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Preface

English Nature is grateful to Ed Mountford for the opportunity to include this report in its research report series. This should help to ensure that knowledge of the permanent transect at Denny 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

Acknowledgements

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Summary

Changes in the vegetation of Denny Wood, an ancient beech-oak-holly wood-pasture in the New Forest were recorded by means of a permanent transect established in 1959 and recorded last in 1999. In 1959-64, the stand was mostly closed, maturing high forest. Beech and oak dominated the canopy, holly was abundant and expanding in the understorey, and a few tree saplings were present. The canopy altered little, but in the understorey small holly stems, low-growing holly-scrub and minor tree/shrub species were reduced. Deadwood was scarce and only oak provided any larger snags or fallen trunks. Seedlings were numerous and of several species (mostly holly and beech), but these declined also. Ground vegetation mainly remained limited to a scatter of grassland, scrub and woodland species, with a few patches of grass, *Pteridium aquilinum* or (rarely) *Rubus fruticosus* agg.

By 1999 the canopy and understorey had been greatly reduced. Gaps were widespread and the ground vegetation had spread virtually over the whole area, though standing and fallen dead wood and minor trees and shrubs remained limited. Beech and holly had suffered most. Both declined across their size-range and many of their surviving stems had been severely debarked either by grey squirrels (beech) or ponies and/or deer (holly). In contrast, oak survived well and accounted for most of the remaining large, healthy trees. Although recruitment had been rare, it included a few hawthorn saplings that developed in the open, a few birches that developed in protected locations, and the density and species represented by seedlings had risen substantially. The ground vegetation occurred mainly as *Pteridium* dominated stands or *Agrostis* dominated lawns, the latter being rich in associated species. Although *Rubus* had increased, it included only a few moderate-sized clumps. Of the numerous species that increased in occurrence, many were associated with acidic dry grassland, slightly damper conditions, or disturbed ground. Several plants declined, most credible of which were *Ruscus aculeatus, Anthoxanthum odoratum, Carex pilulifera, Euphorbia amygdaloides, Melampyrum pratense* and *Oxalis acetosella*.

These changes were associated mainly with:

1. *Increased grazing by deer and ponies.* This might have accounted partly for the decline in holly and seedlings before 1964. Afterwards it reduced holly and prevented potential regeneration developing.
2. *Direct cutting.* This was at least partly responsible for the decline in holly and minor tree/shrub species during 1959-64, and the same might have occurred afterwards, though it was probably not widespread.
3. *Severe drought in 1976.* This killed or weakened many beech, particularly large, canopy trees. These were judged to be a hazard and in winter 1980/81 were felled, extracted and the brash burnt. Dead wood volumes in 1999 thus remained a fifth of what they might have been. The opening of the stand after the drought facilitated the expansion of the ground vegetation and increase in tree and shrub seedlings. It also freed most mature oaks that had been suffering in competition with beech, and these looked set to develop into massive crowned, long-lived specimens.
4. *Grey squirrels.* They stripped bark from beech and especially medium-sized trees, many of which were damaged severely.
5. *Windstorms.* These uprooted or snapped a few oaks.

Contents

1. Introduction

The New Forest is one of the finest surviving wood-pastures in temperate Europe. It contains over 3,000 hectares of grazed ancient woodland, much of which is dominated by old-growth beech, oak and holly (Tubbs 1968, 1986; Flower 1980; Peterken, Spencer and Field 1999). Regeneration rates in these wood-pastures have fluctuated in response to changing populations of deer, cattle and ponies, and other factors, such as canopy closure (Peterken & Tubbs 1965). During the past two centuries, periodic declines in grazing have allowed many areas to infill and develop into high forest. However, in recent decades deer and pony numbers have once again increased, to the extent that concern has been voiced about the lack of regeneration and general condition of the wood-pastures, many of which are mature and have suffered from drought- and storm-damage (Peterken, Spencer & Field 1999).

Several studies have focused on changes in the vegetation of the New Forest wood-pastures. Historical documents, pollen and soil profiles, and stand characteristics have been used to quantify long-term changes in their general composition (Dimbleby & Gill 1955; Peterken & Tubbs 1965; Tubbs 1968, 1986; Rose & James 1974; Barber 1975; Flower 1980; Koop 1989; Peterken, Spencer & Field 1999). In the late 1980s Morgan (1987a, 1987b) developed a general tree regeneration model for the wood-pastures based on samples of their composition, structure, regeneration characteristics and human activities. Based on a detailed study in Ridley Wood, Morgan (1991) also reported on the possible role that a protective understorey could have on regeneration in these wood-pastures. Putman *et al* (1989) examined vegetation changes over a twenty-two year period in two contrastingly grazed areas in Denny Wood, one of which had large herbivores excluded. Detailed records from a permanent transect in a portion of Denny Wood that was enclosed in 1870 were used by Mountford *et al* (1999) to describe the long-term stand change. This report aims to add to these studies by describing developments over a forty-year period in a part of Denny Wood that has remained open to common grazing.

2. Site details

The study area is in Denny Wood (50^{o} 51.5’ N and 1^{o} 32.5’ W, national grid reference SU 335 058), located in the south-east quarter of the New Forest. The area lies at the edge of a plateau at about 30-40m above sea level. It has gentle mainly 1-2^{o} slopes. The soil (Chadwick 1955, Tremlett 1961) typically includes a shallow humus layer over 3-5cm of sandy, brown, slightly gritty, loam in the upper horizon and 3-5cm of leached, sandy-loam in the middle horizon. Below the subsoil is sticky, gleyed, light yellow-grey-brown clay-marl, with iron-orange mottling and flinty chert. This makes the site prone to water-logging in winter and severe drying in summer. Soil pH ranges from strongly acid (pH 3.5-4.5) under beech where conditions are podsolic, to moderately acid (pH 4.5-5.0) under oak where mull brown earth soil occurs.

The area is an old-growth wood-pasture dominated by beech (*Fagus sylvatica*) and pedunculate oak (*Quercus robur*), growing over an underwood of holly (*Ilex aquifolium*). Minor species include ash (*Fraxinus excelsior)*, birch (*Betula pendula/ pubescens*), hawthorn (*Crataegus monogyna*), crab apple (*Malus sylvestris*), field maple (*Acer campestre*), sycamore (*Acer psuedoplatanus*), and yew (*Taxus baccata*). The ground vegetation has developed strongly and comprises mainly *Agrostis* dominated lawns and stands of *Pteridium aquilinum*. The vegetation conforms most closely to the W14 community of the National Vegetation Classification (Rodwell 1991) and stand type 8D of Peterken (1981).

Mountford *et al* (1999) provide details of the site history. Denny is reasonably typical of ancient wood-pastures in the New Forest. In the 16-18th centuries it was open with both pollard and maiden oak and beech trees and some regeneration. During the 19th and 20th centuries pollarding ceased, gaps were part-filled by natural regeneration, and beech generally increased. Although part of Denny was enclosed in 1870, much remained open to the changing populations of deer, cattle and ponies in the New Forest, including the recent increase in deer and pony numbers. Recent direct management has included the occasional cutting of understorey holly to provide material for Christmas decoration and winter browse for livestock. In addition, two major fellings occurred: (i) a strip of trees was cut to make way for a proposed power-line, and (ii) beech trees debilitated by a severe drought in 1976 were removed for salvage/safety purposes.

3. Recording

The study is based on a permanent 20m-wide transect (Figure 1) established in 1959 and last recorded in 1999. It comprises sixteen contiguous 20m-long sections that formed a near-straight transect covering 0.64ha. The section are numbered from 51-52 (west end) to 66-67 (east end), following on from the numbering system used in a nearby transect in the enclosed part of Denny Wood. The transect was not initially marked by permanent posts, but charts that showed the location, species and size of each individual, allowed it to be precisely relocated in 1999 after a 35 year lapse in recording. The centre line now has permanent markers.

Recording took place on five occasions and was carried out by different recorders (some of which were able to confirm details of the early methodology). The recording dates were:
5-7 July 1959; 6-8 July 1960; 30 June-1 July 1961; 1-2 July 1964; and 11-19 August 1999.

Trees and shrubs were recorded in 1959 and 1964. Their location within the transect was mapped and the diameter of all stems at breast (1.3m) height (dbh) was measured. For small stems the average of the widest and narrowest diameter was taken using callipers. Medium stems were measured in the same way but less precisely, and large stems were measured as girths with string and converted to diameters by assuming the cross-section was circular. Each stem was identified as live standing, live fallen, or dead standing (probably including those alive only at the base). In addition, the extent of low-growing holly scrub was mapped, with some emergent stems ≥1.3m height within large patches of scrub being listed rather than mapped. This scrub generally formed discrete thickets, >30cm and <1.3m height, which were part-browsed by ponies and deer, especially around the periphery. Notes were made for some stems, recording those that had been cut off, were leaning over or were with scrub. Some large fallen dead oak trees were mapped and a diameter given. Most of this information was recorded on charts, with each transect section being recorded on a separate A4 sheet. In 1959, 1960 and 1961 the number of seedlings in each transect section was counted and their age estimated (1, 2, 3, 4, 5, >5 years). At all these recordings notes were made of understorey cutting, and an aerial photograph of the area was taken in the summer of 1970.

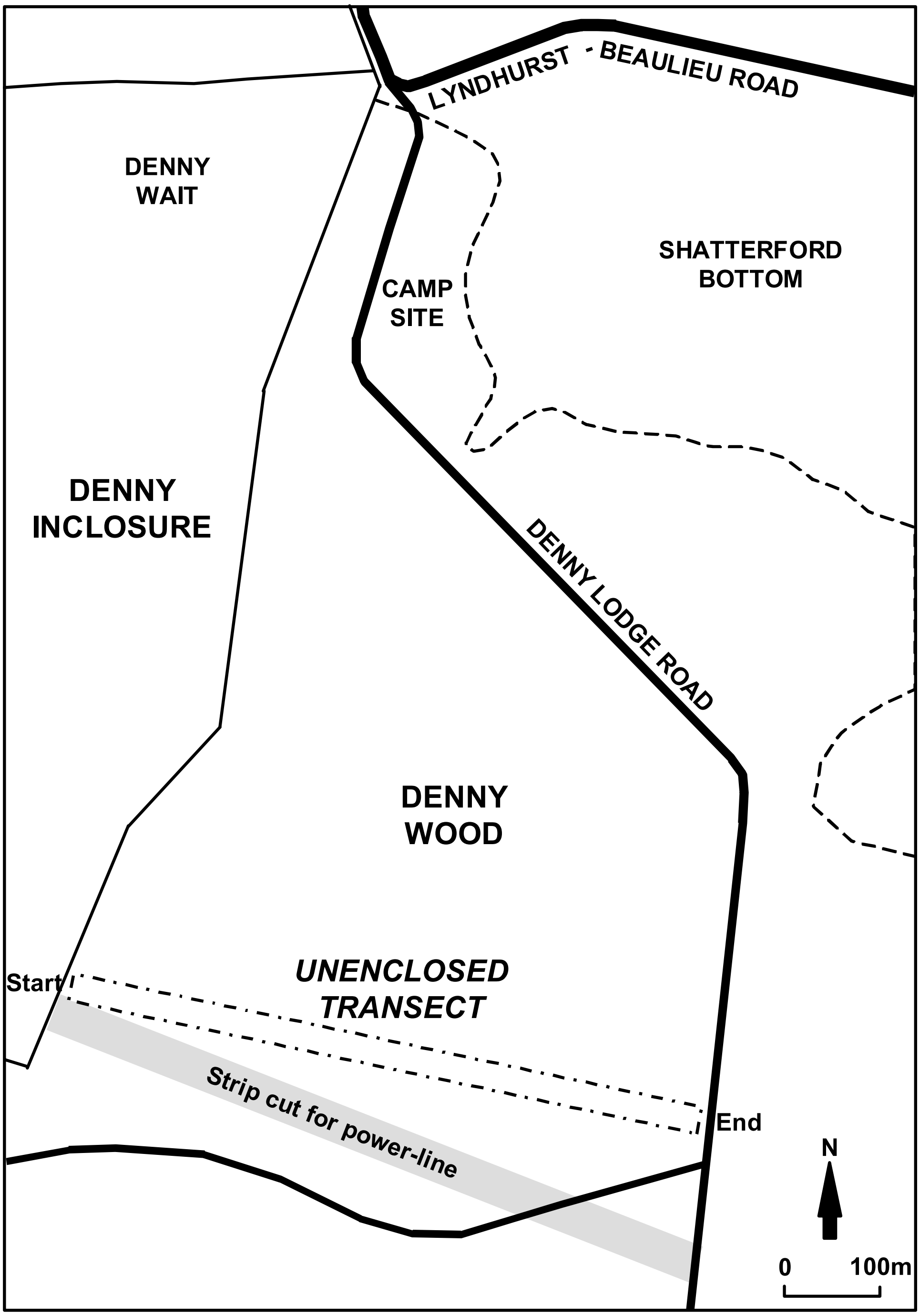

Figure 1 Location map showing the position of the permanent transect within Denny Wood

The clear-felled strip for the proposed power-line through Denny Wood is shown together with metalled roads, livestock fences around the Inclosure, and the approximate limit of woodland (dashed line) around Denny Wood

Trees and shrubs were recorded again in 1999. The remains of stems 'lost' since the 1959/64 recordings were searched for and an assessment made as to the cause of decline. Surviving and recruiting stems were mapped, the g.b.h. of those attaining 1.3m height measured, and each was identified as either live standing, live fallen, alive only at base, or dead standing. In addition, a brief description was made for each stem describing the form, crown condition, damage, debarking, and other salient features. Each was also given a canopy position, crown size and dieback score based on the:

- location of the main part of the crown (*canopy* = in uppermost layer and not overtopped; *sub-canopy* = just below and mostly overtopped by canopy layer; *understorey* = below sub-canopy layer and >2m height; and *ground* = mostly <2m height);
- lateral spread with adjustments made the abundance of foliage and dieback (*very large* = crown spread above 10m diameter; *large* = 6-10m diameter; *medium* = 3-5m diameter; *small* = 2m diameter; *very small* = <1m diameter);
- crown loss due to storms, drought, and debarking (*very severe* = >90% crown loss; *severe* = 60-90% loss; *moderate* = 30-60% loss; *limited* = <30% loss).

Live beech stems were scored for bark-stripping damage by grey squirrels (*Sciurus carolinensis*) 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.

The lower trunk (<2m height) was assessed separately from the upper trunk (>2m height), and the maximum score used to categorise overall damage, ie scores of 1/3, 3/3 and 3/1 were all categorised as severe damage.

Charts were prepared on A3 graph paper showing the location of individuals in each 20m x 20m transect section. On these the following information was mapped:

- low-growing (<1.3m height) holly scrub (generally >20cm and several years old);
- established seedlings (≥40cm and <1.3m height and several years old);
- large fallen dead logs (≥1m length and ≥12.5cm mid-diameter) giving their species, mid-diameter (nearest cm), length (nearest 0.1m), decay state (solid, part-rotten, rotten, very rotten), and amount of bark (percent);
- gaps in the upper canopy layer as viewed by eye from the ground;

- other salient features including layering stems, large stumps, root plates and hollows, and vehicle ruts.

Ground vegetation was recorded during the 1959 and 1960 recordings. For each transect section, a list of graminoid and herb species and an estimate of their percentage cover was made. In 1999, ground vegetation was recorded by visually estimating the percentage cover of *Pteridium* dominated, grass dominated, *Rubus* dominated or unvegetated ground, and by making a list of all herb and graminoid species based on a ten-minute search. In addition, a continuous line of 160, 2m x 2m quadrats, was recorded down the transect mid-line and offset to the north (or if large tree in quadrat to the south). In each of these the percentage cover was estimated separately for:

- all herb and graminoid species (except *Agrostis* grasses which were aggregated);
- mosses as a group;
- sprout growth on trees and shrubs <1.3m tall;
- unvegetated ground covered by leaf litter, mineral soil, horse dung, or dead wood (separated into twigs, branches, trunks, stumps).

In addition, in each of these the number of tree and shrub seedlings (most <50cm and all <1.3m tall) was counted, and notes made on the canopy cover directly overhead and salient features.

4. Analysis

Analysis details and difficulties encountered were the same as given by Mountford *et al* (1999). The main problem was that interpretation was required to track holly stems, especially because the 1964 charts were of poor legibility and precision, and also because separate stems on multi-stemmed individuals were not always drawn separately. In dealing with the latter, it was assumed that the largest stem in the first survey remained as such. In dealing with size anomalies, amendments were made where records were missing or the difference was considered implausible, and by interpolating from the known performance of similar stems located nearby.

Ground vegetation was recorded in each transect section in 1959, 1960 and 1999, even though the approach presented several problems. Tracing all species within the 400m^2 sections in 1959 and 1960 was plausible because ground vegetation was generally sparse, but by 1999 it was extensive and included dense *Pteridium* stands. This meant that some species were probably overlooked and those that had apparently disappeared since 1959-60 were looked for with extra vigilance. In addition, some records appeared misleading; *Agrostis* was always recorded as *A.stolonifera* in 1959 and 1960, but this probably included some *A.capillaris* which was the dominant *Agrostis* in 1999; *Carex, Luzula, Hypericum* and *Galium* species often pose difficulties in identification, especially non-flowering plants in July-August (for example in 1959 and 1960 *Luzula pilosa* appeared to have possibly been confused with *Luzula campestris*); *Cardamine* was always recorded as *C.pratensis* in 1959, and as *C.flexuosa* in 1960; *Festuca* was always recorded as *F.ovina* in 1959 and *F.rubra* in

1960, but in 1999 no *Festuca* was present perhaps because at earlier recordings it had been confused with *Agrostis canina*; traces of vernal species, notably *Anemone nemorosa*, may have disappeared in some plots; *Holcus mollis* was recorded at 45% cover in section 66-67 in 1960, but otherwise occurred only as <5% cover suggesting it had been recorded wrongly or confused with *Agrostis*.

Statistical procedure followed Zar (1984). Differences in average growth rates were tested using single-factor Analysis of Variance (ANOVA), pinpointed by Tukey Honestly Significantly Different tests. The Mann-Whitney U test was used to determine the significance of differences between median species counts. 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, Burslem & Alder (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. Data sorting and statistical calculations were carried out using Microsoft Excel Version 7.0 computer package.

5. Results

5.1 Initial stand condition

In 1959 the stand mainly comprised a scatter of medium-large beech and oak over a dense and developing understorey of holly. The stand was largely closed, save for the first and last sections that were open-canopied and section 63-64 that had an opening on the north side. Basal area was high and stem density moderate-high. Half the basal area was beech, 40% oak, and 9% holly. Most live stems were holly (Tables 1-2).

The largest trees were a beech at 93cm dbh and three oaks at 103-143cm dbh. Except for one twin-stemmed beech individual, all beech and oak grew as single-stemmed trees. Their size-class distributions (Tables 3-4) suggested that both had recruited irregularly in the past, but that only beech had recruited recently and in limited numbers.

The size-class distribution of holly (Table 5) suggested that there had been abundant regeneration over the past few decades, along with a few small (<10cm dbh) hawthorn, birch and ash recruits. Only holly had a large number of multi-stemmed individuals: 53 of the 568 live standing and 10 live fallen individuals were certainly multi-stemmed, ie had two or more live stems ≥1cm dbh, though many individuals grew close to each other forming groups that could have been colonial. There were notes of holly cutting in two transect sections: some stems had been cut off, including some which were sprouting, whilst a few others had been bent flat to the ground and remained alive. Some holly stems and stem groups were surrounded by low-growing holly scrub, and several separate patches of holly scrub occurred elsewhere. Collectively these covered 349.5m^2 or 5% of the transect, most (55 out of 95 patches) were ≤1m^2, and only three large patches covered 30-49m^2. Apart from holly, there were two small patches of low-growing beech, probably derived from root nodules or stump sprouts.

Most snags were small (Table 6), implying that competitive exclusion had been dominant in the development of the stand: all 50 holly snags were <10cm dbh and 39 were <5cm dbh, all four hawthorn snags were ≤10cm dbh, both beech snags were ≤6cm dbh, and 4 out of 8 oak snags were ≤17cm dbh. Similarly, most recorded stumps, which were mainly holly, were small-sized (23 out of 35 were <10cm diameter), and at least some of these survived as low sprouts (12 out of 35) whilst others may have been sprouting but were not recorded as such. Though these stumps may have been the product of competitive exclusion, many could have been the result of active cutting. Only oak provided larger sized pieces of dead wood: four snags were 31-56cm dbh, two stumps were 20 and 70cm diameter, and a large windblown tree was 90cm diameter.

5.2 Changes in the stand from 1959 to 1964

5.3 General changes

By 1964 the stand had increased further in stature. Basal area was 14% up on 1959 and at its highest level, whilst the density of live standing stems ≥5cm dbh remained virtually unchanged.

5.3.1 Changes in beech and oak

In the overstorey, medium-large beech and oak remained dominant and the canopy largely closed. Only two oak and six beech individuals had died (Table 7), of which only the oaks and two beeches were ≥20cm dbh in 1959. Three of these at 20-39cm dbh died standing and were probably excluded. A large fire lit during cutting of the understorey might have damaged the largest beech at 71cm dbh that also died standing. The four smallest beech <10cm dbh could have been cut. Most survivors (51 out of 56 beech and 21 out of 23 oak) that had reliable size measurements increased in dbh and consequently the size-class distributions of both generally shifted upwards, and four beeches and five oaks grew to ≥100cm dbh (Tables 3-4).

5.3.2 Changes in holly and other species

In contrast, changes in the understorey appeared more substantial, although the 1964 records for holly were of poor legibility and precision and often needed interpretation. Nevertheless, mortality was clearly high: 197 holly individuals were lost, birch was reduced to a single surviving 10cm dbh sapling, and hawthorn and ash both died out (Table 7). The large 71% decline in small stems <5cm dbh was mainly due to losses in understorey holly (Tables 2 and 5), with 44 out of 368 holly stems sized ≥5cm dbh and 188 out of 311 holly stems <5cm dbh being lost.

Holly scrub also declined substantially. The area covered fell by 54% from 1959 to 161.5m^2 (3% of the transect area), and more patches (56 out of 82) were ≤1m^2. The main changes were the reduction of most surviving patches amounting to a 63% loss of the area present in 1959, including the reduction of 2 out of 3 largest patches ≥30m^2 to just 4-5m^2 and the largest from $49m^2$ to $31m^2$, and the complete loss of 48% of patches present in 1959. Some new small scrub patches did arise, principally where standing live stems had been reduced, and 7 new holly individuals and 13 new holly stems recruited, mostly developing from scrub patches or on live individuals recorded in 1959.

The reduction in holly coincided with notes made in 1961 that recorded cutting of holly in 8 transect sections: these suffered both high losses of small-sized holly stems (5 out of 7 sections with highest mortality rates) and of holly individuals (3 out of 4 sections with highest mortality rates). Cutting may also have been involved in the loss of holly scrub and the small beech, hawthorn and birch stems, whilst the small ash sapling was certainly cut.

Growth and consequent size-class changes in holly were limited: only 265 out of 373 surviving holly stems with reliable dbh measurements showed an increase in size, albeit that this partly reflected the imprecision with which holly was recorded.

5.3.3 Changes in snags

The basal area of snags increased (Table 6), mainly because all larger oak snags of 14-56cm dbh survived and two new 22-33cm dbh oak snags and two new 36-64cm dbh beech snags recruited. Small snags <5cm dbh dropped to a low level because 36 out of 39 of such holly snags disappeared and only one new one formed, despite the mortality of 172 such small holly stems during 1959-64. This suggested that such small dead stems were not thoroughly recorded in 1964, although some were probably cut down.

5.4 Changes in the stand from 1964 to 1999

5.4.1 General changes

Major changes occurred during 1964-99. A large area of beech dominated canopy broke-up and much of the holly understorey was destroyed. Basal area dropped dramatically by over 50% and the density of live standing stems ≥5cm dbh fell by almost 70%. Losses were greatest in beech and holly, which respectively decreased in basal area by 79% and 53% and in density by 53% and 73%. Corresponding losses in oak were only 18-20%. In 1999 canopy gaps covered 64% of the transect.

5.4.2 Changes in beech and oak

Mortality in beech amounted to 47 stems and 46 individuals, which produced a near five-fold increase in the mortality rate (Table 7). Losses included both small and large sized stems, with no beech >75cm dbh in 1999 surviving, and all size-classes except 20-29.9cm dbh having decreased in number (Table 3). The largest losses appeared to have died or deteriorated following a severe drought in 1976. Widespread drought-damage to large beech is known to have occurred in the vicinity triggered by this exceptional drought (Manners & Edwards 1986; Mountford *et al* 1999), and an aerial photograph from the summer of 1970 confirmed that the stand was essentially intact before this event. In 1999, much of area beyond the transect was open and in places where medium-large beech had not been salvaged, groves of snags stood.

Felling of presumed drought victims occurred in winter 1980/81, as a safety measure because at the north end of Denny Wood a camp site had been established. This operation may have provided an opportunity to fell relatively healthy trees and/or those that had been badly damaged by grey squirrel debarking (see below). Tractors extracted felled trees and some ground was left rutted. Photographs of felled trees lying on the ground in January 1981 suggested that at least some trees were alive when cut, though their crown condition could not be determined because the lop and top had been piled up and burnt. Within the transect in 1999, stump felling notches and/or fallen cut off trunks were found on 21 beech sized 34-100cm in 1964, including 2 on the edge of a clear-felled strip that was made for a power line to Denny Lodge (which was never installed, due to local protests). There were no or few remains of 19 trees, including 8 ≥40cm dbh that potentially suffered the same fate.

Three beech trees sized 56-83cm dbh might have died due to drought, but were not cut and cleared and appeared to have been wind-snapped perhaps in severe storms in 1987 or 1990. Two losses sized 27-38 cm dbh were probably killed when a 100cm dbh oak was windthrown: these were located 1-2m away and an adjacent 14cm dbh beech that survived was left tipped over at 25 degrees from the ground. Two smaller stems at 4-11cm dbh that remained as a short snag and snapped fallen trunk, had been severely debarked by squirrels before death. Squirrels may also have finished off some of the 11 trees sized 4-26 cm dbh that left no trace or few remains: these were within the most vulnerable size-range for attack by squirrels (see below), though they were probably under most competitive stress and could have been destroyed by deer and/or pony debarking whose numbers increased substantially during this period.

Only six oaks died during 1964, which represented a slight decline on the 1959-64 mortality rate (Table 7). These included three trees sized 100-150 cm dbh in 1964, which were windthrown or windsnapped probably soon after 1964 and then mostly cut off and cleared away. Also a 71cm dbh tree in 1964, which died standing, was apparently snapped at 8m up, perhaps during severe storms in either 1987 or 1990, following a period of suppression by beeches up to 1976. The other two losses included a 56cm dbh tree that was probably excluded pre-1976 by adjacent beeches, and a 12cm dbh tree that probably suffered a similar fate. Though this resulted in a decline in numbers in the smallest and largest size-classes of oak, there was little change in numbers across the mid-size range, and in 1999 four oaks achieved 100cm dbh (Table 4).

For surviving standing beech and oak that had reliable size measurements in 1964 and 1999, diameter and basal area increment rates were highly variable even amongst similar sized stems. The polynomial regression gave the best fit for both relationships, indicating that highest growth rates occurred in some mid-sized stems, though some of the relationships were marginally significant (diameter increase, beech $y = -0.0002x^2 + 0.0128x + 0.1413$, $F = 1.91$, $p = 0.18$, $R^2 = 0.193$; oak $y = -0.0002x^2 + 0.0191x + 0.0266$, $F = 2.6$, $p = 0.11$, $R^2 = 0.274$; basal area increase, beech $y = -0.000002x^2 + 0.0002x - 0.0007$, $F = 2.80$, $p = 0.09$, $R^2 = 0.259$; oak $y = -0.000002x^2 + 0.0002x - 0.0008$, $F = 0.96$, $p = 0.41$, $R^2 = 0.120$). Average growth increment rates were slightly higher in oak (diameter = 0.301 v 0.268cm a^{-1}, basal area = 0.00245 v 0.00160cm^2 a^{-1}), but the differences were not significant ($F_{diameter} = 0.16$, $p = 0.69$, $F_{basal\ area} = 1.56$, $p = 0.22$).

Slightly more oak than beech (n = 23 v 21) survived in 1999 (Table 3) and most were larger and healthier trees. Only oak included large trees >80cm dbh, and 18 retained healthy, released, medium or larger crowns in the canopy, compared to eight beech. 14 canopy oak retained numerous vigorous trunk sprouts following release, compared to four beech. A single small leaning oak was in the understorey, compared to ten beech, including two that had been tipped when a large oak was windblown and five that had been reduced to the understorey by squirrel debarking. In fact, grey squirrels had debarked all beech, either by removing bark from the upper trunk and crown branches and/or from the lower trunk including the root buttresses, but no oak. Nine beech had been severely debarked or ringed and had early crown yellowing and/or a dead top. The worst damage was associated with stems sized 20-30cm dbh, though three other stems at 11, 34 and 51cm g.b.h. were also severely debarked (Table 8). Of the 11 (out of 21) surviving beeches in the canopy layer, seven had moderate or severe crown dieback mainly in response to squirrel debarking. Debarking by squirrels was not mentioned in the 1959 and 1964 records, and the damage observed in 1999 was mostly of old scars probably at least a decade old.

5.4.3 Changes in holly

Changes in the understorey included the loss of many hollies, and although the mortality rate declined, it was still highest amongst the main species (Table 7). Overall, 310 holly individuals were lost, 276 of which died completely and 34 were reduced to low-growth. In terms of stem loss, out of 463 live holly stems present in 1964, 321 were killed, including all fallen stems, and 49 were reduced to low-growth, leaving just 93 survivors. Stem loss was associated with small-sized stems <10cm dbh in 1964: 262 out of 308 <10cm dbh were killed/reduced compared to 108 out of 155 ≥10cm dbh ($\chi^2 = 15.2$, $p<0.001$). The decline in holly stems was the main cause of the further decline in small stems <5cm dbh and most of the large decline in stems ≥5cm dbh (Tables 2 and 5).

The area covered by holly scrub (including only coherent patches of low-growth attaining 20cm diameter), had fallen to just 2.1m^2 (0.03% of the transect area), and included 18 patches of up to 0.3m^2. Four of these were the remains of scrub patches present in 1964, three were scrubby sprouts around the base of reduced stems, nine were sprout patches from layered stems, and two growing on a root plate face or beside a fallen oak log.

Despite these losses, 57 holly stems recruited, 36 of which were side forks or low trunk shoots that developed on stems present in 1964, and 13 of which were new sprouts/forks that developed from two tipped hollies located beside windblown oak trees, which were cut off after falling and then vigorously reshot. Only four of the stems represented new holly individuals.

The decline in holly corresponded to a forest-wide increase in deer and ponies. 35 out of 36 lost stems that remained as snags or fallen trunks had been severely debarked by deer/ponies, as had many surviving stems (Table 9). All scrub fragments and basal sprouts around surviving stems and on those reduced to low-growth were browsed down. Also, the reduction in holly scrub was obviously due to browsing. Although it is not know if holly cutting as recorded in 1959 and 1961 occurred post-1964, and some stems were possibly cut/crushed in the salvage fellings in winter 1980/81, only 16 out of 104 residual holly stumps in 1999 appeared to have been cut off.

Growth of surviving standing holly with reliable size measurements in 1964 and 1999 was highly variable with no significant regression between initial size and increment, and the average rates were moderate (diameter = 0.116cm a^{-1}, basal area = 0.00021cm^2 a^{-1}). By 1999 all smaller stem size-classes had declined substantially, though a few large stems remained present.

Of the 150 holly stems recorded in 1999 most were <20cm dbh (Table 5). Those >5cm dbh were mainly understorey stems with medium (37 out of 99) or small (52 out of 99) crowns. Smaller stems were mainly low forks or trunk shoots with most in the ground layer with very small crowns (33 out of 51). Ponies and/or deer had debarked 75% of holly stems, including all ≥10cm dbh (Table 9). The most severe damage was associated with stems ≥10cm dbh, and 20 out of 27 ≥20cm dbh had been severely debarked or ringed.

5.4.4 Changes in other species

The birch sapling present in 1964 died by 1999, but 3 new birch and 5 hawthorn saplings recruited. All the new birches were located in protected locations and looked unlikely to grow into canopy trees; one was a poor sapling growing in humus collected in old fork hollow 1.5m up an oak, and the others were leaning saplings growing together on top of a windblown oak trunk and were becoming increasingly checked by trunk sprouts on a nearby beech tree. The five hawthorn saplings grew on the margins of either *Pteridium* or *Rubus* clumps, all having being part-browsed but having grown to 1.3-2.3m high by 1999.

5.4.5 Changes in snags

Snag basal area increased despite density changing little (Table 6), and in 1999 snag volume was 15.6m^3 ha^{-1}. Oak basal area remained highest, though 5 out of 7 snags present in 1964 had toppled, leaving two at 43-45cm dbh which were recorded as snags in 1959, and a recruit at 80cm dbh which died after being windsnapped possibly in 1987 or 1990. Basal area of beech increased, though only two large 50-80cm dbh snags were present. Holly basal area increased, with ten sized 10-21cm dbh recruiting, all the product of trunk debarking by ponies and/or deer. Despite the potential creation of many holly and beech snags since 1964, relatively few remained standing in 1999, partly because of the salvage operations in 1980/81 and other exogenic events (eg during the 1999 fieldwork three holly snags at 11-18cm and an oak at 45cm and beech at 80cm dbh were either broken off or smashed by campers).

5.4.6 Changes in fallen dead wood

Three fallen dead trees were sketched on the 1959 charts: two 34-90cm diameter oaks and a 14cm diameter holly. At least the large oak had been removed by July 1960. On the 1964 charts only a few oak branches were sketched.

The volume and length of large fallen dead logs increased by 1999 and was estimated at 26m^3 ha^{-1} and 394m ha^{-1} (Table 10). Beech and oak accounted for most of the material, with beech more abundant, with more logs ≥30cm mid-diameter, but with more material with abundant decay. The largest log by far was a 2.3m long, 1m mid-diameter, little-decayed oak trunk, which originated from a windsnapped tree that probably fell soon after 1964. The beech logs included some recently snapped trees and branches lost because of squirrel debarking and/or wind-snapping, but a few were from trees left during the salvage felling in 1980/81. Many of the oak were excluded trunk boughs, whilst a few were from windsnapped and/or excluded trees. Most material from large windblown oaks had been cleared.

5.5 Changes in tree and shrub seedlings from 1959-61 to 1999

Seedling counts made along the transect in 1959, 1960 and 1961 (Table 11) showed that the total seedling density dropped from 15,500 to 10,002 ha^{-1}. This trend was followed in most sections, and the same applied to seedlings five or more years old. Overall, holly seedlings steadily declined but remained abundant (range = 7044-9742 ha^{-1}), beech seedlings fluctuated but remained frequent (2403-5392 ha^{-1}), oak seedlings declined and remained mostly scarce (59-123 ha^{-1}), and maple and hawthorn seedlings remained rare. Only on the flushed soils centred on section 61-62 were ash seedlings frequent. Five-year old seedlings remained common only within the holly population, where they were most abundant in 1960. Only a few old beech, oak and ash seedlings occurred, the large number of older beech in section 65-66 in 1961 being inexplicable.

Seedling counts made in 1999 were recorded by a continuous set of 2m x 2m quadrats taken down the transect mid-line (Table 12). Total seedling density was about 2-3 times higher than in 1959-61. Compared to 1959-61, holly remained most numerous, the total density was about 3-4 times higher, beech was less abundant and ranked below both oak and ash, which were both more abundant though ash remained concentrated in section 61-62, hawthorn remained scarce, and maple was not recorded. In addition, a scatter of birch, willow, crab apple, rose, rowan and yew were recorded. Apart from in ash, the density patterns recorded in 1959-61 were not repeated in 1999.

Holly was widespread occurring in 103 out of 160 quadrats, including 50 where 10 or more holly seedlings were present. Holly seedling occurrence was associated with quadrats with 50% or more *Pteridium* cover (χ^2 = 11.9, p<0.001), though some occurred in grass dominated quadrats and high densities (≥10 holly seedlings per quadrat) were associated with at least quarter-shaded quadrats (χ^2 = 17.2, p<<0.001). Oak occurred in 45 quadrats, mostly either mainly open (29) or at least quarter-shaded by mature oak trees (14), and with the ground cover ranging from *Pteridium* dominated (28) to grass dominated (12). Beech seedlings were very localised, occurring mostly in at least quarter-shaded quadrats where *Pteridium* was abundant. Ash seedlings occurred mainly (75 out of 83) in seven continuous sections through a flushed, slight valley area. Here, a few young ash trees just outside the transect provide a seed source. Most grew where the canopy was more-or-less open and *Pteridium* cover was >50% and 1-1.5m tall, though the highest densities were in three open quadrats where protective *Rubus* grew with the *Pteridium*. Birch seedlings occurred in 19 quadrats. Most were at the start of the transect where the canopy was mainly open and the ground cover ranged from grass to *Pteridium* dominated. All 12 willow seedlings were in open areas predominately covered with grass.

5.6 Initial ground vegetation condition

Ground vegetation was recorded in each transect section in 1959 and 1960 (Table 14). Despite some problems in interpreting the inherited data (see Analysis Section), the records clearly showed that ground vegetation was generally limited, with *Hedera helix, Rubus fruticosus* agg., *Pteridium aquilinium, Oxalis acetosella, Agrostis* spp., and *Carex pilulifera* the most widespread species, consistent with the generally closed conditions. Only four sections had any notable cover, principally of *Agrostis* and/or *Pteridium*. *Rubus* was the only other species to make 5% cover in any one section (assuming the 45% record in section 66-67 for *Holcus mollis* to be an error), and only section 66-67, which was described as having hardly any tree canopy, had consistently high cover values. Differences between the two recordings were limited. *Agrostis* increased considerably in the first section and also possibly the last section (assuming the *Holcus mollis* to be *Agrostis canina*), with section 51-52 also being described as having good exposure to sunlight. Only one record (*Dryopteris carthusiana* in section 62-63) suggested a localised extinction, the others (*Carex sylvatica, Festuca ovina* and *Cardamine* pratensis) are probably explained by identification errors. Thirty-one records suggested localised recruitment of many species, though ten of these could be explained by identification errors, and others could have been due to inattention or over-sight in 1959.

5.7 Changes in ground vegetation from 1959-60 to 1999

The ground vegetation changed greatly by 1999 (Tables 14 and 15). Below the now open-canopy conditions, *Pteridium* dominated stands and *Agrostis* dominated lawns covered around 52% and 43% of the ground respectively. These species now occurred in every transect section, along with *Hedera helix* and *Rubus fruticosus* agg., though only *Rubus* had increased in total cover and now included a few moderate-sized clumps.

Many other species had increased in occurrence, including 29 that had spread into between 5-15 new sections. Many of these were associated with acidic dry grassland (eg *Danthonia decumbens, Galium saxatile, Potentilla erecta, Rumex acetosella, Veronica officinalis*) or slightly damper conditions (eg *Juncus* spp., *Hydrocotyle vulgaris, Ranunculus flammula, Scutellaria minor*). The remaining few were ruderals mainly associated with disturbed ground along open tracks, etc (eg *Digitalis purpurea, Plantago major, Poa annua, Rumex sanguineus, Sagina procumbens*). Many of the 36 species that had moderate gains in occurrence and many of the 47 newly recorded species were associated with the same habitats. Otherwise, ferns increased with *Dryopteris carthusiana* showing a large increase in occurrence and *Athyrium filix-femina, Blechnum spicant, Oreopteris limbosperma* recruiting.

Four species showed large declines in occurrence of between 5-7 sections, five by 3-4 sections, and eight others that occurred in 1-2 sections in 1959/60 could not be re-found. Identification errors in 1959/60, oversight in 1999, or other difficulties (see Analysis Section) could explain some of the losses and slight declines. The most credible declines were for

Ruscus aculeatus and *Anthoxanthum odoratum* (declined by 6 sections), and *Carex pilulifera, Euphorbia amygdaloides, Melampyrum pratense* and *Oxalis acetosella* (declined by 3-4 sections).

The most abundant species along the continuous line of 160 smaller quadrats recorded in 1999 were *Pteridium aquilinium* (50%) and *Agrostis* species (39%), mainly *Agrostis capillaris* (Table 16). Most of the quadrats were well-lit (51 were open, 12 near-open, 16 quarter shaded, 11 half shaded, and 11 three-quarters shaded). Less abundant at 2-5% cover were mosses, which were common, *Rubus fruticosus* agg., which was frequent and included some dense patches, and dead wood, which was most often represented by small twigs. In a few places dead trunks, *Galium saxatile* and bare ground made 10-30% of the cover, and other frequent species were *Hedera helix, Potentilla erecta, Oxalis acetosella, Juncus effusus, Ranunculus repens, Carex ovalis, Galium saxatile, Agrostis stolonifera, Holcus mollis* and *Digitalis purpurea*, in addition to pony dung.

The composition of *Pteridium* dominated quadrats (*Pteridium* ≥60% cover) (80 quadrats) and *Agrostis* dominated quadrats (Agrostis ≥60% cover and *Pteridium* <60% cover) (54 quadrats) was compared (Table 17). *Agrostis* dominated quadrats were significantly more species rich and had more species associated with them. In addition, they had six species that were confined to and occurred in three or more quadrats (*Ajuga reptans, Cardamine flexuosa, C.pratensis, Lysimachia nemorum, Poa annua, Sagina procumbens*), compared to three in *Pteridium* dominated quadrats (*Melampyrum pratense, Molinia caerulea, Rosa arvensis/canina*). Ten species were associated with *Agrostis* dominated quadrats (*Carex ovalis, Danthonia decumbens, Juncus bulbosa, Juncus effusus, Luzula campestre, Prunella vulgaris, Veronica chamaedrys, Potentilla erecta, Galium saxatile, Ranunculus repens*), compared to two with *Pteridium* dominated quadrats (*Rubus fruticosus* agg., *Holcus mollis*).

6. Cause of changes

Initially grazing was moderate, but during the 1960s deer and pony numbers increased greatly and remained high. This may have accounted partly for the decline in holly, minor tree/shrub species, and seedling abundance during 1959-64. However, direct cutting was at least partly responsible for this, and a fire associated with the cutting may have killed a canopy beech. Cutting might have occurred afterwards, though there was no evidence to suggest it had been widespread.

After 1964 grazing certainly reduced holly, with both developed stems and low-growing scrub suffering from browsing and debarking. Grazers also prevented potential regeneration from developing. Despite the opening of the stand and increase in seedlings, only a few hawthorns with well developed spines and birches on the tops of trees grew to above 1.3m. Otherwise, a few seedlings have made some vertical growth on the edges of protective clumps of *Pteridium* and *Rubus,* but have been grazed back once they grew further.

Although there has been suggestions that holly, *Rubus, Rosa,* and fallen branches can afforded sufficient protection against grazers in such situations (Morgan 1987a, 1987b, 1991), this has not occurred on the transect. Rather, such prickly plants have retreated in the face of heavy browsing. Much the same has occurred in the Denny Inclosure (Mountford *et al* 1999), and also in a plot lower down in Denny Wood (Putman *et al* 1989) where livestock but not fallow deer were excluded from 1969 to 1985, and no trees established and the shrub layer of holly, hawthorn, *Ulex europeaus, Rosa* and *Rubus*, but not *Pteridium*, almost disappeared. Should grazing be reduced in Denny, it is likely that a mixture of trees and shrubs would regenerate naturally, though the well-established ground vegetation would be a strong competitor. Opportunities to recruit vigorous seedlings growing in *Rubus* clumps using small-scale exclosures is more certain and would avoid the unattractive and even-aged character of larger exclosures.

The most significant impact on the stand was the severe drought in 1976. Apparently, this killed or weakened many beech and particularly those that were large canopy trees. The same occurred widely across southern Britain, particularly on shallow, free-draining or stagno-gley soils: some mature beech were killed immediately, others were so badly damaged that a slow terminal decline ensued, and many survivors were left with poor crowns and grew little for several years afterwards (Lonsdale *et al* 1989; Stribley 1993; Power 1994; Peterken & Mountford 1996). At Denny, the drought-damaged trees were judged to be a hazard, particularly to the public using the campsite at Denny Wait about 700m to the north, and in winter 1980/81 were felled. Although no record was made of the transect around this time, and the felling provided an opportunity to remove trees that were relatively healthy, otherwise damaged (eg by grey squirrel debarking), or sub-lethally affected by the drought, there was little doubt that the drought impacted strongly on the stand and that many of original canopy beeches were already dead or in terminal decline. In addition to felling existing and potential-snags, the felling operation included extracting most useable timber and firewood and burning the brash. Thus, dead wood volumes that potentially would have amounted to over $200m^3\ ha^{-1}$ (Mountford *et al* 1999), measured only $42m^3\ ha^{-1}$ in 1999.

Beech suffered from grey squirrel bark-stripping, which most likely became significant during the 1970/80s. Many medium-sized beech were deformed and some died as a result. Mature trees were damaged less, though crown branches were snapped and large wounds created at the base and higher up. Debarking was probably facilitated by the drought because it opened the stand and released medium-girth beech poles into vigorous growth, making them even more vulnerable to attack (Mountford 1997; Mountford and Peterken 1999). The scale of damage observed in Denny is not untypical of the New Forest (and elsewhere): although medium-sized trees might persist as informal pollards, it is apparent that development of replacement canopy beech is being severely compromised on a wide-scale.

Oak did not suffer significantly from the drought, grey squirrel debarking or salvage felling, though a few large trees were uprooted or snapped during windstorms before and soon after 1964. It was suffering in competition with beech, but after the stands opened many mature oak trees were freed and responded by sprouting and/or putting out new crown growth. These looked set to develop into massive crowned, long-lived specimens.

The opening of the stand after 1976 flooded the ground with light and facilitated the expansion of the ground vegetation and increase in tree and shrub seedlings. By this time grazing was high, such that close-cropped, species-rich lawns spread and ruderal species developed onto poached ground. Nevertheless, grazers caused the decline of several palatable and sensitive plants, notably *Ruscus aculeatus,* which also survived only as hard-browsed plants in the nearby Denny Inclosure (Mountford *et al* 1999). Heavy grazing did not prevent the widespread development of dense *Pteridium* stands. These expanded vigorously and reduced the extent of species-rich lawn areas, though apparently they did provide some protection for grazing-sensitive species, including *Melampyrum pratense, Molinia caerulea, Rubus, Holcus mollis,* and *Rosa arvensis/canina*.

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Appendix: Tables

Table 1 Basal area (m^2 ha^{-1}) of live standing and fallen stems ≥5cm dbh in the unenclosed transect in 1959, 1964 and 1999

	1959	1964	1999
Beech	21.3	24.4	5.2
Oak	16.9	19.2	15.8
Holly	4.0	4.5	2.1
Birch	<0.1	<0.1	-
Hawthorn	<0.1	-	-
Ash	<0.1	-	-
Total	42.2	48.2	23.2

Table 2 Density of live stems (n ha^{-1}) in the unenclosed transect in 1959, 1964 and 1999

	Density live standing stems ≥5cm dbh			Density live standing stems <5cm dbh			Density live fallen stems		
	1959	1964	1999	1959	1964	1999	1959	1964	1999
Holly	563	572	153	484	142	77	19	9	5
Beech	105	103	33	11	5	-	-	-	-
Oak	48	45	36	-	-	-	-	-	-
Hawthorn	2	-	-	3	-	9	-	-	-
Birch	2	2	-	2	-	5	-	-	-
Ash	2	-	-	-	-	-	-	-	-
Total	720	722	222	500	147	91	19	9	5

Table 3 Size-class distribution (dbh cm) of live beech stems in the unenclosed transect in 1959, 1964 and 1999

	1959	1964	1999
<10	16	7	-
10-19.9	8	13	2
20-29.9	7	4	7
30-39.9	10	5	2
40-49.9	7	10	1
50-59.9	4	5	4
60-69.9	8	5	3
70-79.9	6	8	2
80-89.9	7	7	-
90-99.9	1	-	-
100-109.9	-	3	-
110-119.9	-	-	-
120-129.9	-	1	-
130-139.9	-	-	-

Table 4 Size-class distribution (dbh cm) of live oak stems in the unenclosed transect in 1959, 1964 and 1999

	1959	1964	1999
<10	-	-	-
10-19.9	2	2	1
20-29.9	7	3	-
30-39.9	4	3	4
40-49.9	1	3	-
50-59.9	1	1	4
60-69.9	3	1	1
70-79.9	3	4	4
80-89.9	7	4	3
90-99.9	-	3	2
100-109.9	2	4	3
110-119.9	-	-	1
120-129.9	-	-	-
130-139.9	-	-	-
140-149.9	1	-	-
150-159.9	-	1	-
160-169.9	-	-	-

Table 5 Size-class distribution (dbh cm) of live holly stems (standing and fallen) in the unenclosed transect in 1959, 1964 and 1999

	1959	1964	1999
<5	311	91	50
5-9.9	240	217	28
10-14.9	107	113	45
15-19.9	20	40	22
20-24.9	1	2	4
25-29.9	-	-	1
30-34.9	-	-	-

Table 6 Basal area (m^2 ha^{-1}) and density (n ha^{-1}) of snags in the unenclosed transect in 1959, 1964 and 1999

	Basal area snags ≥5cm dbh			Density snags ≥5cm dbh			Density snags <5cm dbh		
	1959	**1964**	**1999**	**1959**	**1964**	**1999**	**1959**	**1964**	**1999**
Holly	0.1	0.1	0.3	17	16	20	61	5	8
Oak	1.0	1.3	1.3	13	11	5	0	0	0
Hawthorn	<0.1	-	-	5	0	0	2	2	0
Beech	<0.1	0.7	1.1	2	3	3	2	0	0
Total	1.1	2.0	2.7	36	30	28	64	6	8

Table 7 Number, mortality and recruitment of live individuals in the unenclosed transect from 1959 to 1964 and 1964 to 1999. Holly numbers include both standing and fallen live individuals

	Oak	**Beech**	**Holly**	**Birch**	**Hawthorn**	**Ash**
Number of live individuals						
1959	31	73	576	2	3	1
1964	29	67	388	1	0	0
1999	23	21	82	3	5	0
Mortality						
1959-64 number died	2	6	195	1	3	1
1964-99 number died	6	46	310	1	0	0
1959-64 mortality rate (m % a^{-1})	1.3	1.7	7.9	12.9	100	100
1964-99 mortality rate (m % a^{-1})	0.7	3.3	4.5	100	-	-
1959-99 half-life rate (years)	93	22	14	-	-	-
Recruitment						
1959-64 number recruited	-	-	7	-	-	-
1964-99 number recruited	-	-	4	3	5	-

Table 8 Grey squirrel debarking damage to all surviving beech stems in the unenclosed transect in 1999. Comparing stems with none, limited and moderate damage against stems with severe and very severe damage, the latter was associated with the 20-29.9cm dbh size-class compared to all other classes combined ($\chi^2 = 7.9$, $p<0.01$)

	Maximum damage					
Dbh class (cm)	**None**	**Limited**	**Moderate**	**Severe**	**Very severe**	**Totals**
10-19.9	0	1	0	1	0	2
20-29.9	0	0	1	5	1	7
30-39.9	0	0	1	0	1	2
40-49.9	0	1	0	0	0	1
50-59.9	0	0	3	1	0	4
60-69.9	0	3	0	0	0	3
70-79.9	0	2	0	0	0	2
Totals	0	7	5	7	2	21

Table 9 Trunk debarking damage to all surviving holly stems in the unenclosed transect in 1999. Comparing stems with none, limited and moderate damage against stems with severe and very severe damage, the latter was most strongly associated with size-classes ≥10cm dbh compared to all other size-classes combined ($\chi^2 = 23.2$, $p<<0.001$)

Dbh class (cm)	None	Limited	Moderate	Severe	Very severe	Totals
<5	35	4	6	6	0	51
5-9.9	3	6	11	7	0	27
10-14.9	0	9	17	16	3	45
15-19.9	0	3	4	13	2	22
20+	0	0	0	4	1	5
Totals	38	22	38	46	6	150

Table 10 Volume (m^3 ha^{-1}), length (m ha^{-1}), size distribution and condition of fallen dead logs attaining 1m length and 12.5cm mid-diameter in the unenclosed transect in 1999

	Beech	Oak	Holly	Total
Volume	15.4	9.8	0.8	26.0
Length	183.0	172.2	38.9	394.1
Number logs ≥30cm mid-diameter	14	5	0	19
Number logs <30cm mid-diameter	25	26	10	71
% volume limited decay	83	100	100	90
% volume abundant decay	17	0	0	10

Table 11 Tree and shrub seedling counts for each 20m x 20m (0.04ha) section of the unenclosed transect in 1959, 1960 and 1961. Numbers of seedlings five or more years old are shown in brackets

Section	Holly			Beech			Oak			Ash			Maple			Hawthorn		
	1959	1960	1961	1959	1960	1961	1959	1960	1961	1959	1960	1961	1959	1960	1961	1959	1960	1961
51-52	215 (7)	232 (15)	293 (2)	123	48 (3)	88 (4)	7	3	4 (1)	-	-	-	-	-	-	-	-	-
52-53	217 (17)	299 (32)	534 (3)	86	68	294 (1)	1	-	2	-	-	-	-	-	-	-	-	-
53-54	326 (13)	303 (16)	285 (1)	131 (1)	63 (1)	130 (2)	1	1	1	-	-	-	-	-	-	-	-	-
54-55	543 (12)	317 (14)	331 (2)	63	28	102 (1)	-	-	1	-	-	-	-	-	-	-	-	-
55-56	272 (10)	228 (16)	266	76	38	92 (4)	-	2	-	-	-	-	-	-	-	-	-	-
56-57	320 (52)	248 (60)	151 (42)	272 (1)	122 (1)	205 (2)	4	5	4	-	-	-	-	-	-	-	1	-
57-58	380 (30)	271 (28)	172 (6)	289	130 (2)	77	-	3	-	-	-	-	-	-	1	-	-	-
58-59	549 (38)	387 (na)	456 (2)	215 (1)	76 (na)	105 (1)	2	3	2	-	-	-	-	-	-	-	1	-
59-60	783 (33)	428 (47)	304 (6)	165	86	89	1	1	4	-	-	-	-	-	-	-	1	-
60-61	839 (27)	471 (31)	412 (1)	73	43	44	3	2	-	15	9	6	2	-	6	1	2	-
61-62	498 (16)	357 (25)	312 (2)	105	50	72	-	-	2	120 (18)	175 (24)	96 (2)	-	-	1	-	-	-
62-63	285 (12)	254 (16)	105	299 (1)	155 (3)	187	4	1	-	16 (1)	23	9	-	-	-	-	-	-
63-64	282 (29)	242 (18)	192 (5)	337	132 (1)	178 (2)	1	1	-	-	-	1	-	-	-	-	-	-
64-65	437 (9)	340 (24)	314 (3)	315	137	219 (3)	-	2	1	-	-	2	-	1	-	-	-	-
65-66	186 (17)	155 (35)	186 (3)	775	248	433 (105)	8	-	3 (2)	-	-	1	1	-	-	-	-	-
66-67	105 (2)	64 (3)	195 (2)	127 (1)	114 (1)	71 (6)	47	30 (1)	15	-	-	-	-	-	-	-	-	-
Total	6235	4596	4508	3451	1538	2386	79	54	38	151	207	115	3	1	8	1	5	-
Density ha^{-1}	9742	7181	7044	5392	2403	3728	123	84	59	236	323	180	5	2	12	2	8	-

Table 12 Tree and shrub seedling counts along the unenclosed transect in 1999. Based on a continuous line of one hundred and sixty 2m x 2m quadrats (number per section = 10 = 0.004ha) taken along the transect mid-line

Section	Holly	Oak	Ash	Birch	Beech	Will-ow	Crab apple	Haw-thorn	Rose	Row-an	Yew	All
51-52	206	3	0	2	5	0	0	0	0	0	0	216
52-53	19	3	0	8	0	4	6	0	0	0	0	40
53-54	359	3	0	5	0	0	1	0	0	0	0	368
54-55	178	22	0	0	0	0	0	0	0	1	1	202
55-56	47	0	0	1	0	0	0	0	1	0	0	49
56-57	326	5	0	1	8	0	0	1	1	0	0	342
57-58	37	6	0	1	0	2	0	0	0	0	0	46
58-59	132	25	0	2	1	6	0	0	0	0	0	166
59-60	28	2	1	2	0	0	0	2	0	0	0	35
60-61	4	5	1	0	0	0	0	0	0	0	0	10
61-62	47	14	69	0	0	0	0	3	0	0	0	133
62-63	11	2	10	0	0	0	0	1	0	0	0	24
63-64	82	6	2	1	3	0	0	0	0	0	0	94
64-65	25	2	0	0	0	0	0	0	0	0	0	27
65-66	68	0	0	4	0	0	1	0	0	0	0	73
66-67	193	2	0	0	3	0	0	0	0	0	0	198
Total	1762	100	83	27	20	12	8	7	2	1	1	2023
Density (ha^{-1})	27531	1563	1297	422	313	188	125	109	31	16	16	31609
Occurrence (% quadrats)	64	28	8	12	7	5	2	4	1	1	1	72

Table 13 Number of tree and shrub seedlings ≥40cm height in the unenclosed transect in 1999

	Height class (cm)				
	40-59	60-79	80-99	100-129	Total
Oak	2	2	1	1	6
Hawthorn	2	2	1	-	5
Willow	1	2	-	-	3
Birch	2	-	-	-	2
Beech	2	-	-	-	2
Ash	-	-	1	1	2
Crab apple	1	-	-	-	1
Total	10	6	3	2	21

Table 14 Summary of ground vegetation (graminoids and herbs) records for each 20m x 20m (0.04ha) section of the unenclosed transect in 1959 (left), 1960 (centre) and 1999 (right). Percentage cover was recorded in 1959 and 1960, whereas in 1999 the cover of the three main communities was recorded and a list made of all other species present. (+) = <5% cover

	Section															
	51-52	**52-53**	**53-54**	**54-55**	**55-56**	**56-57**	**57-58**	**58-59**	**59-60**	**60-61**	**61-62**	**62-63**	**63-64**	**64-65**	**65-66**	**66-67**
Abundant species in 1959/60 and main communities in 1999																
Agrostis spp./*Agrostis* dominated grassland	+ 30 30	+ + 55	+ + 35	+ + 35	+ + 35	20 20 25	+ 5 25	+ 60	70	70	+ + 60	10 10 50	+ + 30	+ + 25	30 + 55	50 30 20
Pteridium aquilinium/ Pteridium dominated stands	+ + 60	+ + 45	+ + 65	+ + 65	5 5 65	20 20 75	+ + 75	+ 30	+ + 10	+ + 25	+ + 40	35	+ + 65	+ + 70	+ + 40	30 15 70
Rubus fruticosus agg./*Rubus* dominated stands	+ + +	+ + +	+ + +	+ + +	+ + +	5 + +	+ + +	+ + 5	+ + 20	+ + +	+ + +	+ + 5	+ + 5	+ + 5	+ + +	+ + +
Graminoid species recorded in 1959/60 and 1999																
Anthoxanthum odoratum	+ +	+ +	+ +	+ +	+ +	+ + +		+				+			+	+ + +
Carex pilulifera	+ + +	+ +	+ + +	+ + +	+ + +	+ +	+ +	+ +		+	+ +	+ + +		+ + +	+ + +	+ +
Dactylis glomerata			+ +	+	+	+ +	+ +									+ +
Holcus mollis	+ + +	+	+	+	+	+	+ + +	+	+	+	+	+	+	+	+ + +	+ 45 +
Juncus effuses	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+ + +	+
Graminoid species recorded only in 1959/60																
Carex sylvatica								+ +							+	
Festuca ovina	+	+			+											
Festuca rubra	+	+			+							+	+		+	+
Luzula pilosa	+ +				+ +	+	+ +									+ +
Poa trivialis											+ +					
Graminoid species recorded only in 1999																
Carex demissa		+	+		+										+	
Carex flacca															+	
Carex nigra								+								
Carex ovalis	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+
Carex panicea	+		+													
Carex remota			+	+								+				
Danthonia decumbens	+	+	+	+	+	+	+	+	+	+	+					
Deschampsia cespitosa										+						
Deschampsia flexuosa			+		+											
Juncus acutiflorus			+	+			+	+				+		+	+	

	Section															
	51-52	52-53	53-54	54-55	55-56	56-57	57-58	58-59	59-60	60-61	61-62	62-63	63-64	64-65	65-66	66-67
Juncus articulatus								+	+							
Juncus bulbosa	+	+	+		+		+	+	+		+			+	+	
Juncus squarrosus		+														
Luzula campestris	+	+	+	+	+		+		+	+					+	
Molinia caerulea	+		+		+											
Poa annua						+			+	+	+		+	+	+	+
Herb species recorded in 1959/60 and 1999																
Ajuga reptans			+							+	+ + +	+ + +			+ +	+
Cardamine flexuosa											+	+	+	+	+	
Cardamine pratensis		+							+		+		+	+	+	+
Circaea lutetiana											+ +				+	+
Digitalis purpurea		+	+	+	+	+	+	+	+	+	+ + +	+	+	+	+	+
Euphorbia amygdaloides	+	+					+ +		+ +		+	+	+ +	+ +		
Galium palustre			+ +								+ + +	+ +		+ +		
Hedera helix	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Hypericum androsaemum						+ +				+						
Hypericum humifusum			+			+			+							+ +
Lonicera periclymenum	+ + +	+ + +	+ +	+ + +		+			+ +		+	+	+ + +	+ + +	+ +	+ + +
Lysimachia nemorum					+				+			+ +	+	+	+	+
Melampyrum pratense	+ + +	+ + +	+ +		+ +	+ + +	+ + +			+	+				+ +	+ + +
Oxalis acetosella	+ +	+ +	+ +	+ +	+ + +	+ + +	+ + +	+ +	+ + +	+	+ + +	+ + +	+ +	+ + +	+ + +	+ + +
Potentilla erecta	+ + +	+ + +	+ + +	+ +	+	+	+	+	+	+	+	+ + +	+	+	+ + +	+ + +
Ranunculus flammula		+	+	+					+		+ + +			+	+ + +	+ +
Ranunculus repens		+			+	+	+	+ + +	+	+	+ + +	+ + +	+	+	+ + +	+ + +
Rosa arvensis/canina					+	+	+		+ +	+		+ +		+ + +	+ +	
Rumex sanguineus					+		+	+ +	+		+ + +	+	+	+	+	+
Ruscus aculeatus	+ +				+ + +	+ + +	+ +	+ + +	+ +		+		+ + +	+ +	+ + +	+
Scutellariua minor	+ + +	+	+	+			+			+	+		+	+	+ + +	+ + +
Stellaria media								+			+ + +		+	+	+ + +	+ +
Veronica chamaedrys		+			+	+ + +	+	+ +	+ +	+	+ + +	+ + +	+ + +	+	+ + +	+
Viola riviniana	+			+	+	+ + +	+	+ + +	+	+	+ + +	+ + +	+	+ + +	+	+ + +

	Section															
	51-52	**52-53**	**53-54**	**54-55**	**55-56**	**56-57**	**57-58**	**58-59**	**59-60**	**60-61**	**61-62**	**62-63**	**63-64**	**64-65**	**65-66**	**66-67**
Herb species recorded only in 1959/60																
Anemone nemorosa						+ +										
Conopodium majus						+ +										
Mercurialis perennis																+
Succisa pratensis																+ +
Herb species recorded only in 1999																
Bellis perennis									+		+		+	+	+	
Calluna vulgaris	+	+														
Cerastium holosteoides										+		+	+	+	+	
Cirsium palustre			+					+	+		+			+	+	
Erica cinerea	+				+						+					
Galium debile										+	+		+			
Galium saxatile		+	+	+	+		+	+	+	+	+	+	+	+	+	+
Gnaphalium uliginosum															+	
Hydrocotyle vulgaris	+	+	+	+	+		+		+	+			+	+	+	
Hypericum hirsutum		+														
Hypericum perforatum														+		
Hypochoeris radicata	+	+	+	+	+	+		+	+	+	+					
Lotus corniculatus								+							+	
Lotus pedunculatus							+		+							
Peplis portula					+						+					
Plantago lanceolata				+		+		+								
Plantago major		+	+	+	+		+	+	+	+		+	+	+	+	
Prunella vulgaris		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Rumex acetosella		+		+	+				+	+						
Sagina procumbens		+	+		+			+	+		+		+	+	+	
Senecio jacobaea								+								
Stellaria graminea													+	+	+	
Stellaria holosteoides							+									
Taraxacum officinale agg.		+			+				+	+	+	+	+	+		
Trifolium repens								+							+	
Urtica diocia										+						
Veronica officinalis		+	+	+	+	+	+	+	+	+	+					

	Section															
	51-52	**52-53**	**53-54**	**54-55**	**55-56**	**56-57**	**57-58**	**58-59**	**59-60**	**60-61**	**61-62**	**62-63**	**63-64**	**64-65**	**65-66**	**66-67**
Veronica serpyllifolia		+	+				+		+		+	+				
Fern species recorded in 1959/60 and 1999																
Dryopteris carthusiana									+		+	+ +	+	+	+	+
Drypoteris filix-mas										+			+	+ +	+ +	
Fern species recorded only in 1959/60																
Polypodium vulgare	+ +															
Fern species recorded only in 1999																
Athyrium filix-femina									+				+	+	+	
Blechnum spicant														+		
Dryopteris dilitata					+				+				+		+	
Oreopteris limbosperma														+		

Table 15 Summary of changes in occurrence of ground vegetation species (graminoids and herbs) in each 20m x 20m (0.04ha) section of the unenclosed transect from 1959/60 to 1999

	Number sections 1959/60	Number still present	Number lost from	Number recruited in	Number in 1999
Species common in 1959/60 and 1999					
Hedera helix	16	16	0	0	16
Rubus fruticosus agg.	16	16	0	0	16
Pteridium aquilinium	15	15	0	1	16
Agrostis spp.	14	14	0	2	16
Species showing large decline in occurrence					
Festuca spp.	7	0	7	0	0
Ruscus aculeatus	11	5	6	0	5
Anthoxanthum odoratum	9	2	7	1	3
Luzula pilosa	5	0	5	0	0
Species showing large increase in occurrence					
Carex ovalis	0	0	0	15	15
Prunella vulgaris	0	0	0	15	15
Juncus effusus	1	1	0	15	16
Galium saxatile	0	0	0	14	14
Plantago major	0	0	0	12	12
Digitalis purpurea	2	1	1	13	14
Holcus mollis	4	4	0	12	16
Danthonia decumbens	0	0	0	11	11
Hydrocotyle vulgaris	0	0	0	11	11
Juncus bulbosa	0	0	0	10	10
Hypochoeris radicata	0	0	0	10	10
Veronica officinalis	0	0	0	10	10
Luzula campestris	0	0	0	9	9
Sagina procumbens	0	0	0	9	9
Potentilla erecta	7	7	0	9	16
Poa annua	0	0	0	8	8
Taraxacum officinale agg.	0	0	0	8	8
Scutellariua minor	3	3	0	8	11
Ranunculus repens	5	5	0	8	13
Juncus acutiflorus	0	0	0	7	7
Rumex sanguineus	2	1	1	8	9
Cirsium palustre	0	0	0	6	6
Veronica serpyllifolia	0	0	0	6	6
Dryopteris carthusiana	1	1	0	6	7
Bellis perennis	0	0	0	5	5
Cerastium holosteoides	0	0	0	5	5
Rumex acetosella	0	0	0	5	5
Cardamine pratensis	1	0	1	6	6
Lysimachia nemorum	1	0	1	6	6

	Number sections 1959/60	Number still present	Number lost from	Number recruited in	Number in 1999
Species showing moderate decline in occurrence					
Carex pilulifera	13	8	5	1	9
Euphorbia amygdaloides	6	0	6	2	2
Oxalis acetosella	15	11	4	1	12
Melampyrum pratense	9	5	3	1	6
Galium palustre	4	1	3	0	1
Dactylis glomerata	4	0	4	2	2
Carex sylvatica	2	0	2	0	0
Lonicera periclymenum	10	7	3	2	9
Rosa arvensis/canina	5	1	4	3	4
Anemone nemorosa	1	0	1	0	0
Carex flacca	1	0	1	0	0
Conopodium majus	1	0	1	0	0
Mercurialis perennis	1	0	1	0	0
Succisa pratensis	1	0	1	0	0
Poa trivialis	1	0	1	0	0
Polypodium vulgare	1	0	1	0	0
Species showing no change in occurrence					
Drypoteris filix-mas	2	0	2	2	2
Hypericum androsaemum	1	0	1	1	1
Species showing moderate increase in occurrence					
Athyrium filix-femina	0	0	0	4	4
Carex demissa	0	0	0	4	4
Dryopteris dilitata	0	0	0	4	4
Ranunculus flammula	3	2	1	5	7
Viola riviniana	8	6	2	6	12
Carex remota	0	0	0	3	3
Erica cinerea	0	0	0	3	3
Galium debile	0	0	0	3	3
Molinia caerulea	0	0	0	3	3
Plantago lanceolata	0	0	0	3	3
Stellaria graminea	0	0	0	3	3
Cardamine flexuosa	1	0	1	4	4
Calluna vulgaris	0	0	0	2	2
Carex panicea	0	0	0	2	2
Deschampsia flexuosa	0	0	0	2	2
Juncus articulatus	0	0	0	2	2
Lotus corniculatus	0	0	0	2	2
Lotus pedunculatus	0	0	0	2	2
Peplis portula	0	0	0	2	2
Trifolium repens	0	0	0	2	2
Hypericum humifusum	1	0	1	3	3
Ajuga reptans	3	2	1	3	5

	Number sections 1959/60	Number still present	Number lost from	Number recruited in	Number in 1999
Stellaria media	3	2	1	3	5
Blechnum spicant	0	0	0	1	1
Carex nigra	0	0	0	1	1
Deschampsia cespitosa	0	0	0	1	1
Gnaphalium uliginosum	0	0	0	1	1
Hypericum hirsutum	0	0	0	1	1
Hypericum perforatum	0	0	0	1	1
Juncus squarrosus	0	0	0	1	1
Oreopteris limbosperma	0	0	0	1	1
Senecio jacobaea	0	0	0	1	1
Stellaria holosteoides	0	0	0	1	1
Urtica diocia	0	0	0	1	1
Circaea lutetiana	1	0	1	2	2
Veronica chamaedrys	9	6	3	4	10

Table 16 Ground cover and occurrence of main features along the unenclosed transect in 1999. Based on a continuous line of one hundred and sixty 2m x 2m quadrats (number per section = 10 = 0.004ha) taken along the transect mid-line. Only features ≥1% cover or ≥20% occurrence are shown. Covers of <1% were scored as 0.5% for calculation

	Average % cover	**Range % cover**	**% occurrence**
Pteridium aquilinium	50.3	0-100	79
Agrostis spp.	38.9	0-99	97
Agrostis capillaries	-	-	95
Mosses	5.3	0-40	73
Dead wood	2.4	0-30	79
Rubus fruticosus agg.	1.7	0-70	46
Dead trunks	1.4	0-30	18
Dead twigs	<1	0-<1	59
Hedera helix	<1	0-1	59
Potentilla erecta	<1	0-1	51
Oxalis acetosella	<1	0-3	38
Bare ground	<1	0-10	36
Dung	<1	0-5	36
Juncus effusus	<1	0-<1	31
Ranunculus repens	<1	0-1	30
Dead branches	<1	0-5	28
Carex ovalis	<1	0-<1	26
Galium saxatile	<1	0-20	24
Agrostis stolonifera	<1	0-4	23
Holcus mollis	<1	0-1	23
Digitalis purpurea	<1	0-2	22

Table 17 Occurrence of ground vegetation species in *Pteridium* dominated quadrats (*Pteridium* ≥60% cover) (n = 80) or *Agrostis* dominated quadrats (Agrostis ≥60% cover and *Pteridium* <60% cover) (n = 54) along the unenclosed transect in 1999. Based on a continuous line of 2m x 2m quadrats taken along the transect mid-line. Includes only species that occurred in ≥15 quadrats. P = probability of significance based on Mann-Whitney test for medians and chi-square test for species associations

	***Pteridium* dominated quadrats**	***Agrostis* dominated quadrats**	**P**
Median number of species	6	10.5	<0.00001
Species associated with *Agrostis* dominated quadrats			
Carex ovalis	8	29	<0.001
Danthonia decumbens	7	17	<0.001
Juncus bulbosa	1	15	<0.001
Juncus effusus	12	30	<0.001
Luzula campestre	2	14	<0.001
Prunella vulgaris	6	17	<0.001
Veronica chamaedrys	5	16	<0.001
Potentilla erecta	34	37	<0.005
Galium saxatile	11	18	<0.01
Ranunculus repens	17	23	<0.01
Species associated with *Pteridium* dominated quadrats			
Rubus fruticosus agg.	44	13	<0.001
Holcus mollis	24	7	<0.01
Species with no association			
Agrostis stolonifera	15	13	Not sig.
Digitalis purpurea	15	11	Not sig.
Hedera helix	46	29	Not sig.
Oxalis acetosella	31	14	Not sig.
Veronica officinalis	7	7	Not sig.
Viola riviniana	15	9	Not sig.