplain and lower slope stands, and produced basal area declines in all (Table 15). Additional wind-damage was recorded in an apparently part-rotten beech in 1988 located on the east riverside terrace stand: this surviving tree had one of its two forks from 2m up snapped away leaving a badly damaged and half-rotten trunk.

Beech recruited more saplings than any other species and numerous beech seedlings established (Tables 15-16). At the margins of a windblow gap in the west floodplain stand, a recruit grew to 4cm gbh from a branch tip layer located on an oak root mound, though it had been badly debarked by deer or sheep, and a scatter of seedlings established. At the edge of a wind-damage gap beside the river on the west riverside terrace, six beech recruits grew to 1-3cm gbh, though four were being browsed, and a scatter of established seedlings. Recruitment and seedling establishment was greatest in the open conditions on the east riverside terrace, adding to the group of young saplings and probably partly developing from seedlings already established in 1988. Fourteen beech recruited and 33 seedlings established, the largest making 17cm gbh and eight others 7-11cm gbh. However, deer/sheep grazing and squirrel debarking curtailed both and prevented development of young saplings present in 1988: no seedlings recruited or survived in an area marked with 'lots of beech seedlings' in 1988; six recruits had been damaged by grazing; 20 out of 33 established seedlings had been grazed down; six saplings <8cm gbh in 1988 and another four would be recruits that grew to 10-16cm gbh and 2.5-4m height by 1998 were transformed to snags after being severely debarked by squirrels; and the largest recruit and all of the nine largest beech poles at 17-39cm gbh had been severely or very severely debarked by squirrels.

Oak declined slightly overall. Despite all twelve trees surviving and the basal area slightly increasing on floodplain/riverside terrace stands, two trees were lost due to wind-damage on Elvan Bank, one of which was snapped prior to 1988, and this resulted in an overall fall in basal area and density (Tables 12-13 and 15). Although fewer oak than beech were lost, the mortality rate was higher in oak (m = 0.77% v 0.53%), and the population half-life was 90 years compared to 129 years for beech. Growth of surviving large oak was generally exceeded by equivalent chestnut and beech (Figure 4). In 1998 oak accounted for only 21 out of 93 canopy trees, with just two being large-crowned (Table 14). 9 surviving trees located beside canopy gaps showed signs of release through new crown growth and/or branch or trunk sprouting, but one on the upper slopes at 250cm gbh had lost a large bough due to windsnap. No oak saplings had recruited or seedlings established.

The performance of the minor tree species varied (Tables 12-15). Chestnut increased in importance, especially in the upper slope stand. All trees survived and generally grew rapidly (Figure 4). 7 out of 8 remained in the canopy, four having medium-large crowns, and only one tree suffering any notable wind-damage with a large low fork being snapped out, perhaps in the 1990 storms. The two young birch located on the east bank of the River Yealm grew vigorously, though their roots had become exposed due to undercutting by the river. Fir remained scarce. The small weak fir sapling on the west riverside terrace was hit by beech debris and died. On the east riverside terrace the 34cm gbh fir pole remained vigorous and grew to 57cm gbh despite being overtopped by beech, and just into the adjacent floodplain stand a fir sapling recruited, growing to 8cm gbh and 2.5m height though it was badly frayed

by deer. On the upper slope stand the smallest two 30-62cm gbh fir were excluded and the next at 64cm gbh grew little and was left with a poor, suppressed, overtopped crown. However, the two largest fir here grew well, and survived as 229-260cm gbh, large-crowned, tall, canopy trees with only the lower branches shaded out. With the exclusion of one of the sycamore from the upper slope stand, just one tree survived and this was overtopped and strongly suppressed. The single larch in this stand survived as a medium-crown canopy tree, though it appeared to be struggling in competition with adjacent beech.

Holly remained as the main understorey species (Tables 12-15). Although numbers remained low, no holly individuals died and it increased in basal area. However, 17 out of 21 surviving stems ≥10cm gbh were damaged. Deer or sheep debarking killed a small stem, left another at 58.5cm gbh ring-barked and nearly dead, three others severely debarked, and eight more with some debarking. Others had old damage: three at 43-121cm gbh had been damaged long ago at the base and this was now causing rot, and five others at 62-121cm gbh had been damaged by falling trees or branches. In addition, the two strips of low-growing holly regeneration recorded in 1988 had been grazed out. Nevertheless, most surviving holly stems retained healthy crowns, albeit above a distinct browse line, and had grown by a small amount. Three holly managed to recruit by growing in protected sites: (i) on the west floodplain a horizontal-grown sapling with a browsed top established on the mound of an uprooted oak; (ii) on the east riverside terrace a lateral-grown sapling with a browsed at base established on the riverbank face; and (iii) on the lower slopes a weak sapling established on the face of tipped oak root plate. Numerous holly seedlings established, with most recorded on the margins of canopy gaps in the west floodplain stand. Rowan remained as a scarce understorey species. The two smallest saplings present on the riverside terraces disappeared, one being washed away and the other probably being eaten by deer/sheep. The largest of the two that survived grew from 18 to 39cm gbh, despite its roots being exposed at the riverbank, and the smallest developed into a 6-12cm gbh four-stemmed individual. A spindly rowan sapling recruited on the west terrace, but, along with both survivors, had been part-debarked by deer/sheep.

6.6 Changes in dead wood

The compartment enumerations in 1977 estimated snag basal area at 2.1-3.2m^2 ha^{-1} (Table 4). Oak was abundant in Fernfires Wood and on Elvan Bank, and fir and beech on Clam Flat. The largest snags were a few 77.5-137.5cm gbh fir and beech on Clam Flat, and some oak and a few beech and sycamore at 47.5-67.5cm gbh in the other compartments (Table 6).

Snag basal area was higher on the permanent transect, changing from 8.8 to 7.4m^2 ha^{-1} during 1988-98 (Tables 9 and 12), and snag volume in 1998 measured 66.4m^3 ha^{-1} (Table 18). In all stands, basal area reached 4.6m^2 ha^{-1} and volume 25.1m^3 ha^{-1}, but levels varied and were exceptionally high on the east riverside terrace where two large beech remained standing following windsnap. Most (72%) of the total volume was in six large snags, sized 167-418cm gbh and 4-18m height: three windsnapped beech on the riverside terraces, two excluded oaks in the west floodplain, and a windsnapped fir in the east floodplain. Of 41 snags, 6 were 125-200cm gbh and 6 >200cm gbh.

Large fallen dead logs measured on the permanent transect in 1998 amounted to an estimated 61.5m^3 ha^{-1} volume and 739m ha^{-1} length, with most being oak or beech (Table 19). Stand

volumes ranged from 23-174m^3 ha^{-1} and reflected localised patterns of storm-damage. Oak was abundant in the west floodplain and lower slope stands, with most material derived from exclusion in the former and windthrow in the later. Windsnapped beech was very abundant on the west riverside terraces and abundant on the lower slopes.

The line transect estimates of fallen dead wood ≥5cm diameter in Fernfires Wood, Clam Flat and Elvan Bank compartments in 1998, recorded a length of 2932-3560m ha^{-1} and volume of 30.3-48.6m^3 ha^{-1} (Table 20). Length was greater on Clam Flat, and volume highest on Elvan Bank and least in Fernfires Wood. In comparison to the permanent transect measurements, volume was much less abundant and a more equal mixture of oak and beech in Fernfires Wood compartment, less abundant and a more equal mixture of oak and beech in Clam Flat compartment, and less abundant and with much less oak and more chestnut on Elvan Bank compartment. This indicated that the transect reported on areas where wind-damage had been concentrated.

7. Discussion

The compartment, permanent plot and line transect recordings provide a basis to reconstruct past-stand change and postulate on future development in the southern part of Dendles Wood. Although the coverage and detail of the records varied, and their interpretation inevitably thus remains uncertain and possibly biased, they do provide considerable information on various components of stand change, over a three decade period, and from a range of beech-dominated stands.

7.1 Stand history

The history of beech at Dendles Wood is of considerable scientific interest because although there are prehistoric records of beech in the vicinity, there is little evidence of later survival (Godwin 1975, Rackham 1997). The majority of trees in the mixed beech stands in the southern part of Dendles Wood appear to have established on pasture around 150 years ago. Fernfires Wood was recorded as such in 1842, and the size of the present trees infers that grazing must have stopped and stand initiation started soon after this. Set within the extant stands are some large beech and oak, including a few out-grown pollards, and a few large holly that were probably part of the original pasture landscape. The 1842 map classifies the floodplain and slopes east of the river in a single wooded compartment. However, the floodplain stand on Clam Flat appears little different from Fernfires, and the more likely area of ancient woodland is on the slopes of Elvan Bank as evidenced by a scatter of old oak coppice stools. No boundary ruins have been recorded at the foot of the slope between these areas, though past-exclosure may have been informal and achieved by temporary fencing.

It is not clear if the present stands developed from natural regeneration and/or planting. Searches have revealed no historical records of tree planting, though this had become a popular activity in the late 18th century (Jones 1961), and the widespread occurrence of sweet chestnut, silver fir, European larch, or Scots pine shows that at least some, and therefore perhaps much, planting occurred including beech. Nevertheless, the original wood-pasture beech and oak trees would have provided local seed sources and both are capable of invading abandoned pasture (Watt 1934, Tansely 1939). The size-distribution of trees and limited

information on tree ages suggests some variation in tree age, as would be expected from natural invasion. Even if planting had occurred, it is likely to have been supplemented by natural regeneration of beech, oak, birch, ash, sycamore, holly, rowan, hazel, and willow.

Existing information therefore suggests that the site should be treated as an outlying examp of 'native' beech woodland, albeit that at least part of the wood is not strictly 'ancient' (*se* Peterken 1993) and planting of non-native stock potentially occurred. The 'native' lineage beech is indicated by the presence of pre-1600 trees, though the aging is based on uncorroborated evidence.

7.2 Species performance in stand development

By the 1960/70s, perhaps a century after initiation, all stands had grown into high forest. Beech had become dominant on Clam Flat and co-dominant with oak in Fernfires Wood an Elvan Bank. All stands retained some planted non-native sweet chestnut, silver fir, Europea larch, and Scots pine, a scatter of large old beech and oak, and sufficient small trees, especially of beech, to suggest some recent regeneration, possibly coincident with evidence of silvicultural thinning many decades ago. In Fernfires Wood, two birch snags were recorded, indicating that this species could have been abundant in the early development of the stand, which would be expected (Watt 1934, Tansley 1939). In the understorey, a few holly and very few rowan were probably widespread, but other minor species could have been more marginal: the few ash, hazel, hawthorn and sycamore in Fernfires were possibly associated with the stretch of woodland boundary, and the ash, hazel, sallow and elder on Clam Flat probably grew on boggy ground around Wellbrook mire.

During the next thirty years most areas remained as maturing high forest with the beech and, sometimes, oak dominant. However, it was evident that prior to and during these decades a competitive change from oak-beech to beech dominance, and a similar reduction in most minor tree species, was in progress. By 1998 beech had increased its dominance of the permanent transect: it was the most abundant species, accounted for most medium-large tree dominated all canopy layers, had suffered low mortality in the previous decade, made moderate-good growth on surviving trees, and been able to expand into most canopy gaps created. Evidence of exclusion of oak by beech was shown by the relative abundance of snag and size-distributions of surviving trees at initial recordings, and by the slow-growth of surviving oak, the relative number of surviving canopy and smaller-crowned trees, and the higher mortality and lower half-life rates for oak compared to beech on the transect during 1988-98. Nevertheless, some surviving oaks located beside canopy gaps did show signs of release, and several commanded dominant positions in the canopy layer from which exclusion by beech in the foreseeable future seemed unlikely.

Amongst the minor trees, only chestnut remained locally prominent on the transect on upper slopes of Elvan Bank, with all trees on the permanent transect in 1988 surviving, most making good growth, and many retaining healthy, medium-large crowns in the canopy layer. Although silver fir was locally prominent on Clam Flat and Elvan Bank and having produced a few very large trees, it was already declining on Clam Flat by 1975, and by 1998 had become scarce in both stands. On the permanent transect the only firs that survived, grew well, and retained healthy crowns were a second-generation pole on Clam Flat and two large trees on the upper slopes of Elvan Bank. Sycamore and larch appeared to have both declined

substantially being reduced on the permanent transect to single, suppressed surviving trees on the upper slopes of Elvan Bank. Holly remained widespread though infrequent, and rowan remained in low numbers on the permanent transect in Fernfires and Clam Flat. The only species to re-establish was birch: on the permanent transect on the east riverbank two young poles, which established in a large canopy gap probably created in the 1980s, made vigorous growth to 1998 despite being part-undercut by the river. Although ash, hawthorn, hazel, sallow and elder were not recorded on the permanent transect, at least ash, hawthorn and hazel survived in other parts of Fernfires Wood.

7.3 Impact of storms

During these thirty years storm-damage increased. Nevertheless, competitive exclusion has remained the main cause of stand change wherever the canopy remained more-or-less closed: here mortality has been concentrated in smaller suppressed trees and basal area growth greatest in larger trees. Initially, during 1967-1975, some large fir and beech on Clam Flat were possibly killed by storms, and very possibly these included the two large windsnapped silver fir snags recorded on the permanent transect in 1988. Storm-damage as recorded in beech stands at the start of the 1980s in the site archive was probably responsible for snapping two large beech just east of the river, bringing down an oak in Fernfires Wood, two oaks on the lower slope of Elvan Bank, and an oak and a pine on the upper slopes of Elvan Bank. During 1989/90 the site archive also recorded and mapped areas of severe winter storm-damage caused by winds up to 130-140km h^{-1} (Figure 1). These included a stand of mainly larch and Scots pine in the north-east of the reserve and several patches in the centre and south where beech and some sweet chestnut grew on floodplain areas or adjacent steep-slopes. Presumably these storms were also responsible for the records of wind-damage on the transect during 1988-98: beside the river a large beech was snapped off and another had one its main forks snapped, around the base of Elvan Bank three large beech and a large oak were snapped/thrown, and on the upper slopes of Elvan Bank a large beech was snapped and a bough broken from a large oak. Falling trees or boughs struck and damaged or toppled several sub-ordinate oak and beech and understorey holly. Only holly and beech showed some resilience to such damage, with two crushed beech and five part-broken holly surviving in 1998.

7.4 Impact of debarking by mammals

Although there are no archive records of when grey squirrel debarking began, by 1998 they had debarked many beech stems, including 28 that had large amounts of bark missing, caused snapping of boughs or trunks on several trees, and left nine vigorous young poles ringed and dead. The worst damage was associated with medium stems <120cm gbh, and especially those that had grown rapidly.

Deer/sheep debarked and reduced understorey holly. Two medium-large holly snags were recorded in 1988 in Fernfires Wood, and during 1988-98 a small holly stem was killed, and one medium stem was ringed and left near-dead, three others were severely debarked, and eight more moderately debarked. Throughout the area holly had a distinct browse line evidently produced by deer.

7.5 Recent regeneration

Despite the maturing of the stands and opening of the canopy during storms, regeneration recorded on the permanent transect was limited, restricted mainly to shade-tolerant species, and predominately of beech. The most successful regeneration developed east of the river in the largest area of well-lit ground that appeared to be the product of storms in the early 1980s. By 1988, several pole and sapling beech and a few downy birch, rowan and silver fir had developed strongly here, and by 1998 fourteen further beech saplings recruited and 33 established beech seedlings were recorded. However, by 1998 debarking by squirrels had compromised the development of this cohort: some of the beech from 1988 and several would be recruits were dead, and the nine largest surviving beech poles were severely damaged or ring-barked.

Other regeneration by 1998 amounted to a few beech, holly, rowan and silver fir recruits and scatter of established holly and beech seedlings. These were also associated with better-lit gaps or gap margins, indicating that the closed canopy conditions across much of the stands had inhibited regeneration. However, grazing by fallow deer, roe deer and sheep was also to blame. In the large gap east of the river they had probably destroyed beech seedlings established in 1988, and also left several beech recruits damaged and many of the established beech seedlings recorded in 1998 browsed down. Deer/sheep also inhibited the general development of holly scrub under closed stands, as evidenced by the differences between the fenced and unfenced seedling plots, the loss of the two strips of low-growing holly regeneration from the permanent transect, and the restriction of holly recruits to protected sites. Rowan saplings were also eaten by deer/sheep and the single fir recruit was left badly frayed by deer.

7.6 Changes in dead wood

Dead wood generally increased, reaching an estimated total volume of 128 m^3 ha^{-1} on the permanent transect in 1998, sub-equally divided between snags and fallen logs. The distribution of snags and fallen logs was highly localised, with, for example, the fallen dead wood volume ranging from 30-49m^3 ha^{-1} at the compartment scale, and from 23-174m^3 ha^{-1} at the transect stand level, depending largely on localised patterns of storm-damage to beech, oak and fir, and the occurrence of slow-decaying excluded oaks.

Dead wood on the permanent transect is 'high' compared to the benchmark level for British broadleaved forests proposed by Kirby *et al* (1998), which require a fallen dead wood volume of >40m^3 ha^{-1}, and a snag density of >50 ha^{-1} with some >40cm dbh. Dead wood volumes in comparable minimum-intervention stands at Lady Park Wood depend mainly on localised drought impact and are quite similar (15-81 m^3 ha^{-1} fallen and 20-42 m^3 ha^{-1} snag) (Green and Peterken 1997), but at Denny Wood where drought and windstorm disturbance has been greater, levels are far higher (201 m^3 ha^{-1} fallen and 92 m^3 ha^{-1} snag) (Mountford *et al* 1999). In centuries-untreated, mixed-aged, acid, beech-oak stands at Fontainebleau, France, Koop & Hilgren (1987) recorded fallen and snag dead wood volumes of 145 and 28 m^3 ha^{-1} respectively.

7.7 General trends

The observed increase in shade-tolerant species is typical in the long-term development of relatively undisturbed temperate forest stands (Oliver 1981, Oliver & Larsen 1996). Beech is widely recognised as the main competitive shade-bearing tree on such soils in north-west Europe, and in untreated stands generally proves the most competitive species (e.g. Pontailler *et al* 1997, Mountford *et al* 1999). The main disturbance has been windstorms, which have predictably increased in impact as the stands have reached old-growth. Despite the free-draining character of the soils and general impact of drought elsewhere in southern Britain the mid-1970s, there is no evidence of a major drought-decline at Dendles (Ling 1991). Development into old-growth has expectedly increased the amount of dead wood, and a continued supply of slow-decaying oak logs in humid conditions for the resident internationally rare blue ground beetle *Carabus intricatus* is assured for the foreseeable future. Regeneration, which has been principally gap-phase beech, is struggling to develop because of grey squirrel debarking, which, as at other sites in southern Britain, has been focused on vigorous-growing, small-medium poles (Mountford 1997, Mountford & Peterken 1999, Mountford *et al* 1999). The expected development of shade-tolerant understorey holly and rowan and advance regeneration beech has not occurred below the maturing stands, principally because of grazing and debarking by deer and sheep. Thus, the observed developments at Dendles have been most akin to those recorded in untreated wood-pasture stands in the New Forest (Mountford *et al* 1999). If gaps continue to expand and mammal damage remains high, it seems there will be few opportunities for successful regeneration, though if this occurred and grazing was curtailed in the several decades time, opportunities for birch and possibly oak and other species light-demanding species would increase.

8. Recommendations for research and monitoring

The southern part of Dendles Wood has provided valuable as a Research Natural Area, providing information on natural stand development that combines with research and monitoring at other minimum intervention woodland reserves (Mountford 2000). Accordingly the following items are recommended:

- Continued monitoring of the permanent transect and seedling plots based on the methods used in this report and given below.
- Continued use of the site archive to record general impacts and changes (e.g. deer, sheep, storms, drought, tree fall, mammal debarking), perhaps including an annual report based on an inspection of the transect, transect markers, and the general area.
- Consideration of the value in repeating the total and sample stand enumerations reported in this study.
- Consideration of further research into the development of beech woodland, perhaps including studies of (1) sites where stratified pollen might have been suitably preserved, (2) the age-pattern of extant trees, and (3) archaeological features, including the location of old pollards, coppice stools, ruined walls, charcoal hearths, etc.
- Consideration of establishment of (1) further permanent transects to increase the area of stands under direct observation, (2) monitoring of ground vegetation along the permanent transect, (3) a set of representative smaller plots where trees, shrubs, dead

wood and ground vegetation can be recorded, (4) larger enclosures including some of the permanent transects to show developments under contrasting grazing regimes, and (5) monitoring/research of associated features (see Mountford (2000) for details).

- The combination of fenced and unfenced plots should be maintained though with some adjustments to the recording methodology are suggested:

a. Check stock-proofing of the enclosures annually.

b. Record seedlings/saplings and take photos of plots every 5-10 years.

c. Count the number of seedlings in three height-classes (<15cm, 15-<50cm, 50-<130cm), and count and take the gbh of all stems attaining 1.3m. Count all stems unless numbers in a plot are high for one species in a particular size-class, then estimate numbers from a representative sample of quadrats.

d. Record canopy condition above and around the plots based on a description and an estimate of the percentage openness.

e. Record changes in ground vegetation based on a description and perhaps several representative quadrats giving percentage cover of each species, leaf litter, exposed mineral soil, etc.

f. Make notes of other salient features.

g. Make precise records of the methodology, archive everything, and write the recording into the management plan.

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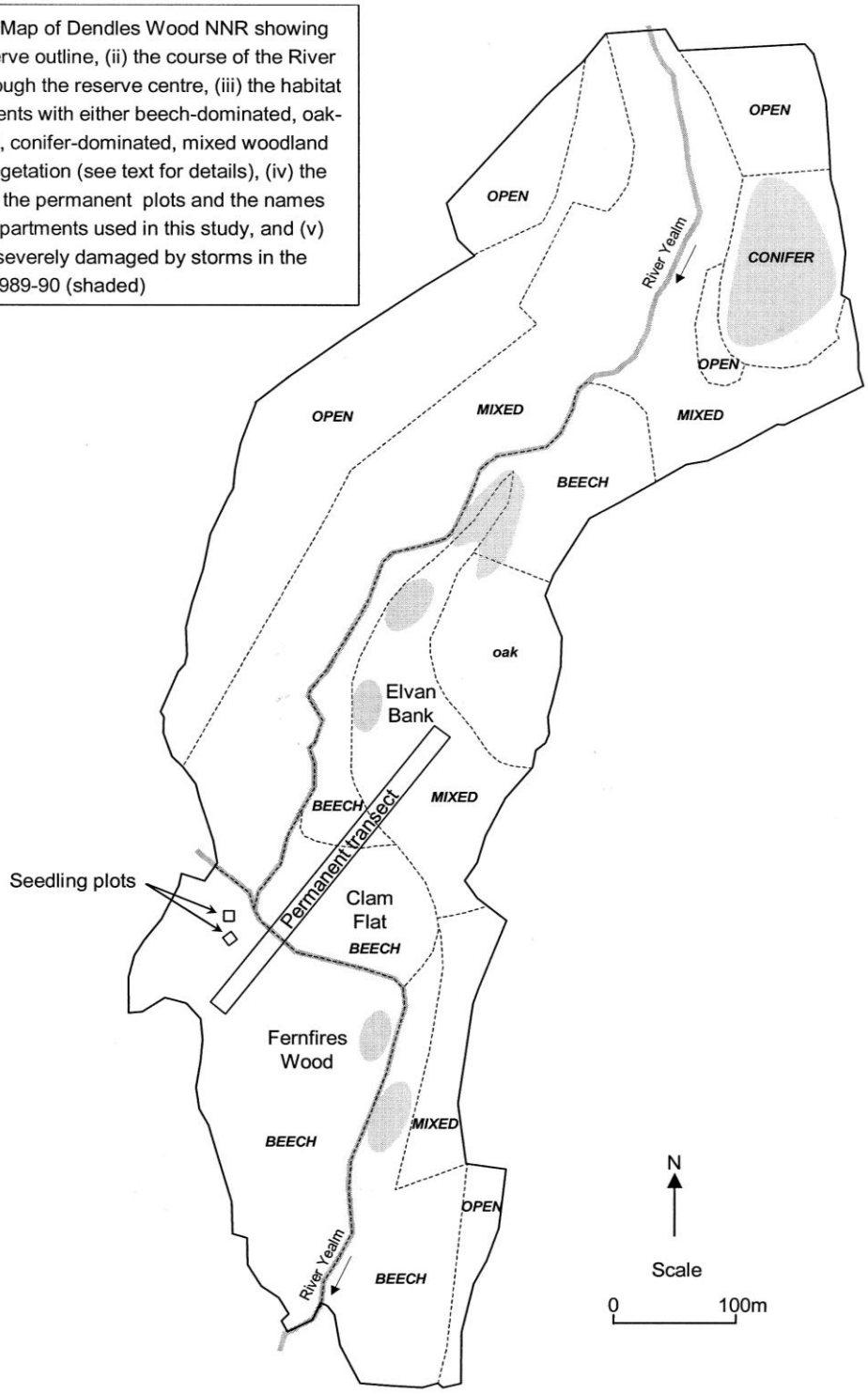
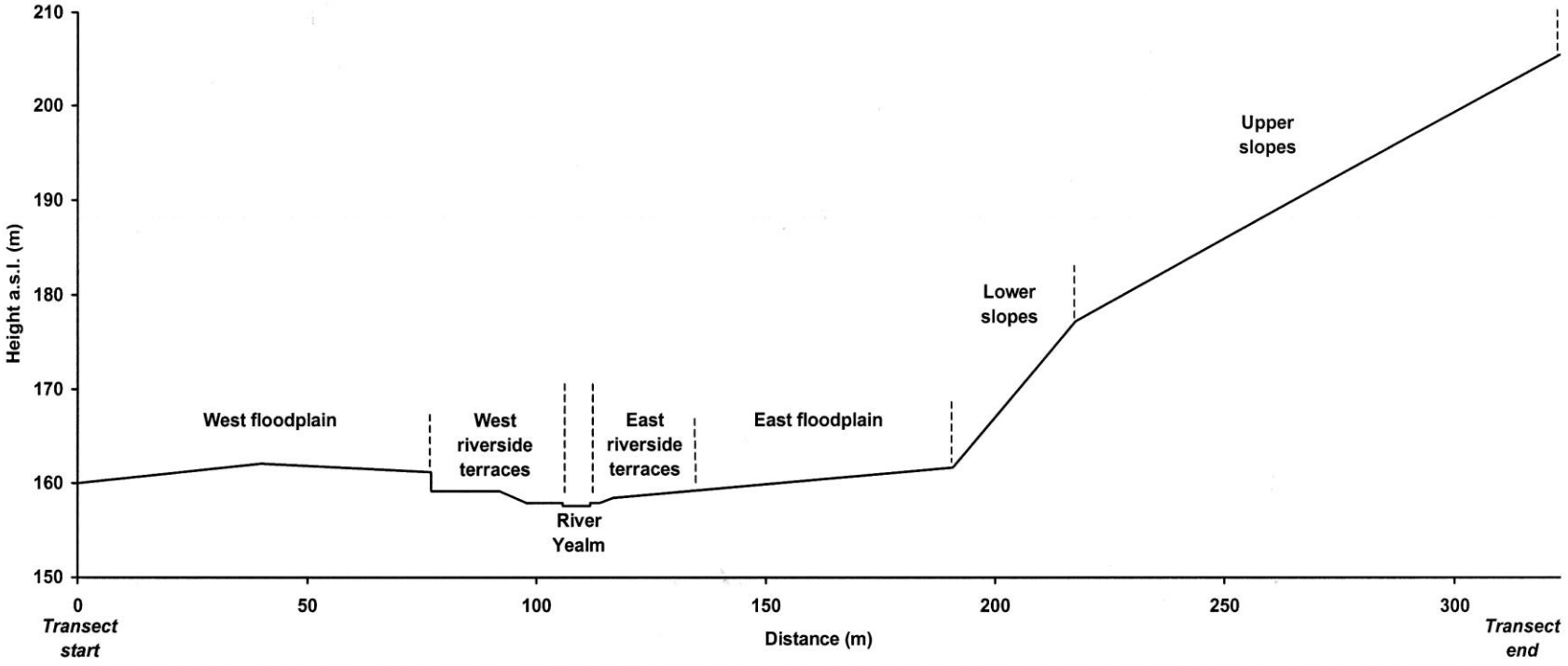
Appendix 1: Figures

Figure 1 Map of Dendles Wood NNR showing (i) the reserve outline, (ii) the course of the River Yealm through the reserve centre, (iii) the habitat compartments with either beech-dominated, oak-dominated, conifer-dominated, mixed woodland or open vegetation (see text for details), (iv) the location of the permanent plots and the names of the compartments used in this study, and (v) the areas severely damaged by storms in the winter of 1989-90 (shaded)





	Fernfires Wood	Clam Flat		Elvan Bank
Stand (NVC type)	Mature beech-oak (W15)	Regener-ating beech (W15)	Mature beech-oak (W15)	Mature beech-oak-chestnut stands (W15/11/10)
Main soils	Well-drained, moderately acid, brown, fine loams and fine silts, with signs of incipient becoming and becoming gritty on riverside terraces; some wall ruins to west and some piles and scattered granite boulders to east; slopes range from 1.5-3° on the floodplains and from level to 12° on the river terraces			Well-drained, moderately acid, brown, silty loam, tending toward humic brown podzol; shallow with rock fragments and some exposed bedrock below; slope 30° below and 15° above

Figure 2 Cross-sectional profile of the 20m x 331m permanent transect in the southern part of Dendles Wood. The location of Fernfires Wood, the River Yealm, Clam Flat, and Elvan Bank are shown along with the different stands and topographical features crossed by the transect. Soil information is based on site assessments and information from the Soil Survey of England and Wales. NB: vertical height is exaggerated approximately two times.

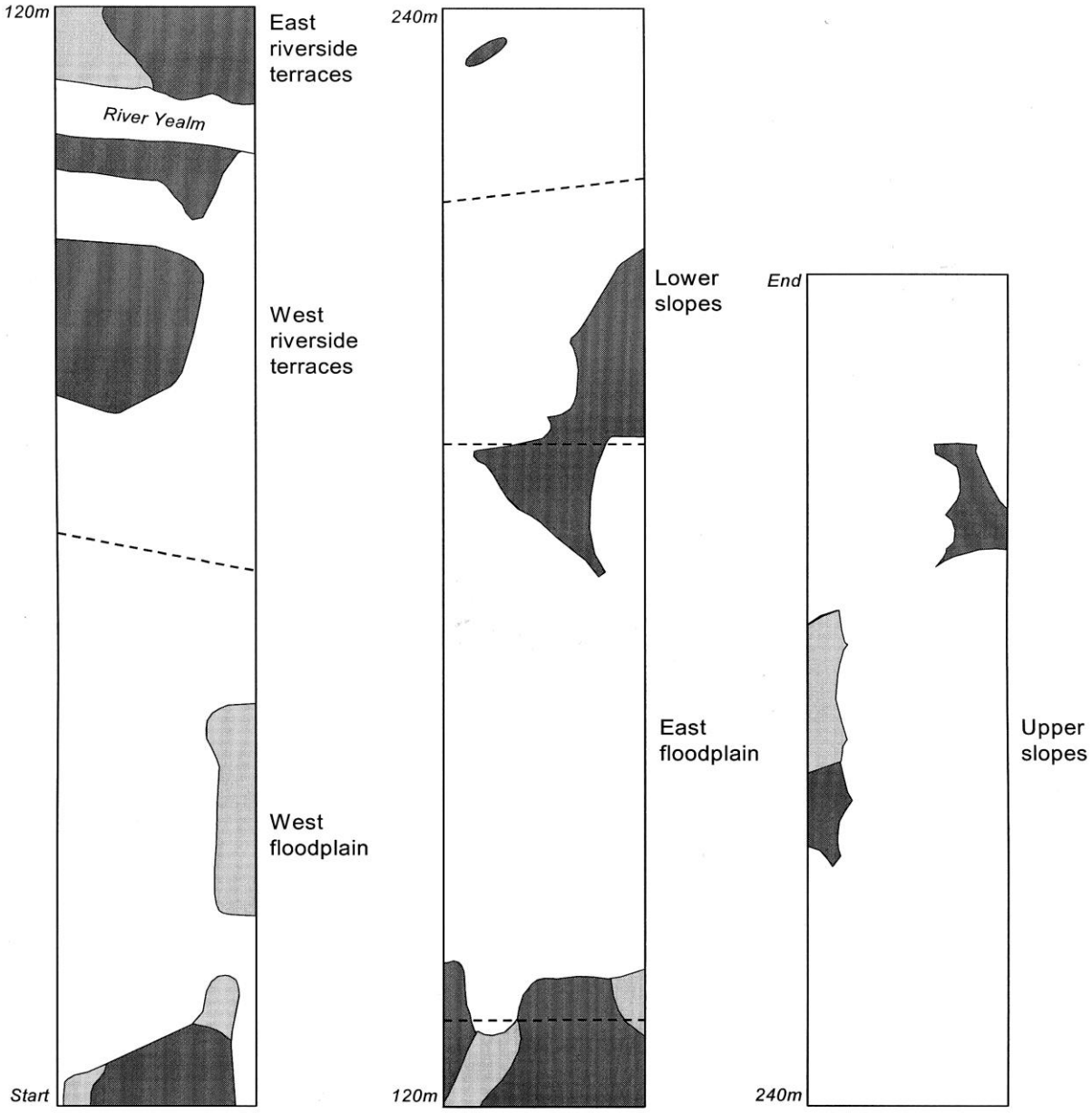


Figure 3 Distribution of gaps in the upper canopy in 1998 along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location). Areas of gaps that were open (heavy shade) are distinguished from those with under-filling (light shade). Also shown are the six distinct stand areas, the distance along the transect, and the River Yealm.

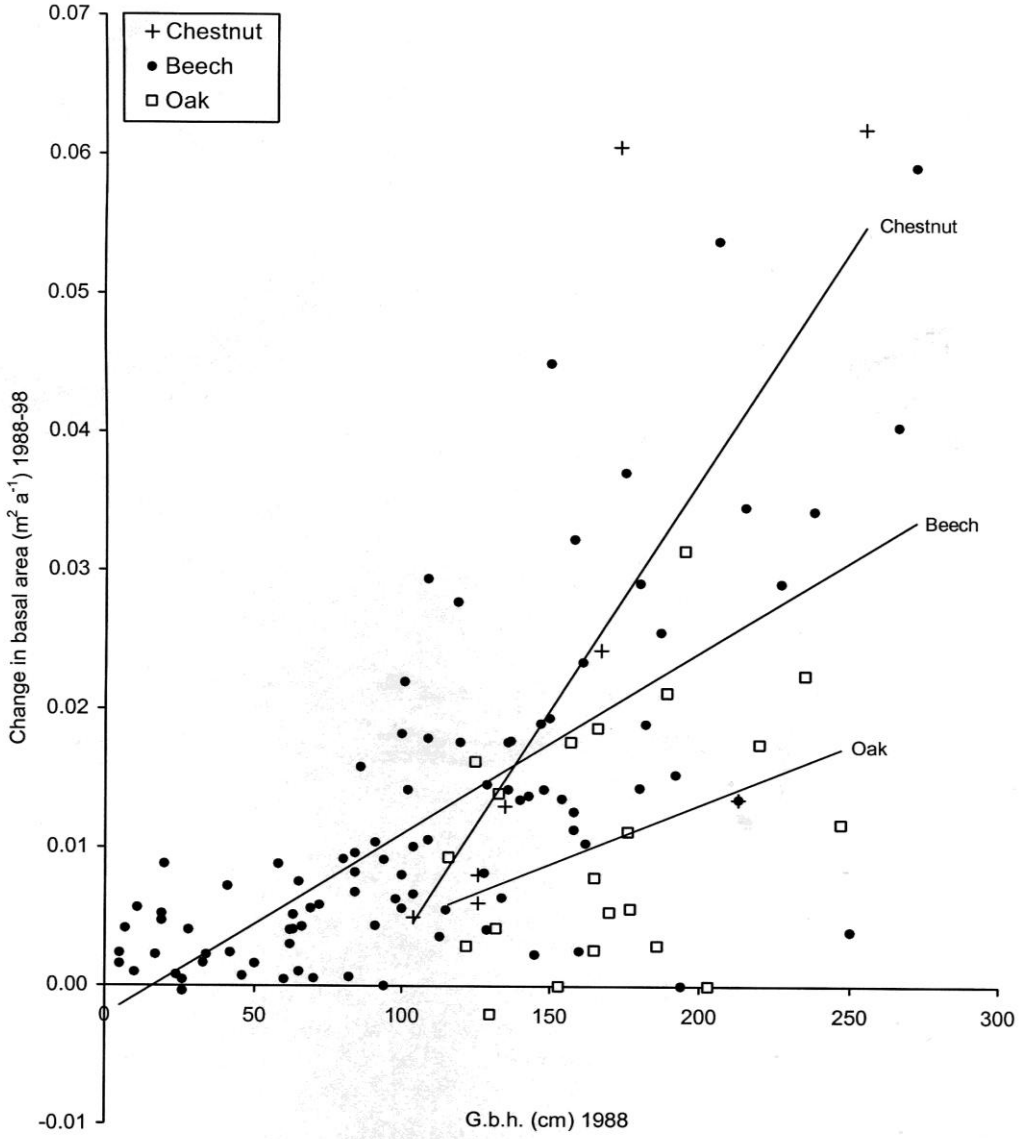


Figure 4 Growth of chestnut, beech and oak stems during 1988-98 in the permanent transect in the southern part of Dendles Wood (see Figure 1 for location). The relationship between initial gbh and change in basal area is shown. The lines represent the best fitting regressions: chestnut, $y = -0.00033x - 0.0300$, $n = 8$, $F = 6.18$, $p = 0.047$, $R^2 = 0.507$; beech, $y = 0.00013x - 0.0021$, $n = 93$, $F = 83.5$, $p \ll 0.0001$, $R^2 = 0.478$; oak, $y = 0.00009x - 0.0041$, $n = 21$, $F = 2.81$, $p = 0.11$, $R^2 = 0.129$. Basal area increase for trees initially >150cm g.b.h. differed significantly (ANOVA $F = 6.76$, $p = 0.003$) with chestnut ($n = 4$, average = $0.0400 m^2 a^{-1}$) and beech ($n = 24$, average = $0.0241 m^2 a^{-1}$) having similar increases (Tukey $q = 2.81$, $p < 0.20$) but both exceeded oak ($n = 15$, average = $0.0117 m^2 a^{-1}$) (Tukey $q_{min} = 3.59$, $p < 0.05$).

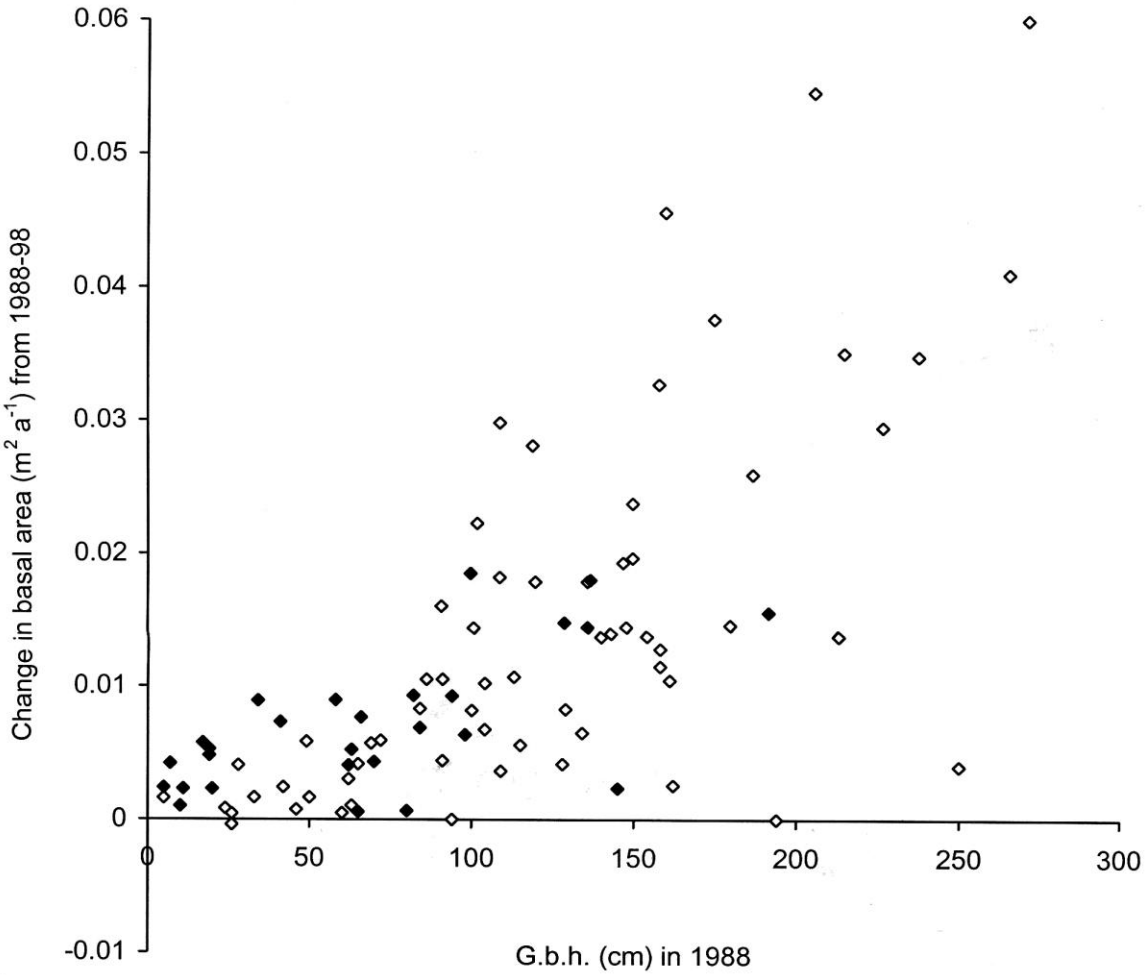


Figure 5 Growth of beech stems in the permanent transect in the southern part of Dendles Wood (see Figure 1 for location) during 1988-98 in relation to debarking by squirrels. The relationship between initial g.b.h. and change in basal area is shown for stems that were severely or very severely debarked by squirrels in 1998 (black diamonds) and those with less or no debarking (white diamonds) (see Methods for details of debarking categories).

Appendix 2: Tables

Table 1 Estimated age of selected trees in Dendles Wood in about 1975 (from unpublished data in site archive). These are based on ring-counts made on single 15-25cm cores and measurements of the mean trunk diameter taken from two opposite sides. Age was estimated by dividing the trunk radius by the average ring width.

Age class (years)	Beech	Oak	Sweet chestnut	Larch	Oak coppice
50-74	-	-	-	-	2
75-99	1	1	3	1	-
100-124	9	1	4	2	2
125-149	4	3	4	2	-
150-174	6	8	3	-	-
175-199	5	6	-	-	-
200-224	-	6	-	-	-
225-249	3	2	-	-	-
250-274	1	1	-	-	-
275-299	1	1	-	-	-
300-384	3	-	-	-	-

Table 2 Age and girth of selected windblown beech trees in Dendles Wood in spring 1991 (Ling 1991). These are based on ring-counts made on single cores and measurements of the trunk girth. Where the core missed early growth rings, age was estimated using the average ring width.

Age (years)	Tree girth (cm)	Location	Comments
92	210	Elvan bank, lower slopes	Core quite close to middle
98	105	South of reserve, lower slopes	Core very close to middle
99	177	Elvan bank, lower slopes	Core quite close to middle
105	184	Centre of reserve, floodplain	Core poor, quite close to middle
118	186	Fernfires Wood, floodplain	Core hit middle
136	190	Centre of reserve, floodplain	Core hit middle
137	266	Fernfires Wood, floodplain	Core very poor, not close to middle
146	224	North of reserve, lower slopes	Core very close to middle

Table 3 Size-class distribution (n ha^{-1}) and basal area (m^2 ha^{-1}) of live stems ≥7.5cm dbh in 1967/8 and 1977 in three compartments in the southern part of Dendles Wood (see Figure 1 for location).

Dbh-class	Fernfires Wood		Clam Flat		Elvan Bank	
(cm)	1968	1977	1967	1977	1968	1977
7.5-12.5	34	31	42	41	28	14
12.5-17.5	35	32	27	18	28	16
17.5-22.5	32	29	22	18	22	20
22.5-27.5	16	17	17	11	22	19
27.5-32.5	22	18	15	14	30	24
32.5-37.5	24	22	10	19	18	18
37.5-42.5	23	23	13	8	15	19
42.5-47.5	22	24	5	9	15	11
47.5-52.5	24	23	8	2	17	16
52.5-57.5	15	21	8	5	16	15
57.5-62.5	10	15	6	8	11	12
62.5-67.5	7	8	3	5	8	12
67.5-72.5	4	7	-	2	7	6
72.5-77.5	3	4	2	4	2	6
77.5-82.5	3	3	<1	4	2	4
82.5-87.5	<1	<1	5	2	-	<1
87.5-92.5	<1	<1	2	2	<1	2
92.5-97.5	<1	<1	2	<1	<1	-
97.5-102.5	-	<1	-	-	-	-
102.5-107.5	<1	-	-	-	<1	-
107.5-112.5	<1	<1	2	<1	<1	-
112.5-117.5	-	<1	-	-	<1	-
117.5-122.5	<1	-	-	-	-	<1
122.5-127.5	<1	-	-	-	-	-
127.5-132.5	-	-	<1	-	-	-
132.5-137.5	-	<1	-	-	-	-
137.5-142.5	-	-	-	-	-	<1
All classes	276	279	188	172	244	214
Basal area	32.8	36.9	21.6	20.2	30.7	33.0

Table 4 Basal area (m^2 ha^{-1}) of live stems ≥7.5cm dbh in 1977 in three compartments in the southern part of Dendles Wood (see Figure 1 for location).

	Fernfires Wood	**Clam Flat**	**Elvan Bank**
Live stems			
Beech	20.8	13.9	17.3
Oak	12.8	4.6	10.1
Sycamore	1.1	-	0.8
Holly	0.9	0.3	0.7
Ash	0.7	0.7	0.1
Chestnut	0.4	-	2.6
Pine	0.2	-	-
Hazel	0.1	0.2	<0.1
Larch	0.1	-	0.9
Fir	<0.1	0.4	0.4
Hawthorn	<0.1	-	<0.1
Rowan	<0.1	<0.1	<0.1
Sallow	-	0.1	-
Elder	-	<0.1	-
All species	36.9	20.2	33.0
Snags			
Oak	1.8	0.1	1.6
Beech	0.1	1.2	0.3
Fir	<0.1	1.7	0.2
Holly	0.2	<0.1	0.1
Hazel	<0.1	-	<0.1
Sycamore	<0.1	-	<0.1
Ash	<0.1	-	-
Chestnut	<0.1	-	-
Birch	<0.1	-	-
Larch	-	-	<0.1
Pine	<0.1	-	-
All species	2.3	3.2	2.1

Table 5 Size-class distribution (n ha^{-1}) of live stems ≥7.5cm dbh in 1977 in three compartments in the southern part of Dendles Wood (see Figure 1 for location).

	Dbh-class (cm)													
	7.5-17.5	**17.5-27.5**	**27.5-37.5**	**37.5-47.5**	**47.5-57.5**	**57.5-67.5**	**67.5-77.5**	**77.5-87.5**	**87.5-97.5**	**97.5-107.5**	**107.5-117.5**	**117.5-127.5**	**127.5-137.5**	**137.5-147.5**
Fernfires Wood														
Beech	27	20	22	25	27	12	6	2	<1	-	<1	-	<1	-
Oak	-	4	11	17	15	10	4	1	-	<1	<1	-	-	-
Sycamore	4	3	3	2	<1	<1	<1	-	-	-	-	-	-	-
Ash	2	3	2	1	<1	<1	-	-	-	-	-	-	-	-
Larch	-	-	<1	<1	-	<1	-	-	-	-	-	-	-	-
Chestnut	<1	<1	1	1	<1	-	-	-	-	-	-	-	-	-
Fir	<1	-	-	<1	-	-	-	-	-	-	-	-	-	-
Pine	-	-	-	<1	<1	-	-	-	-	-	-	-	-	-
Holly	22	15	-	<1	-	-	-	-	-	-	-	-	-	-
Hazel	6	<1	-	-	-	-	-	-	-	-	-	-	-	-
Hawthorn	<1	<1	-	-	-	-	-	-	-	-	-	-	-	-
Rowan	<1	-	-	-	-	-	-	-	-	-	-	-	-	-
Clam Flat														
Beech	20	15	19	8	4	8	5	5	2	-	<1	-		-
Oak	<1	-	7	8	4	5	-	<1	-	-	-	-	-	-
Fir	2	<1	-	-	-	-	<1	-	-	-	-	-	-	-
Ash	4	7	5	-	-	-	-	-	-	-	-	-	-	-
Holly	8	5	<1	-	-	-	-	-	-	-	-	-	-	-
Sallow	2	<1	<1	-	-	-	-	-	-	-	-	-	-	-
Hazel	20	-	-	-	-	-	-	-	-	-	-	-	-	-
Rowan	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Elder	<1	-	-	-	-	-	-	-	-	-	-	-	-	-

Elvan Bank														
Beech	10	13	16	12	16	14	5	3	2	-	-	<1	-	<1
Oak	2	13	14	9	11	5	6	2	-	-	-	-	-	-
Chestnut	<1	1	3	2	3	3	<1	<1	-	-	-	-	-	-
Fir	<1	<1	<1	<1	<1	-	<1	-	-	-	-	-	-	-
Larch	-	-	4	2	<1	<1	-	-	-	-	-	-	-	-
Sycamore	8	3	2	3	-	-	-	-	-	-	-	-	-	-
Ash	-	-	<1	-	-	-	-	-	-	-	-	-	-	-
Holly	4	7	3	1	<1	-	-	-	-	-	-	-	-	-
Rowan	<1	<1	-	-	-	-	-	-	-	-	-	-	-	-
Hawthorn	<1	-	-	-	-	-	-	-	-	-	-	-	-	-
Hazel	4	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 6 Size-class distribution (n ha^{-1}) of snags ≥7.5cm dbh in 1977 in three compartments in the southern part of Dendles Wood (see Figure 1 for location).

	Dbh-class (cm)												
	7.5-17.5	17.5-27.5	27.5-37.5	37.5-47.5	47.5-57.5	57.5-67.5	67.5-77.5	77.5-87.5	87.5-97.5	97.5-107.5	107.5-117.5	117.5-127.5	127.5-137.5
Fernfires Wood													
Oak	<1	4	7	5	1	<1	-	-	-	-	-	-	-
Beech	2	<1	<1	<1	-	-	-	-	-	-	-	-	-
Sycamore	<1	<1	-	-	-	<1	-	-	-	-	-	-	-
Chestnut	-	<1	<1	-	-	-	-	-	-	-	-	-	-
Ash	<1	-	<1	-	-	-	-	-	-	-	-	-	-
Birch	-	-	<1	-	-	-	-	-	-	-	-	-	-
Fir	<1	<1	-	-	-	-	-	-	-	-	-	-	-
Scots pine	-	<1	-	-	-	-	-	-	-	-	-	-	-
Holly	3	1	<1	-	-	-	-	-	-	-	-	-	-
Hazel	<1	-	-	-	-	-	-	-	-	-	-	-	-
Clam Flat													
Beech	2	<1	-	-	-	-	-	-	-	-	-	-	<1
Fir	4	-	-	-	-	-	-	<1	<1	-	<1	-	-
Oak	2	2	<1	-	-	-	-	-	-	-	-	-	-
Holly	2	-	-	-	-	-	-	-	-	-	-	-	-
Elvan Bank													
Oak	5	7	4	2	1	<1	<1	-	-	-	-	-	-
Beech	1	<1	<1	-	-	-	<1	-	-	-	-	-	-
Fir	2	<1	<1	<1	-	-	-	-	-	-	-	-	-
Larch	1	<1	-	-	-	-	-	-	-	-	-	-	-
Sycamore	<1	<1	-	-	-	-	-	-	-	-	-	-	-
Holly	<1	<1	-	-	-	-	-	-	-	-	-	-	-
Hazel	<1	-	-	-	-	-	-	-	-	-	-	-	-

Table 7 Size-class distribution (n ha^{-1}) and basal area (m^2 ha^{-1}) of live stems in 1975 in a sample plot in the southern part of Dendles Wood (see Figure 1 for location).

Gbh-class (cm)	Beech	Oak	Holly
<20	-	-	-
20-39.9	8	-	-
40-59.9	16	-	8
60-79.9	-	-	-
80-99.9	-	8	-
100-119.9	-	33	-
120-139.9	8	8	-
140-159.9	8	-	-
160-179.9	16	-	-
180-199.9	25	16	-
200-219.9	8	-	-
220-239.9	8	-	-
240-259.9	8	-	-
All classes	107	66	8
Basal area	23.9	9.2	0.2

Table 8 Number of live seedlings at four dates between 1976 and 1995 in two nearby $100m^2$ plots in the southern part of Dendles Wood (see Figure 1 for location). Plot A1 was fenced with 1m high netting in 1975 and plot A2 was left unfenced.

Seedlings <15cm height	**Holly**	**Beech**	**Sycamore**	**Ash**
Fenced plot (A1)				
1976	10	-	1	-
1982	52	-	4	-
1988	45	-	-	-
Unfenced plot (A2)				
1976	13	-	1	-
1982	167	4	-	1
1988	177	7	11	-
Seedlings >15cm height	**Holly**	**Beech**	**Sycamore**	**Ash**
Fenced plot (A1)				
1976	56	-	-	-
1982	217	-	-	-
1988	233	-	-	-
1995	592	48	16	-
Unfenced plot (A2)				-
1976	32	-	-	-
1982	66	-	-	-
1988	89	-	-	-
1995	432	-	-	-

Table 9 Basal area (m^2 ha^{-1}) of live stems and snags ≥5cm gbh in 1988 in six stands along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location).

	West floodplain	West riverside terraces	East riverside terraces	East floodplain	Lower slopes	Upper slopes	All stands
Live stems							
Beech	15.88	17.98	3.55	35.97	34.78	25.42	24.17
Oak	15.20	8.53	-	3.04	7.59	16.75	11.21
Chestnut	0.82	-	-	-	-	7.96	2.82
Fir	-	<0.01	0.26	-	-	4.20	1.40
Holly	1.82	<0.01	-	0.30	1.29	0.90	0.91
Larch	-	-	-	-	-	1.18	0.39
Sycamore	-	-	-	-	-	0.12	0.04
Birch	-	-	0.39	-	-	-	0.02
Rowan	-	<0.01	0.07	-	-	-	<0.01
All species	33.72	26.52	4.26	39.31	43.66	56.53	40.97
Snags							
Beech	-	2.36	54.31	-	3.35	0.07	3.58
Fir	-	-	-	11.59	-	1.10	2.58
Oak	4.50	-	-	-	5.87	1.00	1.96
Larch	-	-	-	-	-	0.59	0.20
Pine	-	-	-	-	-	0.56	0.18
Chestnut	-	-	-	-	-	0.41	0.13
Holly	0.49	-	-	0.06	-	0.02	0.13
All species	4.99	2.36	54.31	11.65	9.22	3.75	8.77

Table 10 Density (n ha^{-1}) of live individuals ≥1.3m height and live stems and snags ≥5cm gbh in 1988 in six stands along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location).

	West floodplain	West riverside terraces	East riverside terraces	East floodplain	Lower slopes	Upper slopes	All stands
Live individuals							
Beech	130	69	556	202	146	155	172
Oak	46	52	-	16	33	61	42
Holly	52	17	-	8	49	9	23
Chestnut	7	-	-	-	-	33	12
Fir	-	17	28	-	-	23	11
Rowan	-	34	56	-	-	-	6
Birch	-	-	56	-	-	-	3
Sycamore	-	-	-	-	-	9	3
Larch	-	-	-	-	-	5	2
All species	235	190	694	227	228	296	274
Live stems							
Beech	130	69	389	211	211	178	178
Oak	46	52	-	16	33	61	42
Holly	59	17	-	8	98	19	33
Chestnut	7	-	-	-	-	33	12
Fir	-	17	28	-	-	23	11
Birch	-	-	83	-	-	-	5
Rowan	-	17	28	-	-	-	3
Sycamore	-	-	-	-	-	9	3
Larch	-	-	-	-	-	5	2
All species	241	172	528	235	341	329	288
Snags							
Oak	13	-	-	-	16	33	15
Fir	-	-	-	24	-	19	11
Beech	-	34	56	-	16	5	9
Holly	26	-	-	8	-	5	9
Larch	-	-	-	-	-	19	6
Chestnut	-	-	-	-	-	9	3
Pine	-	-	-	-	-	5	2
All species	39	34	56	32	33	94	56

Table 11 Size-class distribution (n ha^{-1}) of live stems ≥5cm gbh in 1988 in six stands along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location).

	Gbh-class (cm)																	
	<20	**20-39.9**	**40-59.9**	**60-79.9**	**80-99.9**	**100-119.9**	**120-139.9**	**140-159.9**	**160-179.9**	**180-199.9**	**200-219.9**	**220-239.9**	**240-259.9**	**260-279.9**	**280-299.9**	**300-319.9**	**320-339.9**	**340-359.9**
West floodplain																		
Beech	-	7	13	13	13	13	7	26	20	20	-	-	-	-	-	-	-	-
Oak	-	-	-	-	-	-	13	-	13	7	-	7	-	-	-	-	-	7
Chestnut	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-
Holly	7	-	13	39	-	-	-	-	-	-	-	-	-	-	-	-	-	-
West riverside																		
Beech	-	-	-	-	-	-	34	17	-	-	-	-	-	17	-	-	-	-
Oak	-	-	-	-	-	-	17	34	-	-	-	-	-	-	-	-	-	-
Holly	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rowan	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fir	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
East riverside																		
Beech	278	56	-	28	28	-	-	-	-	-	-	-	-	-	-	-	-	-
Birch	28	56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fir	-	28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rowan	28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
East floodplain																		
Beech	-	-	8	24	49	32	8	16	8	16	16	8	8	8	-	-	-	-
Oak	-	-	-	-	-	8	-	-	-	8	-	-	-	-	-	-	-	-
Holly	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lower slopes																		
Beech	-	16	16	16	16	16	33	49	16	-	33	-	-	-	-	-	-	-
Oak	-	-	-	-	-	-	-	16	-	16	-	-	-	-	-	-	-	-
Holly	33	49	-	-	16	-	-	-	-	-	-	-	-	-	-	-	-	-

	Gbh-class (cm)																	
	<20	**20-39.9**	**40-59.9**	**60-79.9**	**80-99.9**	**100-119.9**	**120-139.9**	**140-159.9**	**160-179.9**	**180-199.9**	**200-219.9**	**220-239.9**	**240-259.9**	**260-279.9**	**280-299.9**	**300-319.9**	**320-339.9**	**340-359.9**
Upper slopes																		
Beech	-	28	9	28	19	33	19	5	-	5	9	9	5	5	-	-	-	5
Oak	-	-	-	-	-	5	9	9	19	-	5	9	5	-	-	-	-	-
Chestnut	-	-	-	-	-	9	5	-	9	-	5	-	5	-	-	-	-	-
Fir	-	5	-	9	-	-	-	-	-	-	5	-	5	-	-	-	-	-
Larch	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-
Sycamore	-	5	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holly	5	5	-	-	5	-	5	-	-	-	-	-	-	-	-	-	-	-

Table 12 Change in basal area (m^2 ha^{-1}) of live stems and snags ≥5cm gbh between 1988 and 1998 in six stands along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location).

	West floodplain	**West riverside terraces**	**East riverside terraces**	**East floodplain**	**Lower slopes**	**Upper slopes**	**All stands**
Live stems							
Beech	3.35	-8.77	2.11	-0.91	-8.55	4.42	0.60
Chestnut	0.05	-	-	-	-	0.88	0.30
Fir	-	-0.003	0.46	0.01	-	0.44	0.17
Birch	-	-	1.16	-	-	-	0.06
Holly	0.08	0.03	-	0.02	0.19	0.02	0.05
Rowan	-	0.05	0.26	-	-	-	0.02
Larch	-	-	-	-	-	0.04	0.01
Sycamore	-	-	-	-	-	-0.06	-0.02
Oak	0.95	0.05	-	0.48	-3.06	-1.32	-0.40
All species	4.44	-8.63	3.99	-0.41	-11.42	4.42	0.79
Snags							
Beech	-	9.21	-2.55	-	1.81	-0.01	1.38
Chestnut	-	-	-	-	-	1.01	0.33
Larch	-	-	-	-	-	-0.03	-0.01
Holly	-0.03	-	-	-0.06	-	-0.02	-0.02
Pine	-	-	-	-	-	-0.56	-0.02
Oak	-0.17	-	-	-	-5.87	0.29	-0.50
Fir	-	-	-	-7.37	-	-0.36	-1.53
All species	-0.20	9.22	-2.55	-4.69	-4.06	0.82	-0.37

Table 13 Change in density (n ha^{-1}) of live individuals ≥1.3m height and live stems and snags ≥5cm gbh between 1988 and 1998 for each stand along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location).

	West floodplain	West riverside terraces	East riverside terraces	East floodplain	Lower slopes	Upper slopes	All stands
Live individuals							
Beech	7	86	222	-8	-16	0	19
Holly	7	0	28	0	16	0	5
Birch	-	-	0	-	-	-	0
Chestnut	0	-	-	-	-	0	0
Larch	-	-	-	-	-	0	0
Rowan	-	0	-28	-	-	-	-2
Sycamore	-	-	-	-	-	-5	-2
Oak	0	0	-	0	-16	-5	-3
Fir	-	-17	0	8	-	-9	-3
All species	13	69	222	0	-16	-19	14
Live stems							
Beech	0	-17	583	-8	-33	14	31
Rowan	-	52	0	-	-	-	5
Birch	-	-	0	-	-		0
Chestnut	0	-	-	-	-	0	0
Holly	0	0	-	0	0	0	0
Larch	-	-	-	-	-	0	0
Sycamore	-	-	-	-	-	-5	-2
Oak	0	0	-	0	-16	-5	-3
Fir	-	-17	0	8	-	-9	-3
All species	0	17	583	0	-49	-5	28
Snags							
Beech	-	0	278	8	16	0	19
Chestnut	-	-	-	-	-	0	0
Larch	-	-	-	-	-	0	0
Holly	0	17	-	-8	-	-5	-2
Oak	0	-	-	-	-16	0	-2
Fir	-	-	-	-16	0	-9	-6
All species	0	17	278	-16	0	-9	11

Table 14 Stratification and size of crowns on all live stems recorded in 1998 in six stands along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location). Cells show the number of stems in each category.

Strata:	Canopy				Sub-canopy		Understorey				Ground
Crown size:	Large	Medium	Small	Very small	Medium	Small	Large	Medium	Small	Very small	All
West floodplain											
Beech	4	6	1	2	1	1	1	1	2	-	2
Oak	2	2	2	1	-	-	-	-	-	-	-
Chestnut	-	-	-	1	-	-	-	-	-	-	-
Holly	-	-	-	-	-	-	-	6	2	1	1
West riverside											
Beech	-	2	-	1	-	-	-	-	-	-	6
Oak	-	-	1	1	-	-	-	-	1	-	-
Rowan	-	-	-	-	-	-	-	-	1	3	1
Holly	-	-	-	-	-	-	-	-	1	-	-
East riverside											
Beech	-	-	-	-	1	-	1	6	15	6	11
Birch	-	-	-	-	1	-	-	1	1	-	-
Fir	-	-	-	-	-	-	1	-	-	-	-
Rowan	-	-	-	-	-	-	-	1	-	-	-
Holly	-	-	-	-	-	-	-	-	-	-	1
East floodplain											
Beech	2	5	6	4	2	3	-	2	1	-	-
Oak	-	1	-	-	1	-	-	-	-	-	-
Holly	-	-	-	-	-	-	-	1	-	-	-
Fir	-	-	-	-	-	-	-	-	-	-	1
Lower slopes											
Beech	-	4	4	-	-	-	-	3	-	-	-
Oak	-	-	1	-	-	-	-	-	-	-	-
Holly	-	-	-	-	-	-	-	2	2	1	2
Upper slopes											
Beech [1]	6	4	6	5	1	6	2	2	7	-	1
Oak	-	6	4	-	-	2	-	-	-	-	-
Chestnut	1	3	1	1	-	1	-	-	-	-	-
Fir	2	-	-	-	-	-	-	1	-	-	-
Larch	-	1	-	-	-	-	-	-	-	-	-
Holly	-	-	-	-	-	-	-	2	-	-	2
Sycamore	-	-	-	-	-	-	-	-	1	-	-
All stands											
All species	17	34	26	16	7	13	5	28	34	11	28

[1] a 185cm gbh beech was not recorded

Table 15 Recruitment and mortality of live individuals ≥1.3m height and stems ≥5cm gbh between 1988 and 1998 in six stands along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location).

	Recruits (n)	Stems alive in 1988 (n)	Stems lost by 1998 (n)	Gbh (cm) of individuals lost	Cause of death
West floodplain					
Beech	1	20	-	-	
Holly	1	9	-	-	
Oak	-	7	-	-	
Chestnut	-	1	-	-	
West riverside terraces					
Beech	6	4	1	266	windsnap
Fir	-	1	1	5	hit
Oak	-	3	-	-	
Holly	-	1	-	-	
Rowan	1	1	0	<5, <5	erosion, eaten(?)
East riverside terraces					
Beech	14	12	2	8, 6, <5, <5, <5, <5	squirrel debarking
Birch	-	3	-	-	
Rowan	-	1	-	-	
Fir	-	1	-	-	
Holly	1	0	-	-	
East floodplain					
Beech	-	25	1	207	windsnap
Oak	-	2	-	-	
Holly	-	1	-	-	
Fir	1	0	-	-	
Lower slopes					
Beech	-	13	2	207, 118	windthrow, windsnap
Holly	1	6	-	-	
Oak	-	2	1	155	windthrow
Upper slopes					
Beech	-	41	-	-	
Oak	-	13	1	154	windsnap
Chestnut	-	7	-	-	
Fir	-	5	2	62, 30	exclusion
Holly	-	4	-	-	
Sycamore	-	2	1	44	exclusion
Larch	-	1	-	-	
Total	26	186	12		

Table 16 Density (n ha^{-1}) of established seedlings (≥20cm and <1.3m height) in 1998 in six stands along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location).

	West floodplain	West riverside terraces	East riverside terraces	East floodplain	Lower slopes	Upper slopes	All stands
Holly	384	207	139	-	114	-	129
Beech	111	362	917	16	-	-	113
Fir	-	-	-	-	16	-	2
All species	495	569	1056	16	130	-	243

Table 17 Grey squirrel bark-stripping damage scores to live beech stems in 1998 for the whole permanent transect in the southern part of Dendles Wood (see Figure 1 for location). Stem numbers in various damage-categories and size-classes are shown.

Gbh-class (cm)	Bark-stripping category					Total
	None	Limited	Moderate	Severe	Very severe	
<20	15	8	1	5	1	30
20-39.9	4	1	1	5	3	14
40-59.9	4	0	1	1	0	6
60-79.9	4	2	1	5	1	13
80-99.9	5	3	0	3	0	11
100-119.9	4	5	0	3	0	12
120-139.9	3	2	3	1	0	9
140-159.9	2	3	5	0	0	10
160-179.9	1	2	5	0	0	8
180-199.9	1	1	3	0	0	5
200+	3	7	2	0	0	12
Total	46	34	22	23	5	130

Table 18 Volume (m^3 ha^{-1}) of snags ≥10cm gbh in 1998 for each stand along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location).

	West floodplain	West riverside terraces	East riverside terraces	East floodplain	Lower slopes	Upper slopes	All stands
Beech	-	60.0	425.5	8.2	49.5	0.1	35.4
Oak	66.4	-	-	-	-	8.0	18.4
Fir	-	-	-	16.9	-	6.1	5.2
Larch	-	-	-	-	-	11.6	3.8
Chestnut	-	-	-	-	-	4.6	1.5
Pine	-	-	-	-	-	4.4	1.5
Holly	1.8	-	-	-	-	-	0.4
All species	68.2	60.0	425.5	25.1	49.5	34.9	66.4

Table 19 Volume (m^3 ha^{-1}) and length (m ha^{-1}) of fallen logs ≥1m length and ≥40cm mid-girth in 1998 for each stand along the permanent transect in the southern part of Dendles Wood (see Figures 1 and 2 for location).

	West floodplain	West riverside terraces	East riverside terraces	East floodplain	Lower slopes	Upper slopes	All stands
Volume							
Oak	63.7	18.8	-	18.3	63.3	11.2	30.1
Beech	1.3	155.2	43.5	13.2	31.2	-	22.2
Fir	-	-	-	27.0	-	1.0	5.5
Scots pine	-	-	-	-	-	4.4	1.4
Sweet chestnut	-	-	-	-	-	4.1	1.3
Larch	-	-	-	-	-	2.3	0.8
Holly	1.1	-	-	-	-	-	0.3
All species	66.1	174.0	43.5	58.5	94.5	23.0	61.5
Length							
Oak	807	283	-	144	502	225	367
Beech	52	966	556	213	459	-	215
Fir	-	-	-	317	-	47	76
Scots pine	-	-	-	-	-	99	33
Sweet chestnut	-	-	-	-	-	94	31
Larch	-	-	-	-	-	31	10
Holly	30	-	-	-	-	-	7
All species	889	1248	556	674	961	495	739

Table 20 Estimated volume (m^3 ha^{-1}) and length (m ha^{-1}) of fallen dead wood for three compartments in the southern part of Dendles Wood (see Figure 1 for location).

	Oak	Beech	Chestnut	Larch	Fir	Total
Volume						
Fernfires Wood	18.9	11.4	-	-	-	30.3
Clam Flat	21.2	12.7	-	-	-	33.8
Elvan Bank	7.4	23.1	13.3	3.6	1.1	48.6
Length						
Fernfires Wood	1257	1676	-	-	-	2932
Clam Flat	1571	1990	-	-	-	3560
Elvan Bank	1047	1047	209	314	314	2932